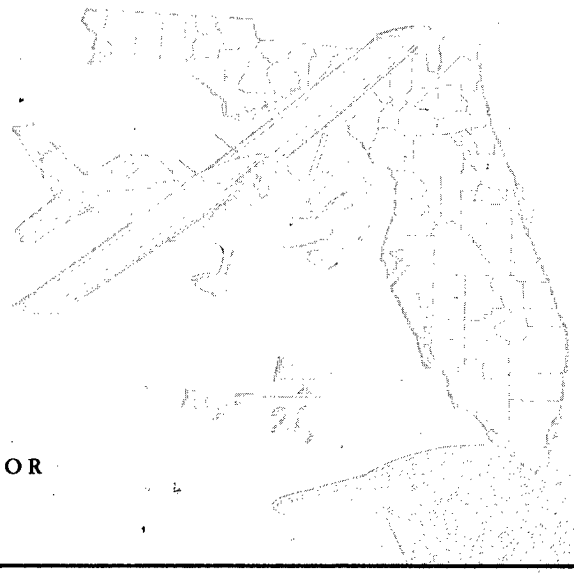


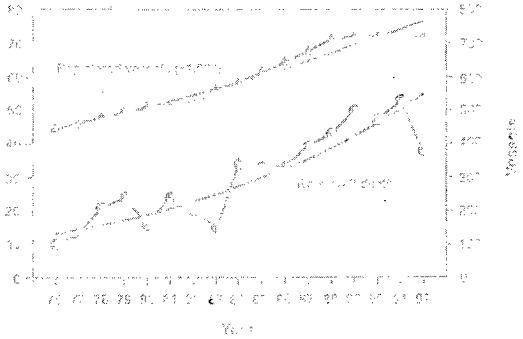
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INFORMATION AND TECHNOLOGY REPORT 1

POPULATION BIOLOGY OF THE FLORIDA MANATEE

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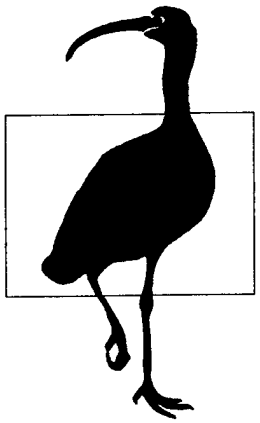
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INFORMATION AND TECHNOLOGY REPORT 1
AUGUST 1995

POPULATION BIOLOGY OF THE FLORIDA MANATEE

Edited by

Thomas J. O'Shea,

Bruce B. Ackerman,

and

H. Franklin Percival

Dedication

Dedicated to colleagues in some 50 developing nations of the world who strive to maintain manatees in their faunal heritage and to the memory of Tammy Dominguez and Amaury Villalba who lost their lives during an aerial survey of manatees on the southern coast of the Dominican Republic, January 1995.

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Frontispiece: *Female Florida manatee (*Trichechus manatus latirostris*) with nursing calf. Photo by P. M. Rose.*

Introduction

by

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Florida Manatees

The Florida manatee (*Trichechus manatus latirostris*) is a unique element of the U.S. fauna. It is a distinct subspecies of the West Indian manatee (Domning and Hayek 1986) and one of the largest inshore mammals of the continent, reaching weights to 1,650 kg (Rathbun et al. 1990). Annual migratory circuits of some individuals through the intracoastal waterways of the Atlantic Coast are 1,700 km round trips at seasonal travel rates as high as 50 km/day (*[3]Reid and O'Shea 1989; Reid et al. 1991), resulting in one of the longest remaining intact mammalian migrations in the eastern United States. Manatees are the only living North American representatives of the small mammalian Order Sirenia and are therefore the only embodiment of the unique suite of biological features that define the distinctive adaptive syndrome at the ordinal level of the taxonomic hierarchy. Features of this adaptive syndrome can be directly related to the lifestyle of aquatic herbivory (O'Shea and Reep 1990). In manatees, these features include unique aspects of morphology (pachyostosis; horizontal, unilobular lungs and diaphragm; indeterminate numbers of molars undergoing continuous replacement; dexterous forelimbs and prehensile lips; and a hind-gut as long or longer than 30 m), physiology (in particular an unusually low metabolic rate and a high thermal conductance that lead to energetic stresses in winter, ameliorated by migrations and aggregations in warm-water refugia), and behavioral ecology (lack of a rigid social organization, seasonal migrations, absence of strong circadian rhythms). Hartman (1979) and Reynolds

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and Odell (1991) provided further details on distinctive features of manatee biology. Other aspects of this adaptive syndrome include life-history traits, such as litter size, age at first reproduction, interbirth intervals, and longevity, which profoundly dictate the population consequences of human intrusion on the manatee's unique lifestyle.

Human intrusions on manatees in Florida have been substantial. Many manatees are accidentally killed by watercraft and other anthropogenic causes; traditional migrations have been preempted or modified by coastal development and industrially heated water (where aggregations of hundreds of animals may form and are liable to catastrophic losses), and human activities have impinged on habitat quality throughout the range of the Florida manatee. Nevertheless, quantification of these impacts on the population has been elusive, and available data frequently lead to enigmas about some of the seemingly simplest questions (O'Shea 1988). How many are there? Is the population decreasing or increasing? What are the potential rates of population growth? What rates of mortality can manatees sustain without being driven closer to extinction? How do these compare with existing information on population size, observed numbers of dead manatees, and life-history traits?

These questions have high priorities for research on Florida manatees. Manatees are protected under the Florida Manatee Sanctuary Act of 1978, the U.S. Endangered Species Act of 1973, and the U.S. Marine Mammal Protection Act of 1972 and their amendments (*U.S. Fish and Wildlife Service 1989). Federal management is directed to improve the population status of Florida manatees so that the subspecies can be removed from the endangered-species list. The U.S. Marine Mammal Protection Act also requires that Florida manatees must be maintained at optimum sustainable population levels and that the marine ecosystems of which they are a part also remain healthy and stable. Manatees have become increasingly popular with the public because of their biological uniqueness and their ability to exist in densely populated areas, where some individuals become accustomed to people and provide them with some of the most singular, inspiring wildlife encounters of their lifetimes. Some of these animals, however, also bear inhumane and gruesome wounds from boat propellers, and images of manatees killed by these means are given substantial media attention, leading to deepening public concern.

Information on Manatee Population Biology

Increasing public concern and requirements of legislation notwithstanding, the answers that can be provided to questions about manatee population biology are only as good as the quality of available information. Recognizing this need for a new assessment of information about manatee population dynamics, the U.S. Fish and Wildlife Service and the Florida Department of Natural Resources held a technical workshop on manatee population biology at the Austin Cary Forest of the University of Florida during 4–6 February 1992.[4]

This was the first workshop on the topic since a meeting in Orlando in 1978 (*Brownell and Ralls 1981). At the 1978 meeting, several recommendations were made for further research, and conclusions were drawn about certain aspects of manatee population biology, but these conclusions were tentative because of the scant amount of then-available data. Also in 1978, the U.S. Fish and Wildlife Service organized the Sirenia Project at the Gainesville Field Station of the National Fish and Wildlife Laboratory.[5] One of the major objectives for the Sirenia Project was long-term research to expand databases on manatee life history, population size, and mortality. Subsequently, in the early 1980's, the service and the U.S. Marine Mammal Commission (through the Florida Cooperative Fish and Wildlife Research Unit) embarked on a series of studies to address other issues in manatee population biology, particularly aerial survey, census, estimation of trends, and development of a preliminary population model. These studies resulted in a series of publications and reports, including those by Eberhardt (*1982), Packard and Mulholland (*1983), Packard and Nichols (*1983), Packard (*1984, *1985a, *1985b), and Packard et al. (1985, 1986). However, conclusions of many of these studies remained preliminary because of the large degree of uncertainty about manatee population attributes. Although databases had moved from being scant to modest by the mid-1980's, continued long-term research and additional experimentation were necessary to improve certainty. Population research was significantly augmented in 1985 when the state of Florida initiated manatee research at what is now the Florida Marine Research Institute. This program encompasses several areas of study in manatee population biology, including aerial surveys, research with telemetry, habitat studies, and the statewide recovery of carcasses and analyses of mortality data.

[4] In 1993, the research functions of the U.S. Fish and Wildlife Service were transferred to the National Biological Service, and the Florida Department of Natural Resources was merged with the Florida Department of Environmental Regulation to form the Department of Environmental Protection.

[5] The National Fish and Wildlife Laboratory of the U.S. Fish and Wildlife Service was responsible for all of the service's marine mammal research under the Marine Mammal Protection Act and began federal manatee research in 1973 prior to formal establishment of the Sirenia Project in 1978. The Sirenia Project was subsequently administered by the Denver Wildlife Research Center of the service after the Denver Wildlife Research Center and the National Fish and Wildlife Laboratory were merged. The National Ecology Research Center of the service later administered the Sirenia Project after the transfer of many other Denver Wildlife Research Center programs to the U.S. Department of Agriculture. Currently the Sirenia Project is conducted by the Southeastern Biological Science Center of the National Biological Service.

Because the Sirenia Project, the Florida Marine Research Institute, and the Florida Cooperative Fish and Wildlife Research Unit have been involved in much of the past and present research about manatee population biology, sponsorship of the 1992 workshop by these institutions was appropriate. However, significant progress in understanding manatee population biology has also been due to the contributions of many other individuals and organizations. In addition to findings of federal and state agencies, the workshop also included contributions by oceanaria, industry, and the academic community. Much of the research on manatee population biology presented at the workshop was called for in the revised Florida Manatee Recovery Plan (*U.S. Fish and Wildlife Service 1989).

Objectives of Workshop Participants

The goals for the 1992 workshop were (1) a synthesis of information about manatee population biology, (2) an evaluation of the strengths and weaknesses of data sets and approaches to manatee-population research, and (3) recommendations for future research. The primary objective for the revised Florida Manatee Recovery Plan (*U.S. Fish and Wildlife Service 1989) was to change the status of the subspecies from endangered to threatened. According to the plan, this objective is met when viable, self-sustaining populations are maintained on Florida's Gulf and Atlantic coasts. The criteria for a change of status encompasses four elements: the population is growing or stable, mortality factors are controlled at acceptable levels or decreasing, habitats are secure, and threats to habitats are controlled or decreasing. The recovery plan also called for the development of population models to assist in assessing progress toward meeting the first of these criteria if methodology and data are available. One of the tasks of the workshop participants was the assessment of existing data and research.

The duration of the workshop was 3 days. On the first day, 14 invited papers were delivered to an audience of approximately 75 individuals, including members of the recovery team, researchers and managers from government agencies, members of the academic community, and representatives of industry and conservation groups. The paper session was followed by a 2-day retreat of group meetings and informal evening sessions. The group sessions were devoted to aerial-survey techniques and estimation of population size and growth trend, reproduction, age structure, mortality, photo identification, estimation of survival, and integration of life-history data and population modeling. The groups were limited to a small number of researchers in manatee population biology and experts in statistics and mammalian population dynamics. Individuals were assigned to various groups and were provided a list of topics for discussion. Each group provided a written summary and set of recommendations. Abstracts of presentations, group reports, and lists of attendees were assembled in an interim report with limited distribution (*O'Shea et al. 1992).

The proceedings contain the peer-reviewed presented papers, except the information on reproduction in captive manatees (summarized by Odell et al. 1995) and the life-history information based on field studies of the wild population at Blue Spring (O'Shea and Hartley 1995). Development of the latter paper was a recommendation of the workshop participants. Several papers include results through calendar year 1992 or later, but most papers report findings through 1991. Most papers benefitted from comments by participants in the 1992 workshop and were modified with feedback in response to their verbal presentation. The contribution on population modeling (Eberhardt and O'Shea 1995) was completed after results of related studies became available in manuscript form. Participants in the 1992 working group sessions were: B. B. Ackerman, Florida Marine Research Institute; C. A. Beck, Sirenia Project; I. E. Beeler, Florida Marine Research Institute; R. K. Bonde, Sirenia Project; D. P. DeMaster, National Marine Fisheries Service, La Jolla, California; L. L. Eberhardt, Battelle Northwest, Kennewick, Washington; C. W. Fowler, National Marine Fisheries Service, Seattle, Washington; R. A. Garrott, University of Wisconsin; T. Gerrodette, National Marine Fisheries Service, La Jolla, California; S. R. Humphrey, University of Florida; H. I. Kochman, Sirenia Project; C. A. Langtimm, Sirenia Project; L. W. Lefebvre, Sirenia Project; M. Marmontel, University of Florida; H. Marsh, James Cook University, Townsville, Australia; J. D. Nichols, Patuxent Wildlife Research Center, Laurel, Maryland; D. K. Odell, Sea World of Florida, Orlando; T. J. O'Shea, Sirenia Project; K. H. Pollock, North Carolina State University, Raleigh; K. M. Portier, University of Florida; G. B. Rathbun, National Biological Service, San Simeon, California; J. P. Reid, Sirenia Project; J. E. Reynolds, III, Eckerd College, St. Petersburg, Florida and U.S. Marine Mammal Commission, Washington, D.C.; P. M. Rose, Florida Department of Environmental Protection, Tallahassee; B. L. Weigle, Florida Marine Research Institute; and S. D. Wright, Florida Marine Research Institute.

Articles in the current volume provide the most intensive analyses of original data and overview perspectives yet available on the topic of the population biology of the Florida manatee. Contents are arranged to provide an overview of the numerous programs and institutions in manatee research and related conservation in Florida to the time of the workshop, information about manatee aerial-survey techniques and estimation of population size and

trend, background information on research approaches and current understanding of the population biology of the closely related dugong (*Dugong dugon*, that for years provided the best standard and proxy for evaluating sirenian population biology), anatomical studies of manatee age-related reproduction, techniques in assembling photo-identification records for life-history studies in the field, longitudinal field studies of manatee reproduction, field studies of survival, analyses of manatee mortality databases, and integration of manatee population and life-history data with a classical approach to population dynamics modeling. The volume is concluded with an overview, including summaries of recommendations from the workshop and a brief synopsis of pertinent work that has been published elsewhere since the workshop.

Acknowledgments

In addition to working group participants, we thank the numerous individuals who contributed to the success of the 1992 workshop: R. L. Brownell, Jr., L. Buckle, C. Campbell, R. Carthy, D. Easton, B. Fesler, J. Grear, R. J. Hofman, W. Jones, M. Klaips, D. Laist, P. Lefebvre, M. Mangel, J. Serino, T. D. Smith, M. Suarez, R. O. Turner, Jr., J. R. Twiss, Jr., P. A. Underwood, J. R. Wilcox, and K. Wood. We also thank the many peer reviewers for helpful comments on each of the manuscripts. The workshop was administered in part through Research Work Order No. 88 issued by the National Ecology Research Center to the Florida Cooperative Fish and Wildlife Research Unit at the University of Florida. Logistics and administration were eased by participation of the Florida Wildlife Federation. The use of Mace Lodge at the Austin Cary Forest was provided by the School of Forest Resources and Conservation, University of Florida. We are especially grateful to our families for tolerating our absences while assembling and editing the material for this volume. Assistance with the preparation of final versions of the manuscripts was provided by B. Coen and D. Medellin. J. Shoemaker, D. Crawford, and J. Goehring assisted with the final preparation of the figures and the cover art.

Cited References[6]

*Brownell, R. L., Jr., and K. Ralls, editors. 1981. The West Indian manatee in Florida. Proceedings of a workshop held in Orlando, Florida, 27–29 March 1978. Florida Department of Natural Resources, Tallahassee. 154 pp.

Domning, D. P., and L. C. Hayek. 1986. Interspecific and intraspecific morphological variation in manatees (Sirenia: *Trichechus*). Marine Mammal Science 2:87–144.

*Eberhardt, L. L. 1982. Censusing manatees. Manatee Population Research Report 1, Florida Cooperative Fish and Wildlife Research Unit, University of Florida, Gainesville. 18 pp.

Eberhardt, L. L., and T. J. O'Shea. 1995. Integration of manatee life-history data and population modeling. Pages 269–279 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Hartman, D. S. 1979. Ecology and behavior of the manatee (*Trichechus manatus*) in Florida. American Society of Mammalogists, Special Publication 5. Lawrence, Kans. 153 pp.

Odell, D. K., G. D. Bossart, M. T. Lowe, and T. D. Hopkins. 1995. Reproduction of the West Indian manatee in captivity. Pages 192–193 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

O'Shea, T. J. 1988. The past, present, and future of manatees in the southeastern United States: realities, misunderstandings and enigmas. Pages 184–204 *in* R. R. Odom, K. A. Riddleberger, and J. C. Ozier, editors. Proceedings of the Third Southeastern Nongame and Endangered Wildlife Symposium. Georgia Department of Natural Resources, Game and Fish Division, Social Circle.

*O'Shea, T. J., B. B. Ackerman, and H. F. Percival, editors. 1992. Interim report of the technical workshop on manatee population biology. Manatee Population Research Report 10, Florida Cooperative Fish and Wildlife Research Unit, University of Florida, Gainesville. 83 pp.

O'Shea, T. J., and W. C. Hartley. 1995. Reproduction and early-age survival of manatees at Blue Spring, upper St. Johns River, Florida. Pages 157–170 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

O'Shea, T. J., and R. L. Reep. 1990. Encephalization quotients and life-history traits in the Sirenia. Journal of Mammalogy 71:534–543.

*Packard, J. M. 1984. Review of manatee marking techniques. Manatee Population Research Report 6, Florida Cooperative Fish and Wildlife Research Unit, University of Florida, Gainesville. 29 pp.

*Packard, J. M. 1985a. Development of manatee aerial survey techniques. Manatee Population Research Report 7, Florida Cooperative Fish and Wildlife Research Unit, University of Florida, Gainesville. 68 pp.

*Packard, J. M. 1985b. Preliminary assessment of uncertainty involved in modeling manatee populations. Manatee Population Research Report 9, Florida Cooperative Fish and Wildlife Research Unit, University of Florida, Gainesville. 19 pp.

*Packard, J. M., and R. Mulholland. 1983. Analysis of manatee aerial surveys: a compilation and preliminary analysis of winter aerial surveys conducted in Florida between 1977 and 1982.

[6] An asterisk denotes unpublished material.

Manatee Population Research Report 2, Florida Cooperative Fish and Wildlife Research Unit, University of Florida, Gainesville. 119 pp.

*Packard, J. M., and J. D. Nichols. 1983. A preliminary analysis of sample sizes required for mark–recovery and mark–resighting studies of manatees (*Trichechus manatus*) in Florida. Manatee Population Research Report 4, Florida Cooperative Fish and Wildlife Research Unit, University of Florida, Gainesville. 14 pp.

Packard, J. M., D. B. Siniff, and J. A. Cornell. 1986. Use of replicate counts to improve indices of trends in manatee abundance. Wildlife Society Bulletin 14:265–275.

Packard, J. M., R. C. Summers, and L. B. Barnes. 1985. Variation of visibility bias during aerial surveys of manatees. Journal of Wildlife Management 49:347–351.

Rathbun, G. B., J. P. Reid, and G. Carowan. 1990. Distribution and movement patterns of manatees (*Trichechus manatus*) in northwestern peninsular Florida. Florida Marine Research Publications 48:1–38.

*Reid, J. P., and T. J. O'Shea. 1989. Three years operational use of satellite telemetry on Florida manatees: tag improvements based on challenges from the field. Pages 217–232 *in* Proceedings of the 1989 North American Argos Users Conference. Service Argos, Inc., Landover, Md. 361 pp.

Reid, J. P., G. B. Rathbun, and J. R. Wilcox. 1991. Distribution patterns of individually identifiable West Indian manatees (*Trichechus manatus*) in Florida. Marine Mammal Science 7:180–190.

Reynolds, J. E., III, and D. K. Odell. 1991. Manatees and dugongs. Facts On File, Inc., New York. 192 pp.

*U.S. Fish and Wildlife Service. 1989. Florida manatee (*Trichechus manatus latirostris*) Recovery Plan. Prepared by the Florida Manatee Recovery Team for the U.S. Fish and Wildlife Service, Atlanta, Ga. 98 pp.

Florida Manatee Population Biology: Research Progress, Infrastructure, and Applications for Conservation and Management

by

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Abstract. Twenty-five years ago, a single scientist focused his research on Florida manatees (*Trichechus manatus latirostris*). Today, millions of dollars are spent annually on research and management of this endangered species. In the meantime, several databases with valuable information about manatee population biology, including some particularly valuable long-term databases, were created. Cooperation and interaction among various individuals, agencies, and institutions have been great strengths of the overall research and the management of manatees in Florida. The presentation and evaluation of the collectively gathered information about the population biology of manatees in this workshop are therefore appropriate. The recovery of the subspecies is not assured; with some justification, it has been portrayed in grim terms. I hope that this workshop provides new insights, new syntheses, and new directions for research and management and that these, in turn, establish new hope for the recovery of Florida manatees.

Key words: Manatee, *Trichechus*, Florida, population biology, recovery plan, trends.

The first and, to my knowledge, only workshop that focused on population biology of manatees in Florida was held almost exactly 14 years ago in March 1978 ([2]*Brownell and Ralls 1981). The attending individuals and represented institutions and agencies at the workshop were different from those of today's workshop. In fact, fewer than a half dozen individuals appear on both rosters, and only two institutions, the U.S. Fish and Wildlife Service and Sea World, provided representatives to both workshops.

The players but not the objectives changed with time. The objectives, reflected in the revised Florida Manatee Recovery Plan (*U.S. Fish and Wildlife Service 1989), include assessment of the causes of manatee mortality, population size and distribution, habitat-use patterns, reproduction, behavior, life history, and application of available data to the management of the subspecies. I provide a brief historical context for manatee research and management, describe the current status of activities, and speculate about the future.

History and Organization of Manatee Research

Modern manatee research can be traced to Daniel S. Hartman who began to study manatees in the Crystal River in the mid-1960's. In 1974, he prophetically stated that "the manatee is protected...but its survival is still threatened by the propellers of power boats...and habitat alteration. Recommendations for the manatee's conservation include the regulation of boat speeds on strategic bodies of water and the establishment of sanctuaries..." (*Hartman 1974:239). His insightful observations and advice for manatee protection and his descriptions of manatee behavior (Hartman 1979) still stand.

The year 1974 marked the beginnings of multifaceted manatee research at the University of Miami and at the Gainesville Field Station of the U.S. Fish and Wildlife Service, a program that in 1978 was recognized as the Sirenia Project. The 1978 workshop mentioned earlier,

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[2] An asterisk denotes unpublished material.

in fact, helped catalyze the reorganization of the Sirenia Project.

Research by the U.S. Fish and Wildlife Service and University of Miami personnel has been on behavior and ecology, causes of death, distribution and abundance, functional anatomy, food habits, movement patterns, acoustics, growth, and recently, age determination. Most long-term databases, which are essential for population assessment, were begun by scientists of the U.S. Fish and Wildlife Service and the University of Miami and were covered in the 1978 workshop (*Brownell and Ralls 1981). The state of Florida demonstrated increased involvement in studies of manatees with the passage of the Florida Manatee Sanctuary Act in 1978.

By 1984, the Florida Department of Natural Resources (now the Florida Department of Environmental Protection) began to assume a more active role in manatee management and various types of research, including the operation of the carcass-salvage network in mid-1985. Note that 1990 amendments of certain state statutes, including the Florida Manatee Sanctuary Act, gave the department more authority, more funding, and more positions, such that the department has a larger budget and more people for manatee research and management than other agencies or organizations in manatee conservation.

Over time, several other players joined the conservation, research, or education programs on manatees. Many organizations and individuals are involved in research, management, education, or public awareness efforts on manatees in Florida (Tables 1–4). These organizations generally work well together.

Cooperation among the various agencies has been demonstrated in many ways. Recently the development and adoption of a revised Florida Manatee Recovery Plan (signed by heads or representatives of 13 agencies, conservation organizations, and industry groups) and the multiagency support of proposed regulations by the Florida Department of Natural Resources to the Florida Governor and Cabinet have provided good examples of cooperation and shared goals (*U.S. Fish and Wildlife Service 1989).

The history of manatee conservation can be divided into three eras. From the late 1960's until 1980, various activities got underway, setting the stage for cooperative, focused conservation. In 1980, with the direction of the Marine Mammal Commission, the first Manatee Recovery Plan was adopted and a coordinator was hired (*U.S. Fish and Wildlife Service 1980); from that date until 1989, joint studies increased in which the state began to participate in 1984. Finally, in 1989, the revised Recovery Plan was adopted (*U.S. Fish and Wildlife Service 1989); it focused even better on specific research or management. The transition to each new stage, marked by increased research and management, was promoted and guided by the Marine Mammal Commission, the agency with oversight of all marine mammal conservation in this country (*Marine Mammal Commission 1980, 1981, 1991). Since the late 1970's, the commission has been concerned about the status of manatees and manatee management in Florida and, as a result, has devoted time and funding to research and recovery of the manatee. In fact, the bulk of the commission's 1988 research budget was spent on manatees (*Marine Mammal Commission 1991). In 1980, 1987, and 1992, the commission held its annual meeting in Florida to focus on manatee issues.

All the individual and collective efforts to date advanced our knowledge about manatees. In the 1970's, popular and technical publications may well have given the impression that the common name of the animal was not simply "manatee" but "the poorly studied manatee." That situation changed. Unanswered questions remain, but important databases exist. For example, several long-term manatee databases were initiated at least 15 years ago by the Sirenia Project, by Daniel Odell at the University of Miami, and by the Florida Power and Light Company. They include the causes and locations of mortality; distribution and abundance in winter; numbers of calves in aggregations in winter; reproduction and behavior of distinctly marked manatees; and movement patterns and high use at sites on the eastern coast of Florida, the Crystal River, Blue Spring, Fort Myers, and in Tampa Bay. Recent studies provided valuable insight into manatee population biology and conservation; papers in this volume describe many of the newer databases. For this particular workshop on manatee population biology, it is important to note the pioneering work of J. M. Packard, who compared a variety of survey techniques to determine their value in assessing manatee abundance and trends (*Packard and Mulholland 1983; Packard et al. 1986).

Applications of Manatee Research to Conservation and Management

The existing databases and technology facilitate studies to determine the following:

1) the number of manatees that died where, when, and how to highlight specific areas and key counties where manatee abundance or mortality is highest,
2) locations of warm-water refugia and other high-use areas where protection of manatees is especially important,
3) approximate age and reproductive status of manatees,
4) the number of calves in warm-water refugia in winter, and
5) characteristics of basic life-history events such as reproductive intervals, age at first reproduction, and survival.

Table 1. Summary of research or research-related activities conducted now or in the recent past by the federal government and the state of Florida on manatees (*Trichechus manatus latirostris*; updated from Reynolds and Gluckman 1988).

Agency	Topics
U.S. Fish and Wildlife Service (under National Biological Service as of 1993), Sirenia Project	Life-history studies Carcass salvage Development and application of telemetry Behavior Ecosystems Aerial surveys Scar catalog Technical assistance Age determination
Florida Cooperative Fish and Wildlife Research Unit (National Biological Service)	Human recreational activities (Crystal River) Research and management plans (Crystal River) Aerial surveys (Caloosahatchee and Crystal Rivers) Aerial surveys/human activities (Northeastern Florida) Radio tracking (Cumberland Sound) Description of habitat types and manatee distribution (Crystal River)
Florida Department of Natural Resources (under Department of Environmental Protection as of 1993)	Carcass salvage Aerial surveys Geographic information systems Telemetry (central, western Florida) Ecosystem studies (Hobe Sound) Human activities (boat use patterns)
U.S. Army Corps of Engineers (Jacksonville, Florida District)	Overview of manatee status Aerial surveys (eastern Florida) Telemetry support (eastern Florida)
National Aeronautics and Space Administration	Aerial surveys (Banana River) Ecosystem studies (Banana River)
U.S. Marine Mammal Commission	Constituting/convening the Manatee Technical Advisory Council Studies to enhance protection and management of manatees Research and management plans (Crystal River) Food sources and feeding habits (Hobe Sound)
National Marine Fisheries Service	Ecosystems studies (Hobe Sound)
National Park Service	Aerial surveys (Cumberland Island, Everglades National Park) Telemetry applications (Cumberland Sound)
U.S. Navy	Telemetry applications (Cumberland Sound)
Chassahowitzka National Wildlife Refuge	Aerial surveys (Citrus County)

The databases also provide much additional information. The manatee entered a new era when the term "poorly studied" was no longer an apt description.

Good biological data permit more and better management. The U.S. Fish and Wildlife Service continues to use the best available data to formulate endangered species act jeopardy opinions. To date, more opinions (99 between 1984 and November 1991) were issued for manatees than for all other endangered species in this country combined (R. Turner, U.S. Fish and Wildlife Service, personal communication). Similarly, the state continues to work with local governments to implement local management for the adequate protection of the manatee and its habitats. To date, plans that regulate boat speeds and boat access in areas known to be frequented by manatees were approved for six counties by the state; three other plans will probably be approved soon. These plans should reduce fatal and non-fatal collisions between watercraft and manatees. As mandated by Florida's Growth Management Act of 1985, local regulations for watercraft will be incorporated into management to control the effects of human population growth in local areas (*Reynolds and Gluckman 1988).

Table 2. Research conducted or sponsored by private organizations or by scientists (updated from Reynolds and Gluckman 1988).

Organization or individual	Topic
Florida Power & Light Company	Aerial surveys Scar catalog Applications of telemetry Water temperatures
Save the Manatee Club	Aerial surveys, support to various other projects including international efforts
Sea World (D. Odell, others)	Clinical parameters Carcass salvage Morphometrics Parasites Aerial surveys Behavior and ecology
Miami Seaquarium (G. Bossart)	Clinical parameters, immunology
J. Reynolds (Eckerd College)	Carcass salvage Aerial surveys Functional anatomy Behavior and ecology
D. Domning (Howard University)	Anatomy Paleontology and systematics Feeding ecology Bibliography and index
G. Patton (Mote Marine Laboratory)	Aerial surveys Means of detecting manatees Acoustics
J. Morris (Florida Institute of Technology)	Ecology and behavior Analysis of vocalizations Nutrition
E. Gerstein (Florida Atlantic University)	Acoustics
J. and M. Provancha (Bionetics Corp.)	Aerial surveys Habitat assessment

Public support is important for the passing of regulations to protect manatees or their habitat. The Save the Manatee Club now has more than 30,000 members (J. Vallee, Save the Manatee Club, personal communication) and more than 130,000 special state of Florida auto tags depicting a manatee were sold (B. Weigle, Florida Marine Research Institute, personal communication).

The biological data on manatees increased, efforts to conserve manatees have broad support and should reduce manatee deaths, public support and interest in manatees are widespread, and several agencies and institutions work hard to protect manatees. Nonetheless, I consider that manatee recovery and protection are, in fact, in jeopardy for four fundamental reasons: (1) the poorly managed human population growth in Florida, (2) insufficient funds for acquisition of habitat and enforcement of regulations, (3) the increasing strength and effectiveness of opposition, and (4) the size of the problem. A better understanding of manatee population biology would permit a measure of progress in the face of these limitations.

In recent years, the human population of Florida increased by nearly 1,000 new residents a day (Anonymous 1987). About 90% of Florida's residents live within 16 km of the coast, concentrating impacts of human activities on coastal habitats. Human activities continue to kill and injure manatees; the number of manatee deaths attributable to human factors grows with the human population.

A conference titled *Managing Cumulative Effects in Florida Wetlands* (*Estevez et al. 1986a, 1986b) revealed that in the early 1970's the average annual loss of wetlands was approximately 29,160 ha. The loss of Florida wetlands continues today at a reduced rate. However, cumulative effects of development and other human

Table 3. Primary state and federal agencies that manage Florida manatees (*Trichechus manatus latirostris*) or manatee habitat, and examples of duties (Reynolds and Gluckman 1988).

Agency	Duties
Florida Department of Community Affairs	Approval of local growth management plans; approval of major developments with regional impact.
Florida Department of Environmental Regulation	Administers permits for dredging and filling of wetlands; designates aquatic preserves as Outstanding Florida Waterways
Florida Department of Natural Resources	Develop local management plans for Florida manatees; enforce state laws affecting manatees and their habitats; use of state-owned lands; review of permit applications, and other regulatory activities that can enhance manatee protection
Florida Game and Freshwater Fish Commission	Enforcement of boat speed zones and other manatee protection activities on inland waterways
Marine Mammal Commission	Oversight for all federal agency activities affecting marine mammals
U.S. Army Corps of Engineers	Federal permits for activities in coastal areas with potential impacts on manatees; initiate Section 7 consultations
U.S. Fish and Wildlife Service	Consultations with other federal agencies on activities with potential impacts on manatees as required under Section 7 of the Endangered Species Act; federal wildlife law enforcement; review of permit applications under various federal statutes; development and updating of Recovery Plan; coordination of a wide array of management activities

Table 4. Organizations involved in education and awareness programs about Florida manatees (*Trichechus manatus latirostris*) in Florida. A brief statement of efforts to date is included. More complete information about education and awareness is in Reynolds and Gluckman (1988).

Organization	Efforts
Colleges and Universities	Classes; public lectures
Florida Department of Natural Resources	Brochures, bumper stickers, posters, public lectures, etc.
Florida Power & Light Company	Booklets, bumper stickers, Educator's Guide, films, public workshops
Marine Mammal Commission	Funding support for development of educational materials and for *Sirenews*; distribution of annual reports and other literature
Marine Zoological Parks	Tours, efforts focused on children and teachers, educational displays
Port Everglades Authority	Bumper stickers, brochures, public tours, and lectures
Save the Manatee Club	Newsletter, public service announcements, signs, press releases, in-service programs for teachers, brochures
Tampa Electric Company	Manatee viewing platform, lectures, displays
U.S. Fish and Wildlife Service	Interpretive/Education Center literature distribution

activities have been devastating. In Tampa Bay, for example, Lewis (*1986) estimated that more than 80% of the seagrass community was destroyed by human activities. The status of the manatee is not unique but symptomatic of the status of all coastal and estuarine resources in Florida. Efforts focused entirely on manatee protection are doomed to failure if erosion of habitat extent and quality is allowed to continue.

Important solutions to manatees' woes and to coastal degradation include the acquisition of habitat and subsequent creation of reserves and further development and enforcement of regulations to protect habitat and manatees. Where true sanctuaries (i.e., no entry areas, such as at the Crystal River, the Banana River, and the Tampa Electric Company's Apollo Beach plant) were created and incorporate adequate resources for manatees, manatee use increased profoundly.

Lack of money is a problem for habitat acquisition and enforcement. The state's Conservation and Recreational Lands Acquisition List includes properties valued

at more than $900 million, but the program has an annual budget of about $50 million (*Reynolds and Gluckman 1988). These are large sums but perhaps not large enough to secure sufficient habitat for Florida wildlife. Funding has been insufficient to hire adequate enforcement staff. An additional 250 field officers (the number needed in 1988; *Reynolds and Gluckman 1988) for the Florida Marine Patrol would cost more than $11 million a year. A state that is currently implementing significant cutbacks in education and other programs to control its budget will probably not make these expenditures.

Damaging the protection of manatees are reports in various media that basically state that humans cause little damage to manatees and manatee habitat. Some articles simply contain false information. Others take advantage of the fact that precise population data on size and trends are unavailable. Scientists may be reluctant to speculate on insufficient data; many journalists are not so reticent. Therefore, the public does not know what to believe. A solution is to continue research to provide more definitive population data.

Some people in Florida are openly antagonistic toward regulations that restrict human activities. The attitude has been publicly expressed: waterways belong to humans and, if manatees and other creatures cannot exist where people want to boat or ski, that is unfortunate. The boating industry, among others, has a strong and effective lobby in a state with 750,000 registered boats. However, a survey by scientists (*Parker 1989) at the Florida State University revealed that, in reality, most boaters support protection of manatees.

The magnitude of the problem is immense. Almost any human activity in any inshore body of water or wetland in Florida can and does harm manatees or their habitat. Significant progress in regulating human activities to protect wildlife and habitat in the last 20 years is a tribute to those who have worked in this area. Whereas some other marine mammal-human interactions may be limited to a small number of activities or particular locations, human–manatee interactions cover all activities along Florida's lengthy waterways (*Marine Mammal Commission 1991). People who are unfamiliar with Florida may be surprised to learn that Florida and Georgia have more coastline (2,333 km) than California, Oregon, and Washington combined (2,080 km; Anonymous 1991).

The current research and management must continue and expand. In particular, the valuable long-term databases must be maintained. Enforcement must increase. Habitat protection with regulations or acquisition must continue. Education must expand. But currently the question remains: Will all this be enough? I worry that it may not. I also worry that by the time we have enough pieces of the puzzle in place and then evaluate their effects in terms of habitat and manatee recovery, years will have passed. If our efforts do not work, those years of continued high mortality and continued habitat destruction may be irreversible.

This workshop and its proceedings take advantage of the degree of interagency cooperation and the existence of certain data to attempt to better understand Florida manatee population biology. Let us hope that the effort results not only in increased scientific insight but also in contributions to better management and conservation of this endangered species.

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Cited References[3]

Anonymous. 1987. Keys to Florida's future. Winning in a competitive world. Final report of the State Comprehensive Planning Committee. Florida Department of Community Affairs, Tallahassee. 46 pp.

Anonymous. 1991. Information please almanac. Forty-fourth edition. Houghton Mifflin Company, Boston, Mass. 992 pp.

*Brownell, R. L., Jr., and K. Ralls, editors. 1981. The West Indian manatee in Florida. Proceedings of a workshop held in Orlando, Florida, 27–29 March 1978. Florida Department of Natural Resources, Tallahassee. 154 pp.

*Estevez, E. D, J. Miller, J. Morris, and R. Hammen. 1986a. Proceedings of the conference: managing cumulative effects in Florida wetlands. October 1985, Sarasota, Fla. New College Environmental Studies Program Publication 37, Omnipress, Madison, Wis. 326 pp. + appendix.

*Estevez, E. D., J. Miller, J. Morris, and R. Hammen. 1986b. Executive summary of the conference: managing cumulative effects in Florida wetlands. October 1985, Sarasota, Fla. New College Environmental Studies Program Publication 37, Omnipress, Madison, Wis. 50 pp. + appendix.

*Hartman, D. S. 1974. Distribution, status, and conservation of the manatee in the United States. Document PB 81-140725, National Technical Information Service, Springfield, Va. 246 pp.

Hartman, D. S. 1979. Ecology and behavior of the manatee (*Trichechus manatus*) in Florida. Special Publication 5, American Society of Mammalogists. Lawrence, Kans. 153 pp.

*Lewis, R. R., III. 1986. Marine wetland loss in Tampa Bay and management/restoration recommendation. Pages 159–174 *in*

[3] An asterisk denotes unpublished material.

E. D. Estevez, et al., editors. Proceedings of the conference: managing cumulative effects in Florida wetlands. October 1985, Sarasota, Fla. New College Environmental Studies Program Publication 37, Omnipress, Madison, Wis.

*Marine Mammal Commission. 1980. Annual report of the Marine Mammal Commission, calendar year 1979. A report to Congress. Washington, D.C.

*Marine Mammal Commission. 1981. Annual report of the Marine Mammal Commission, calendar year 1980. A report to Congress. Washington, D.C.

*Marine Mammal Commission. 1991. Annual report of the Marine Mammal Commission, calendar year 1990. A report to Congress. Washington, D.C.

*Packard, J. M., and R. Mulholland. 1983. Analysis of manatee aerial surveys. Prepared for U.S. Fish and Wildlife Service, Cooperative Agreement 14-16-0009-1544. 32 pp.

Packard, J. M., D. B. Siniff, and J. A. Cornell. 1986. Use of replicate counts to improve indices of trends in manatee abundance. Wildlife Society Bulletin 14:165–175.

*Parker, S. L. 1989. Report on a survey of Florida's licensed boat owners for the Save the Manatee Committee. Survey Research Laboratory, Florida State University, Tallahassee. 52 pp.

*Reynolds, J. E., III, and C. J. Gluckman. 1988. Protection of the West Indian manatee (*Trichechus manatus*) in Florida. Document PB 88-222922, National Technical Information Service, Springfield, Va. 85 pp.

Reynolds, J. E., III, and K. D. Haddad, editors. 1990. Report of the workshop on geographic information systems as an aid to managing habitat for West Indian manatees in Florida and Georgia. Florida Marine Research Publication 49, St. Petersburg. 98 pp.

*U.S. Fish and Wildlife Service. 1980. West Indian manatee recovery plan. Prepared by the U.S. Fish and Wildlife Service in cooperation with the Recovery Team. 27 pp.

*U.S. Fish and Wildlife Service. 1989. Florida manatee (*Trichechus manatus latirostris*) recovery plan. Prepared by the Florida Manatee Recovery Team for the U.S. Fish and Wildlife Service, Atlanta, Ga. 98 pp.

Aerial Surveys of Manatees: A Summary and Progress Report

by

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Abstract. Aerial surveys are used to document the distribution and relative abundance of Florida manatees *(Trichechus manatus latirostris)* and to assess population trends. Recent research included aerial surveys by various agencies to determine the distributions of manatees in 10 areas of Florida. In most of these studies, twice-monthly flights were made for at least 2 years. Surveys of distributions have now been made in all areas of the state that are extensively used by manatees. The resulting data have been used for the protection of manatees. Various groups conducted counts of manatees at aggregation sites in winter at selected power plants and at the Crystal River and Blue Spring. These counts have been used to assess population-size trends. Based on mandates by the state legislature, a 2-day, synoptic aerial survey was made to obtain a single annual high count by maximizing survey effort under optimal conditions. These surveys followed two major cold fronts each winter in 1991 and 1992. On 17–18 January 1992, a high count of 1,856 manatees was made (907 on the eastern coast, 949 on the western coast, 8.7% calves). Although not statistical estimates, these counts provide new information about the minimum size of the population. The higher synoptic-survey counts are not proof of an increase of the population through time but are consistent with increases in long-term counts in some areas of the state, including aerial counts at the Crystal River, ground counts at Blue Spring, and counts of aggregations at power plants adjusted for temperature covariates. Current research on aerial surveys is focused on new techniques to improve estimates of population size and trend.

Key words: Aerial surveys, Florida manatee, synoptic survey, trends, *Trichechus manatus latirostris*, warm-water refuges.

Aerial surveys to count and map the distribution of Florida manatees (*Trichechus manatus latirostris*) have been used since 1967 (Hartman 1979). Various methods to survey manatees were used by subsequent researchers (*[1]Hartman 1974; Irvine and Campbell 1978; *Rose and McCutcheon 1980; Irvine 1982; Irvine et al. 1982; Shane 1983; Kinnaird 1985; *Packard 1985; Reynolds and Wilcox 1985, 1986, 1994; Packard et al. 1986). Aerial surveys are useful and cost-effective for counting manatees and for mapping manatee distribution and seem to be the only method with which large numbers of manatees in large areas can be counted. Distribution data have been used extensively for the protection and management of manatees. However, aerial surveys have significant drawbacks for obtaining precise population-size estimates (*Eberhardt 1982; Packard et al. *1984, 1985; Lefebvre et al. 1995). Manatees are difficult to detect and, once seen, are often difficult to count accurately (Packard et al. 1985, 1986). Therefore, aerial counts are generally assumed to be too low. Lefebvre et al. (1995) discussed the theory and the problems of aerial surveys of manatees, particularly for the estimation of population sizes and trends.

My objectives were to provide descriptions of recent and ongoing aerial surveys of manatee distribution, surveys of manatee aggregations in winter, and synoptic surveys. Descriptions of each of these survey categories include statements of survey objectives, summaries of employed procedures, results, and inherent problems and limitations. I also provided information on population size and trend based on

[1] An asterisk denotes unpublished material.

aerial surveys and gave brief descriptions of new research to improve survey techniques.

This paper is largely a summary of all recent information on aerial surveys of manatees and interpretation of results of these surveys, particularly as they relate to estimation of manatee distribution, population size, and trend. Considerable resources are expended on this topic by several organizations, but many of the results appear in technical documents, agency files, or other unpublished sources. I examined these sources and tabulated descriptions to provide a comprehensive overview of aerial survey activities, focusing on work carried out since 1986. Studies prior to 1986 were previously reviewed by Packard (*1985), Beeler and O'Shea (*1988), and O'Shea (1988).

Reviews of methodology employed in previous studies are included under the heading of procedures in descriptions of surveys of manatee distribution and surveys of manatee aggregations in winter. I present original information, including the first published description of the objectives, procedures, and results of synoptic surveys. I also analyzed data on trends in counts of manatees in the Crystal River and at Blue Spring with regression techniques. Details on methods for obtaining and analyzing original information are provided in the sections devoted to these topics.

Recent and Ongoing Aerial Surveys

Surveys of Distribution

Objectives

The purpose of surveys of distribution (extended-area surveys, *Packard 1985) is to document the spatial distribution and seasonal habitat use of manatees. Although these surveys do not give accurate population-size estimates, they provide a minimum estimate of the number of animals in an area on a given day. Abundance is usually considered to be relative because it is believed (or hoped) to include a roughly constant proportion of the animals. Surveys over a large area are made repeatedly during 1 or more years and provide data on seasonal and yearly changes of relative abundance. Data from these surveys have been useful for management because they reveal areas of high seasonal usage and support the protection of manatees (e.g., restrictions on boat speeds or conditions for development).

Procedures

The following is a summary of procedures by the Florida Department of Environmental Protection; the procedures are similar to those of other agencies. The procedures typically followed protocols established by earlier studies such as those by Shane (1983), Kinnaird (1985), Provancha and Provancha (1988), and Rathbun et al. (1990). Some studies may vary from these guidelines, but for each study, procedures are kept as consistent as possible to maximize comparability of counts.

Most aerial surveys are conducted with a Cessna 172 or with a similar small, high-winged, 4-seat airplane with good downward visibility (Irvine 1982). Small helicopters have also been used but are more expensive (Rathbun 1988). Helicopters are useful for surveys in urban or residential areas and in congested airspaces such as near major airports. Pilots experienced in low-altitude, slow-speed, circling flight are used. One or two experienced observers are usually seated on the right side of the aircraft; the door is attached and the window is open. Observers wear polarized sunglasses to reduce glare. The primary (most experienced) observer has a minimum of 30 hours experience in aerial surveys of manatees, has detailed knowledge of the survey area, and sits in the right front seat. A secondary observer is not required for most survey areas but, if used, usually sits in the right rear seat. However, if wide expanses of shallow water are covered, the second observer can view from the left rear seat to help cover the area more effectively (Irvine 1982; Shane 1983; *Packard et al. 1984). A higher proportion of manatees is seen with two experienced observers than with one.

Flights are usually at an altitude of 150 m and at an air speed of 130 km/h. When manatees are seen, the airplane slows and circles the area clockwise until the observer is reasonably sure that an accurate count was made (i.e., until repetitive counts become consistent). Manatees may be spotted by any observer or by the pilot, but manatees are officially counted and mapped only when confirmed by the primary observer (*Packard et al. 1984). Counts are more consistent when the same observers are used each time.

Surveys follow a standardized flight path and are designed to cover the most probable manatee habitats in an area, as described by Irvine (1982), Shane (1983), Packard (*1985), and Rathbun et al. (1990). The route is marked in advance on National Oceanic and Atmospheric Administration 1:40,000 navigation charts or U.S. Geological Survey 1:24,000 topographic maps, and observations are written on the maps. Since 1992, the Florida Department of Environmental Protection has used a portable global positioning system unit (Trimble Pathfinder Basic Plus, Trimble Navigation, Sunnyvale, California) to accurately store information on the position of sightings and the flight path. Routes may include coastal areas, major rivers and estuaries (usually to depths of 3 m) and their tributaries, and freshwater and saltwater canals. Surveys are intensified over aggregation sites in winter, areas within 500 m of shore, offshore areas (shoals) that are shallower than

2 m, areas with aquatic vegetation, freshwater sources, and areas in which manatees have been sighted historically.

High-density concentrations of manatees such as those at power plants are surveyed intensively (intensive-area method; *Packard 1985). Each small area is circled clockwise at least twice before the aircraft moves on. This technique takes more time but gives a higher probability of detecting manatees, including manatees that rest on the bottom and must rise for a breath while the aircraft is passing over. Surveys in areas of low manatee density are less intensive (extended-area method; *Packard 1985). Only one pass is made over each area, which reduces the probability of seeing all manatees but allows sampling in a larger area.

Wide expanses of shallow water (e.g., Indian River, Whitewater Bay) have been covered in a series of transects that were 0.8 km apart (Odell 1979; Shane 1983). Wide expanses of deeper water, such as Tampa Bay, are only covered along the shoreline and around spoil islands (*Reynolds et al. 1991). This allows coverage of a larger area in a given amount of time but decreases the probability of detecting all the manatees.

Recent Florida Department of Environmental Protection surveys were typically conducted twice per month for 2 or more years. The unpublished protocols are similar to those of other agencies (Shane 1983; Provancha and Provancha 1988; Rathbun et al. 1990). Data about each survey flight are recorded on standardized forms and include date; start and end time; observer and pilot names; and aircraft type, speed, and altitude. Weather and water conditions recorded for each segment of the flight include wind speed and direction, air temperature, percentage of clouds, water clarity (depth to which a manatee can be seen), and water-surface conditions. A scale of water-surface conditions was adapted from the Beaufort Scale (Woolf 1977:98): (0) smooth like glass; (1) ripples with appearance of scales, no foam crests; (2) small wavelets, crests of glossy appearance, not breaking, no whitecaps; and (3) large wavelets, crests beginning to break, scattered whitecaps. Flights are canceled at conditions rated 3 or higher. The best visibility below the water surface occurs in smooth, clear water in the presence of few clouds and a bright sun. Flying conditions are best in the presence of little wind and no fog or precipitation.

Data about each observed group are recorded on maps and include the number of adult and calf manatees and their locations and behavior. Calves are defined as animals closely associated with an adult but less than about half the adult's length (Irvine and Campbell 1978; Irvine 1982). Behavior categories include resting (motionless manatees), traveling (swimming manatees), feeding (recognized by the presence of a manatee in a vegetated area and a nearby plume of suspended sediment), and cavorting (group of manatees rolling, splashing, or swimming in tight circles). Most manatees are seen close to the flight path but not directly under the aircraft. Splashes, surface wakes, mud trails, and mud plumes may draw the observer's attention to more distant manatees (Irvine 1982). Manatees in aggregations or in clear water are easiest to find. In winter, aggregations occur at or near warm-water refuges and are often accompanied by large amounts of stirred-up mud. Photographs can confirm counts of groups in clear water but are not of much value for large groups in turbid water.

Results

More than 30 studies were made between 1984 and 1993 (Table 1). Studies through 1986 were reviewed by Beeler and O'Shea (*1988). Surveys have been conducted in most areas of the state since that time. In most studies, twice-monthly surveys were conducted year-round for 2 or more years. Results of many studies have not yet been published (see Table 1 for unpublished sources). Examples of long-term or extensive studies follow.

On the western coast of Florida, the U.S. Fish and Wildlife Service conducted surveys in Lee County during 1984–85 (R. K. Frohlich, Florida Department of Environmental Protection, unpublished data). Subsequent surveys by the department were of manatees in Charlotte, Lee, and Collier counties (Florida Department of Environmental Protection, unpublished data). The Mote Marine Laboratory conducted surveys in Manatee, Sarasota, and Charlotte counties from 1985 to the present (*Kadel and Patton 1992). Eckerd College and the department conducted surveys in Tampa Bay from 1987 to 1994 (*Reynolds et al. 1991; Eckerd College and Florida Department of Environmental Protection, unpublished data). A series of studies of distribution were conducted in northwestern Florida beginning in 1967, covering aggregation sites in winter and warm-season habitats (Charlotte, Dixie, and Levy counties; Powell and Rathbun 1984; Kochman et al. 1985; Rathbun et al. 1990; Chassahowitzka National Wildlife Refuge, unpublished data).

On the eastern coast of Florida, four teams from different agencies conducted simultaneous counts twice-monthly for 1 year during 1986 in five adjacent counties from Volusia to Martin counties (B. L. Weigle, Florida Department of Environmental Protection, St. Petersburg, Florida, and R. K. Bonde, National Biological Service, Gainesville, Florida, unpublished data). These coordinated surveys provided information about seasonal migrations of manatees. Provancha and Provancha (1988, *1989) conducted surveys of manatees in the Banana River from 1984 to the present, expanding the database provided by surveys conducted during 1978–80 by Shane (1983). These surveys revealed high use by manatees of the Banana River, especially during spring migration.

Table 1. Recent aerial surveys of distribution of the Florida manatee (*Trichechus manatus latirostris*).

Area	Dates	Citations
Eastern coast		
Southeastern Georgia (Camden County, Cumberland Sound, warm seasons)	May 1988–Aug 1989	Zoodsma (1991)
Southeastern Georgia (Camden, Glynn, McIntosh counties)	Jun 1989–May 1990	*[a]Valade (1990)
Nassau County	Oct 1986–Oct 1988	Zoodsma (1991)
Duval County	May 1988–Apr 1990	City of Jacksonville, Florida, unpublished report
Duval, Clay, St. Johns counties (lower St. Johns River)	Jul 1982–Jun 1983	Kinnaird (1985)
Duval County (lower St. Johns River)	May 1993–May 1994	Florida Department of Environmental Protection, unpublished data
St. Johns, Clay, Putnam counties (middle St. Johns River)	Jun 1985–Jun 1986	*CH_2M Hill (1986)
Nassau, Duval, St. Johns, Flagler, Volusia counties (ICW, coast)	Jul 1982–Jun 1983	Kinnaird (1985)
St. Johns, Flagler, Volusia counties (ICW, coast)	Mar 1991–Nov 1993	Florida Department of Environmental Protection, unpublished data
Volusia County (Tomoka River)	May 1985–Dec 1985	Florida Department of Environmental Protection, unpublished data
Brevard County	Jan 1978–Feb 1980	U.S. Fish and Wildlife Service, Shane (1983)
Brevard County (Banana River, warm seasons)	Jun 1984–Apr 1986; Feb 1987–ongoing	Provancha and Provancha (1988, *1989); National Aeronautic and Space Administration, unpublished data
Interagency cooperative aerial survey		
Volusia County (Halifax River, Tomoka River, Mosquito Lagoon) Brevard County (northern Indian River, Banana River, Banana Creek)	Dec 1985–Jan 1987	U.S. Fish and Wildlife Service, unpublished data
Brevard County (southern Indian River)	Jan 1986–Jan 1987	Brevard County, unpublished data
Indian River, St. Lucie counties	Jun 1985–Dec 1987	Florida Department of Environmental Protection, unpublished data
St. Lucie, Martin counties	Jan 1986–Jan 1987	U.S. Fish and Wildlife Service, unpublished data
St. Lucie, Martin counties	Aug 1990–Jun 1993	Florida Department of Environmental Protection, unpublished data
Palm Beach County	Aug 1990–Jun 1993	Palm Beach County, unpublished data
Broward, northern Dade counties	Jan 1988–Mar 1990	Florida Department of Environmental Protection, unpublished data
Broward County	Nov 1991–Jun 1993	Broward County, unpublished data
Dade County (Biscayne Bay)	Jul 1974–Jun 1975	*Odell (1976)
Dade County (County-wide)	Jun 1989–ongoing	Dade County, unpublished data
Western coast		
Citrus, Levy, Dixie counties Winter (Crystal River, Homosassa River) Summer (coast and rivers)	1967–ongoing	Hartman (1979); *Powell (1981); Powell and Rathbun (1984); Kochman et al. (1985); Rathbun et al. (1990); Chassahowitzka National Wildlife Refuge, unpublished data
Northern Manatee County	Apr 1985–Dec 1986	Florida Department of Environmental Protection, unpublished data
Pinellas, Hillsborough, northern Manatee counties	Nov 1987–May 1994	Reynolds et al. (1991); Florida Department of Environmental Protection and Eckerd College, unpublished data
Southern Manatee, Sarasota, northern Charlotte counties	Jan 1985–ongoing	Kadel and Patton (1992)

Table 1. *Continued.*

Area	Dates	Citations
Charlotte County	Jan 1987–Dec 1988	Florida Department of Environmental Protection, unpublished report
Lee County		
Core area	Jan 1984–Dec 1985	Florida Department of Environmental Protection, unpublished report
Hendry Creek	May 1988–Dec 1988	
Imperial River	Mar 1987–Feb 1988	
Deep Lagoon	Jul 1986–Feb 1988	
Collier County		
North Collier	Feb 1987–Feb 1988	Florida Department of Environmental Protection, unpublished report
Naples area	Jan 1986–Jan 1987	
Wiggins Pass area	Feb 1987–Sep 1987	
Marco Island area	Jan 1989–Dec 1990	
Everglades City	Jan 1986–Jan 1987	
Ochopee	Mar 1987–Feb 1988	
Port of the Islands	Jan 1986–Dec 1990	
Ten Thousand Islands (includes Everglades City, Ochopee, Port of the Islands)	Jan 1991–Nov 1993	
Everglades National Park	Sep 1973–Jun 1976	Odell (1979)
Everglades National Park	Dec 1979–Sep 1981	Everglades National Park, unpublished report
Everglades National Park	Mar 1990–Mar 1993	*Snow (1992)

[a] An asterisk denotes unpublished material.

In 1992, 10 surveys of distribution were in progress (3 by the Florida Department of Environmental Protection, 3 by other agencies, and 4 jointly by the department and other agencies; Table 1). The department conducted surveys in 1992 in St. Johns, Flagler, and Volusia counties (unpublished data); St. Lucie and Martin counties (unpublished data); Tampa Bay (*Reynolds et al. 1991; Florida Department of Environmental Protection and Eckerd College, unpublished data); and the Ten Thousand Islands in Collier County (unpublished data). Surveys were conducted in 1992 by the Broward County Office of Planning (D. Burgess, unpublished data), Palm Beach County Department of Environmental Resources (D. Carson, unpublished data), and the Everglades National Park (*Snow 1992), each co-sponsored by the Florida Department of Environmental Protection. Surveys were also conducted in Dade County by the Dade County Department of Environmental Resources Management (S. Markley, unpublished data), in the Crystal River area by the Chassahowitzka National Wildlife Refuge (J. Kleen, unpublished data), and in the Banana River by the National Aeronautic and Space Administration (Provancha and Provancha 1988, *1989, unpublished data).

These surveys provided a detailed, up-to-date coverage of all counties in the typical range of manatees. An extensive database of counts and distribution maps now exists for most of the state (Table 1; Fig. 1). These data were needed to support intensive manatee protection proposed in 1989 to regulate watercraft speeds in 13 counties in Florida (*Florida Department of Natural Resources 1989). Sighting data from all surveys conducted by the Florida Department of Environmental Protection and numerous other groups were digitized and entered into the department's Marine Resources Geographic Information System (O'Shea and Kochman 1990; Weigle and Haddad 1990). Maps were created that display manatee sightings from aerial surveys and locations where dead manatees were reported, locations of manatees tracked by telemetry, shorelines, aquatic habitats, shoreline development, boat ramps, sources of fresh and warm water, and water depths. The Marine Resources Geographic Information System has been used extensively by the department to develop protection of manatees in concentration areas and to plan watercraft and shoreline developments (Weigle and Haddad 1990; B. Ackerman and K. Clifton, in preparation).

Problems and Limitations

Surveys provide valuable data on the seasonal distribution and abundance of manatees and have now been conducted in all major areas in the typical range of Florida manatees around the state. They also provide detailed information on habitat use and have been used extensively to define areas that require legal protection. However, a major criticism of surveys of distribution is that they usually do not provide accurate or statistical

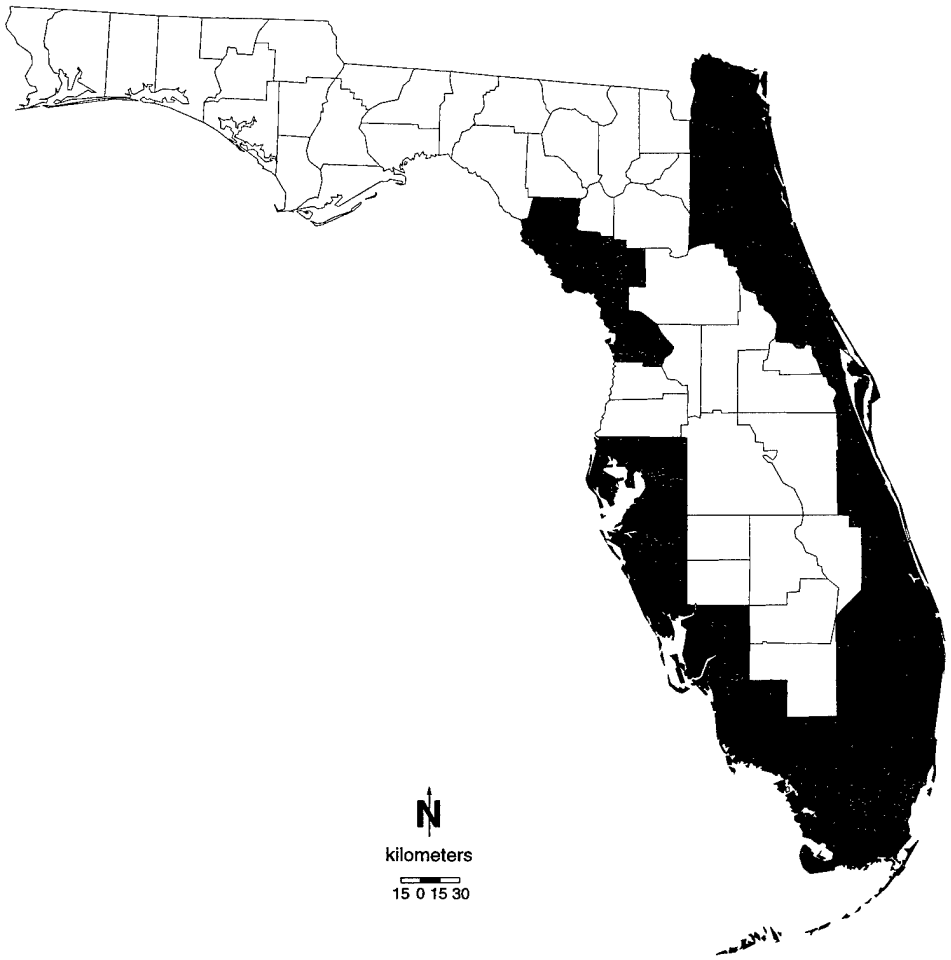


Fig. 1. Counties (*shaded*) in Florida where aerial surveys of manatee (*Trichechus manatus latirostris*) distribution were conducted.

estimates of the number of manatees present (*Eberhardt 1982; *Packard 1985; Lefebvre et al. 1995). Effort varies by flight and by area. Visibility biases are probably not equal among various habitats. Therefore, surveys of distribution do not provide good population-size estimates, especially where visibility bias is large.

Surveys by the Florida Department of Environmental Protection and others were usually conducted twice monthly for 2 years. This provided a sample of the manatees' seasonal distribution; however, a determination of whether this is a sufficient sample has not been possible. Twice-monthly surveys for 2 years seem more adequate than a smaller sample (less frequent or shorter duration surveys) for documenting manatee distribution. This schedule at least compensates for short-term weather changes between months and between consecutive years. But longer-term studies are needed to monitor changes in numbers or shifts in habitat use (Provancha and Provancha 1988, *1989; Rathbun et al. 1990; *Reynolds et al. 1991; *Kadel and Patton 1992). Limited resources require trade-offs between surveys in many study areas for a short time each or surveys in few areas for longer periods.

Because of resource limitations, in 1992 the Florida Department of Environmental Protection began shifting its emphasis from these surveys to the improvement of techniques. However, this temporary moratorium on new surveys of distribution by the department is not without costs. Long-term monitoring is probably needed to assess changes in populations and habitat use. At least, additional distribution data are probably needed on a rotating schedule, perhaps every 5 years, to update data used for the protection of manatees. Many existing data are now older than 5 years, and additional distribution information may soon be required.

Surveys of Manatee Aggregations in Winter

In winter, Florida manatees are forced to travel to warm water because of the low water temperatures in much of the state (*Lefebvre and Frohlich 1986; Reid et al. 1991;

Ackerman et al. 1995; Reid et al. 1995). Manatees migrate either far to the south (e.g., Dade, Monroe, and Collier counties), to a few natural springs (principally the Crystal River and Blue Spring), or to industrial warm-water effluents (Fig. 2). Aggregations in these areas allow the counting of large numbers of manatees from the air with relatively short, concentrated efforts. Some long-term studies provided information on trends in the sizes of these aggregations. Best results should be obtained from a regional population that aggregates in one small area where clear water allows accurate counting.

Objectives

Surveys of manatee aggregations in winter serve to determine the changing numbers of the animals at warm-water sites. Surveys may also be useful for assessing trends in counts. These objectives are primarily useful for measuring progress toward long-term recovery goals. However, these surveys are also valuable for management, such as defining boundaries of seasonal sanctuaries to protect manatee aggregations in winter. Intensive counts were made at aggregation sites in winter as early as 1967 (Hartman 1979). These counts allow the economical counting of a high proportion of all animals in a large region. Long-term studies have been made at the Crystal River, at Blue Spring, and at power plants on the eastern coast and near Fort Myers. These surveys were initially used to determine the number of manatees near aggregation sites throughout the year but later were focused on counts only in winter.

Procedures

Surveys of manatees at power plants on the eastern and southwestern coasts of Florida have been conducted from 1977 to the present (*Rose and McCutcheon 1980; *Raymond 1981; *McGehee 1982; Reynolds and Wilcox 1985, 1986, 1994; *Reynolds 1993, 1994). These surveys were a part of larger research to determine the year-round distribution and abundance of manatees. Surveys were funded by the Florida Power and Light Company. Surveys took place at six major power-generating stations, including five Florida Power and Light Company plants and one Orlando Utility Commission plant (Fig. 2) and their adjacent waters. Manatees were surveyed at several other sites, including smaller power plants at Fort Pierce and Vero Beach and in the Hobe Sound area. Areas within about 8 km of each power plant were included in surveys of manatees (*Rose and McCutcheon 1980; Reynolds and Wilcox 1994) with intensive-area methods (*Packard 1985). Water clarity, general visibility, air traffic problems, and attractiveness to manatees varied among sites.

Details of survey timing and methodology were provided by Rose and McCutcheon (*1980), *Raymond (1981),



Fig. 2. Warmwater sites in Florida that manatees (*Trichechus manatus latirostris*) frequented in winter. Symbols indicate natural springs (*triangles*) and power plants (*circles*) that were included in surveys by the Florida Power and Light Company in winter.

*Packard and Mulholland (1983), and Reynolds and Wilcox (1985, 1986, 1994). Surveys of manatees at power plants were initially 2-day surveys in each week in winter and 2/month in summer. In 1980, these were reduced to 1-day surveys in each week in winter. By 1982 a schedule was achieved that consisted of 4–10 flights each year, only after winter cold fronts. Except for scheduling, the same survey methods have been used since 1977, and the same biologist has conducted the surveys since 1982. This is the longest series of available counts of manatees on the eastern and southwestern coasts of Florida.

Results

Following the suggestions of Eberhardt (*1982), Packard and Mulholland (*1983) conducted preliminary statistical analyses of the survey counts during 1977–82. They attempted to adjust or correct the counts at each power plant, based on air and water temperatures (*Packard and Mulholland 1983; *Packard et al. 1984). Their analyses showed complex relations between the counts at each plant and air and water temperatures and other environmental factors, but counts could not be adjusted for these factors. The numbers of manatees at each plant increased from fall to winter but were highly variable at each plant between consecutive flights and among years. Cold fronts caused manatees to aggregate at certain plants, resulting in high counts. More manatees stayed near the plants on cold days but dispersed from the plants on warmer days to feed. More recent studies with telemetry revealed that some manatees migrate farther southward during the coldest part of the winter, moving among southern plants for a few days, then migrating back northward in spring (Reid et al. 1991, 1995).

The highest summation of counts of manatees at all eastern coast power plants on a single date each winter showed an upward trend (linear regression, $r^2 = 0.39$, $n = 17$, $P = 0.01$; Fig. 3). Annual high counts at the Fort Myers plant were too variable to show a trend ($r^2 = 0.01$, $n = 17$, $P = 0.78$; Fig. 4). However, without correcting for short-term and long-term temperature effects on counts, the annual high counts did not reveal convincing trends (Figs. 3 and 4).

Garrott et al. (1995) improved trend information from data from the surveys at power plants during 1982–91 by developing statistical models that adjust the counts based on short-term and long-term air and water temperature patterns. The adjusted counts in 1982–91 at the power plants on the Atlantic Coast of Florida significantly increased when corrected for temperature. This suggested but did not prove that the actual size of the Atlantic Coast manatee population also increased. The adjusted counts at the Fort Myers plant did not show a significant trend.

Problems and Limitations

The percentage of manatees that is in aggregations in winter to be counted at any given time and the percentage of animals that are actually observed are not known (*Eberhardt 1982; *Packard 1985; Lefebvre et al. 1995). These counts are the only long-term data from the eastern-coast and southwestern aggregation sites, and considerable effort is justifiable to develop an index to past and future population-size trends from these data (*Packard 1985; Packard et al. *1984, 1986, 1989). An increase in knowledge of factors that influence these counts is important. Analysis of counts with telemetry data on locations and behavior of manatees by the area (Reid et al. 1995) and air and water temperatures may provide further information for correcting for possible biases in these counts.

Synoptic Survey

The synoptic survey is designed to obtain statewide counts of manatees in all winter habitats at one time. De-

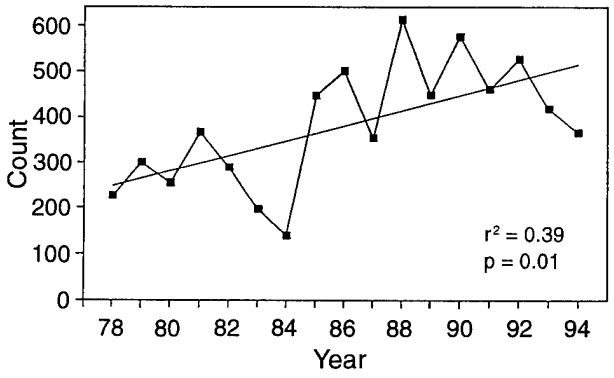


Fig. 3. Largest numbers of manatees (*Trichechus manatus latirostris*) in aggregation areas at power plants on the eastern coast of Florida, 1977–1994. Data were collected during aerial surveys in winter (Reynolds and Wilcox 1994 and sources therein). Data from 10 power plants were combined.

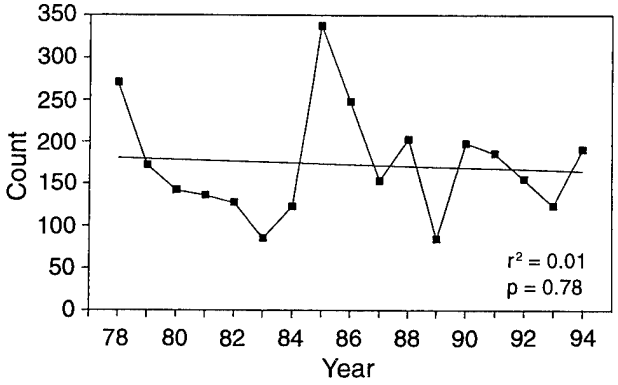


Fig. 4. Largest numbers of manatees (*Trichechus manatus latirostris*) at the Fort Myers power plant, Lee County, southwestern Florida, 1977–1994. Data were collected during aerial surveys in winter (Reynolds and Wilcox 1994 and sources therein).

scriptions of the synoptic survey have not been published. This procedure combines some features of the intensive counts of manatees in aggregations in winter and extended-area surveys of manatee distribution. The goal is to obtain the highest, presumably most accurate count, which then serves as a new baseline to evaluate indexes from other surveys. Plans were initially made by the Florida Department of Environmental Protection to conduct a synoptic survey in 1989. Surveys were not made until 1991, however, because of the lack of weather patterns suitable for synoptic surveys in 1989 or 1990. In 1990, the Florida State Legislature mandated "an impartial scientific benchmark census of the manatee population to be conducted annually" by the Florida Department of Environmental Protection (Florida Statute §370.12.5a). The subsequent synoptic surveys were made to comply with this mandate.

Procedures

The term *synoptic* was used to designate comprehensive coverage of a large area at one time. Plans were made to cover the entire potential winter range of manatees in Florida and in southeastern Georgia in 2 days (Fig. 1). Most routes followed those of recent surveys, principally over rivers, estuaries, bays, streams, and canals along most of the coastline of peninsular Florida. Most aircraft were Cessna 172's, although in a few areas manatees were surveyed from helicopters. Ground-based observers searched Blue Spring and two industrial sites in southeastern Georgia where vertical visibility was poor. Planes flew at an altitude of 150 m and at a speed of 130 km/h. Transects were used to cover some wider areas. These methods were flexible and were altered in some cases to accommodate local conditions. Routes were planned and teams were on standby for 2 months each winter. Each count was planned to follow two cold fronts or a prolonged cold period in January or February when manatees were concentrated at warm-water aggregation sites and when the winter migration was probably completed. The desired weather pattern usually was forecast with only 2–3 days notice, which made planning difficult.

Manatees on the eastern coast of Florida were surveyed on the first day and on the western coast on the second day. Surveys required nearly simultaneous counts by biologists from numerous agencies. Whenever possible, manatees in adjacent areas were simultaneously surveyed to minimize the effects on counts from manatee movements between areas. The survey was made on 2 days because of the limited number of available biologists and aircraft. Movement of manatees between the eastern and western coasts was assumed to be minimal (O'Shea 1988). Counts of manatees in all areas were tallied, and possible duplicate counts were eliminated by taking into consideration the manatees' mapped positions and the distance the manatees may travel in the elapsed time between adjacent surveys.

Synoptic surveys of manatees were conducted three times, twice in 1991 and once in 1992. Following successful surveys in 1991, the flight window in 1992 was shortened to the period from early January to mid-February, and planned coverage was reduced in a few areas. After 1991, surveys conducted north of Tampa on the western coast and north of Fort Pierce on the Atlantic Coast covered only warm-water aggregation sites. This reduced the number of teams and the cost. Few manatees were in the omitted areas during the two previous surveys. Conditions on the most recent survey in 1992 were more conducive to higher counts of manatees than during previous synoptic surveys. A significant cold front passed across Florida on 14 January 1992, and a second on 16 January. Weather conditions were good; several weeks of cool weather were followed by several days of steadily decreasing temperatures. The survey was conducted during 17–18 January; the weather was clear and cold and winds diminished in most areas. Counts were made on 21 survey routes. Ten aircraft flew simultaneously on the first day, nine on the second day. Surveys were not conducted during the winters of 1992–93 or 1993–94 because of weather conditions.

Results

Two surveys were completed in 1991 (23–24 January and 17–18 February). Counts during the first survey were 679 manatees on the eastern coast and 589 on the western coast or a total of 1,268 manatees (8.6% calves; Table 2). A second survey was conducted during 17–18 February 1991. Weather had been warm for almost a month, and a strong cold front passed on 15 February. A total of 1,465 manatees (8.8% calves) was seen, 813 on the eastern coast and 652 on the western coast. This was about 20% more than in any

Table 2. Counts of Florida manatees (*Trichechus manatus latirostris*) from synoptic aerial surveys on the eastern and western coasts of Florida, 1991–1992.

Date	Eastern	Western	Total	Percent calves	Number of Teams	Number of Observers
23–24 Jan 1991	679	589	1,268	8.6	27	32
17–18 Feb 1991	813	652	1,465	8.8	27	32
17–18 Jan 1992	907	949	1,856	8.7	21	28

previous statewide count (Table 2). During both surveys, almost all of the manatees seen in the northern part of the state were at warm-water aggregation sites (Table 3). During the second survey in the southern part of the state, about half were away from warm water (Table 3), particularly in the southeast.

The largest number of Florida manatees ever recorded was seen during the synoptic survey during 17–18 January 1992. A total of 1,856 manatees (8.7% calves) was counted, 907 on the eastern coast (7.6% calves) and 949 on the western coast (9.6% calves; Tables 2–4; Fig. 5).

Problems and Limitations of the Synoptic Survey

The synoptic surveys provided new information on the minimum size of the manatee population in Florida: 1,856 manatees in January 1992. Until that time, only 1,200 were known to exist. The greatest value of the surveys may be as a snapshot of the whole state population at once, reducing the possibility of movements among areas between adjacent count segments. However, these counts seem to be highly variable among surveys, depending on weather conditions. Weather conditions will never be optimal in all areas at once, and counts in some areas may be maximized under opposite weather conditions. In several areas, higher counts were obtained on dates other than during synoptic surveys. Optimal conditions are difficult to predict, and the best conditions in each winter are easily missed. Surveys were not conducted during some winters because of inadequate weather conditions. The results are not statistical estimates of population size and will probably not provide estimates of population-size trends. They are more costly than many other surveys because of the required large number of aircraft and biologists and the large amounts of coordination.

Population Size and Size Trends

Trends Based on Surveys of Aggregations in Winter

Crystal River Area

Aerial surveys of manatees have been conducted in the Crystal River region in winter since 1967, except during the three winters from 1970–71 to 1972–73. Surveys covered the Crystal and Homosassa rivers and surrounding areas (Hartman 1979; *Powell 1981; Powell and Rathbun 1984; Kochman et al. 1985; Rathbun et al. 1990; Chassahowitzka National Wildlife Refuge, unpublished data). These are the only aggregation sites in winter in northwestern Florida and are characterized by clear water. This area is largely isolated in winter from other aggregation sites; however, counts and distribution in the Crystal River area markedly change during and between winters. Animals leave on feeding excursions, and changes in counts can be substantial from week to week (Rathbun et al. 1990).

I used exponential regression to examine maximum aerial counts in each winter from 1967 to 1994 for trends. Maximum aerial counts each winter in the Crystal River area were based on data from Hartman (1979), Powell (*1981), Powell and Rathbun (1984), Rathbun et al. (1990), and unpublished data of the Chassahowitzka National Wildlife Refuge. Exponential regression was used because populations often change exponentially and because it allows simpler expression of the annual percentage change in numbers. The formula for exponential regression is

$$y = a \times e^{bt} \quad (1)$$

where y is the count, t is the year, and a and b are regression coefficients (Eberhardt and Simmons 1992). This is equivalent to the linear regression form

$$\ln(y) = \ln(a) + bt \quad (2)$$

This further gives

$$\text{annual percent change} = (e^{b} - 1) \times 100\%. \quad (3)$$

Manatee counts in the Crystal River area showed a significant upward trend with low variability (Fig. 6; +9.7%/year; $r^2 = 0.93$, $n = 23$, $P < 0.001$). Maximum counts increased from 38 during 1967–68 to 292 during 1992–93. Similarly, the total number of manatees identified during each winter (Hartman 1979; *Powell 1981; Powell and Rathbun 1984; Rathbun et al. 1990) increased through time.

Moore (1951) described manatee sightings as rare in the Crystal River area in the 1940's and earlier. Increasing populations were noted by later researchers (Hartman 1979; Powell and Rathbun 1984; *Beeler and O'Shea 1988; O'Shea 1988; Rathbun et al. 1990). Life-history studies of known individuals suggested that most of this increase could

Table 3. Percentage of Florida manatees (*Trichechus manatus latirostris*) at warm-water sources during synoptic surveys in northern and southern zones of Florida, 1991.

Date	Northern zone	Southern zone	Statewide
23–24 Jan 1991	93	7	53
17–18 Feb 1991	97	47	85

Table 4. Synoptic aerial survey of Florida manatees (*Trichechus manatus latirostris*) in Florida and Georgia, 17 (eastern and coast) 18 (western coast) January 1992, unless otherwise noted.

Location of survey	Total number of manatees	Number of calves	Comments
Eastern coast			
Camden/Glynn counties, Georgia	5	0	Count from shore at four industrial plants
Nassau/Duval counties	2	0	Five industrial plants and vicinity
St. Johns/Flagler/Volusia counties	0	0	Conducted 18 Jan
Volusia County (St. Johns River) Blue Spring Run	67	7	Count made from canoe
Brevard County			Aerial counts at power plants, warm-water sites, known use areas, and immediate vicinity
OUC plant	122	[a]	
Cape Canaveral plant	59	[a]	
Indian River County			
Vero Beach plant	23	2	
Other sites	32	4	
St. Lucie/Martin counties			
Fort Pierce plant	20	3	
Other sites	20	[a]	
Palm Beach County			
Riviera Beach plant	245	15	
Other sites	38	4	
Broward County			
Port Everglades plant	167	8	Survey using helicopter
Fort Lauderdale plant	7	0	
Other sites	5	0	
Dade County	86	11	Survey using helicopter
Monroe County (Florida Keys)	9	1	
Eastern total	907	55	
Western coast			
Citrus/Levy counties	260	24	
Western Tampa Bay	15	0	
Eastern Tampa Bay	111	13	
Manatee/Sarasota counties	2	0	
Sarasota/Charlotte counties	17	3	
Charlotte/Lee counties	190	20	
Lee/Collier counties	246	22	
Monroe County (western Everglades)	77	7	
Monroe County (eastern Everglades)	29	2	Conducted 17 Jan
Okeechobee Waterway/Lee/Hendry/ Glades/ Okeechobee/Martin/ Palm Beach counties	2	0	Conducted 17 Jan
Western total	949	91	
Grand total	1,856	146	

[a] Calf counts were not obtained at three sites.

result from reproduction and survival of resident manatees (Eberhardt and O'Shea 1995), but some of the increase probably also resulted from permanent immigration by adults from areas farther south and recruitment of their descendants (Powell and Rathbun 1984; O'Shea 1988; Rathbun et al. 1990; Rathbun et al. 1995). At the Crystal River, food supplies are abundant, unlike at most other winter aggregation sites (Hartman 1979; O'Shea 1988), and increases in manatee numbers in the region have been attributed in part to the introduction of exotic aquatic vegetation in the mid-1960's (Hartman 1979; Powell and Rathbun 1984; O'Shea 1988).

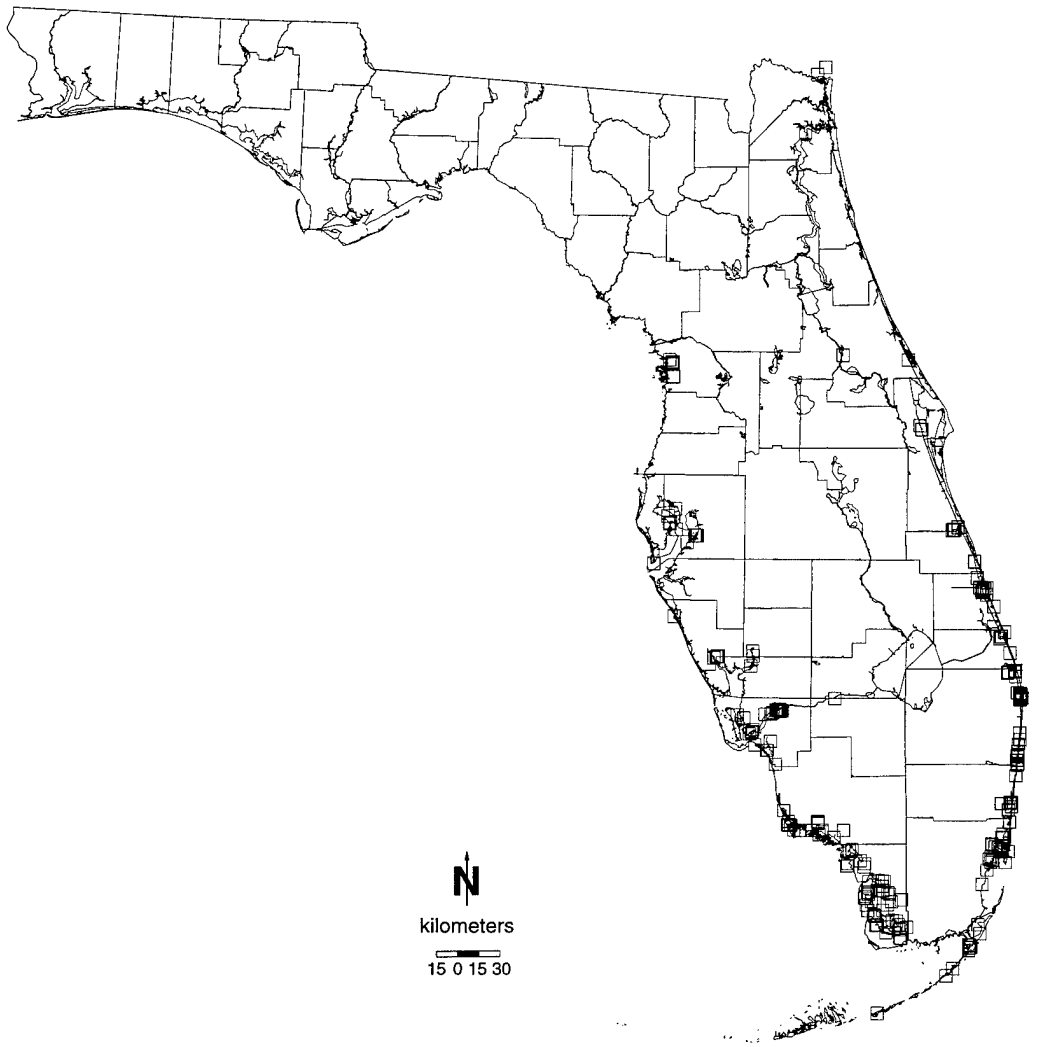


Fig. 5. Locations of 1,856 manatees (*Trichechus manatus latirostris*) seen during the third synoptic aerial survey in Florida and in southeastern Georgia, 17–18 January 1992. Each symbol indicates one group.

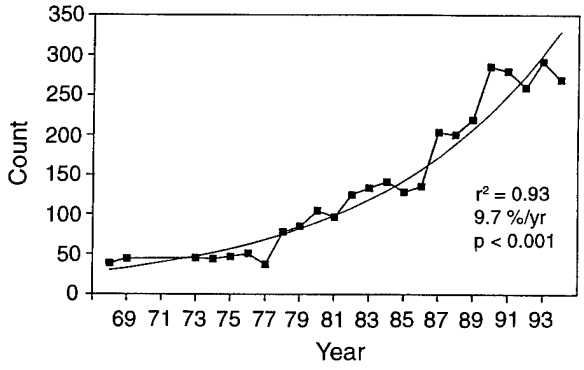


Fig. 6. Trend (exponential regression) in counts of Florida manatees (*Trichechus manatus latirostris*) made during aerial surveys at winter aggregation sites in the Crystal River area, Citrus County, 1967–1994. Highest count obtained during each winter is shown. Data were collected by Hartman (1979), Powell (*1981), Powell and Rathbun (1984), Rathbun et al. (1990), and the Chassahowitzka National Wildlife Refuge (unpublished data).

Blue Spring

Counts of manatees at the aggregation site at Blue Spring State Park provide the only long-term trend data about manatees in the St. Johns River. The spring run is shaded by a tree canopy, and aerial surveys are therefore not practical. However, the clear water allows accurate counts from canoes and shore, and all individuals are identifiable (T. J. O'Shea, National Biological Service, Fort Collins, Colorado, personal communication). Counts have been conducted almost daily in winter since 1970 except during the winters of 1972–73 and 1973–74. Analysis of the total number of manatees identified during each winter was based on data obtained from Hartman (1979), Powell and Waldron (*1981), O'Shea (1988), T. J. O'Shea (National Biological Service, Fort Collins, Colorado, personal communication), and W. C. Hartley (Florida Park Service, Orange City, Florida, personal communication).

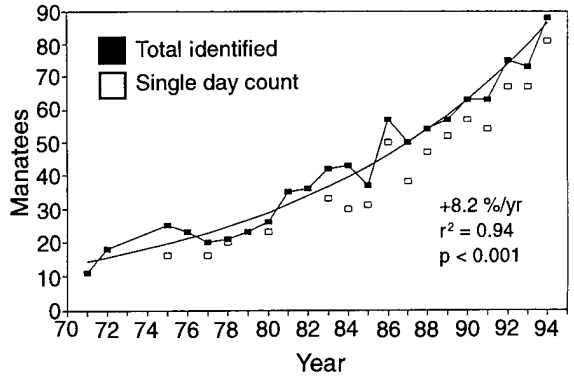


Fig. 7. Trend (exponential regression) in counts (highest total number of animals identified during each winter) of Florida manatees (*Trichechus manatus latirostris*) at the winter aggregation site in Blue Spring State Park, Volusia County, 1970–1994. Highest counts of manatees on a single day each winter at Blue Spring are also shown. Data were collected during surveys by canoe and snorkeling by Hartman (1979), Powell and Waldron (*1981), O'Shea (1988) and the National Biological Service and Florida Park Service (unpublished data).

The number of manatees identified at Blue Spring each winter showed an upward trend with low variability (+8.2%/year; $r^2 = 0.94$, $n = 22$, $P < 0.001$; Fig. 7), increasing from 11 during 1970–71 to 88 during 1993–94. Similarly, highest single-day counts each year increased from 11 during 1970–71 to 81 during 1993–94 (+8.7%/year; $r^2 = 0.96$, $n = 19$, $P < 0.001$).

Increases in counts at Blue Spring were discussed by Beeler and O'Shea (*1988), O'Shea (1988), O'Shea and Hartley (1995) and O'Shea and Langtimm (1995). Studies of known individuals showed that most of this increase resulted from reproduction and survival of resident animals, but part was also from permanent immigration of adults (O'Shea 1988). A maximum of about one-third of the increase in counts at Blue Spring may be due to immigration and subsequent reproduction by the immigrants (T. J. O'Shea, National Biological Service, Fort Collins, Colorado, personal communication). Forty-two of the 63 manatees identified at Blue Spring during the 1990–91 winter season were present during the first 3 years of intensive study (winters 1978–79 through 1980–81, $n = 14$ animals) or were descendants ($n = 28$) of those animals. The remaining 21 were immigrants or their offspring. Therefore, during a 10-year period, 67% of the net population growth was from internal recruitment (T. J. O'Shea, National Biological Service, Fort Collins, Colorado, personal communication). This is a minimum estimate because some individuals identified as new immigrants could have been offspring of long-term residents that returned when older but were no longer identifiable as such because of new marks. O'Shea and Langtimm (1995) found high adult survival at Blue Spring. Eberhardt and O'Shea (1995) estimated positive population growth rates at Blue Spring based on demographic data and discussed results in relation to trends in counts. Manatees at Blue Spring have been increasingly protected from direct injury from watercraft and from disturbance by boats, swimmers, and divers (Hartman 1979; *Powell and Waldron 1981; *Beeler and O'Shea 1988; O'Shea 1988). This increased protection may have encouraged more manatees to use these aggregation sites.

Tampa Bay

Weigle et al. (*1988) summarized the highest annual aerial counts of manatees obtained in the Tampa Bay area from 1979 to 1986, and no counts exceeded 76 manatees. Subsequently, counts of manatees during surveys during the winters of 1987–94 were as high as 190 (24 January 1994; *Reynolds et al. 1991; Florida Department of Environmental Protection and Eckerd College, unpublished data). However, major changes also occurred in warm-water sources in the 1980's (*Weigle et al. 1988). The Gardinier Phosphate Plant discharge into the Alafia River ceased in 1986, and a small no-entry zone was created at the Tampa Electric Company's Big Bend plant in 1986 and expanded to the entire discharge canal in 1989 (*Reynolds et al. 1991). These actions probably reduced disturbance to manatees from boats and resulted in a shift in manatee use from the Alafia River to the Big Bend plant during 1985–86 (*Weigle et al. 1988). The increasing levels of protection may have encouraged manatees to immigrate from other wintering areas, although this has not so far been detected by studies with telemetry (*Lefebvre and Frohlich 1986; B. L. Weigle, Florida Department of Environmental Protection, St. Petersburg, Florida, unpublished data) or scar catalog studies (Beck and Reid 1995; B. L. Weigle, Florida Department of Environmental Protection, unpublished data). The number of documented manatee deaths is low in the Tampa Bay area (O'Shea et al. 1985; *Reynolds et al. 1991; Ackerman et al. 1995). Manatee sightings were apparently rare in the Tampa Bay area until the 1950's (Moore 1951), and numbers seemingly were low until the 1970's (Hartman *1974, 1979; Irvine and Campbell 1978; Irvine et al. 1982; *Beeler and O'Shea 1988).

Counts at Power Plants

Trends in counts of aggregations in winter at seven power plants on the eastern coast and at the Fort Myers plant on the western coast were presented above and by Garrott et al. (1995). These are the only long-term trend data in these areas. Results from Garrott et al. (1995) suggested that adjusted counts at the plants on the eastern

coast increased but showed no evidence of change at the Fort Myers plant on the western coast. Although the number of documented deaths in both areas is relatively high (O'Shea et al. 1985; Ackerman et al. 1995), models based on demographic information suggested that past manatee population growth on the eastern coast could have occurred but, if so, at a low rate (Eberhardt and O'Shea 1995).

Trends during Warm Seasons in the Banana River

Intensive surveys of manatees during warm seasons have been made in the northern Banana River since 1977 (Shane 1983; Provancha and Provancha 1988, *1989; National Aeronautical and Space Administration, unpublished data). These are the only long-term counts during warm seasons on the eastern coast. Counts were made from an airplane during 1977–80 and from a helicopter during 1980–81 and from 1984 to the present; similar flight routes were used (Provancha and Provancha 1988). Aerial counts increased through time; the counts were highest in spring each year (Provancha and Provancha 1988, *1989; National Aeronautical and Space Administration, unpublished data). High counts in spring seemed to reflect a temporary influx of manatees in transit during spring migration (Provancha and Provancha 1988). Recent counts in spring were as high as 200–400 manatees. Counts in summer (June to August) north of the NASA Causeway from 1977 to 1981 did not exceed 30 animals (Provancha and Provancha 1988), but recent counts were as high as 139 (J. Provancha, National Aeronautical and Space Administration, Kennedy Space Center, Florida, unpublished data). Provancha and Provancha (1988) suggested that no other area on the eastern coast offers as much protected suitable habitat as the northern Banana River. Much of this area is inside the Kennedy Space Center and has been closed to boating for many years for security reasons. A larger area in the Merritt Island National Wildlife Refuge (north of the Cape Canaveral Barge Canal) was closed in 1990 for manatee protection, substantially decreasing human disturbance. Provancha and Provancha (1988) suggested two possible reasons for increased counts in the northern Banana River: increases in manatee population size and shifts in habitat use by manatees into the northern Banana River because of increased development or disturbance outside this sanctuary.

Problems and Limitations in Long-term Survey Data

Manatee populations in all areas for which long-term data exist seem to be increasing (eastern-coast power plants, Crystal River, Blue Spring, Tampa Bay, Banana River in summer) or appear stable (Fort Myers power plant). Although these data are encouraging, they do not encompass all areas, and trends may differ in populations lacking long-term data. Moreover, interpretations of increases in counts over time are difficult because of various confounding factors (Reynolds and Wilcox 1994; Garrott et al. 1995). Although the increasing counts in most areas where manatees were surveyed suggested that populations increased, alternative explanations exist. Manatees are able to locate and use protected areas. Manatees may have increased use of these areas and avoided other areas in response to improving resources such as availability of warm water, protection from human disturbance, and increasing aquatic plants. Manatees may have become more visible to biologists, perhaps because a higher proportion uses aggregation sites than in the past or because of improved visibility or changes in plant operations (Packard et al. 1989; Reynolds and Wilcox 1994). In most cases, different people conducted surveys, the survey procedures evolved, and skills or techniques for surveying aggregated manatees in winter may have improved. Each of these alternative explanations could also result in the observed upward trends of counts in some refugia in the absence of an actual increase in the manatee population size. Although no data support these alternative speculations on the apparent increases in counts, conclusions that populations actually increased in these parts of the state could be erroneous (Reynolds and Wilcox 1994; Eberhardt and O'Shea 1995; Garrott et al. 1995).

Statewide Population-size Estimates

A population-size estimate of Florida manatees is desirable as a baseline for estimating trends, modeling populations, and assessing the effect of observed mortality. Statewide surveys were designed to provide such a baseline. However, other than the synoptic surveys, only a small number of studies included simultaneous counts of manatees throughout the southeastern United States. Hartman (*1974) counted 255 manatees throughout Florida and southeastern Georgia in summer 1973; he used one plane during six consecutive weeks. A crude correction factor was based on water clarity (*Hartman 1974). Hartman concluded from these counts and interviews of the public that probably 800 manatees (range 750–850) were in Florida and Georgia. Counts in summer have since been lower than counts in the same general areas in winter (Irvine and Campbell 1978; Rathbun et al. 1990; *Reynolds et al. 1991). Manatees are dispersed widely in summer in small groups at low densities in unpredictable locations. Visibility is poor in many areas because of turbid water and overhanging trees.

In winter 1976, Irvine and Campbell (1978) counted 738 manatees in Florida and Georgia. Nine teams

conducted surveys statewide in 6 days after a cold front. Manatees in most areas were counted simultaneously in a single day. These and other data suggested a population of at least 800–1,000 in 1978 (*Brownell et al. 1981). A survey was also conducted in August 1976 (Irvine and Campbell 1978) and included parts of the Florida panhandle, Georgia, and the Carolinas; 245 manatees were seen, similar to Hartman's (*1974) count in summer 1973. After 1976, research shifted to other topics because these mass efforts were too costly and logistically difficult and did not provide data for clear interpretation (*Eberhardt 1982; G. B. Rathbun, National Biological Service, San Simeon, California, personal communication).

High counts at power plants in January 1985 and counts in other areas of the state led experts to revise the minimum statewide estimate to 1,200 in 1985 (O'Shea 1988). However, surveys were not made at the same time in all areas, and manatees in some important areas had not been counted at all in several years. A record single-day count of 717 manatees at selected power plants was made under favorable counting conditions in January 1986, and a higher count of 804 in February 1988 (Reynolds and Wilcox 1994). In December 1989, a composite of counts in various areas during a short time period revealed 1,240 manatees (B. B. Ackerman, Florida Department of Environmental Protection, St. Petersburg, Florida, unpublished data). As discussed above, the synoptic survey in January 1992 revealed a count of 1,856.

Interpretation of the results of these statewide surveys is difficult. In 19 years the best minimum estimate increased from 800 to 1,856, but these data were obtained with survey methods that differed in several important ways. O'Shea (1988) reviewed statewide manatee population counts through 1985. He found no firm evidence of a decrease or increase in manatee populations in spite of the increase in the official minimum estimate because the methods were without a measure of precision.

What does the record count of 1,856 in January 1992 reveal about trends in the statewide manatee population? Perhaps not much. Even though the best minimum counts increased from 800 in 1973 to 1,000 in 1978, to 1,200 in 1985, and to 1,856 in 1992, a basis to determine the statistical significance does not exist (*Eberhardt 1982; O'Shea 1988). Previous surveys were not over as large an area, under as good conditions, as comprehensive, or in as short a time as the 1992 synoptic survey.

This higher count does not provide evidence that the population is no longer endangered. Rescaling to a new baseline does not change the fact that mortality from various anthropogenic causes is still increasing and that these threats may be greater than the population can withstand (*Brownell et al. 1981; O'Shea 1988; Marmontel 1993; Ackerman et al. 1995; Eberhardt and O'Shea 1995). Accurate assessment of the effects of anthropogenic mortality on the manatee population is not yet possible. Therefore, higher statewide counts provide no reason to relax conservation. In the interim, however, methods of statewide surveys must be improved. Goals should be to use statistical sampling methods to reduce the required effort in a wide-scale survey, provide statistically meaningful estimates with confidence limits, correct for counting biases, and reduce the total cost (Lefebvre et al. 1995).

Research to Improve Survey Techniques

Techniques for estimating population sizes of Florida manatees are currently inadequate (*Eberhardt 1982; Packard et al. 1985, 1986; O'Shea 1988; *Reynolds and Gluckman 1988; *U.S. Fish and Wildlife Service 1989; Lefebvre and Kochman 1991; Lefebvre et al. 1995). No basis exists to statistically measure trends in population size, correct for visibility errors (visibility bias), or assign confidence levels to minimum counts (*Eberhardt 1982; *Packard and Mulholland 1983; Packard et al. *1984, 1986; *Packard 1985; Lefebvre et al. 1995). The number of manatees cannot be estimated from a random sample of current surveys. The estimated number of manatees in one subunit cannot be extrapolated to other subunits. Counts are not corrected for visibility bias. The current survey procedures probably lead to an underestimation of the number of manatees and do not provide estimates of the precision of the count (i.e., standard deviation).

Research to Determine Visibility and Absence Bias

Visibility bias (the proportion of missed animals) is one of the largest problems in estimating manatee population sizes (Lefebvre et al. 1995). Visibility bias in aerial counts of other animals was determined with known or marked subpopulations (Eberhardt et al. 1979; Pollock and Kendall 1987). The proportion of a known number of radio-tagged animals observed during counts has also been used to estimate bias in various species of large mammals (Floyd et al. 1979; Gasaway et al. 1985; Packard et al. 1985, 1989; Samuel et al. 1987; Ackerman 1988). Other researchers used known subpopulations comprising groups monitored intensively by another method or from the ground (*Hartman 1974; Samuel and Pollock 1981) or known numbers of penned animals (Packard et al. 1989; Unsworth et al. 1990). Accurate counts are needed to obtain correction factors (Eberhardt et al. 1979; *Eberhardt 1982; Pollock and Kendall 1987). Correction factors were developed for counts of other species—some terrestrial—and were based on group size, behavior, and habitat (Eberhardt et al. 1979; Floyd et al. 1979; Samuel and Pollock 1981; Gasaway et al. 1985; Samuel et al. 1987; Ackerman 1988; Marsh and Sinclair 1989b).

Packard et al. (1985) investigated visibility bias in surveys of manatees in the St. Johns River based on known numbers of radio-tagged and unmarked manatees near Blue Spring. Many manatees were not seen in these turbid waters; an estimated 38–47% were seen. The seen proportion varied by river, lake, and creek habitats. The radio tags were often not visible from aircraft when the peduncle was submerged. Packard et al. (1989) investigated visibility bias in winter near Fort Myers with telemetry. Floating transmitters used then were not easily seen from aircraft (*Packard 1985; Packard et al. 1989). These researchers did not determine the environmental variables that correlate with visibility or suitable correction factors for current surveys.

However, as recommended by Lefebvre et al. (1995), additional assessment of visibility bias is underway. Preliminary tests of visibility bias in aerial counts of manatees were made by the Florida Department of Environmental Protection and collaborators during 1990–92 with radiotelemetry and are planned for the future. Analysis of data will be made with logistic regression to identify variables (covariates) that influence the probability of seeing a given group of manatees. Significant variables will be used to develop an equation (visibility model) to predict the probability of seeing groups under various environmental conditions. This equation can then be converted to a visibility correction factor (Samuel et al. 1987; Ackerman 1988; Steinhorst and Samuel 1989) on a group-by-group basis. Success of this approach depends on the visibility of the tags from the air (*Packard 1985; Pollock and Kendall 1987).

A different approach to estimating the number of animals missed in surveys is a double-sampling technique (Pollock and Kendall 1987; Marsh and Sinclair 1989b; Marsh 1995). Paired observers view the same area, and each counts and maps seen animals. The number of animals seen by each observer is determined, and mark–recapture statistics are used to estimate the number of objects missed by both observers. This provides an estimate with confidence limits of the total number of objects in the surveyed area. When animals are in groups, the number of groups is estimated and is multiplied by the average group size to provide the total number of present animals (Marsh and Sinclair 1989b; Marsh 1995). Correction factors are based on seen or missed groups—not individuals—because sightings of members in a group are not considered independent. Double-observer counts were tested during monthly aerial surveys of manatee distributions in Tampa Bay during 1989–92 (*Reynolds et al. 1991; B. Ackerman, Florida Department of Environmental Protection, St. Petersburg, Florida, unpublished data) and will be made in the future.

Telemetry data can also be used to investigate absence bias in determining whether manatees are present in the survey area as expected (Packard et al. *1984, 1989; Marsh and Sinclair 1989b; Lefebvre et al. 1995; Marsh 1995). For example, locations of radio-tagged animals can be used to estimate the proportion of all animals available to be counted at power plants on a given day.

Use of Novel Approaches

Lefebvre et al. (1995) suggested that standardized surveys during warm seasons should be tested as supplements to counts in winter. Short-term weather patterns probably affect the density of manatees less in summer than in winter. Therefore, counts during warm seasons with a standardized procedure and during a short time period should provide more consistent data for determining annual indices and population-size trends. Strip transects have been used for population-size estimates of dugongs (*Dugong dugong*; Marsh and Sinclair 1989a, 1989b; Marsh 1995) and other species (Eberhardt et al. 1979; Pollock and Kendall 1987; Barlow et al. 1988; Graham and Bell 1989). Strip transects were used for counting bottlenosed dolphins (*Tursiops truncatus*) and manatees in the Indian and Banana rivers, (Leatherwood 1979), but manatee counts were incidental and were not used for calculating estimates. Transects are most suitable in large, homogenous areas. The Florida Department of Environmental Protection and the National Biological Service recently selected three areas—Charlotte Harbor, Ten Thousand Islands, and the Banana River—to test a strip transect methodology for counting manatees in warm seasons. This work was initiated in 1992 and is in progress.

Ongoing research also includes the use of other novel approaches. Recent test flights were conducted to compare counts from an airship and from an airplane, namely a Cessna 172 and the Airship Shamu. The airship is provided by Sea World of Florida and has a length of 58 m and a capacity for two pilots and five passengers. The flights were made over three Tampa Bay power plants and adjacent areas on 12 December 1990 and on 22 and 25 January 1992. Additional flights were made in 1993. The airship was flown along discharge canals and transects across adjacent water bodies. Observers looked out of large, open windows on either side of the airship. Altitudes were usually 150 m but also 20–300 m. Ground speed was 0–15 km/h. Because of the stability and slow speed of the airship, observers were able to use binoculars, long telephoto lenses on still cameras, and video cameras. Preliminary flights demonstrated the usefulness of an airship for counting manatees, although counts from the two aircraft were similar. Manatees had less reaction to the airship than to an airplane. This allowed investigators to observe manatees without repeatedly circling in a small plane or disturbing the animals with the noise and turbulence from a helicopter.

Large airships may not be as effective for surveys of manatee distributions because they are not as maneuverable as an airplane. However, comparisons of the two aircraft must be made to determine the strengths and weaknesses of each kind of aircraft for various tasks. I recommend additional testing of airships. Smaller, more maneuverable and more affordable airships may soon be available for extended observation.

Other technologies are probably useful for aerial surveys of manatees. High-resolution aerial video may be used to record sightings on long transects for later viewing and counting and simultaneous documentation of water conditions (Sidle and Ziewitz 1990). Computer-image analysis may be available for detecting and counting manatees on videotapes and for measuring body lengths (Ratnaswamy and Winn 1993) and quantifying visibility conditions. Use of global positioning systems will improve accuracy of sighting locations and will accurately record the flight path to document the exact areas covered during flights. Advances in sonar may allow accurate detection of manatees in some small areas where aerial counting of the manatees is difficult; counts on the ground could provide verification of counts from aircraft. Sensitive time-depth recorders (Goodyear 1993) may be used to document when manatees are at the surface and to improve correction factors. Previously classified, military remote-sensing technology may eventually be used to detect and count marine mammals with various platforms (military satellites, high-altitude reconnaissance planes, or unoccupied military drones with video or real-time artificial intelligence algorithms) in large areas.

Conclusions

Recommendations for improvements in aerial survey methods periodically have been made (*Eberhardt 1982; *Packard 1985; Packard et al. 1986; Lefebvre et al. 1995). Improvements were made, but progress has been slow. Most survey methods are the same as 10–15 years ago. Surveys of distribution have been made in almost all areas of Florida that manatees use substantially. These data are in demand for developing protection of manatees, particularly for planning boat traffic regulations and coastal development. Long-term, regular monitoring of manatees may be necessary to update distribution data and to reassess manatee protection needs.

The January 1992 synoptic survey revealed more manatees than had ever been recorded. However, the method is not adequate to track statewide trends, and a more standardized method is needed. Counts from future surveys will probably be as variable as those from the three surveys in 1991 and 1992. Estimated population sizes based on surveys at aggregation sites in winter increased in several areas of the state where long-term studies were made, but the trends in population sizes in other areas are unclear. Proposed techniques for monitoring trends must include tests of their statistical power to detect small changes (Gerrodette 1987; Taylor and Gerrodette 1993).

Improvement of aerial-survey techniques is a high priority in manatee-population research. Statistically valid techniques are needed. Development of correction procedures for visibility bias is continuing. These new techniques probably require advanced statistical analyses, more observers in the aircraft, more intensive survey effort, and more funds. Assessment of trends may require more replication of surveys within years.

Recent advances in electronic equipment and computers will make the data more usable. Examples include use of a global positioning system to more accurately record the locations and geographic information system mapping techniques and sighting density maps to display the results. Small airships may improve surveys.

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Cited References[2]

Ackerman, B. B. 1988. Visibility bias of mule deer aerial census procedures in southeast Idaho. Ph.D. dissertation, University of Idaho, Moscow. 106 pp.

Ackerman, B. B., S. D. Wright, R. K. Bonde, D. K. Odell, and D. J. Banowetz. 1995. Trends and patterns in mortality of manatees in Florida, 1974–1992. Pages 223–258 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Barlow, J., C. W. Oliver, T. D. Jackson, and B. L. Taylor. 1988. Harbor porpoise, *Phocoena phocoena*, abundance estimation for California, Oregon, and Washington: II. Aerial surveys. Fishery Bulletin 86:433–444.

Beck, C. A., and J. P. Reid. 1995. An automated photo-identification catalog for studies of the life history of the Florida manatee. Pages 120–134 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

*Beeler, I. E., and T. J. O'Shea. 1988. Distribution and mortality of the West Indian manatee (*Trichechus manatus*) in the southeastern United States: a compilation and review of recent information. Document Number PB 88-207980/AS, National Technical Information Service, Springfield, Va. 613 pp.

*Brownell, R. L., Jr., K. Ralls, and R. R. Reeves. 1981. Report of the West Indian manatee workshop. Pages 3–16 *in* *R. L. Brownell, Jr., and K. Ralls, editors. 1981. The West Indian manatee in Florida. Proceedings of a workshop held in Orlando, Florida, 27–29 March 1978. Florida Department of Natural Resources, Tallahassee. 154 pp.

CH_2M Hill. 1986. Aerial census of manatees in the vicinity of Six Mile Creek, in the lower middle St. Johns River, Florida. CH_2M Hill, Gainesville, Fla. Report for St. Johns Harbour, Inc. Unnumbered.

*Eberhardt, L. L. 1982. Censusing manatees. Manatee Population Research Report 1, Florida Cooperative Fish and Wildlife Research Unit, University of Florida, Gainesville. 18 pp.

Eberhardt, L. L., D. G. Chapman, and J. R. Gilbert. 1979. A review of marine mammal census methods. Wildlife Monographs 63. 46 pp.

Eberhardt, L. L., and T. J. O'Shea. 1995. Integration of manatee life-history data and population modeling. Pages 269–279 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Eberhardt, L. L., and M. A. Simmons. 1992. Assessing rates of increase from trend data. Journal of Wildlife Management 56:603–610.

*Florida Department of Natural Resources. 1989. Recommendations to improve boating safety and manatee protection for Florida waterways. Report to the Governor and Cabinet. Final report. 20 pp.

Floyd, T. J., L. D. Mech, and M. E. Nelson. 1979. An improved method of censusing deer in deciduous–coniferous forests. Journal of Wildlife Management 43:258–261.

Garrott, R. A., B. B. Ackerman, J. R. Cary, D. M. Heisey, J. E. Reynolds, III, and J. R. Wilcox. 1995. Assessment of trends in sizes of manatee populations at several Florida aggregation sites. Pages 34–55 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Gasaway, W. C., S. D. Dubois, and S. J. Harbo. 1985. Biases in aerial transect surveys for moose during May and June. Journal of Wildlife Management 49:777–784.

Gerrodette, T. 1987. A power analysis for detecting trends. Ecology 68:1364–1372.

Goodyear, J. D. 1993. A sonic/radio tag for monitoring dive depths and underwater movements of whales. Journal of Wildlife Management 57:502–513.

Graham, A., and R. Bell. 1989. Investigating observer bias in aerial survey by simultaneous double-counts. Journal of Wildlife Management 53:1009–1016.

*Hartman, D. S. 1974. Distribution, status, and conservation of the manatee in the United States. Document Number PB 81-140725, National Technical Information Service, Springfield, Va. 246 pp.

Hartman, D. S. 1979. Ecology and behavior of the manatee (*Trichechus manatus*) in Florida. American Society of Mammalogy Special Publication 5. 153 pp.

[2] An asterisk denotes unpublished material.

Irvine, A. B. 1982. West Indian manatee. Pages 241–242 *in* D. E. Davis, editor. Handbook of census methods for terrestrial vertebrates. CRC Press, Boca Raton, Fla.

Irvine, A. B., J. E. Caffin, and H. I. Kochman. 1982. Aerial surveys for manatees and dolphins in western peninsular Florida. Fishery Bulletin 80:621–630.

Irvine, A. B., and H. W. Campbell. 1978. Aerial census of the West Indian manatee, *Trichechus manatus*, in the southeastern United States. Journal of Mammalogy 59:613–617.

*Kadel, J. J., and G. W. Patton. 1992. Aerial studies of the West Indian manatee (*Trichechus manatus*) on the west coast of Florida from 1985–90: a comprehensive six year study. Mote Marine Laboratory Technical Report 246. Report to Sarasota County Natural Resources Department. 39 pp. + appendixes.

Kinnaird, M. F. 1985. Aerial census of manatees in northeastern Florida. Biological Conservation 32:59–79.

Kochman, H. I., G. B. Rathbun, and J. A. Powell. 1985. Temporal and spatial distribution of manatees in Kings Bay, Crystal River, Florida. Journal of Wildlife Management 49:921–924.

Leatherwood, S. 1979. Aerial survey of the bottlenosed dolphin, *Tursiops truncatus*, and the West Indian manatee, *Trichechus manatus*, in the Indian and Banana rivers, Florida. Fishery Bulletin 77:47–59.

Lefebvre, L. W., B. B. Ackerman, K. M. Portier, and K. H. Pollock. 1995. Aerial survey as a technique for estimating trends in manatee population size—problems and prospects. Pages 63–74 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

*Lefebvre, L. W., and R. K. Frohlich. 1986. Movements of radio-tagged manatees in southwest Florida, January 1985–March 1986. U.S. Fish and Wildlife Service, unpublished report. 87 pp.

Lefebvre, L. W., and H. I. Kochman. 1991. An evaluation of aerial survey replicate count methodology to determine trends in manatee abundance. Wildlife Society Bulletin 19:298–309.

Marmontel, M. 1993. Age determination and population biology of the Florida manatee, *Trichechus manatus latirostris*. Ph.D. dissertation, University of Florida, Gainesville. 408 pp.

Marsh, H. 1995. Fixed-width aerial transects for determining dugong population sizes and distribution patterns. Pages 56–62 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Marsh, H., and D. F. Sinclair. 1989a. An experimental evaluation of dugong and sea turtle aerial survey techniques. Australian Wildlife Research 16:639–650.

Marsh, H., and D. F. Sinclair. 1989b. Correcting for visibility bias in strip transect aerial surveys of aquatic fauna. Journal of Wildlife Management 53:1017–1024.

*McGehee, M. A. 1982. Manatees (*Trichechus manatus*): abundance and distribution in and around several Florida power plant effluents during the winter of 1981–1982. Final report prepared for the Florida Power and Light Company, Contract 31534-86419. 67 pp.

Moore, J. C. 1951. The range of the Florida manatee. Quarterly Journal of the Florida Academy of Science 14:1–19.

*Odell, D. K. 1976. Distribution and abundance of marine mammals in South Florida: Preliminary results. Pages 203–212 *in* A. Thorhaug and A. Volker, editors. Biscayne Bay: past/present/future. Proceedings of a symposium, 2–3 April 1976. Special Report 5. University of Miami, Sea Grant Program.

Odell, D. K. 1979. Distribution and abundance of marine mammals in the waters of the Everglades National Park. Pages 673–678 *in* R. M. Linn, editor. Proceedings of the First Conference on Scientific Research in the National Parks, New Orleans, Louisiana, 9–12 November 1976. U.S. Department of the Interior, National Park Service, Transactions and Proceedings Series 5, Volume 1.

O'Shea, T. J. 1988. The past, present, and future of manatees in the southeastern United States: realities, misunderstandings, and enigmas. Pages 184–204 *in* R. R. Odom, K. A. Riddleberger, and J. C. Ozier, editors. Proceedings of the Third Southeastern Nongame and Endangered Wildlife Symposium, Georgia Department of Natural Resources, Social Circle.

O'Shea, T. J., C. A. Beck, R. K. Bonde, H. I. Kochman, and D. K. Odell. 1985. An analysis of manatee mortality patterns in Florida, 1976–81. Journal of Wildlife Management 49:1–11.

O'Shea, T. J., and W. C. Hartley. 1995. Reproduction and early-age survival of manatees at Blue Spring, St. Johns River, Florida. Pages 157–170 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

O'Shea, T. J., and H. I. Kochman. 1990. Florida manatees: Distribution, geographically referenced data sets, and ecological and behavioral aspects of habitat use. Pages 11–22 *in* J. E. Reynolds, III and K. Haddad, editors. Report of the workshop on geographic information systems as an aid to managing habitat for West Indian manatees in Florida and Georgia. Florida Marine Research Publications 49.

O'Shea, T. J., and C. A. Langtimm. 1995. Estimation of survival of adult Florida manatees in the Crystal River, at Blue Spring, and on the Atlantic Coast. Pages 194–222 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

*Packard, J. M. 1985. Development of manatee aerial survey techniques. Manatee Population Research Report 7, Technical Report 8-7. Florida Cooperative Fish and Wildlife Research Unit, University of Florida, Gainesville. 68 pp.

*Packard, J. M., R. K. Frohlich, J. E. Reynolds, III, and J. R. Wilcox. 1984. Factors influencing indices of manatee abundance of manatees in the Fort Myers region, winter 1983/84. Manatee Population Research Report 5, Technical Report 8-5. Florida Cooperative Fish and Wildlife Research Unit, University of Florida, Gainesville. 63 pp.

Packard, J. M., R. K. Frohlich, J. E. Reynolds, III, and J. R. Wilcox. 1989. Manatee response to interruption of a thermal effluent. Journal of Wildlife Management 53:692–700.

*Packard, J. M., and R. Mulholland. 1983. Analysis of manatee aerial surveys: a compilation and preliminary analysis of winter aerial surveys conducted in Florida between 1977 and 1982. Manatee Population Research Report 2, Technical Re-

port 8-2. Florida Cooperative Fish and Wildlife Research Unit, University of Florida, Gainesville. 119 pp.

Packard, J. M., D. B. Siniff, and J. A. Cornell. 1986. Use of replicate counts to improve indices of trends in manatee abundance. Wildlife Society Bulletin 14:265–275.

Packard, J. M., R. C. Summers, and L. B. Barnes. 1985. Variation in visibility bias during aerial surveys of manatees. Journal of Wildlife Management 49:347–351.

Pollock, K. H., and W. L. Kendall. 1987. Visibility bias in aerial surveys: a review of estimation procedures. Journal of Wildlife Management 51:502–510.

*Powell, J. A. 1981. The manatee population in Crystal River, Citrus County, Florida. Pages 33–40 *in* *R. L. Brownell, Jr. and K. Ralls, editors. The West Indian manatee in Florida. Proceedings of a workshop held in Orlando, Fla., 27–29 March 1978. Florida Department of Natural Resources, Tallahassee. 154 pp.

Powell, J. A., and G. B. Rathbun. 1984. Distribution and abundance of manatees along the northern coast of the Gulf of Mexico. Northeast Gulf Science 7:1–28.

*Powell, J. A., and J. C. Waldron. 1981. The manatee population in Blue Spring, Volusia County, Florida. Pages 41–51 *in* *R. L. Brownell, Jr. and K. Ralls, editors. The West Indian manatee in Florida. Proceedings of a workshop held in Orlando, Fla., 27–29 March 1978. Florida Department of Natural Resources, Tallahassee. 154 pp.

Provancha, J. A., and M. J. Provancha. 1988. Long-term trends in abundance and distribution of manatees (*Trichechus manatus*) in the northern Banana River, Brevard County, Florida. Marine Mammal Science 4:323–338.

*Provancha, J. A., and M. J. Provancha. 1989. Summary of 1987 and 1988 manatee aerial surveys at Kennedy Space Center. National Aeronautical and Space Administration Technical Memorandum 102783. 17 pp.

Rathbun, G. B. 1988. Fixed-wing airplane versus helicopter surveys of manatees *Trichechus manatus*. Marine Mammal Science 4:71–75.

Rathbun, G. B., J. P. Reid, R. K. Bonde, and J. A. Powell. 1995. Reproduction in free-ranging Florida manatees. Pages 135–156 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Rathbun, G. B., J. P. Reid, and G. Carowan. 1990. Distribution and movement patterns of manatees (*Trichechus manatus*) in northwestern peninsular Florida. Florida Marine Research Publications 48:1–33.

Ratnaswamy, M. J., and H. E. Winn. 1993. Photogrammetric estimates of allometry and calf production in fin whales, *Balaenoptera physalus*. Journal of Mammalogy 74:323–330.

*Raymond, P. W. 1981. Manatees (*Trichechus manatus*): abundance and distribution in and around several Florida power plant effluents during the winter of 1981–82. Final report prepared for the Florida Power and Light Company, Contract 31534-81511. 62 pp.

Reid, J. P., R. K. Bonde, and T. J. O'Shea. 1995. Reproduction and mortality of radio-tagged and recognizable manatees on the Atlantic coast of Florida. Pages 171–191 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Reid, J. P., G. B. Rathbun, and J. R. Wilcox. 1991. Distribution patterns of individually identifiable West Indian manatees (*Trichechus manatus*) in Florida. Marine Mammal Science 7:180–190.

*Reynolds, J. E., III. 1993. Distribution and abundance of Florida manatees (*Trichechus manatus latirostris*) around selected power plants following winter cold fronts: 1992–1993. Report for Florida Power and Light Company, Order B91135-00073. 36 pp.

*Reynolds, J. E., III. 1994. Distribution and abundance of Florida manatees (*Trichechus manatus latirostris*) around selected power plants following winter cold fronts: 1993–1994. Report for Florida Power and Light Company, Order B91135-00139. 37 pp.

*Reynolds, J. E., III, B. B. Ackerman, I. E. Beeler, B. L. Weigle, and P. F. Houhoulis. 1991. Assessment and management of manatees (*Trichechus manatus*) in Tampa Bay. Pages 289–306 *in* S. F. Treat and P. A. Clark, editors. Proceedings of the Second Tampa Bay Area Scientific Information Symposium, 27 February–1 March 1991, Tampa, Fla.

*Reynolds, J. E., III, and C. J. Gluckman. 1988. Protection of the West Indian manatee in Florida. Document Number PB 88-222922, National Technical Information Service, Springfield, Va. 85 pp.

Reynolds, J. E., III, and J. R. Wilcox. 1985. Abundance of West Indian manatees (*Trichechus manatus*) around selected Florida power plants following winter cold fronts: 1982–1983. Bulletin of Marine Science 36:413–422.

Reynolds, J. E., III, and J. R. Wilcox. 1986. Distribution and abundance of the West Indian manatees (*Trichechus manatus*) around selected Florida power plants following winter cold fronts: 1984–1985. Biological Conservation 38:103–113.

Reynolds, J. E., III, and J. R. Wilcox. 1994. Observations of Florida manatees (*Trichechus manatus latirostris*) around selected power plants in winter. Marine Mammal Science 10:163–177.

*Rose, P. M., and S. P. McCutcheon. 1980. Manatees (*Trichechus manatus*) abundance and distribution in and around several Florida power plant effluents. Final report prepared for the Florida Power and Light Company, Contract 31534-86626 128 pp.

Samuel, M. D., E. O. Garton, M. W. Schlegel, and R. G. Carson. 1987. Visibility bias during aerial surveys of elk in northcentral Idaho. Journal of Wildlife Management 51:622–630.

Samuel, M. D., and K. H. Pollock. 1981. Correction of visibility bias in aerial surveys where animals occur in groups. Journal of Wildlife Management 45:993–997.

Shane, S. H. 1983. Abundance, distribution, and movements of manatees in Brevard County, Florida. Bulletin of Marine Science 33:1–9.

Sidle, J. G., and J. W. Ziewitz. 1990. Use of aerial videography in wildlife habitat studies. Wildlife Society Bulletin 18:56–62.

*Snow, R. W. 1992. The distribution and relative abundance of the Florida manatee in Everglades National Park. Interim report, March 1991 to February 1992. South Florida Research Center, Everglades National Park. Unnumbered.

Steinhorst, R. K., and M. D. Samuel. 1989. Sightability adjustment methods for aerial surveys of wildlife populations. Biometrics 45:415–425.

Taylor, B. L., and T. Gerrodette. 1993. The uses of statistical power in conservation biology: the vaquita and northern spotted owl. Conservation Biology 7:489–500.

Unsworth, J. W., L. Kuck, and E. O. Garton. 1990. Elk sightability model validation at the National Bison Range, Montana. Wildlife Society Bulletin 18:113–115.

*U.S. Fish and Wildlife Service. 1989. Florida manatee (*Trichechus manatus latirostris*) recovery plan. U.S. Fish and Wildlife Service, Atlanta, Ga. 98 pp.

*Valade, J. A. 1990. Coastal Georgia manatee assessment. Final report for Georgia Department of Natural Resources, Contract 462-511-960966. Unnumbered.

Weigle, B. L., and K. D. Haddad. 1990. Applications of the Florida Department of Natural Resources' Marine Resources Geographic Information System to manatee biology and management. Pages 23–27 *in* J. E. Reynolds, III and K. D. Haddad, editors. Report of the workshop on geographic information systems as an aid to managing habitat for West Indian manatees in Florida and Georgia. Florida Marine Research Publications 49:23–27.

*Weigle, B. L., J. E. Reynolds, III, G. W. Patton, and J. R. Wilcox. 1988. Manatee (*Trichechus manatus*) winter use of warm water discharges in Tampa Bay. Pages 153–164 *in* K. Mahadevan, R. K. Evans, P. Behrens, T. Biffar, and L. Olsen, editors. Proceedings Southeastern Workshop on Aquatic Ecological Effects of Power Generation, 3–5 December 1986, Sarasota, Fla. Mote Marine Lab. Report 124.

Woolf, H. B., editor. 1977. Webster's New Collegiate Dictionary. G. & C. Merriam Company, Springfield, Mass. 1,536 pp.

Zoodsma, B. J. 1991. Distribution and behavioral ecology of manatees in southern Georgia. M.S. thesis, University of Florida, Gainesville. 202 pp.

Assessment of Trends in Sizes of Manatee Populations at Several Florida Aggregation Sites

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Abstract. Temporal trends in sizes of Florida manatee (*Trichechus manatus latirostris*) populations were assessed with counts from aerial surveys at nine aggregation sites in winter. Manatees that winter along the eastern coast of Florida are considered one population; therefore, counts from all survey sites in eastern Florida were pooled. Results from counts at Fort Myers in southwestern Florida were treated separately. Simple log-linear models were used to identify physical covariates that explained a significant amount of variability in the counts adjusted to yearly means. Then the counts were adjusted for these covariates and, if present, a test for temporal pattern in the year coefficients was made. Covariates included survey conditions, short-term (1- to 3-day) air and water temperatures at each survey site, and a series of time-lagged air and water temperature variables. National Oceanic and Atmospheric Administration degree-day summations for periods of 5–40 days prior to the survey were used. Most temperature variables contributed significantly to the model. Based on the correlation coefficient, however, the best general models for counts of manatees in eastern Florida and at Fort Myers incorporated a short- and long-term summation of degree-days. Approximately 50% of the variation in counts could be explained with this simple model. An analysis of temporal trends in the temperature-adjusted counts suggested that population sizes in eastern Florida increased from 1982–83 to 1990–91, whereas population sizes at Fort Myers remained stable. Interpretation of these results is problematic because corroborating evidence that counts at winter aggregation sites are reliable indicators of manatee population size does not yet exist.

Key words: Aerial survey, manatee, power plants, trends, *Trichechus manatus latirostris.*

Increases in the number of recovered dead Florida manatees (*Trichechus manatus latirostris*) throughout Florida in recent years have been interpreted as evidence of increasing mortality rates (Ackerman et al. 1995). Because manatees are long-lived mammals with low rates of reproduction, any significant increase in mortality may lead to a decline in the population (O'Shea 1988). No available indices of population-size trends have been proven reliable. However, an extensive database has been collected by aerial surveys during the past 14 years. Repeated aerial surveys in winter to count aggregations of manatees in the warm-water effluents at power plants have been conducted since 1977 (*[1]Rose and McCutcheon 1980, *Raymond 1981; *McGehee 1982; *Reynolds 1983, 1985, 1991; Reynolds and Wilcox 1985, 1986). These data may provide insights into trends in manatee numbers in several regions of Florida (Ackerman 1995; Lefebvre et al. 1995). However, the variability of the counts has been problematic.

Previous researchers (*Rose and McCutcheon 1980, *Raymond 1981; *McGehee 1982; *Reynolds 1983) regressed manatee counts at each major site within each year against daily air and water temperatures. They clearly demonstrated that the highest counts occurred at lowest temperatures, but sample sizes in any one year were not sufficiently large to indicate more specific patterns. Counts did not vary solely in response to single-day temperatures. Packard and Mulholland (*1983) compiled the first 5 years of data (1977–82) and performed extensive statistical analyses. Multiple regression was used to separately regress counts from each site against air and water temperatures on the survey date and each of the two previous days, time of year, and other weather and visibility factors. However, regressions on water temperatures seemed to differ among years at some sites, and trends in maximum counts and mean-adjusted counts seemed to substantially differ among sites. These complications were thought to be the result of large-scale movements among sites within and between years or responses to longer-term weather patterns. Subsequently, Reynolds and colleagues (*Reynolds 1983, 1985, 1991; Reynolds and Wilcox 1985, 1986) regressed manatee counts at each major site each year against 1- and 3-day mean air and water temperatures.

Although these studies provided important insights into the factors of the variability of the counts, none of the studies provided a means of integrating data to develop a population index. Our objectives were the identification of environmental variables that influenced counts, development of a statistical model to adjust counts for these effects, and testing of the adjusted counts for a significant temporal trend in the index. These studies were recommended in the Florida Manatee Recovery Plan (*U.S. Fish and Wildlife Service 1989, Tasks 42 and 421) and by Eberhardt (*1982).

Methods

Aerial Survey Methodology

Since 1977, 1- to 2-day aerial surveys have been conducted to count manatees associated with warm-water sources during cold weather. These surveys can be segregated into two fundamentally different periods. During the 5-year interval from 1977 to 1982, counts were conducted

[1] An asterisk denotes unpublished material.

first year-round at regularly scheduled weekly intervals and later weekly only in winter. Survey methodology also evolved, and several different personnel performed the counts (*Rose and McCutcheon 1980; *Raymond 1981; *McGehee 1982). Beginning in winter 1982–83, the scheduling of surveys was changed so that flights were conducted only immediately after cold fronts when the highest counts were obtained. We began conducting surveys at that time and standardized the methodology. The difference in survey scheduling and the changes that occurred in personnel and methodology during 1977–82 suggested that pooling data from all years in a single analysis would be problematic. Hence, only survey data from winter 1982–83 through winter 1990–91 were used in this analysis.

Surveys were conducted at four major manatee aggregation sites at power plants along the eastern coast of Florida: the Orlando Utility Commission's Indian River plant (IR) and the Florida Power and Light Company's Cape Canaveral (CC), Riviera Beach (RV), and Port Everglades (PE) plants (Table 1; Fig. 1). Minor aggregations at three eastern-coast plants were also surveyed: Vero Beach Municipal Plant (VB), H. D. King Municipal Plant at Fort Pierce (FP), and the Florida Power and Light Company's Fort Lauderdale plant (FL). Manatees were also counted at the Harbor Branch Oceanographic Institute (HB), at the Hobe Sound National Wildlife Refuge (HS), and along the Intracoastal Waterway (IW) between the plants, although none of these had a source of warm water (Fig. 1). These sites are believed to include most areas along the eastern coast where manatees are known to aggregate during winter. The Indian River and Cape Canaveral power plants are only 3 km apart, and counts at these two plants were pooled. Surveys were also conducted at a single power plant on the southwestern coast of Florida, the Florida Power and Light Company's Fort Myers (FM) plant, believed to be the only warm-water site in the area where manatees aggregate. In winter, manatees are more isolated there than at eastern-coast sites.

Aerial counts were conducted by continuously circling manatee groups detected in each area until a maximum count was obtained. The primary observer was the same individual during all surveys. Each survey area extended about 8 km from one of the major plants. Recorded data included the total number of observed manatees, the number of calves, and a subjective ranking of survey conditions (SURVCOND, combining wind conditions, water turbidity, and surface conditions) ranging from 1 (excellent) to 5 (very poor; Table 2; *Reynolds 1983). A more detailed description of the survey procedures appears in Reynolds and Wilcox (1986), and discussions of survey limitations are presented elsewhere (Ackerman 1995; Lefebvre et al. 1995).

Because temperature may strongly influence the number of manatees counted on surveys, several temperature variables were recorded during surveys (Table 2; Hartman 1979; *Rose and McCutcheon 1980; *Packard and Mulholland 1983). National Oceanic and Atmospheric Administration air temperatures were obtained from sites nearest the four major power plants (National Oceanic and Atmospheric Administration 1982–91). Air temperatures were the average of the maximum and minimum temperatures on the survey day and average temperature on the survey day and on the two previous days. Water temperatures were measured at the power-plant intakes and were representative of ambient temperatures in the area. The water temperature

Table 1. Florida manatee (*Trichechus manatus latirostris*) aggregation sites in winter.

Site number	Site identifier	Site name	City	County
Eastern coast				
1	IR	OUC[a] Indian River plant	Titusville	Brevard
2	CC	FPL[b] Cape Canaveral plant	Titusville	Brevard
3	VB	Vero Beach Municipal plant	Vero Beach	Indian River
4	FP	H. D. King Municipal plant	Ft. Pierce	St. Lucie
5	HB	Harbor Branch Oceanographic Institute	Ft. Pierce	St. Lucie
6	HS	Hobe Sound National Wildlife Refuge (feeding area)	Jupiter	Martin
7	RV	FPL Riviera Beach plant	West Palm Beach	Palm Beach
8	PE	FPL Port Everglades plant	Ft. Lauderdale	Broward
9	FL	FPL Ft. Lauderdale plant	Ft. Lauderdale	Broward
10	IW	Intracoastal Waterway (Titusville to Ft. Lauderdale)		
Western coast				
11	FM	FPL Ft. Myers plant	Ft. Myers	Lee

[a] OUC = Orlando Utility Commission.
[b] FPL = Florida Power and Light Company.

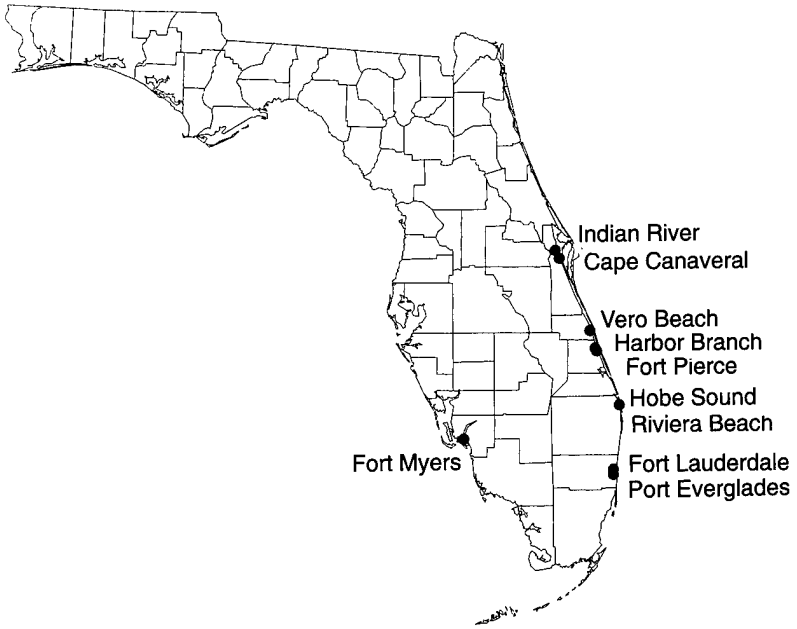


Fig. 1. Aggregation sites of Florida manatees (*Trichechus manatus latirostris*) where counts were made by aerial surveys in winters, 1982–1983 to 1990–1991.

Table 2. Definitions of variables.

Variable name	Definition
ATEMP	Mean of high and low air temperature ° C at a given site on survey date
ATEMP3	Mean air temperature ° C at a given site, averaged over survey date and 2 previous days
NATEMP	Same as ATEMP, at northern site (CC)
NATEMP3	Same as ATEMP3, at northern site (CC)
SATEMP	Same as ATEMP, averaged over two southern sites (RV, PE)
SATEMP3	Same as ATEMP3, averaged over two southern sites (RV, PE)
COUNT	Total number of manatees counted at a site on a given date, including adults and calves
DD5, ..., DD40	Cumulative heating degree-days ° F. Cumulative degrees that daily mean air temperature is below 65° F (18.3° C), summed for 5, ..., 40 days previous to survey date at each site. Calculated for Titusville and Fort Myers
TOTDD	Cumulative heating degree-days ° F, summed over entire year
DD10	DD 10 (1–10 previous days)
DD10S	DD 10 (1–10 previous days) squared
DX30	DD 11-30 (11–30 previous days; DD30 with DD10 removed)
DX30S	DD 11-30 squared (11–30 previous days)
SURVCOND	Subjective evaluation of survey conditions for each major site on day of survey, based on water turbidity, surface glare and chop, and wind conditions (1 = excellent or very good, 2 = good, 3 = fair, 4 = poor, 5 = very poor)
NSUVCOND	Same as SURVCOND, at northern site (CC)
SSUVCOND	Same as SURVCOND, averaged over two southern sites (RV, PE)
WTEMP	Intake water temperature ° C, at a given site, on survey date
WTEMP3	Intake water temperature ° C, at a given site, averaged over survey date and 2 previous days
NWTEMP	Same as WTEMP, at northern site (CC)
NWTEMP3	Same as WTEMP3, at northern site (CC)
SWTEMP	Same as WTEMP, averaged over two southern sites (RV, PE)
SWTEMP3	Same as WTEMP3, averaged over two southern sites (RV, PE)
YEAR	Year of survey, 83 indicates November 1982–March 1983

indices were the average temperature on the survey day and the average temperature on the survey day and on the two previous days. Complete air and water temperature variables were available only at three of the eastern-coast power plants (Cape Canaveral, Riviera Beach, and Port Everglades) and the Fort Myers power plant in southwestern Florida. Each of the eastern Florida sites is close to a second survey area (Indian River plant, Hobe Sound, and Ft. Lauderdale plant). Thus, the temperatures generally also reflected conditions at nearby sites.

The air temperature variables provided a measure of the severity of the cold fronts that instigated each survey, whereas water temperature variables provided a more direct measure of the immediate thermal conditions that manatees were experiencing. Cumulative heating degree-days were calculated with National Oceanic and Atmospheric Administration (1982–91) air temperatures (original measurements in ° F) at Titusville (near Cape Canaveral) and Fort Myers (Table 2). Heating degree-days were used as another measure of the winter severity. Heating degree-days are the cumulative total of degrees that the daily average air temperature is below 18.3° C each day and summed over all days of the year (primarily occurs October–March). The National Oceanic and Atmospheric Administration (1982–91) provides degree-days on a monthly and yearly basis as an index to the severity of each winter. However, degree-day data were recalculated here to create a series of time-lag variables that represent temperature conditions on various numbers of days prior to each aerial survey. Eight time-lag temperature variables were calculated by summing the degree-days (daily number of degrees below 18.3° C) over the 5–40 day intervals prior to each survey (5-day increments, DD5, DD10, ..., and DD40). Occasionally missing National Oceanic and Atmospheric Administration temperatures were replaced with temperatures from the most appropriate nearby weather station.

General Approach

A population index is a statistic that correlates with the true population level (Lancia et al. 1994). The higher the correlation is, the more reliable is the index. Extraneous sources of variation may weaken the correlation to the point that the index is no longer useful. However, if the causes of the extraneous sources of variation are largely known, it may be possible to adjust for these causes, and some of the reliability of the index may be recovered. Thus, an index that poorly correlates with the population level may still be useful if a high partial correlation with the true population level can be achieved after appropriate adjustment for covariates.

Adjusting for covariates involves risks. The primary goal is to find a model of the index for which the covariates explain a large portion of the variability of the index. After adjustment for these covariates, the remaining or residual variability in the index should be caused by variations in the true population level. However, this may not be the case. The greater the proportion of variability in the index that is due to covariates, the greater are the consequences of model misspecification. Undocumented lurking variables also remain a problem. Furthermore, if the covariates also correlate with the true population level, adjustment may weaken the reliability of the index. Only a comparison with accurate population data allows a true test of the reliability of the index (Lancia et al. 1994).

With these cautions in mind, we developed an adjusted aerial count index for manatees. We initially pursued a descriptive, statistical model of the count data rather than a more biological, model-based approach because we wanted as simple and assumption-free a model as possible. We used a semi-parametric approach, imposing no model structure by year; yearly levels were nonparametrically modeled. A nonparametric approach ensures that an assumed model does not force the appearance of a temporal pattern (e.g., a linear trend) that does not exist. We worked primarily with the logarithm of counts, which is a natural scale for many rate processes such as population growth (Lancia et al. 1994).

The proportional-rates model we developed is similar to the semi-parametric Cox proportional-hazards model (Cox and Oakes 1984). We assumed that, if temperatures and survey conditions were always average, the expected number of manatees that is counted in any given place (one site or several pooled sites) at time t is $M(t)$. We assumed that $M(t)$ remains constant during a year (at least during the counting period), represented as M_i, where i = year. M_i should correlate with the true manatee population level and must be assumed. We let $C(t, X(t))$ be the expected number of manatees counted at time t, given conditions $X(t)$, where $X(t)$ is a row vector of covariate values at time t. This can be modeled as follows:

$$C(t, X(t)) = M_i R(t, X(t))$$

The function $R(.)$ is a rate function (range 0 to ∞) that takes the value 1 when the conditions are at their averages. When $R(.)$ is greater than 1, conditions favored high counts, and vice versa. $R(.)$ must be nonnegative. A convenient form for $R(t, X(t))$ is $R(t) = exp(x(t)'B)$, where $x(t)$ is a row vector of the covariates centered at their long-term means and B is a row vector of regression parameters. Thus, the model becomes

$$C(t, X(t)) = M_i \exp(x(t)'B) \text{ or}$$
$$\ln C(t, X(t)) = \ln M_i + x(t)'B,$$

a simple log-linear model. The M_i's are the baseline annual population index levels.

Before attempting to fit a given model to the count data, we conducted a variety of exploratory investigations of the

covariate data in an attempt to understand the variations in these variables and their potential relations to each other and to the counts. Because temperature data at the two southern power plants (RV, PE) were similar, these data were averaged into a single southern site temperature variable to contrast with the pooled northern site (IR, CC) data.

The sampling design is such that it seems difficult to accurately model the anticipated error structure. The timing of counts is erratic and based on subjective factors (*Reynolds 1983). Some surveys were conducted soon after others, whereas others were more temporally isolated. This no doubt results in varying degrees of temporal auto-correlation. The fact that the timing of the surveys was based on the values of covariates that may enter into the model is also problematic. Despite these problems, we believed that statistical modeling was useful for exploring some features of this data set. We tried a wide variety of models but report only on those we believe are the most valid. We caution that the analysis is purely exploratory and that the data are from observations; we use hypothesis- testing statistics (*P*-values) only as relative measures of model merit.

Trends in the population size may be detected by treating data from each site separately, adjusting counts with site-specific covariates, and looking for trends at each site (*Packard and Mulholland 1983). This relatively rigorous strategy allows modeling different relations of populations at each site and provides the most detailed use of the data. Data from individually identifiable animals, however, indicate that manatees move among the sites in each winter (Reid et al. 1991, 1995). Another confounding factor is the possibility that factors far from each survey site may influence the number of manatees.

Manatee aggregations on the eastern coast of Florida in winter are considered a single population that is relatively closed to emigration or immigration (Ackerman 1995). For our analysis, therefore, we had to determine whether the count data provided an indication of trend in the population size of manatees of the entire eastern coast of Florida. During each survey, counts were conducted at the major aggregation sites along the eastern coast. Counts were conducted immediately after cold fronts because it is believed that almost all manatees in the population are concentrated at these warm-water refuges because of thermal stress. The structure of the surveys and the regional dynamics of the population suggested modeling the counts with a generalized model that summed counts from all sites in each survey.

The strategy of our analysis was the identification of the physical covariates that significantly contributed to the variability of the natural logarithm of the total number of manatees counted at a site on a given date (COUNT in Table 2) after adjusting to the yearly means, the adjustment of counts for these covariates, and the determination of any temporal pattern in the year coefficients. The covariates included the 1- and 3-day air and water temperatures and survey conditions from the northern power plants (sites IR and CC; NATEMP, NATEMP3, NWTEMP, NWTEMP3, NSUVCOND). The means of the same variables from the two major southern power plants (sites RV and PE) were also considered (SATEMP, SATEMP3, SWTEMP, SWTEMP3, SSUVCOND). In addition, nine time-lag variables with degree-days from the northern site summed over 5- to 40-day intervals (DD5, DD10, ..., DD40) and the total number of degree-days (TOTDD) in winter were considered. Model selection was performed by manually conducting a series of forward stepwise regressions to identify the best model. The first step was to include the categorical variable YEAR for the baseline parameter M_i. In Step 2, we constructed models for each of the 19 possible covariates and their quadratic terms and performed an F test to determine whether a covariate significantly contributed to the simple model. The covariate that contributed the most (i.e., had the highest correlation coefficient) was added to the model. In further steps, we continued to search for the next most important physical covariate, only stopping when no further covariates could be identified at the $P \leq 0.05$ level.

Results

Eastern Florida Aggregation Sites

Count Data

Each winter, 4–10 surveys were conducted between December and early March (Appendix A). Three surveys, when counts were not made at all sites (19 January 1983, 23 January 1989, 11 February 1989), and the first survey (14 December 1982), when only a single manatee was observed at a warm-water aggregation site, were excluded from the analysis (Appendix A). Principal aggregation areas included the combined IR (Site 1) and CC (Site 2) power plants in the northern part of the study area and the RV (Site 7) and PE (Site 8) plants in southern Florida (Table 1; Fig. 1). Counts at these sites were highly variable within and among years (Fig. 2). The high variability of the counts was also present when counts from each survey at all survey sites were pooled (Fig. 3). Seasonal patterns in winter counts within years were not obvious. Survey conditions were usually recorded only at sites CC, Hobe Sound (Site 6, HS), RV, PE, and Fort Lauderdale (Site 9, FL). Survey conditions were intermediate during most flights; only 12% of surveys in all years were conducted under excellent (1) conditions and only 6% under very poor conditions (5; Tables 3 and 4). Survey conditions were similar among sites.

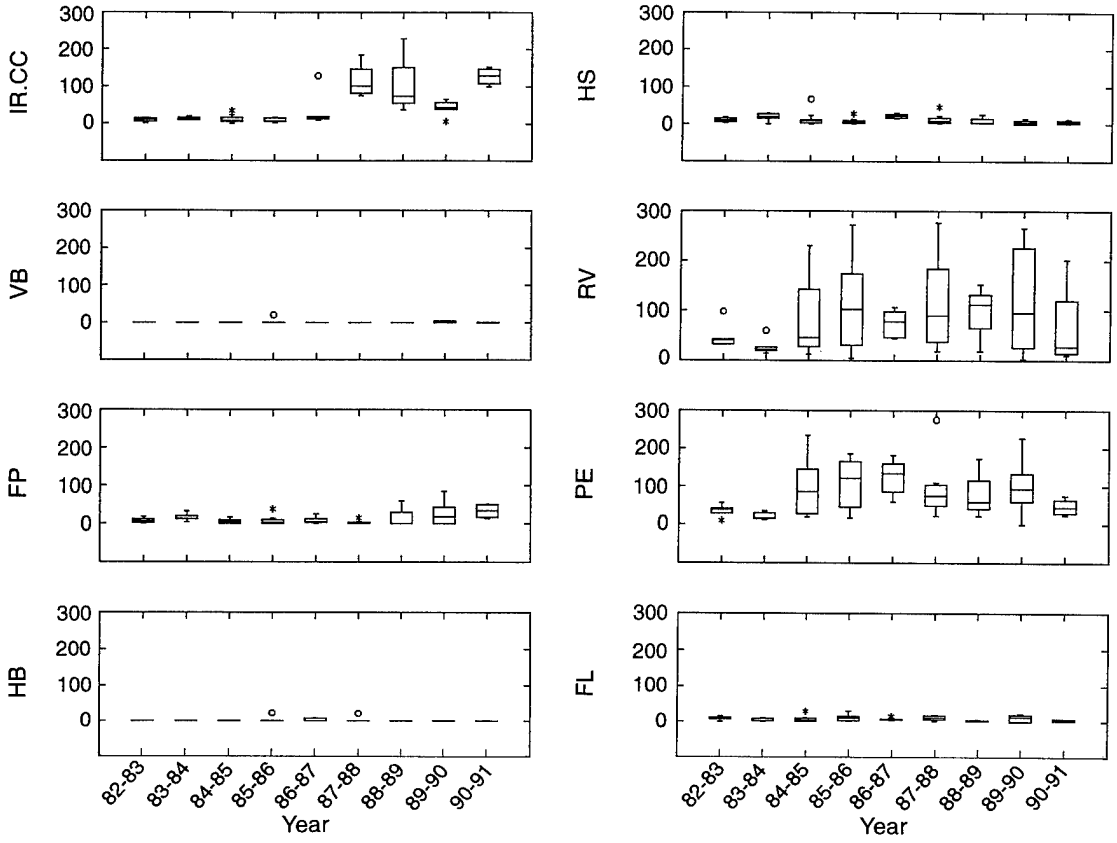


Fig. 2. Frequency distribution of number of manatees (*Trichechus manatus latirostris*) counted at survey sites along the eastern coast of Florida during aerial surveys in winter 1982–1991. Data are presented in standard box plots. Individual survey counts are shown as *solid squares*; extreme values are plotted as an *asterisk* or *open circle*. For each sample, the bottom and top edges of the box are located at the sample 25th and 75th percentiles. The center *horizontal line* is drawn at the sample median. The central *vertical lines* extend from the 5th to the 95th percentile.

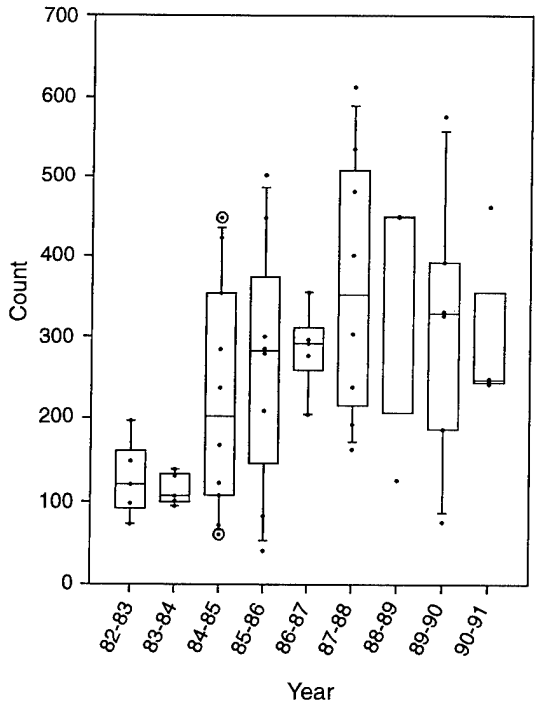


Fig. 3. Summary statistics on number of manatees (*Trichechus manatus latirostris*) counted at seven aggregation sites along the eastern coast of Florida during each winter, 1982–1991. Counts at all sites were made on the same day from a fixed-wing aircraft; 4–10 surveys were conducted each winter. Data are presented in standard box plots (see Fig. 2 caption).

Table 3. Survey conditions during aerial counts at seven Florida manatee (*Trichechus manatus latirostris*) aggregation sites along the Florida coast, by site, during winters 1982–1983 to 1990–1991. Survey-condition scores were a subjective evaluation of visibility based on water turbidity, surface glare and chop, and wind conditions (*Reynolds 1983). A score of 1 indicated excellent conditions and a score of 5, very poor conditions. Counts are identified in each category and are followed by the percentage of the row total in parentheses.

	Survey conditions					
Site	1 Excellent	2 Good	3 Fair	4 Poor	5 Very poor	Total
IR 1		2 (20.0)	4 (40.0)	4 (40.0)		10
CC 2	2 (3.4)	13 (22.4)	23 (39.7)	16 (27.6)	4 (6.9)	58
HS 6	1 (1.8)	17 (29.8)	23 (40.4)	16 (28.1)		57
RV 7	19 (32.8)	19 (32.8)	9 (15.5)	3 (5.2)	8 (13.8)	58
PE 8	12 (21.4)	27 (48.2)	7 (12.5)	5 (8.9)	5 (8.9)	56
FL 9		13 (24.1)	27 (50.0)	14 (25.9)		54
FM 11	1 (1.7)	6 (10.2)	26 (44.1)	24 (40.7)	2 (3.4)	59
Total	35 (9.9)	97 (27.6)	119 (33.8)	82 (23.3)	19 (5.4)	352

Temperature

Although we examined 1-day and 3-day air and water temperature variables, the patterns and relations of both were similar, and we present in detail only the 3-day variables (ATEMP3, WTEMP3). Median 3-day water temperatures were approximately 5–6° C warmer than median air temperatures in the southern and northern areas (Fig. 4). Air and water temperatures were cooler at the northern site than at the southern site (median air temperature 4.4° C cooler, Fig. 5; water 5.8° C cooler, Fig. 6). Air temperatures were more variable than water temperatures (Fig. 4), and the range of temperatures during each survey in winter was similar in the northern and southern areas (Fig. 5). Water temperatures at the southern sites usually varied by no more than 2–3° C during surveys in winter, whereas water temperatures at the northern site usually varied 5–7° C (Fig. 6).

Manatees seem to be thermally stressed at water temperatures below 18° C. Hartman (1979) found that manatees aggregated at the Crystal River and Blue Spring warm-water sites when the daily low air temperatures were below 10° C; the number of manatees was largest at temperatures below 0° C. Manatees used the refuges when water temperatures outside the refuges were below 16–18° C but occasionally left the refuges to feed when outside waters were as cool as 11–13.5° C. Irvine (1983) found that manatees must increase their metabolic rates in water below 20° C but did not increase metabolism at air

Table 4. Survey conditions during aerial counts at seven Florida manatee (*Trichechus manatus latirostris*) aggregation sites along the Florida coast in each winter 1982–1983 to 1990–1991. Survey-condition scores were a subjective evaluation of visibility based on water turbidity, surface glare and chop, and wind conditions (*Reynolds 1983). A score of 1 indicated excellent conditions and a score of 5, very poor conditions. Counts are identified in each category and are followed by the percentage of the row total in parentheses.

	Survey conditions					
Year	1 Excellent	2 Good	3 Fair	4 Poor	5 Very poor	Total
1982–83	2 (5.0)	21 (52.5)	6 (15.0)	10 (25.0)	1 (2.5)	40
1983–84	4 (13.3)	13 (43.3)	12 (40.0)	1 (3.3)		30
1984–85	6 (10.0)	14 (23.3)	27 (45.0)	11 (18.3)	2 (3.3)	60
1985–86	7 (14.6)	6 (12.5)	21 (43.8)	13 (27.1)	1 (2.1)	48
1986–87	3 (10.0)	9 (30.0)	12 (40.0)	5 (16.7)	1 (3.3)	30
1987–88	6 (12.5)	15 (31.3)	11 (22.9)	16 (33.3)		48
1988–89	7 (25.9)	3 (11.1)	12 (44.4)	5 (18.5)		27
1989–90		9 (22.0)	11 (26.8)	13 (31.7)	8 (19.5)	41
1990–91		7 (25.0)	7 (25.0)	8 (28.6)	6 (21.4)	28
Total	35 (9.9)	97 (27.6)	119 (33.8)	82 (23.3)	19 (5.4)	352

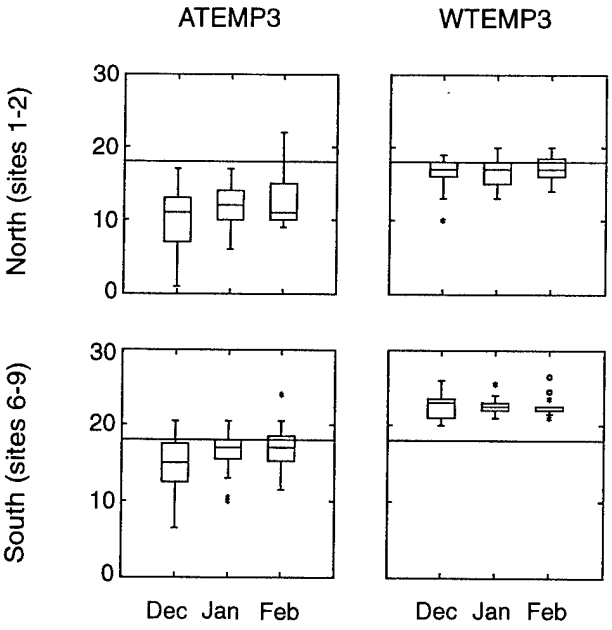


Fig. 4. Comparison of 3-day mean air (ATEMP3) and water (WTEMP3) temperatures recorded at northern and southern survey sites along the eastern coast of Florida, 1982–1991. Data are presented in standard box plots (see Fig. 2 caption).

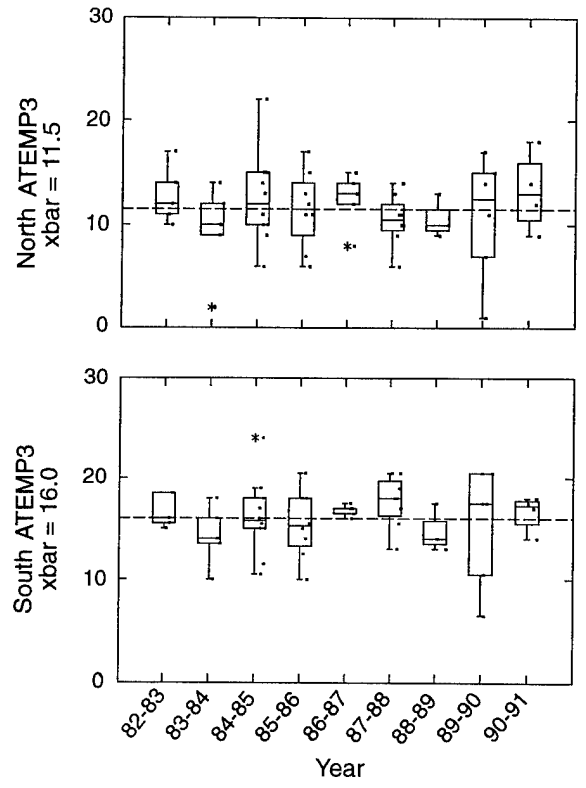


Fig. 5. Annual variation in 3-day mean air temperatures (ATEMP3) recorded on each survey date at northern and southern survey sites along the eastern coast of Florida, 1982–1991. Data are presented in standard box plots (see Fig. 2 caption).

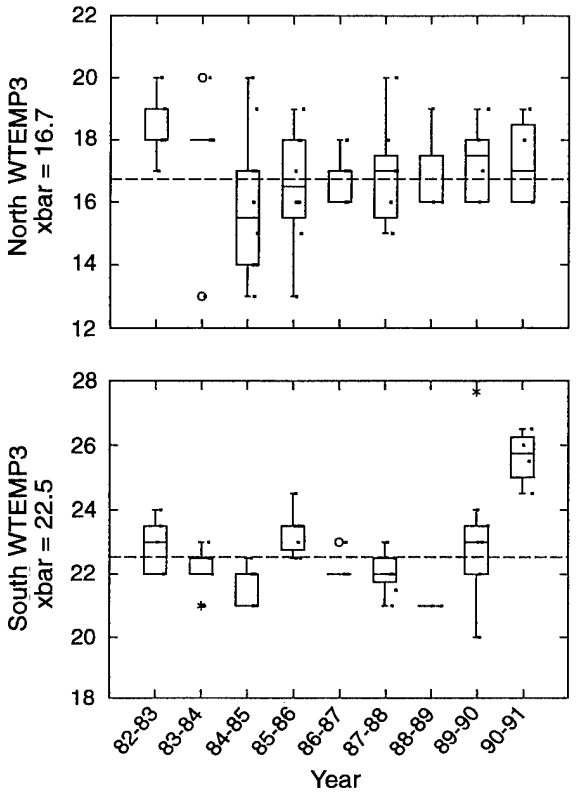


Fig. 6. Annual variation in 3-day mean water temperatures (WTEMP3) recorded on each survey date at northern and southern survey sites along the eastern coast of Florida, 1982–1991. Data are presented in standard box plots (see Fig. 2 caption).

temperatures as low as 10° C. Campbell and Irvine (*1981) reported that captive manatees exposed to water temperatures below 16–18° C for several days experienced lethargy and anorexia.

During cold fronts, water temperatures were usually below 18° C at the northern sites but remained considerably warmer in the southern area. Air temperatures during cold fronts were generally below this reference point in the northern and southern areas. Southern areas are warmed by their proximity to the Florida Current. No trends in air temperatures were apparent at the northern or southern sites during the 9-year survey (Fig. 5); water temperatures at the southern sites were also without trends (Fig. 6). However, 3-day water temperatures at the northern site suggested a general increase in temperature during 1984–85 and 1990–91 (Fig. 6).

The cumulative total number of heating degree-days in winter (TOTDD in Table 2) recorded at Titusville during 1982–83 through 1986–87 were near the 30-year mean of 712 (Table 5). Departures from the 30-year mean were notable during several winters. Winter 1987–88 was abnormally severe, and winters 1988–89 and 1990–91 were

Table 5. Number of heating degree-days at Titusville and Fort Myers, Florida, during winters 1982–1983 to 1990–1991 (National Oceanic and Atmospheric Administration 1982–1991).

Year	December	January	February	Total[a]
Titusville				
1982–83	110	260	170	699
1983–84	184	301	200	869
1984–85	98	401	176	767
1985–86	252	232	112	768
1986–87	49	276	136	540
1987–88	173	314	304	983
1988–89	130	22	116	318
1989–90	302	118	57	541
1990–91	75	93	78	314
9-year mean	153	224	150	644
30-year mean (NOAA 1991)				712
Fort Myers				
1982–83	61	133	87	347
1983–84	101	141	79	384
1984–85	38	177	77	316
1985–86	128	91	38	329
1986–87	22	116	43	198
1987–88	65	129	105	353
1988–89	70	9	73	180
1989–90	178	33	9	229
1990–91	57	24	44	146
30-year mean (NOAA 1991)	107	150	120	441

[a] Total degree-days represents the entire year (July–June), although almost all degree-days are accumulated from November to March.

unusually mild (Table 5). The number of heating degree-days also increased through time similar to the northern water temperature variable.

Model Development and Trend Analysis

Year as a categorical variable contributed significantly ($P = 0.036$) to the model, accounting for 29% of the variation in the ln(COUNT) and identifying significant differences in counts among years (Table 6). In Step 2, the correlation coefficients suggested that nearly all temperature variables explained a significant amount of the remaining variation. DD10, the summation of degree-days of the 10-day period just prior to the survey, was the temperature variable that explained the largest proportion of the variation and was added to the model (Table 6). For Step 3, we subtracted the DD10 value from the remaining degree-day variables to exclude the information that was incorporated into the model at Step 2. The next iteration identified DX30, the new variable summing degree-days for the 20-day period from 11 to 30 days prior to the survey, as the largest remaining contributor to the correlation coefficient. Although the F test indicated that DX30 contributed significantly to the model ($P < 0.001$), it only accounted for an additional 13% of the variation in the ln(COUNT), raising the question whether this covariate should be added to the model (Table 6). A plot of DX30 against the DD10 variable already incorporated into the model, however, showed little correlation between the two variables (Fig. 7a). In addition, a plot of DX30 against the residuals from the Step 2 model suggested a general correlation (Fig. 7b). Therefore, we chose to add DX30 as a second temperature covariate to the model. No other variables contributed significantly to the model, thus our best model was

$$E\{\ln(COUNT)\} = \beta_0 + \beta_1\,(\text{YEAR}) + \beta_2\,(\text{DD10}) + \beta_3\,(\text{DD10})^2 + \beta_4\,(\text{DX30}) + \beta_5\,(\text{DX30})^2 \quad (1)$$

This model required estimating 13 parameters (year as categorical variable required eight parameters; Table 7) and accounted for 78% of the variation in the ln(COUNT) data (Table 6). Residual plots for this model indicated a relatively good fit to the data.

Plots of the unadjusted and adjusted counts on logarithmic and natural scales against year, adjusted for the temperature covariates, suggested an increasing trend in the data (Figs. 8 and 9). The model had the most significant effect on counts that were conducted under abnormally warm conditions (Fig. 10). Polynomial contrasts indicated that most of the between-year variation could be explained by a linear trend ($P < 0.001$) and that a quadratic trend was not significant ($P = 0.498$).

Table 6. Forward step-wise regressions to select covariates to be included into a log-linear model of total counts of Florida manatees (*Trichechus manatus latirostris*) along the eastern coast of Florida during winters 1982–1983 to 1990–1991. Year was treated as a categorical variable, and linear and quadratic terms were included when testing each of the other 19 possible covariates. *Underlined* values are variables that were entered into the model at each step.

Covariate	Correlation coefficient (R^2)		
	Step 1	Step 2	Step 3
YEAR (categorical)	<u>0.291</u>		
NATEMP		0.433	0.671
NATEMP3		0.456	0.662
NWTEMP		0.475	0.672
NWTEMP3		0.332	0.663
NSUVCOND		0.313	0.658
SATEMP		0.475	0.701
SATEMP3		0.536	0.696
SWTEMP		0.432	0.696
SWTEMP3		0.433	0.663
SSUVCOND		0.351	0.729
DD5		0.503	
DD10		<u>0.651</u>	
DD15		0.577	0.660
DD20		0.493	0.706
DD25		0.517	0.762
DD30		0.532	<u>0.782</u>
DD35		0.508	0.741
DD40		0.482	0.723
TOTDD		0.369	0.699
F value	2.31	22.11	12.43
df	8, 45	2, 43	2, 41
P	0.036	<0.001	<0.001
R^2	0.29	0.65	0.782

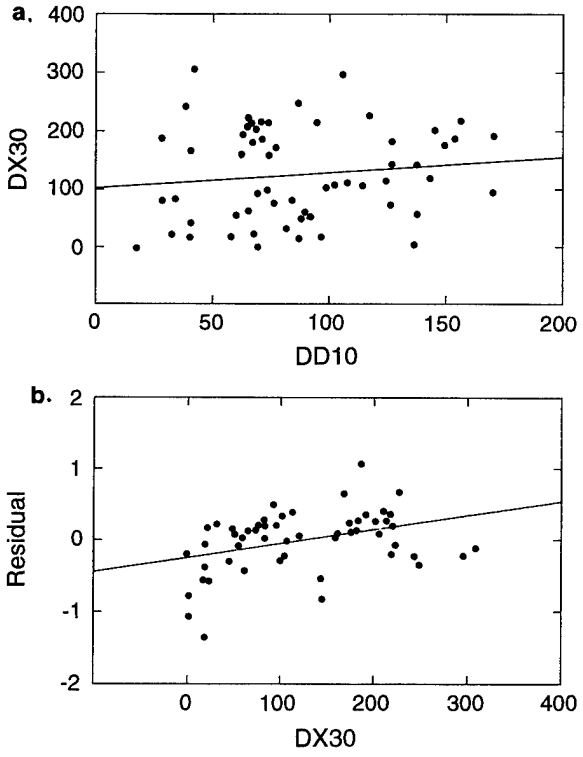


Fig. 7. Plots of manatee (*Trichechus manatus latirostris*) counts pooled at all sites along the eastern coast of Florida, 1982–1991, showing the relation between (a) DX30, the summation of degree-days during the 20-day period from 10 to 30 days prior to the survey, and DD10, the summation of degree-days from 1 to 10 days prior to the survey, and (b) the residuals from a simple log-linear model (Step 2, Table 6) and DD10, incorporated into the model as a covariate.

Table 7. Comparison of best models fit to counts of Florida manatees *(Trichechus manatus latirostris)* at aggregation sites on the eastern coast of Florida and at Fort Myers. Values of year and temperature coefficients in scientific notation.

Independent variable	Coefficient value	
	Eastern coast	Fort Myers
Constant	3.18	2.81
1982–83	-5.84×10^{-1}	-7.71×10^{-1}
1983–84	-7.75×10^{-1}	-1.68×10^{-1}
1984–85	-3.13×10^{-1}	3.55×10^{-1}
1985–86	-1.00×10^{-2}	3.32×10^{-1}
1986–87	-6.00×10^{-3}	1.33×10^{-1}
1987–88	-1.16×10^{-1}	-1.55×10^{-1}
1988–89	6.44×10^{-1}	-1.40×10^{-1}
1989–90	1.97×10^{-1}	2.71×10^{-1}
1990–91	9.63×10^{-1}	1.43×10^{-1}
DD10	2.65×10^{-2}	5.18×10^{-2}
DD10S	-8.40×10^{-5}	-4.30×10^{-4}
DX30	1.22×10^{-2}	1.72×10^{-2}
DX30S	-3.68×10^{-5}	-1.04×10^{-4}
R^2	0.78	0.68

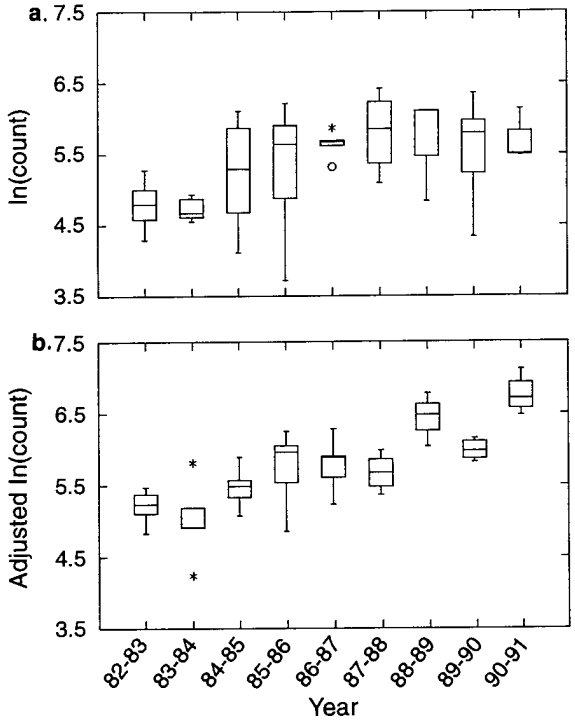


Fig. 8. Comparison of ln(COUNT) of numbers of manatees *(Trichechus manatus latirostris)* seen during aerial surveys in winter 1982–1991, (a) before and (b) after adjustment for temperature covariates. Data from all sites along the eastern coast of Florida were pooled. Note the large adjustments of counts during 1988–1989 and 1990–1991.

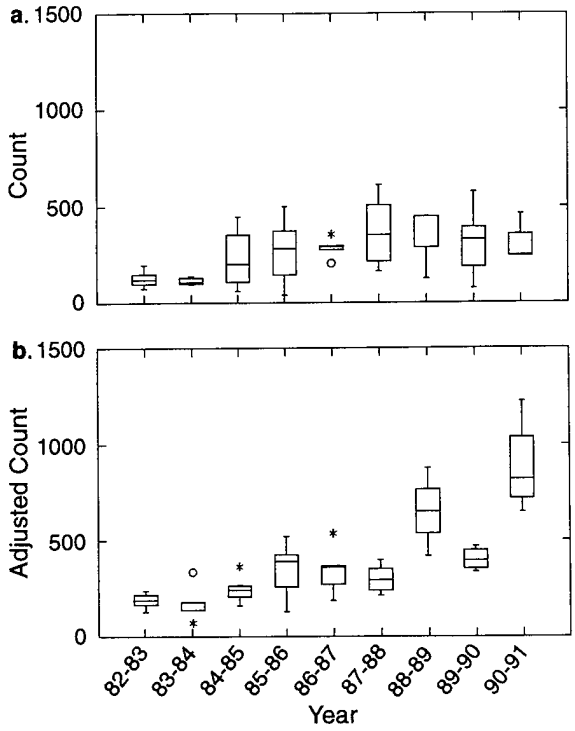


Fig. 9. Comparison of counts of manatees *(Trichechus manatus latirostris)* during aerial surveys in winter 1982–1991, (a) before and (b) after adjustment for temperature covariates. Data from all sites along the eastern coast of Florida were pooled. Note the large adjustments of counts during 1988–1989 and 1990–1991.

Given these results, we developed a more parsimonious model by treating year as a continuous variable and manually performing a backwards stepwise regression to identify parameters that could be dropped from the model. Our final model, therefore, was

$$E\{\ln(\text{COUNT})\} = \beta_0 + \beta_1(\text{YEAR}) + \beta_2(\text{DD}10) + \beta_3(\text{DX}30) + \beta_4(\text{DX}30)^2. \quad (2)$$

This model required the estimation of five parameters (year as continuous variable requires only one parameter) and had an R^2 of 0.678, which is only slightly lower than the best model that required the estimation of 13 parameters. Again, residual plots indicated that the model fit the data relatively well. Because the estimates are on a logarithmic scale, the linear trend translated to an increasing exponential (geometric) trend on the original scale, providing no evidence that the manatee population in eastern Florida is decreasing.

Fort Myers Aggregation Site

Numbers of Manatees and Temperature

Because manatees at the Fort Myers site were counted during the same flights as those on the eastern coast, the

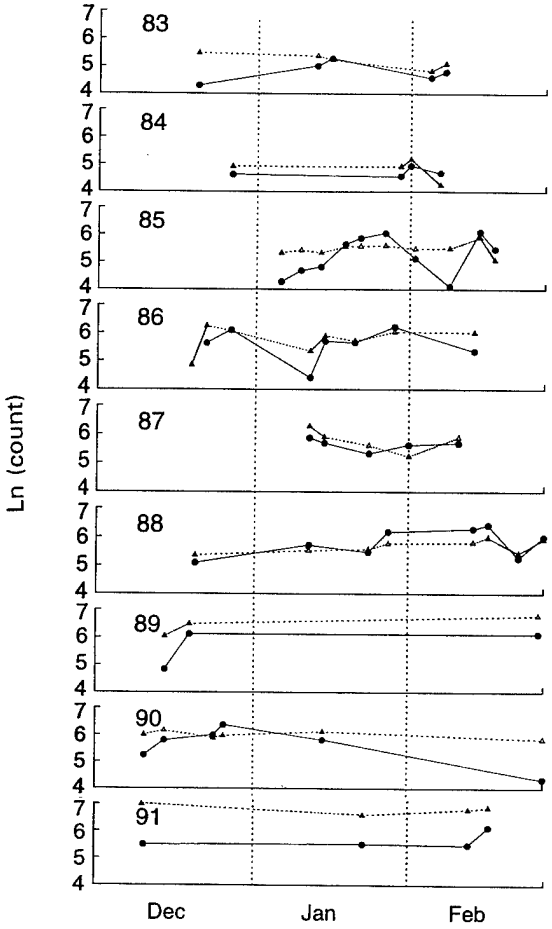


Fig. 10. Comparison of ln(COUNT) of numbers of manatees (*Trichechus manatus latirostris*) seen during aerial surveys before and after adjustment for temperature covariates. Data from all sites along the eastern coast of Florida during 1982–1991 were pooled. *Circles* connected by *solid lines* represent the observed counts, and *triangles* connected by *dotted lines* represent the counts adjusted for the temperature covariates.

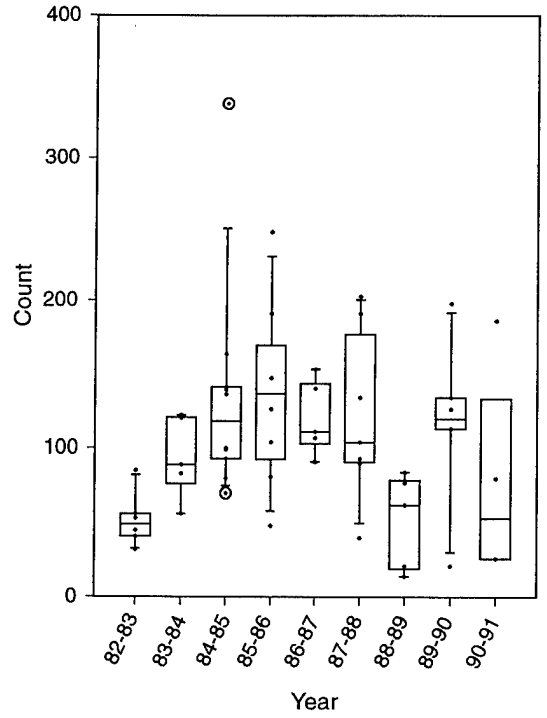


Fig. 11. The number of manatees (*Trichechus manatus latirostris*) counted in the vicinity of the Fort Myers power plant during aerial surveys in winter 1982–1991. A total of 4–10 surveys were conducted each winter. Data are presented in standard box plots (see Fig. 2 caption).

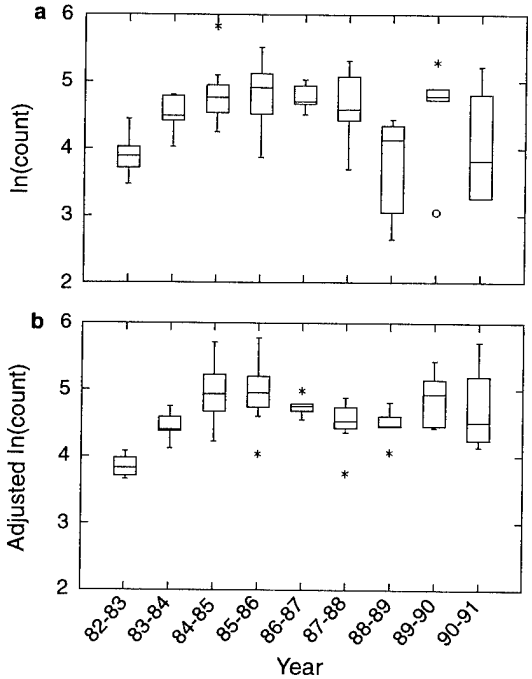


Fig. 12. Comparison of ln(COUNT) of numbers of manatees (*Trichechus manatus latirostris*) observed during aerial surveys at the Fort Myers power plant area in winters 1982–1983 to 1990–1991, (a) before and (b) after adjustment for temperature covariates.

number and timing of surveys were identical (Appendix B). A total of 58 counts was obtained between winters 1982–83 and 1990–91; however, we excluded data from the 14 December 1982 survey because, like during the surveys in eastern Florida, few animals were seen. The general characteristics of the counts were also similar to those obtained on the eastern coast of Florida, and variation within and among years was considerable (Figs. 11–14).

The extreme outlier in these data was observed on 19 January 1985 when 338 manatees were counted in one survey. This was approximately three times the mean number of manatees counted during nine other surveys in winter 1984–85. The 19 January survey was the only survey at Fort Myers during the 9-year period that was judged to have been conducted under excellent survey conditions (Appendix B;

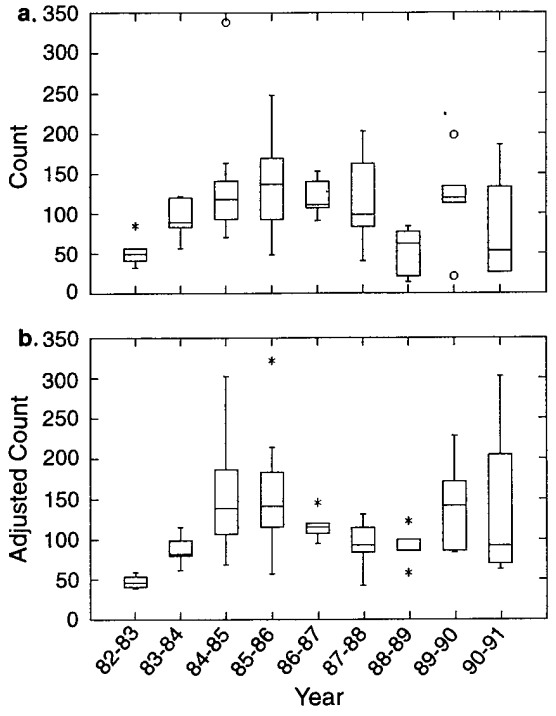


Fig. 13. Comparison of counts of manatees *(Trichechus manatus latirostris)* during aerial surveys at the Fort Myers power plant in winters 1982–1983 to 1990–1991, (a) before and (b) after adjustment for temperature covariates.

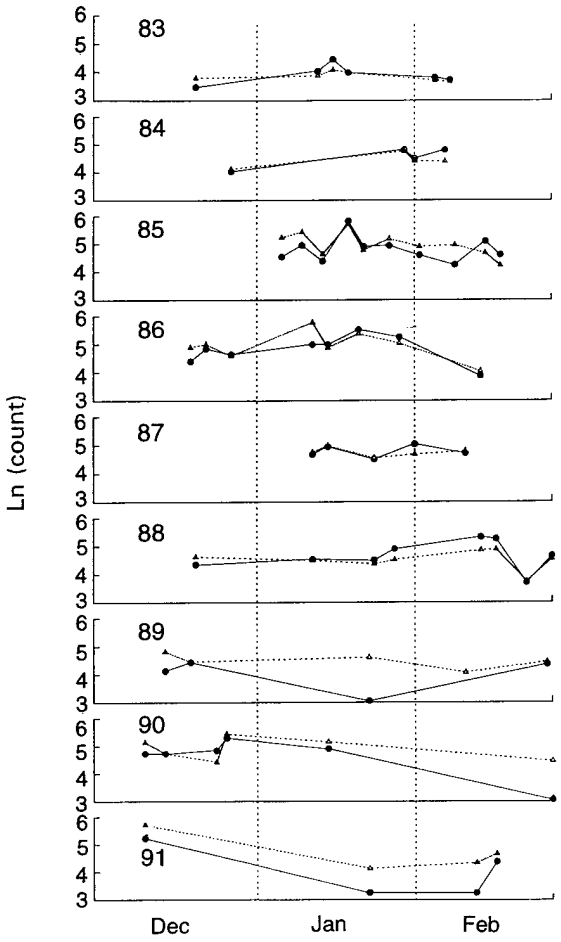


Fig. 14. Comparison of ln(COUNT) of numbers of manatees (*Trichechus manatus latirostris*) observed during aerial surveys at the Fort Myers power plant in winters 1982–1983 to 1990–1991 before and after adjustment for temperature covariates. *Circles* connected by *solid lines* represent the observed counts, and *triangles* connected by *dotted lines* represent the counts adjusted for the temperature covariates.

Table 3). Under typical survey conditions, which were usually rated fair to poor at this site (Table 3), a relatively low proportion of the animals may have been detected. Relatively low counts were obtained during the winters 1988–89 and 1990–91 (Fig. 11). These winters were unusually milder than previous winters, and the lowest counts in each year were made during the warmest months (Table 5; Fig. 14).

Model Development and Trend Analysis

Because the data structure and possible covariates of the Fort Myers manatee population were identical to those of the manatee population on the eastern coast, we initially fit the best model developed for this population to the Fort Myers data. The model fit the data relatively well. However, the covariates accounted only for 68% of the variation, whereas they accounted for 78% of the variation in counts in eastern Florida. We attempted to find a better model by repeating the stepwise procedure to construct the model for counts in eastern Florida. This procedure produced results similar to the analysis of the data from eastern Florida (Table 8), indicating the best model for the data from eastern Florida was also the best model for the data from Fort Myers. The degree-day coefficients had the same signs for the data from Fort Myers and eastern Florida, and the relative magnitude of the coefficients was also similar (Table 7).

Polynomial contrasts of the year coefficients indicated that linear ($P < 0.045$) and quadratic temporal trends in adjusted counts ($P < 0.012$) were significant; however, the plots of the adjusted counts (Figs. 12 and 13) were not convincing. The most significant adjustments to the counts were those obtained during unusually warm weather (Fig. 14). Tukey multiple comparisons revealed the only significant differences among years were between 1982–83 and each of the years 1984–85, 1985–86, 1986–87, and 1989–90. We concluded that no detectable trend was in the counts of manatees in the Fort Myers area between 1983–84 and 1990–91 (although counts in 1982–83 were lower than counts in subsequent years).

To develop a more parsimonious model, we converted year from a categorical to a continuous variable with a linear and quadratic term and performed a backward stepwise

Table 8. Forward stepwise regressions to select covariates to be included into a log-linear model of total counts of Florida manatees *(Trichechus manatus latirostris)* at Fort Myers, Florida during winters 1982–1983 to 1990–1991. Year was treated as a categorical variable, and linear and quadratic terms were included when testing each of the other 14 possible covariates. *Underlined* values are variables that were entered into the model at each step.

Covariate	Correlation coefficient (R^2)		
	Step 1	Step 2	Step 3
YEAR (categorical)	0.335		
ATEMP		0.441	0.716
ATEMP3		0.411	0.717
WTEMP		0.493	0.740
WTEMP3		0.481	0.726
SURVCOND		0.377	0.717
DD5		0.457	
DD10		0.600	
DD15		0.573	0.611
DD20		0.523	0.637
DD25		0.537	0.653
DD30		0.608	0.683
DD35		0.578	0.684
DD40		0.496	0.655
TOTDD		0.358	0.603
F value	3.31	14.82	5.19
df	8, 48	2, 46	2, 44
P	0.004	<0.001	<0.010
R^2	0.34	0.60	0.68

regression. This procedure resulted in dropping the linear year and quadratic DX30 parameters from the model, producing the model

$$E\{\ln(\text{COUNT})\} = \beta_0 + \beta_1(\text{YEAR})^2 + \beta_2(\text{DD}10) + \beta_3(\text{DD}10)^2 + \beta_4(\text{DX}30). \quad (3)$$

This model required estimating five parameters, had an R^2 of 0.501, and fit the data relatively well. Treating year as a continuous variable resulted in a substantial decrease in the correlation coefficient. This result and the results of the post-hoc analysis of the year coefficients suggested that the most appropriate log-linear model for the data from Fort Myers was the model initially developed with the forward stepwise regression procedure.

Discussion

Results of these analyses revealed that approximately 50% of the variation in the counts of manatees in winter on the eastern coast of Florida and at Fort Myers in southwestern Florida can be explained with log-linear models that incorporate measures of temperature. The choice of models is probably not critical because most temperature covariates correlated with each other and contributed significantly to the models. The best general models we could construct for the data sets from eastern Florida and Fort Myers incorporated the same temperature covariates.

The models used a short-term (1–10 days) and a long-term (11–30 days) summation of heating degree-days. Although degree-day variables are artificial because of the relatively arbitrary scaling to 18.3° C, they provided several advantages over the other possible temperature covariates. Degree-days are calculated from standard National Oceanic and Atmospheric Administration temperature data that are recorded daily and are readily available from many locations in Florida (National Oceanic and Atmospheric Administration 1982–91). Summation of degree-days over various time periods also allowed the development of time-lag temperature covariates that can provide a measure of the relative severity of winter temperatures for extended periods prior to each survey. In contrast, water-temperature data obtained from the power plants were available only for the survey date and two prior days. The aerial surveys were standardized for short-term temperatures because they were conducted only immediately after cold fronts had moved into the area. Other problems with power-plant water-temperature data are that they are recorded only when the plant is operating and the quality of the measurements was not tightly controlled (J. R. Wilcox, Florida Power and Light Company, North Palm Beach, personal observation). These considerations

and the comparisons of the correlation coefficients obtained during the stepwise regression procedures led us to conclude that time-lag degree-day covariates in our models were the most appropriate temperature covariates.

These results, however, were influenced by a profound increase in the number of manatees counted at the Indian River and Cape Canaveral power plants during the late 1980's. Manatees in these areas are difficult to count because of turbid water and surface foam from the power-plant discharge. The increase in number of manatees counted at the IR-CC sites may have resulted from changes in counting conditions because the plants underwent major operational changes during the mid-1980's (J. R. Wilcox, Florida Power and Light Company, personal observation). This possibility must be further investigated.

Because a substantial proportion of the variability in these statistical models remains unexplainable, a determination of whether an increase in the population size caused the increase in adjusted counts on the eastern coast of Florida is difficult. Alternate explanations can be suggested for why the increasing counts may not accurately track trends in the size of the population. Although the same observer conducted all surveys, the observer may have become more experienced at conducting the surveys with time. Visibility may have increased. Changes in manatee behavior or traditions may have altered the proportion of manatees in winter aggregations. Random variation in conditions during specific winters may have led to the appearance of a greater-than-observed trend in the temperature-adjusted counts.

More analyses must be made. A primary goal should be to incorporate the previous set of 1977–82 surveys (*Rose and McCutcheon 1980; *Raymond 1981; *McGehee 1982; *Packard and Mulholland 1983). Although those earlier surveys were conducted year-round under a different sampling scheme and surveyors recorded different variables, data should be investigated to determine whether a suitable subset of comparable surveys can be selected. Counts were higher during several months (January 1979, January 1980, January 1981) on the eastern coast of Florida than in the years 1982–84, and their inclusion may reduce the apparent trend from this model.

Conclusions and Recommendations

The major impetus for this study was the determination of whether aerial survey counts of manatees at aggregation sites in winter can provide an index to the size of the manatee population. A consistent increase in the number of dead manatees each year created concern that the populations may be declining (Ackerman et al. 1995). Our analyses of the aerial counts do not provide evidence in support of a trend of a decreasing population size of manatees in eastern Florida or at Fort Myers. Pooled counts of manatees at all survey sites in eastern Florida, adjusted for temperature, increased during the past 8 years. Several other factors may have influenced this trend, such as changing conditions at the IR and CC plants. In contrast, the temperature-adjusted counts from the Fort Myers area suggested that this population remained relatively stable.

The interpretation of the results of this analysis requires caution. Several measures of temperature were identified, each of which seemed to explain a substantial fraction of the variation in the count data. Finding such an influential adjustor by using the counts as a population index was good and bad. The advantage was that much of the observed variation in the counts can be explained and, to some extent, adjusted. The disadvantage was that this indicated the counts were not responding to only the underlying population levels but also to external covariates. The better our covariate model becomes at predicting the counts, the less residual variability remains to predict true population fluctuations. The more influential the covariates become, the more serious becomes the bias induced by model misspecification (e.g., assuming a linear model instead of the appropriate nonlinear one). Even if all year effects observed in count data were caused by fluctuations in the true population levels, the analysis suggests that no more than half of the variability observed in the counts can be attributed to changes in population levels. With the currently available data, statistical analysis alone can shed no light on the question of whether the estimated baseline year effects are truly indicative of the population-size trends. Several relatively extensive databases exist on other demographic characteristics of these manatee populations that include information on age structure, reproduction, and survival (Eberhardt and O'Shea 1995). We caution against accepting the results of our trend analysis unless these independent databases provide reasonable evidence to corroborate our results. We recommend incorporation of other population data in future attempts to support or reject the trend suggested by this work.

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Cited References[2]

Ackerman, B. B. 1995. Aerial surveys of manatees: a summary and progress report. Pages 13–33 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Ackerman, B. B., S. D. Wright, R. K. Bonde, D. K. Odell, and D. J. Banowetz. 1995. Trends and patterns in mortality of manatees in Florida, 1974–1992. Pages 223–258 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

*Campbell, H. W., and A. B. Irvine. 1981. Manatee mortality during the unusually cold winter of 1976–1977. Pages 86–91 *in* *R. L. Brownell, Jr. and K. Ralls, editors. The West Indian manatee in Florida. Proceedings of a workshop held in Orlando, Fla., 27–29 March 1978. Florida Department of Natural Resources, Tallahassee. 154 pp.

Cox, D. R., and D. Oakes. 1984. Analysis of survival data. Chapman and Hall, New York. 201 pp.

*Eberhardt, L. L. 1982. Censusing manatees. Manatee Population Research Report 1, Florida Cooperative Fish and Wildlife Research Unit. University of Florida, Gainesville. 18 pp.

Eberhardt, L. L., and T. J. O'Shea. 1995. Integration of manatee life-history data and population modeling. Pages 269–279 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Hartman, D. S. 1979. Ecology and behavior of the manatee (*Trichechus manatus*) in Florida. American Society of Mammalogists Special Publication 5, Lawrence, Kans. 153 pp.

Irvine, A. B. 1983. Manatee metabolism and its influence on distribution in Florida. Biological Conservation 25:315–334.

Lancia, R. A., J. D. Nichols, and K. H. Pollock. 1994. Estimating the number of animals in wildlife populations. Pages 215–253 *in* T. A. Bookhout, editor. Research and management techniques for wildlife and habitat. The Wildlife Society, Bethesda, Md.

Lefebvre, L. W., B. B. Ackerman, K. M. Portier, and K. H. Pollock. 1995. Aerial survey as a technique for estimating trends in manatee population size—problems and prospects. Pages 63–74 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

*McGehee, M. A. 1982. Manatees (*Trichechus manatus*): abundance and distribution in and around several Florida power plant effluents during the winter of 1981–1982. Final report prepared for the Florida Power and Light Co., Contract 31534–86419. 67 pp.

National Oceanic and Atmospheric Administration. 1982–91. Climatological data, Florida. National Climatic Data Center, Asheville, N.C. Volumes 86–95.

O'Shea, T. J. 1988. The past, present, and future of manatees in the southeastern United States: realities, misunderstandings, and enigmas. Pages 184–204 *in* R. R. Odom, K. A. Riddleberger, and J. C. Ozier, editors. Proceedings of the Third Southeastern Nongame and Endangered Wildlife Symposium, Georgia Department of Natural Resources, Social Circle.

*Packard, J. M., and R. Mulholland. 1983. Analysis of manatee aerial surveys: a compilation and preliminary analysis of winter aerial surveys conducted in Florida between 1977 and 1982. Manatee Population Research Report 2. Technical Report 8–2. Florida Cooperative Fish and Wildlife Research Unit, University of Florida, Gainesville. 119 pp.

*Raymond, P. W. 1981. Manatees (*Trichechus manatus*): Abundance and distribution in and around Florida power plant effluents. Final report prepared for the Florida Power and Light Co. Contract 31534–81511. 62 pp.

Reid, J. P., R. K. Bonde, and T. J. O'Shea. 1995. Reproduction and mortality of radio-tagged and recognizable manatees on the Atlantic Coast of Florida. Pages 171–191 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Reid, J. P., G. B. Rathbun, and J. R. Wilcox. 1991. Distribution patterns of individually identifiable West Indian manatees (*Trichechus manatus*) in Florida. Marine Mammal Science 7:180–190.

*Reynolds, J. E., III. 1983. Distribution and abundance of West Indian manatees (*Trichechus manatus*) around selected Florida power plants following winter cold fronts. Final report prepared for the Florida Power and Light Co., Contract 71527–88609. 75 pp.

*Reynolds, J. E., III. 1985. Distribution and abundance of the West Indian manatee (*Trichechus manatus*) around selected Florida power plants following winter cold fronts: 1984–1985. Final report prepared for the Florida Power and Light Co., Order 01249–87331. 48 pp.

*Reynolds, J. E., III. 1991. Distribution and abundance of the West Indian manatee (*Trichechus manatus*) around selected Florida power plants following winter cold fronts: 1990–1991. Report for Florida Power and Light Co., Order B89806-00264. 39 pp.

Reynolds, J. E., III, and J. R. Wilcox. 1985. Abundance of West Indian manatee *Trichechus manatus* around selected Florida power plants following winter cold fronts: 1982–1983. Bulletin of Marine Science 36:413–422.

Reynolds, J. E., III, and J. R. Wilcox. 1986. Distribution and abundance of the West Indian manatee *Trichechus manatus* around selected Florida power plants following winter cold fronts: 1984–85. Biological Conservation 38:103–113.

*Rose, P. M., and S. P. McCutcheon. 1980. Manatees (*Trichechus manatus*) abundance and distribution in and around several Florida power plant effluents. Final report prepared for the Florida Power and Light Co., Contract 31534-86626. 128 pp.

*U.S. Fish and Wildlife Service. 1989. Florida manatee *(Trichechus manatus latirostris)* Recovery Plan. U.S. Fish and Wildlife Service, Atlanta, Ga. 98 pp.

[2] An asterisk denotes unpublished material.

Appendix A. Aerial counts of Florida manatees (*Trichechus manatus latirostris*) along the eastern coast of Florida and potential adjustment factors.

Survey date	Survey conditions: North[a] A[c]	A3[d]	W[e]	W3[f]	SC[g]	South[b] A	A3	W	W3	SC	Counts by site[h] 1	2	3	4	5	6	7	8	9	10	Cumulative degree days S[i]	−5[j]	−10	−15	−20	−25	−30	−35	−40
821214[k]	15	19	21	22	3	22.0	19.0	24.0	24.0	2.3	0	0	0	0	0	3	1	0	0	6	41	18	18	18	18	18	18	18	41
821220	13	11	16	17	2	15.5	15.0	23.0	23.0	1.8	0	14	0	0	0	5	32	10	0	12	92	48	69	69	69	69	69	69	69
83 113	7	12	18	20	2	11.5	16.0	23.5	24.0	2.5	0	11	0	18	0	19	43	39	10	9	202	33	69	69	69	121	161	179	179
83 116	12	10	17	18	2	14.0	15.5	22.5	23.5	2.5	0	15	0	2	0	3	98	56	16	7	248	78	99	115	115	135	201	225	225
83 119[k]	10	9	15	15	4	17.0	15.0	22.0	22.0	3.5	0	14	0	5	0	17	85	0	0	2	299	77	131	163	166	166	208	256	276
83 2 5	12	17	18	19	2	15.5	18.5	21.5	22.0	2.3	0	1	0	7	0	15	33	29	7	6	422	29	68	112	174	252	273	289	289
83 2 8	10	14	18	18	2	14.5	18.5	22.0	22.0	2.3	0	5	0	12	0	10	41	41	12	0	450	54	66	122	151	227	281	314	317
831227	0	2	12	13	3	14.0	10.0	20.5	21.0	2.3	0	9	0	4	0	0	60	12	0	16	235	90	90	114	140	140	151	166	195
84 130	11	14	20	20	2	17.5	18.0	22.5	23.0	1.8	0	16	0	12	0	28	15	16	2	6	563	27	65	93	148	208	288	361	418
84 2 1	5	9	16	18	3	14.0	16.0	22.0	22.5	2.0	0	14	0	20	0	27	20	35	8	15	601	65	71	113	171	223	290	355	456
84 2 7	6	10	17	18	3	12.0	14.0	22.5	22.5	2.8	0	9	0	13	0	20	27	15	11	12	674	54	137	138	181	228	280	352	427
84 3 1	9	12	17	18	2	10.5	13.5	21.0	22.0	2.0	0	20	0	32	0	15	22	30	2	10	777	26	28	35	58	145	214	241	279
85 1 6	8	14	18	20	5	13.5	16.0	22.0	22.5	2.5	0	8	0	17	0	9	13	20	0	5	192	34	34	34	34	49	117	128	142
85 110	11	11	17	17	3	18.0	17.0	22.5	22.0	2.5	0	12	0	9	0	23	17	30	1	16	245	71	87	87	87	87	104	180	180
85 114	7	10	13	14	3	17.5	15.0	21.5	22.0	3.5	0	5	0	8	0	9	34	62	0	5	295	63	137	137	137	137	140	164	231
85 119	13	15	16	16	4	16.5	19.0	22.0	22.0	2.3	0	34	0	6	0	12	58	144	11	19	358	63	126	200	200	200	200	203	227
85 122	−2	6	11	13	4	4.5	10.5	21.0	21.0	2.5	0	7	0	0	0	0	231	109	5	2	424	75	170	217	266	266	266	266	274
85 127	5	13	12	13	2	13.0	15.5	21.0	21.0	3.0	0	2	0	0	0	3	143	234	29	12	519	95	170	265	312	361	361	361	361
85 2 2	23	22	19	17	4	26.0	24.0	22.0	22.0	2.5	0	0	0	4	0	67	29	28	4	36	559	26	106	211	284	341	401	401	401
85 2 9	8	15	16	19	4	14.5	18.0	21.5	22.0	2.5	0	6	0	0	0	0	28	23	2	2	594	35	42	106	224	279	350	420	436
85 215	11	9	14	14	3	12.0	11.5	21.0	21.0	1.5	0	23	0	12	0	9	191	190	10	13	680	71	117	121	185	292	345	430	488
85 218	14	10	16	15	3	18.5	15.0	21.0	21.0	2.8	0	16	0	0	0	6	85	116	8	6	731	85	156	172	194	256	373	436	499
851219	14	13	17	17	4	19.0	18.0	24.5	23.5	3.3	0	8	0	0	0	7	5	17	2	2	101	58	58	70	77	77	77	77	77
851222	9	11	15	16	4	12.0	15.0	24.5	24.5	2.3	0	16	0	7	0	7	124	109	7	9	139	57	96	102	115	115	115	115	115
851227	2	7	12	13	4	11.5	12.5	22.5	22.5	2.5	0	15	0	0	0	5	217	172	30	9	220	82	138	177	183	197	197	197	197
86 112	15	17	17	18	4	18.5	20.5	22.0	23.0	3.5	0	3	0	1	0	1	11	57	4	6	325	16	38	83	169	232	282	282	302
86 115	13	12	16	16	3	13.5	14.0	23.5	23.5	2.3	0	17	0	0	0	3	131	133	13	3	360	47	73	83	170	239	289	317	330
86 121	12	15	18	18	3	17.0	18.0	23.0	23.5	2.3	0	7	0	5	0	13	81	158	17	4	390	19	77	91	103	170	252	308	347
86 129	2	6	13	15	3	11.5	10.0	22.0	22.5	2.3	0	6	0	14	0	3	272	185	14	8	482	75	108	135	168	194	221	316	371
86 214	6	11	16	19	5	15.5	15.5	23.0	23.5	2.0	0	7	20	38	22	28	52	35	2	5	568	40	40	67	156	190	208	254	280
87 112	8	14	16	17	5	11.5	17.0	22.0	22.0	2.8	0	19	0	25	0	30	107	160	4	10	151	33	88	114	128	132	138	138	151
87 115	16	12	17	16	2	21.0	17.5	20.0	22.0	2.8	0	129	0	5	0	15	45	86	8	8	186	54	84	138	160	166	168	173	173
87 124	6	8	16	18	3	13.0	16.0	22.5	23.0	1.8	0	13	0	13	8	17	78	59	16	1	244	58	62	118	152	201	221	224	226
87 2 1	14	15	16	16	3	16.0	17.0	22.0	22.0	2.5	0	9	0	0	0	27	47	182	5	6	333	56	127	147	182	215	270	296	310
87 211	15	13	16	17	3	18.5	16.5	23.0	22.0	3.0	0	16	0	3	7	22	98	134	6	5	400	56	67	122	194	214	249	282	336

871220	18	13	18	18	1	23.0	20.5	23.0	23.0	3.0	0	83	0	1	0	12	19	27	6	15	203	65	73	88	141	151	174	181	203
88 112	8	9	14	16	4	16.5	18.0	22.5	22.0	2.3	0	81	0	15	0	7	99	71	18	12	353	62	114	148	150	162	219	223	260
88 124	11	11	15	15	3	19.5	18.0	22.0	22.0	2.8	0	85	0	5	0	10	53	78	7	0	438	44	74	138	183	212	235	236	301
88 128	6	6	15	15	3	13.5	13.0	20.5	21.0	3.3	0	76	0	3	0	3	269	110	16	4	521	96	127	163	230	282	308	318	320
88 214	11	10	16	17	1	15.0	15.5	22.0	22.0	2.5	0	137	0	0	0	5	277	99	17	0	699	71	150	158	244	305	326	386	429
88 217	10	11	18	17	2	16.5	19.0	23.0	22.5	2.0	0	156	0	0	0	47	96	276	20	18	740	72	145	191	219	314	346	381	449
88 223	13	14	19	20	2	23.5	20.5	22.5	22.5	2.5	0	117	0	0	0	3	23	23	2	25	772	25	87	160	223	238	334	378	408
88 228	11	10	17	17	2	18.5	17.0	21.5	21.5	3.0	0	185	0	0	21	22	84	72	8	9	843	71	95	158	231	294	308	405	449
881214	15	13	17	19	3	14.0	17.5	21.5	21.0	2.0	0	37	0	0	0	3	19	59	2	6	85	34	41	76	85	85	85	85	85
891219	11	9	16	16	3	14.5	14.0	20.5	21.0	2.0	0	74	0	0	0	26	153	173	3	21	142	57	91	98	133	142	142	142	142
89 123[k]	14	16	19	20	4	17.0	20.0	22.0	22.5	1.5	0	15	0	0	0	2	3	0	0	10	161	14	14	14	20	20	20	20	77
89 211[k]	13	15	18	21	4	19.0	19.5	22.5	22.0	2.5	0	14	7	3	0	1	15	1	0	4	187	24	24	24	33	39	39	39	45
89 227	12	10	16	16	3	15.5	13.0	20.5	21.0	2.0	0	229	0	59	0	4	112	23	6	16	275	81	81	81	112	112	112	114	128
891210	11	17	17	18	3	16.0	20.5	24.0	24.0	2.0	13	25	0	43	1	6	26	60	9	4	115	28	60	66	88	115	115	115	115
891214	6	14	18	18	3	14.0	17.5	22.5	23.0	2.2	5	41	5	32	0	10	118	78	23	14	152	50	76	104	108	130	152	152	152
891224	−1	7	13	16	2	2.5	10.5	20.0	22.0	3.2	5	1	0	5	0	0	226	133	20	2	254	74	102	152	178	205	209	232	254
891226	4	1	9	10	4	10.5	6.5	20.0	20.0	2.2	3	54	4	0	1	0	266	227	17	4	312	125	143	185	217	253	263	281	312
90 115	14	11	17	17	4	21.0	17.5	22.5	23.0	2.2	2	39	1	84	0	15	73	110	0	7	444	51	65	87	132	257	275	317	349
90 228	17	15	20	19	3	22.0	20.5	23.5	23.5	2.3	17	49	4	0	0	3	3	0	0	0	532	38	40	42	53	57	57	78	82
901210	13	14	17	18	3	18.0	17.5	25.0	26.0	2.7	16	84	1	51	1	6	38	35	8	5	53	29	32	32	34	42	53	53	53
91 123	11	12	18	19	3	16.5	17.0	26.0	25.5	1.3	13	129	0	49	0	4	18	24	3	8	170	40	68	74	74	74	89	89	95
91 213	20	18	15	16	3	18.0	18.0	26.0	26.5	2.5	88	28	0	20	0	13	11	54	3	25	219	20	28	30	40	87	110	123	123
91 217	8	9	15	16	4	13.0	14.0	23.5	24.5	2.5	55	97	0	14	0	2	202	75	8	9	260	41	65	70	71	90	130	158	164

[a] Sites 1 and 2.
[b] Sites 7 and 8.
[c] Air temperature (° C) on day of survey.
[d] Average air temperature (° C) for 3 days prior to survey.
[e] Water temperature (° C) on day of survey at power plant intake.
[f] Average intake water temperature (° C) for 3 days prior to survey.
[g] Index to flight and sighting conditions during survey.
[h] Subheadings under counts are 10 different sites surveyed.
[i] From start of winter (1 Nov) to survey date.
[j] −5, ..., −40 are starting points in days relative to the survey date.
[k] Survey unusable for analysis.

Appendix B. Aerial counts of Florida manatees (*Trichechus manatus latirostris*) near Fort Myers, Florida, and potential adjustment factors.

Survey date	Survey conditions					Counts	Cumulative degree days								
	A[a]	A3[b]	W[c]	W3[d]	SC[e]		S[f]	−5[g]	−10	−15	−20	−25	−30	−35	−40
821214[h]	18	17	24	25	4	5	18	11	11	11	11	11	11	11	18
821220	14	13	20	20	4	32	54	36	47	47	47	47	47	47	47
83 113	10	13	21	22	4	56	107	25	39	39	39	60	89	100	100
83 116	12	13	18	18	4	85	134	52	56	66	66	67	108	127	127
83 119	17	15	18	18	5	53	160	43	79	90	93	93	106	142	153
83 2 5	18	20	18	18	4	45	221	20	34	58	88	140	143	154	154
83 2 8	13	16	18	19	4	41	235	31	35	62	75	118	154	165	168
831227	13	7	17	19	3	56	94	68	68	70	74	78	79	80	85
84 130	15	16	21	23	2	122	252	14	31	40	68	90	135	169	227
84 2 1	12	14	19	20	3	89	270	32	32	58	67	96	135	177	245
84 2 7	10	13	19	21	3	120	303	30	61	64	91	96	120	161	209
84 3 1	11	13	20	21	3	83	337	16	23	23	23	64	85	99	116
85 1 6	13	16	20	20	4	93	71	17	17	17	17	17	41	55	55
85 110	17	17	19	19	3	141	91	29	37	37	37	37	37	75	75
85 114	16	13	17	18	3	80	119	31	64	64	64	64	64	66	102
85 119	17	18	18	18	1	338	133	14	45	78	78	78	78	78	80
85 122	6	9	21	20	3	136	184	54	82	104	130	130	130	130	130
85 127	13	15	21	23	3	139	231	47	101	129	151	177	177	177	177
85 2 2	24	24	22	22	5	99	232	1	31	102	118	148	177	177	177
85 2 9	15	16	19	21	3	70	247	16	16	38	109	124	156	185	193
85 215	9	11	20	21	4	163	297	48	66	66	77	137	167	206	226
85 218	19	17	21	21	3	100	309	42	68	77	77	99	176	190	221
851219	18	16	18	18	4	81	37	27	32	37	37	37	37	37	37
851222	11	13	17	17	3	126	62	27	57	57	62	62	62	62	62
851227	10	10	15	16	3	104	116	54	81	111	111	116	116	116	116
86 112	18	19	19	19	3	147	138	4	10	19	66	102	133	133	138
86 115	14	14	18	18	4	147	162	27	33	34	61	113	135	157	160
86 121	16	18	18	19	4	248	170	8	33	36	42	55	109	136	165
86 129	11	10	17	18	3	191	214	44	51	59	79	86	89	135	173
86 214	15	14	18	21	4	48	243	24	24	25	73	77	81	108	114
87 112	11	16	19	20	4	107	71	19	37	59	65	65	65	65	71
87 115	20	17	20	20	2	140	83	31	31	61	76	77	77	77	77
87 124	12	14	20	21	3	91	109	26	26	56	63	90	103	103	103
87 2 1	16	16	20	20	3	153	143	21	60	60	72	91	109	131	137
87 211	16	15	20	20	3	111	168	25	25	46	85	85	97	115	133
871220	22	18	21	21	4	77	67	25	25	33	51	51	62	62	67
88 112	15	14	19	20	4	93	118	28	37	51	51	51	76	76	93
88 124	11	13	19	20	4	90	159	27	36	64	78	80	92	92	117
88 128	11	11	18	18	4	134	202	51	70	83	112	121	130	135	135
88 214	13	13	19	20	4	203	272	32	62	62	111	140	145	170	184
88 217	16	17	20	20	2	191	281	30	48	70	79	130	148	162	191
88 223	21	18	21	21	4	40	290	9	27	50	79	79	131	157	167
88 228	19	15	20	20	4	104	313	23	32	50	73	102	102	154	180
881214	13	15	21	22	3	62	34	20	22	32	34	34	34	34	34
881219	12	11	18	20	3	84	72	38	58	59	70	72	72	72	72
89 123	18	18	22	23	2	21	81	3	3	3	9	9	9	9	47
89 211	16	17	23	24	3	14	88	7	7	7	9	10	10	10	16
89 227	15	12	20	21	3	77	153	64	64	64	73	73	73	73	75

Appendix B. *Continued.*

Survey date	Survey conditions					Counts	Cumulative degree days								
	A[a]	A3[b]	W[c]	W3[d]	SC[e]		S[f]	−5[g]	−10	−15	−20	−25	−30	−35	−40
891210	14	19	21	21	2	113	42	10	34	35	36	42	42	42	42
891214	11	15	20	21	2	113	68	35	44	62	62	62	68	68	68
891224	2	7	17	19	3	126	133	61	65	99	109	126	126	127	133
891226	11	6	14	16	2	198	169	97	97	121	135	161	162	163	169
90 115	20	15	20	20	3	134	211	23	23	25	43	139	140	163	178
90 228	20	19	22	22	3	21	228	8	8	8	9	9	9	17	17
901210	14	15	21	21	2	186	37	28	35	35	35	35	37	37	37
91 123	16	17	21	21	3	26	82	10	19	23	23	23	25	25	25
91 213	19	18	21	22	4	26	93	10	10	10	11	21	26	34	34
91 217	13	13	21	21	3	80	120	28	38	38	38	39	48	58	62

[a] Air temperature (° C) on day of survey.

[b] Average air temperature (° C) for 3 days prior to survey.

[c] Water temperature (° C) on day of survey at power plant intake.

[d] Average intake water temperature (° C) for 3 days prior to survey.

[e] Index to flight and sighting conditions during survey.

[f] From start of winter (1 Nov) to survey date.

[g] −5, ..., −40 are starting points in days relative to the survey date.

[h] Survey unusable for analysis.

Fixed-width Aerial Transects for Determining Dugong Population Sizes and Distribution Patterns

by

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Abstract. The fixed-width transect technique developed for surveying the dugong (*Dugong dugon*) from the air at large spatial scales (tens of thousands of km^2) is described and evaluated. Perception bias (the proportion of groups that is visible in the transect, yet missed by observers) is corrected with a modified Petersen estimate calculated for each of two teams of tandem observers, one on each side of the aircraft. Availability bias (the proportion of animals that is unavailable to observers because of water turbidity) is standardized by comparing the proportion of individuals at the surface during the survey with the proportion at the surface in a clear-water area when all dugongs are potentially visible. This fixed-width transect technique provides a standardized estimate of minimum population size and is useful for producing density-distribution maps for monitoring trends in abundance over large spatial scales and long time periods, and for assessing the probable impact of direct anthropogenic mortality. However, the population size estimated with the technique has a coefficient of variation (S.E./mean) of 12% at best, which means detection of a low-level chronic decline in dugong abundance even at a large spatial scale would take about one decade.

Key words: Aerial survey techniques, bias corrections, dugong, *Dugong dugon.*

The range of the dugong (*Dugong dugon*) extends throughout the tropical and subtropical coastal and island waters of the Indo-west Pacific from east Africa to the Solomon Islands and Vanuatu and between 26° and 27° north and south of the equator (Nishiwaki and Marsh 1985). The distribution spans the waters of more than 40 countries. Over much of this range, dugongs are now believed to be represented by relict populations, separated by large areas in which they are close to extinction or extinct (Nishiwaki and Marsh 1985) or have never occurred. For most countries, however, this assessment is based on anecdotal information and the extent of population declines or range contractions is unknown because quantitative information on the distribution and abundance of dugongs and their habitats is unavailable.

The only quantitative information on dugong population size is from aerial surveys. Hughes and Oxley-Oxland (1971) demonstrated that aerial surveys were useful for studying dugongs in Mozambique. Heinsohn et al. (1976) were the first to survey dugongs from the air in Australia, and most surveys have been in Australian waters. Aerial surveys of dugongs have also been conducted in Kenya (*[1]Ligon 1976), Papua New Guinea (Ligon and Hudson 1977; Hudson 1980a, 1980b), Palau (*Brownell et al. 1981; Rathbun et al. 1988), Irian Jaya in Indonesia (*Salm et al. 1982), the Arabian region (*Preen 1989), and Vanuatu (Chambers et al. 1989).

The designers of the surveys before 1983 assumed that, because dugongs feed primarily on seagrasses (Marsh et al. 1982), they mainly occur in coastal waters within about 2 km of land. The survey technique was broadly similar to the extended-area technique (sensu *Packard 1985 and Lefebvre et al. 1995) used for manatees (*Trichechus manatus latirostris*). Dugongs were counted from aircraft at altitudes of 275–300 m and about 0.8 km from and parallel to the shore. If a large group of dugongs was detected, a count was made while the aircraft circled. In some studies, flights were made over additional transects where suitable habitat was known to extend farther offshore. No corrections were made for dugongs that were not seen by observers (e.g., because of water turbidity).

This technique proved useful for identifying areas in which large numbers of dugongs occurred close to the shore (see Nishiwaki and Marsh [1985] for a summary of

[1] An asterisk denotes unpublished material.

counts in various areas). Because of its ease of implementation, the technique is still useful for identifying inshore areas in developing countries where dugongs occur, particularly in regions where the continental shelf is narrow (Chambers et al. 1989).

Dugongs have been sighted tens of kilometers from the coast in large embayments (e.g., Shark Bay in Western Australia; *Marsh et al. 1991; Marsh et al. 1994) and where the continental shelf is broad (e.g., Torres Strait [Marsh and Saalfeld *1988, *1991] and the northern Great Barrier Reef lagoon [Marsh and Saalfeld 1989]). The number of dugongs sighted during a survey over the shoreline is an unreliable index of abundance because it depends on the degree to which the distribution of the animals follows the coast, which is variable, even where the continental shelf is narrow. Hence, the shoreline method is unsuitable for tracking temporal changes in dugong abundance, especially at large spatial scales.

The shoreline technique has largely been replaced by fixed-width transect surveys (Marsh and Saalfeld 1989; Marsh and Sinclair 1989a, 1989b) designed to provide standardized minimum population-size estimates of dugongs as a basis for monitoring temporal changes in abundance, for the assessment of the impact of direct anthropogenic mortality, and for density-distribution maps at scales required for management by zoning. A fixed-width transect technique was adopted in preference to the line transect technique often used for dolphin surveys (Forney et al. 1991). Dugongs are generally more difficult to sight than dolphins because they are most often seen as solitary individuals or adult female-calf pairs in turbid water. Accordingly, we decided to use a technique with which observers did not have to take their eyes off the water to read an inclinometer.

Here I review the fixed-wing transect technique as a background to the evaluation of the relevance of dugong aerial-survey techniques for estimating manatee population sizes or trends.

Material and Methods

Survey Procedure

Dugongs are counted on either side of an aircraft flying at 185 km/h at an altitude of 137 m over 200-m-wide strip transects. Altitude is maintained with the aid of a radar altimeter. The strip transects, defined by markers on the wing struts (see diagram in Caughley 1977), are sufficiently narrow to preclude detectable variation in dugong sightability across the transect (Marsh and Saalfeld 1990).

The survey crew comprises six people: the pilot, a front-right survey leader, and two teams of tandem observers, one on either side of the aircraft. The survey leader records the data with a portable computer programmed as a data logger and timer and equipped with a printer that produces an immediate hard copy of the data. The mid-seat observers report their sightings to the survey leader via a 2-way intercom system connected to one track of a 2-track tape recorder. The rear-seat observers are usually screened from the mid-seat observers with a curtain and acoustically isolated from the other crew members but can communicate with each other. They report their sightings into the second track of the tape recorder (Fig. 1).

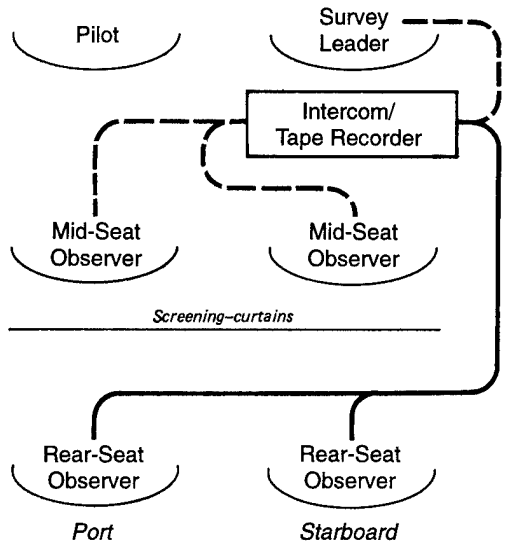
All reports from observers are in standardized format: dugong group size, number of calves, number at the surface, and position of the sighting inside the transect strip. The top (farthest from aircraft), middle, and bottom thirds of the transect are color-marked on the wing strut to facilitate the determination of the position of sightings inside the strip. This information is recorded to increase the probability of distinguishing between different, simultaneously reported sightings by both members of a tandem team. Surveys are made only when the cloud cover is less than 50% and the sea is calm (<Beaufort 3); they are timed to minimize glare off the surface of the water from a low or mid-day sun.

After each flight, the tape record of each transect is used to verify and edit the computer records, so that each sighting can be coded as made by one (specified) member or both members of a tandem observing team. The reports of team members are different if they are unambiguously distinct (usual situation) or if they are separated by 5 or more seconds. Discrepancies between the reports of observers sighting the same group of dugongs are also noted.

When training a new observer (Marsh and Saalfeld 1989), I use a functional tandem team on one side of the aircraft and one trained observer and the trainee on the other side. During training, the intercom system is switched so that the trainee can hear the reports of his or her counterpart on the same side of the aircraft. This system greatly reduces the time to train reliable observers.

Corrections are made for perception bias (dugongs that are visible but missed by observers) and availability bias (dugongs that are unavailable to observers because of water turbidity) with correction factors that are calculated separately for each survey. These corrections compensate for fluctuations in variations in the visibility biases that are due to changes in sea state, glare, and water turbidity within the range of acceptable survey conditions and that cannot be eliminated by the standardization of procedures. They also compensate for differences between observers and reduce the need to use the same observers for each survey.

The correction for perception bias is based on a modified Petersen estimate calculated separately for the two



Pilot

Flys/navigates aircraft
Blows whistle at start and end of transect
Uses stopwatch to check navigation

Survey Leader

Manages survey: Records aircraft height, Landmarks, Beaufort sea state. Standardized observations of mid-seat observers into data-logger

Mid-Seat Observers

Communicate with each other and survey leader during transects

Rear-Seat Observers

Communicate with each other during transects

(All members wear polarized sunglasses)

— — Track 1 Intercom/Tape Recorder

——— Track 2 Intercom/Tape Recorder

Fig. 1. The arrangement and duties of the survey crew during fixed-width aerial transect surveys of dugongs (*Dugong dugon*).

teams of two observers (Marsh and Sinclair 1989a). This correction factor requires the assumption that all groups are equally sightable. Marsh and Sinclair (1989b) showed that this is a reasonable assumption for the small groups of dugongs usually observed.

The correction for availability bias (Marsh and Sinclair 1989a) serves to standardize the results of each survey for the proportion of animals that was unavailable to observers because of water turbidity during that survey. This correction rests on the untested assumption that the proportion of dugongs at the surface is constant within the limits of acceptable survey conditions. This proportion (16.7%) is based on data from an aerial survey over a clear water area in Moreton Bay near Brisbane where all dugongs were assumed to be visible. The proportion is not significantly different from that obtained from vertical aerial photographs of dugongs in the same area (Marsh and Sinclair 1989b). This fraction is, however, much greater than the 1.9% suggested by Anderson and Birtles' (1978) surface observations of diving and surfacing dugongs in muddy water. The differences may be due to the observation platform or spatial variation in diving by dugongs. I believe the corrections for availability bias are probably conservative and the population size obtained with the fixed-wing transect technique is probably underestimated.

Large Groups of Dugongs

The mean size of a group of dugongs sighted in these surveys is between 1.3 and 2.1 animals (Marsh and Sinclair 1989a). Groups of more than 10 dugongs are rare (<2% of groups; Marsh and Saalfeld *1988, 1989, 1990; *Marsh et al. 1990, *1991, 1994). When these groups are sighted (even outside the transect), the flight course is interrupted and the group is circled and photographed to obtain a total count. These groups are then treated as a separate stratum of large herds as suggested by Norton-Griffiths (1978).

Survey Design

The survey areas ranged from about 2,000 to 40,000 km^2 (Table 1). Each area was divided into blocks (sampling strata) based on expected dugong density. The sampling fraction in each block was proportional to dugong density, varying from about 5% where few dugongs were expected to about 20% where the known dugong density was high. The sampling fraction in the entire survey usually averaged about 10%. Dugongs in each block were sampled over systematically spaced transects (the first transect was placed randomly). Because of their logistical advantages and to facilitate the production of density-distribution maps, systematic rather than random transects were used. The transects were aligned across the depth contours to increase the precision of the population-size estimates. The same transects were used on repeated surveys of the same area so that transects could be used as factors in the analyses. I now use a global positioning system to locate the aircraft on the transects.

Analysis

Because transects are variable in area, the Ratio Method (Jolly 1969; Caughley and Grigg 1981) was used to estimate density and population size and their associated standard errors in each block in each survey. Any statistical bias from this method was considered inconsequential because of the high sampling fraction

Table 1. Estimates of the number and densities of dugongs (*Dugong dugon*) and the associated coefficients of variation where surveys were conducted with the fixed-width transect technique.

Location	Area (km^2)	Population estimate ±S.E.	Density km^{-1} ±S.E.	Coefficients of variation	Reference
Shark Bay[a]	14,240	10,146± 1,478	0.71± 0.10	14.6	*Marsh et al. (1991) Marsh et al. (1994)
Exmouth Gulf-Ningaloo[a]	3,397	1,964± 363	0.58± 0.11	18.5	*Marsh et al. (1991)
North coast Northern Territory[b]	28,746	13,800± 2,683	0.48± 0.09	19.4	Bayliss (1986) in Bayliss and Freeland (1989)
Western Gulf of Carpentaria[b]	27,216	16,846± 3,259	0.62± 0.12	19.3	Bayliss and Freeland (1989)
Torres Strait[c]	30,533	12,522± 1,497	0.41± 0.05	11.9	*Marsh and Saalfeld (1988 and 1991)
Northern Great Barrier Reef[c]	31,288	8,110± 1,073	0.26± 0.03	13.2	Marsh and Saalfeld (1989)
Southern Great Barrier Reef[c]	39,396	3,479± 459	0.088± 0.012	13.2	Marsh and Saalfeld (1990)
Southeast Queensland[c]	9,170	2,479± 365	0.26± 0.04	14.7	*Marsh et al. (1990)
Arabian Gulf[d]	34,604	7,310± 1,300	0.25[e]± 0.045	17.8	*Preen (1989)
Saudi Arabian coast of Red Sea	22,370	1,820± 380	0.08[e]± 0.017	20.9	*Preen (1989)

[a] Western Australia.
[b] Northern Territory, Australia.
[c] Queensland, Australia.
[d] Saudi Arabia.
[e] Excluding zones in which too few dugongs were sighted for population-size estimates.

(Caughley and Grigg 1981). Input data were the estimated number of dugongs (in groups of <10) for each tandem team per transect, calculated with the corrections for perception and availability biases. The resultant standard errors were adjusted to incorporate the errors associated with the appropriate estimates of the perception and availability correction factors and mean group size as outlined in Marsh and Sinclair (1989a). At the end of the analyses, the number of dugongs in groups of more than 10 was added to the estimates of the population size and density in the appropriate block, as outlined in Norton-Griffiths (1978).

Density diagrams, adjusted for sampling intensity, were produced with the Arcinfo GIS package. A grid coverage (2.5 km^2 or 5 km^2) was combined with the coastline coverage. The corrected number of dugongs and the transect length in each grid cell were calculated. The density in each grid cell was then calculated as follows:

density/km^2 = corrected number of dugongs sighted in cell/survey area in cell, where survey area = transect length in km × transect width (i.e., 0.4 km).

Results

Distribution of Dugongs

Density distribution maps were produced for the entire survey area (Table 1). High local densities of dugongs occur in inshore waters sheltered from trade winds and in association with offshore reefs and shoals in the northern Great Barrier Reef (Marsh and Saalfeld 1989; *Marsh et al. 1993) and Torres Strait (Marsh and Saalfeld *1988, *1991). Large numbers of dugongs were sighted in more-than-10-m-deep water in several areas including Shark Bay in Western Australia (*Marsh et al. 1991; Marsh et al. 1994), Torres Strait (Marsh and Saalfeld *1988, *1991), the northern Great Barrier Reef region (Marsh and Saalfeld 1989; *Marsh et al. 1993), and Hervey Bay in southeastern Queensland (*Marsh et al. 1990). The proportion of dugongs in these deeper water areas is unknown because we lack information on the relation between diving and surfacing times at different depths. In contrast to their essentially inshore distribution where the continental shelf is narrow, dugongs seen in waters deeper than about 10 m in northern Australia tend to be more than

10 km from land (Marsh and Saalfeld *1988, 1989, *1991; Marsh et al. *1990, *1991, *1993, 1994).

Detection of Population Trends

Temporal changes in density have been studied with repeated surveys of dugongs in the same area and with analysis of variance usually with and without measures of sea state or cloud cover at each transect as continuously distributed covariates (Bayliss and Freeland 1989; Marsh and Saalfeld 1989; *Marsh et al. 1993). Blocks and times were treated as fixed factors and transects as a random factor nested within blocks. Data for all analyses were corrected densities/km^2 based on mean group sizes and the estimated correction factors for perception and availability bias; each transect contributed one density per survey based on the combined corrected counts of both tandem teams. The densities were transformed ($\log_{10}x + 1$) for analysis to equalize the error variances.

The population-size estimates (Table 2; Fig. 2) are consistent, especially in surveys separated by relatively short time intervals (months). The inclusion of sea state and cloud cover as covariates in the analyses made little difference to the results and did not alter the conclusions (Marsh and Saalfeld 1989), suggesting that the method was appropriate for stabilizing most biases in visibility because of weather conditions.

Marsh and Saalfeld (1989) used Gerrodette's (1987) power analysis technique to investigate the length of time to detection of a hypothetical population decline of 5%/year with acceptable levels of confidence (Type 1 and Type 2 errors at 0.05). Assuming that the precision of the population-size estimate is 11% (which is optimistic even for large-scale dugong surveys at the given sampling fractions; Table 1), Marsh and Saalfeld (1989) estimated that 10 annual surveys are required (i.e., 9 years to be able to detect such a decline with 95% confidence). During this period, a dugong population declining at 5%/year would have been reduced to 63% of its size since the time of the first survey. A preliminary indication of this trend could be obtained more quickly by increasing the Type 1 and Type 2 error rates. However, because the consequences of failing to detect a declining trend are more serious than the consequences of deciding that a declining trend is occurring when it is not, the Type 2 error rate must be kept low. Even if the Type 2 error rate were increased to 0.1 and the Type 1 error rate to 0.15, eight annual surveys (7 years) are required to detect a declining trend in the given example.

Discussion

Evaluation of the Technique

Results of the fixed-width transect technique are now used for developing local strategies for dugong conservation. Density-distribution maps of dugongs are used for the zoning and management of marine protected areas in northern Australia, especially in the Great Barrier Reef Marine Park. Distribution maps have also been used to produce recommendations for the conservation and management of dugongs in the Arabian region (*Preen et al. 1989). The distribution of dugongs mirrors the distribution of seagrasses in all survey areas. Indeed, the pattern of dugong sightings has proved a reliable basis for designing recent seagrass surveys in Torres Strait, the northern Great Barrier Reef, and Shark Bay.

The standardized minimum population-size estimates have been used in conjunction with a dugong population model to assess the probable impact of direct anthropogenic mortality of dugongs in the few cases for which a measure of that mortality was available. For example, Smith and Marsh (1990) concluded that the take of Aboriginal communities in Cape York was well below the sustainable yield.

In Australia, dugongs are being resurveyed at regular intervals along fixed transects using the techniques outlined

Table 2. Comparison of the population-size estimates obtained from repeated surveys of dugongs (*Dugong dugon*) with the fixed-width transect technique in the same area.

Location	Survey date	Population estimate ± S.E.	Reference
Western Gulf of Carpentaria[a]	August 1984	16,816 ± 2,946	Bayliss and Freeland (1989)
	February 1985	16,846 ± 3,257	
Cape Bedford-Cape Melville[b]	November 1984	2,899 ± 454	Marsh and Saalfeld (1989)
	November 1985	2,542 ± 634	
Campbell Point-Hunter Point[b]	April 1985	2,172 ± 552	Marsh and Saalfeld (1989)
	November 1985	1,938 ± 491	
Cape Bedford-Hunter Point[b]	November 1985	8,100 ± 1,073	Marsh and Saalfeld (1989)
	November 1990	10,742 ± 1,579	*Marsh et al. (1993)

[a] Northern Territory, Australia.

[b] Northern Great Barrier Reef region, Queensland, Australia.

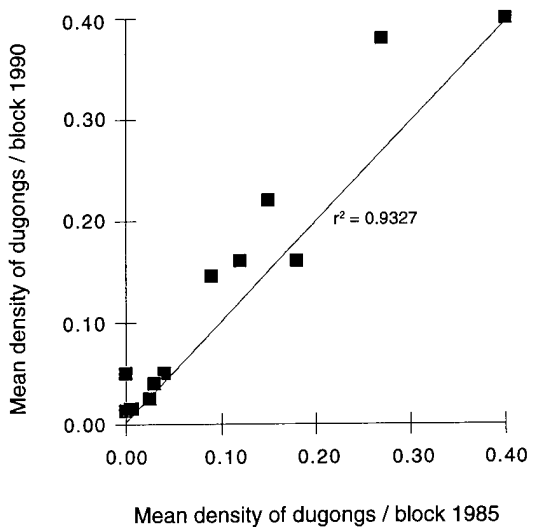


Fig. 2. The estimated density of dugongs (*Dugong dugon*) in each block in the northern Great Barrier Reef region in Australia in 1985 (Marsh and Saalfeld 1989) plotted against the estimated numbers in the same blocks when the survey was repeated in November 1990 (Marsh et al. 1993). The line illustrates equal densities in the two surveys and is not the fitted regression line represented by the r^2 value.

in this paper. I recommended a resurvey interval of 5 years to the management agencies. Although the expected small population-size changes will probably not be detected in less than a decade, a 10-year interval between surveys could cause unwarranted delays in the management response if numbers were declining rapidly. In addition, personnel changes would make it difficult to guarantee continuity of the methodology if the survey interval was much longer than 5 years.

The greatest weakness of the technique is its dependence on the unvalidated assumption that the proportion of dugongs on the surface is constant. Data are urgently needed to examine this assumption and, if it is incorrect, to develop additional methods of compensating for the variability in the proportion of dugongs that are not visible to observers.

The method also must be modified so that local changes in dugong densities can be monitored, a modification that may be relevant to the needs of surveying manatees in large bays, lagoons, and estuaries. Theoretically, this goal can be achieved by increasing the sampling fraction and the frequency of surveys, which have yet to be empirically confirmed.

Applicability of the Technique to Surveys of Manatees

Lefebvre et al. (1995) provided a corresponding review of techniques and problems with surveys and current methods of estimation of population sizes of Florida manatees. Manatees inhabit rivers or coastal and estuarine waters and seemingly require access to freshwater (Hartman 1979), whereas dugongs are strictly marine and in some areas feed tens of kilometers offshore. Thus the spatial dimensions tend to be more linear in manatee habitats than in dugong habitats. The spatial design of manatee surveys must reflect these differences, and parallel transects probably will be useful only in large bays, estuaries, and lagoons. However, the distinction between perception and availability bias (Marsh and Sinclair 1989a) is relevant to manatee surveys, and the methods developed to overcome these biases in dugong surveys have potential application for surveys of manatees.

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Cited References[2]

Anderson, P. K., and A. Birtles. 1978. Behavior and ecology of the dugong, *Dugong dugon* (Sirenia): observations in Shoalwater and Cleveland Bays, Queensland. Australian Wildlife Research 5:1–23.

Bayliss, P. 1986. Factors affecting aerial surveys of marine fauna, and their relationship to a survey of dugongs in the coastal waters of the Northern Territory. Australian Wildlife Research 13:27–37.

Bayliss, P., and W. J. Freeland. 1989. Seasonal distribution and abundance of dugongs in the Gulf of Carpentaria. Australian Wildlife Research 16:141–149.

*Brownell, R. L., P. K. Anderson, R. P. Owen, and K. Ralls. 1981. The status of dugongs at Palau, an isolated island group. Pages 11–23 *in* H. Marsh, editor. The Dugong: Proceedings of a Seminar/Workshop Held at James Cook University, 8–13 May 1979. Townsville, Australia.

Caughley, G. 1977. Analysis of vertebrate populations. John Wiley and Sons, London. 234 pp.

Caughley, G., and G. C. Grigg. 1981. Surveys of the distribution and density of kangaroos in the pastoral zone in South Australia, and their bearing on the feasibility of aerial survey in large and remote areas. Australian Wildlife Research 8:1–11.

Chambers, M. R., E. Bani, and B. E. T. Barker-Hudson. 1989. The status of the dugong in Vanuatu. South-Pacific Regional Environment Program Topic Review 37. 63 pp.

[2] An asterisk denotes unpublished material.

Forney, K. A., D. A. Hanan, J. Barlow. 1991. Detecting trends in harbor porpoise abundance from aerial surveys using analysis of covariance. Fishery Bulletin 89:367–377.

Gerrodette, T. 1987. A power analysis for detecting trends. Ecology 68:1364–1372.

Hartman, D. S. 1979. Ecology and behavior of the manatee (*Trichechus manatus*) in Florida. Special publication, The American Society of Mammalogists 5:1–154.

Heinsohn, G. E., A. V. Spain, and P. K. Anderson. 1976. Populations of dugongs (Mammalia: Sirenia): aerial survey over the inshore waters of tropical Australia. Biological Conservation 9:21–23.

Hudson, B. E. T. 1980a. Dugongs in Papua New Guinea: west New Britain. Wildlife in Papua New Guinea 80/15:1–22.

Hudson, B. E. T. 1980b. Dugongs in Papua New Guinea: Manus Province. Wildlife in Papua New Guinea 80/16.

Hughes, G. R., and R. Oxley-Oxland. 1971. A survey of dugong (*Dugong dugon*) in and around Antonio Enes, Northern Mozambique. Biological Conservation 3:299–301.

Jolly, G. M. 1969. Sampling methods for aerial census of wildlife populations. East African Agriculture and Forestry Journal 34:46–49.

Lefebvre, L. W., B. B. Ackerman, K. M. Portier, and K. H. Pollock. 1995. Aerial survey as a technique for estimating trends in manatee population size—problems and prospects. Pages 63–74 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

*Ligon, S. H. 1976. Aerial survey of the dugong in Kenya. FAO/UN Advisory Committee on Marine Resources Research, Scientific Consultation on Marine Mammals, Bergen. ACMRR/MM/SC/107. 2 pp.

Ligon, S., and B. E. T. Hudson. 1977. Aerial survey of the dugong, *Dugong dugon*, in Papua New Guinea. Wildlife in Papua New Guinea 77/17:1–5.

Marsh, H., P. W. Channells, G. E. Heinsohn, and J. Morrissey. 1982. Analysis of stomach contents of dugongs from Queensland. Australian Wildlife Research 9:55–67.

*Marsh, H., D. Kwan, and I. Lawler. 1993. The status of dugongs, sea turtles and dolphins in the northern Great Barrier Reef region. Unpublished report to the Great Barrier Reef Marine Park Authority.

Marsh, H., R. I. P. Prince, W. K. Saalfeld, and R. Shepherd. 1994. The distribution and abundance of the dugong in Shark Bay. Wildlife Research. 21:149–161.

Marsh, H., and W. K. Saalfeld. 1988. The distribution and abundance of dugongs in the Torres Strait region. Report to the Australian Fisheries Service, the Great Barrier Reef Marine Park Authority and the Fisheries Management Branch of the Queensland Department of Primary Industries. 25 pp.

Marsh, H., and W. K. Saalfeld. 1989. The distribution and abundance of dugongs in the northern Great Barrier Reef Marine Park. Australian Wildlife Research 16:429–440.

Marsh, H., and W. K. Saalfeld. 1990. The distribution and abundance of dugongs in the Great Barrier Reef region south of Cape Bedford. Australian Wildlife Research 17:511–524.

*Marsh, H., and W. K. Saalfeld. 1991. The status of the dugong in Torres Strait. Pages 187–194 *in* D. Lawrence and T. Cansfield-Smith, editors. Sustainable development for traditional inhabitants of the Torres Strait region. Great Barrier Reef Marine Park Authority Workshop Series 10, Townsville, Australia.

*Marsh, H., W. K. Saalfeld, and A. R. Preen. 1990. The distribution and abundance of dugongs in southern Queensland. Final report to the Queensland Department of Primary Industries, Fisheries Management Branch. 14 pp.

*Marsh, H., W. K. Saalfeld, and R. I. P. Prince. 1991. The status of the dugong in Shark Bay and Exmouth Gulf-Ningaloo. Report to the Western Australian Department of Conservation and Land Management. 17 pp.

Marsh, H., and D. F. Sinclair. 1989a. Correcting for visibility bias in strip transect aerial surveys of aquatic fauna. Journal of Wildlife Management 53:1017–1024.

Marsh, H., and D. F. Sinclair. 1989b. An experimental evaluation of dugong and sea turtle aerial survey techniques. Australian Wildlife Research 16:639–650.

Nishiwaki, M., and H. Marsh. 1985. The dugong. Pages 1–31 *in* S. H. Ridgway and R. J. Harrison, editors. Handbook of marine mammals, volume 3. Academic Press, London.

Norton-Griffiths, M. N. 1978. Counting animals. African Wildlife Leadership Federation Handbook 1. 139 pp.

*Packard, J. M. 1985. Development of manatee aerial survey techniques. Manatee Population Research Report 7. Technical Report 8-7. Florida Cooperative Fish and Wildlife Research Unit. University of Florida, Gainesville. 68 pp.

*Preen, A. R. 1989. Dugongs: technical report 10, volume 1. Meteorology and Environmental Protection Administration, Saudi Arabia. 200 pp.

*Preen, A. R., H. Marsh, and G. E. Heinsohn. 1989. Recommendations for the conservation of the Arus Al Bahr (*Dugong dugon*) in the Kingdom of Saudi Arabia and neighboring countries, Dugongs: technical report 10, volume 2. Meteorology and Environmental Protection Administration, Saudi Arabia. 43 pp.

Rathbun, G. B., R. L. Brownell, K. Ralls, and J. Engbring. 1988. Status of dugongs in waters around Palau. Marine Mammal Science 4:265–270.

*Salm, R., R. C. Petocz, and T. Socharlono. 1982. Survey of coastal areas in Irian Jaya (1982). Report for the Directorate of Nature Conservation, Directorate General of Forestry, Republic of Indonesia.

Smith, A. J., and H. Marsh. 1990. Management of the traditional hunting of dugongs [*Dugong dugon* (Muller 1776)] in the Great Barrier Reef Marine Park. Environmental Management.

Aerial Survey as a Technique for Estimating Trends in Manatee Population Size—Problems and Prospects

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Abstract. Aerial surveys are the primary means of obtaining information on Florida manatee (*Trichechus manatus latirostris*) distribution and abundance. Results have been used to derive minimum estimates of population size; these are composite counts with unknown variance which cannot be statistically compared across surveys or years. The need to establish population estimation techniques with aerial surveys or other methods and to control or correct for the many variables that influence counts was identified as a high priority in the Florida Manatee Recovery Plan. Aerial-survey-based estimates of manatee abundance are biased because of visibility and sampling problems. Visibility bias is the proportion of unobserved manatees in the survey area. Two types of visibility bias were defined by Marsh and Sinclair: perception bias (proportion of the target species present and visible in the survey area but not observed) and availability bias (proportion of the target species present but not visible). A third type of bias in surveys of manatees in aggregation sites in winter is absence bias (proportion not present in the survey area and for which the count is not corrected). Several environmental, behavioral, and procedural factors are related to the degree of survey bias. The current approach to compensating for variability in these factors is *variable survey effort*. The greater the difficulty is in counting manatees because of water turbidity, group size, and other factors, the longer the aircraft circles a particular site. Further investigation is needed of the relations among survey effort, environmental variables, manatee behavior, and counts. Research is needed to improve survey design and technique and to reduce survey bias.

Key words: Aerial survey, availability, bias, population estimate, Florida manatees, trend, visibility.

The Florida manatee (*Trichechus manatus latirostris*) is a subspecies of the West Indian manatee (*T. manatus*), which also occurs in coastal waters and rivers of the Gulf coast of Mexico, the Caribbean coast of Central America, northern South America, and the Greater Antilles. The two other species of manatees are the Amazonian manatee (*T. inunguis*) and the West African manatee (*T. senegalensis*). Manatees, like their closest living relative, the dugong (*Dugong dugon*), are tropical to subtropical in distribution and are classified as threatened or endangered. Florida manatees are near the northern limit of the species' range, yet they probably represent one of the most abundant populations of the West Indian manatee (Lefebvre et al. 1989). Aerial surveys are the primary means of obtaining information on manatee distribution and relative abundance in Florida (Ackerman 1995). Aerial survey results have been used to derive minimum estimates of the manatee population size in the state. These are actually composite counts rather than estimates and are biased by a variety of factors that prevent complete enumeration or unbiased extrapolation of manatees in survey areas. The composite counts also have an unknown variance, thus, the population-size trend (upward or downward) cannot be determined from survey results. This is hardly an optimal situation. Managers must detect downward trends before they become irreversible.

The two ultimate goals in aerial-survey research are the development of indices of abundance that accurately reflect trends and the development of population-size estimation procedures that allow comparisons of manatee numbers at different sites within and across years. The objectives of managers who use the results of aerial surveys are the determination of trends in manatee distribution over time, the estimation of total manatee abundance, and the determination of trends in manatee abundance over time, particularly the detection of any decline in manatee abundance. Researchers and managers generally agree that current aerial survey methods are useful for meeting the first objective but not for the second and third objectives.

The U.S. Fish and Wildlife Service and the U.S. Marine Mammal Commission sponsored research during 1982–85 to improve manatee population indices from aerial surveys (*[2]Packard and Mulholland 1983; *Packard 1985; Packard et al. 1985, 1986, 1989). This research revealed many sources of bias in the surveys and indicated that methods to reduce bias in the visibility of manatees should be explored. The need to establish unbiased population-size estimation techniques with aerial surveys or with other methods was identified as a high priority in the revised Florida Manatee Recovery Plan (*U.S. Fish and Wildlife Service 1989). A Manatee Aerial Survey Technical Meeting was held in December 1987 to review the current state of the art in aerial surveys of manatees and to determine whether models of manatee visibility can be developed, tested, and used to correct for various sources of survey bias. We here report the findings of the 1987 meeting and provide a report of research since that meeting, including insights and recommendations provided by the participants of the February 1992 Technical Workshop on Manatee Population Biology. Our intended audience is technical and non-technical personnel, including managers, interested non-scientists, and researchers. Thus we do not attempt to use detailed statistical terms. Readers who wish to learn more about the different types of survey techniques described here should refer to the

[2] An asterisk denotes unpublished material.

cited literature. Results of recent and ongoing aerial surveys of Florida manatees are described by Ackerman (1995).

Types of Aerial Surveys of Manatees

Packard (*1985) described three aerial survey techniques used to assess manatee distribution and abundance: the extended-area, intensive-search, and unit-recount techniques. The extended-area technique is used to determine manatee distribution in areas surrounding a winter refuge or in broad areas that are distant from a winter refuge and is usually conducted throughout the year to detect changes in seasonal and local distribution over several years. Shane's (1983) surveys of the Indian and Banana rivers are examples of extended-area techniques. Intensive-search and unit-recount techniques are used in winter refuges, when manatees are highly aggregated after the passage of cold fronts.

Intensive-search Technique

Irvine (1982) described the intensive-search technique. Surveyors strive for comprehensive coverage of probable manatee habitat in a well-defined region, usually an aggregation site in winter. Manatees in Florida must move to natural or artificial warm-water sites during winter, and biologists have taken advantage of this situation by timing aerial or ground surveys to coincide with periods when manatees are probably aggregated at warm-water sites. The use of warm-water effluents is triggered by drops in ambient water temperature below about 20° C, and manatees may move hundreds of kilometers to reach these refuges (O'Shea 1988; Reid et al. 1991).

Intensive-search techniques follow a general survey route until manatees are sighted; groups are then circled until repetitive counts are consistent. Survey effort may differ among survey dates, so that variation from differences in effort cannot be distinguished from variation in actual abundance (*Packard 1985). Even when surveys are replicated, variation in replicates has been ignored in favor of using the highest count of the series. Packard (*1985) called the obtained numbers a maximum-count index. No estimate of error is associated with a maximum count.

Since 1977, the Florida Power and Light Company has sponsored intensive-search surveys in winter at five of their power plants and at several other warm-water aggregation sites (Fig. 1; *Rose and McCutcheon 1980; *Raymond 1981; *McGehee 1982; Reynolds and Wilcox 1985, 1986; Reynolds *1989, *1990, *1991). Biologists with the Sirenia Project and with the Chassahowitzka National Wildlife Refuge have conducted aerial surveys in winter of the aggregated manatees in Kings Bay and in the Crystal River since 1978 and in the Homosassa River since 1983 (Fig. 1).

Unit-recount Technique

The unit-recount technique was the first attempt to design aerial surveys with standardization, replication, and stratification. The study area is divided into survey units and stratified so that survey effort is consistent among units in each stratum. The primary stratum includes warmer waters (e.g., thermal plumes from power plants) where manatees aggregate during cold periods and receives the greatest survey effort. Manatees are counted five times in primary units and at least once in secondary and tertiary units during each survey (*Packard 1985).

Packard (*1985) and Packard et al. (1986) developed the unit-recount technique to monitor annual trends in manatee abundance at specific winter refuges. Packard (*1985) envisioned the development of standardized unit-recount procedures at six major aggregation sites: Crystal and Homosassa rivers, Tampa Bay, and Fort Myers on the Gulf Coast of Florida; Indian River, Riviera Beach, and Port Everglades on the Atlantic Coast (Fig. 1).

The unit-recount technique was developed in Fort Myers during 1984–85 (Packard et al. 1986), and one of the indices obtained with this method, the sight-resight index, was used again in Fort Myers during the following winter (Packard et al. 1989). However, the sight-resight index has not been used by other survey biologists, and the unit-recount technique has only been tested at one other winter refuge, the Crystal and Homosassa rivers (Lefebvre and Kochman 1991).

Statewide Technique

The first statewide attempt to count manatees by aerial surveys was made in summer 1973 during a 6-week period and resulted in an estimate of 750–850 manatees (Table 1; *Hartman 1974). Hartman was also the first biologist to attempt correction of raw counts based on his best guess that 90% of the manatees in clear water, 50% of those in moderately turbid water, and 10% of those in highly turbid water are visible from the air. He did not provide details of how these correction factors were obtained. Irvine and Campbell's 1976 count in winter (during a 6-day period) of 738 manatees is uncorrected (Table 1), but these researchers assumed that they undercounted and guessed that the manatee population size was between 800 and 1,000 (Irvine and Campbell 1978). The statewide minimum estimate was updated in 1985 to 1200 based on a composite of surveys of manatees in aggregation sites in winter and other data (O'Shea 1988).

The statewide synoptic technique, coordinated by the Florida Marine Research Institute, Florida Department of Environmental Protection, is a marathon event that combines the methods of the intensive-search and extended-area techniques. Three synoptic surveys have been conducted

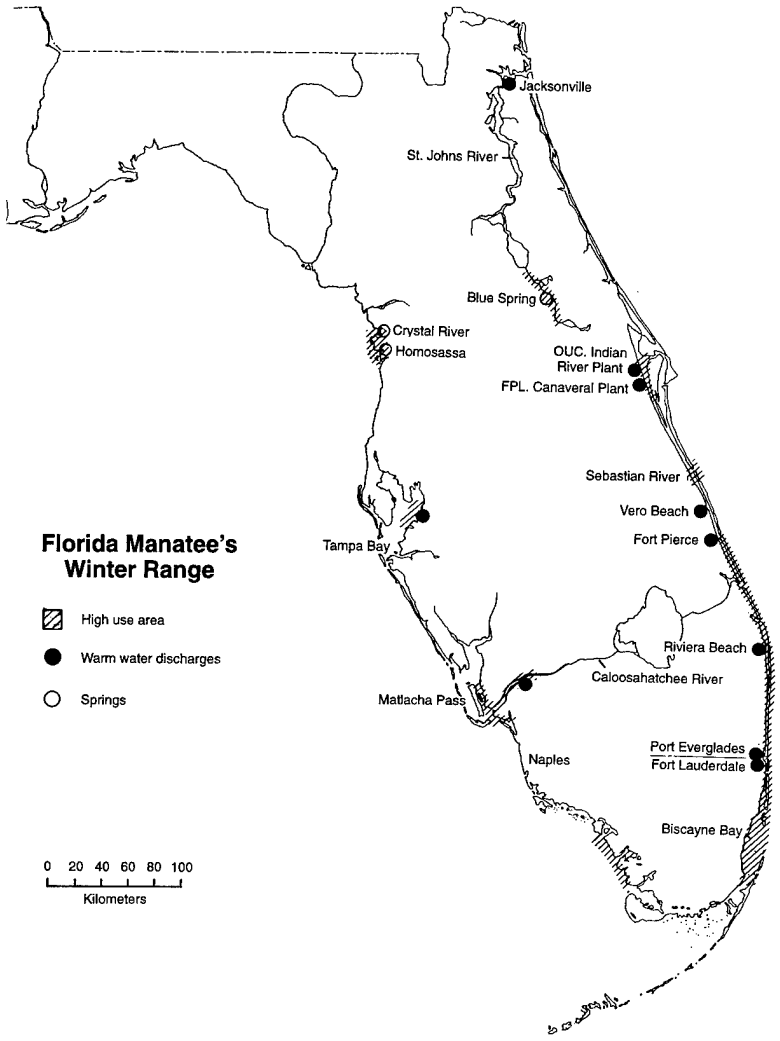


Fig. 1. Important warm water aggregation sites and winter range of the Florida manatee (*Trichechus manatus latirostris*). Aerial surveys are conducted every year over the Crystal and Homosassa rivers and over several coastal power plants. Counts on the ground of manatees at Blue Spring are obtained each winter.

Table 1. Statewide minimum estimates of Florida manatee (*Trichechus manatus latirostris*) abundance based on aerial surveys conducted between 1973 and 1992. Sources of data are shown on the right.

Minimum estimate	Source
750–850	Hartman (1974)
738	Irvine and Campbell (1978)
800–1,000	*Brownell et al. (1981; no new data)
1,200	FP&L[a], FDNR[b], and USFWS[c] surveys (1985)
1,268	FDNR statewide survey, 23–24 January 1991
1,465	FDNR statewide survey, 17–18 February 1991
1,856	FDNR statewide survey, 17–18 January 1992

[a] FP&L = Florida Power and Light Company.
[b] FDNR = Florida Department of Natural Resources.
[c] USFWS = U.S. Fish and Wildlife Service.

through January 1992, two in 1991 and one in 1992. Ackerman (1995) described the objectives and methods of agencies who made the surveys, and provided the results.

Although there is considerable doubt that the counts (Table 1) represent the actual population-size trend, manatee biologists probably agree with Eberhardt's (*1982) conclusion that a substantial fraction of the population is represented in maximum aerial counts of manatees at power plants and warm-water springs. The aggregation at Blue Spring on the St. Johns River (Fig. 1) cannot be surveyed by air because of overhanging branches; however, the relatively small number of manatees that use this site (<90) and the high proportion of distinctly scarred individuals make direct enumeration by ground observation possible. Although surveys have also been conducted at many sites in Florida in non-winter seasons (Shane 1983; Powell and

Rathbun 1984; Kinnaird 1985), the relative effectiveness of aerial surveys in winter or in other seasons for estimating abundance or detecting trends is unknown. At the 1987 Manatee Aerial Survey Technical Meeting, the participants assumed that aerial surveys at aggregation sites in winter would continue to be the primary focus of research, although much of what the participants discussed could also apply to other sites and seasons.

Eberhardt (*1982) noted that an improved size estimate of manatee populations would lead to some confusion and controversy because reported abundance could increase over the years, whereas actual numbers may be decreasing. For example, although recent minimum estimates of manatee abundance were not improved statistically, survey coverage of important manatee wintering sites undoubtedly improved, leading to an apparent increase in counts. Furthermore, even if survey methods are improved so that more accurate, statistically valid size estimates of manatee populations can be made, a statistical detection of a decline may never be possible because of the relatively small population size in a survey region (Taylor and Gerrodette 1993). Estimates with a precision of 12% at best were obtained with the fixed-width transect technique in surveys of dugongs; for example, detection of a 5%/year decline in dugong abundance to a level where only 63% of the population remained would require almost a decade (Marsh 1995).

Survey Bias

Types of Bias

The problems with aerial-survey sampling of manatee population abundance are caused by biases in count-based estimates. Bias is the difference between the estimated value and the true value of a parameter (in this case, population size). Unbiased estimators of population size do not exist in most situations (not even of humans). Unbiased estimates are difficult to obtain because of problems with unequal visibility (also called observability) and sampling. A count-based statistic, C, is related to the true population size, N, by a proportionality constant, β:

$$\hat{N} = C/\beta \quad (1)$$

where β is the proportion of the population represented by the count or the probability that a given manatee will be seen and counted (Lancia et al. 1994).

The closer the surveyor can get physically to the individuals that are counted, the smaller the bias in the estimator. Thus, aerial sampling, which keeps the observer at a distance from individuals in the population, tends to result in biased estimators. The fact that manatees are not always at the surface or visible when submerged obviously compounds the problem. Two types of visibility bias in dugong and sea turtle surveys were defined by Marsh and Sinclair (1989; Table 2). *Perception bias* occurs when a manatee group (of one or more individuals) is present and visible in the survey area but is missed by the observer(s). *Availability bias* is the proportion of manatees that is present but not visible in the survey area. Perception bias is the least problematic source of bias; it can be tested and corrected by using at least 2 observers/survey (Marsh and Sinclair 1989). Availability bias depends on location, environmental conditions, and manatee behavior and is the source of bias that is most difficult to control.

Another major source of bias in many wildlife surveys is the necessity for less-than-complete coverage of the area of interest (Lancia et al. 1994). Typically, sample areas are randomly selected, and the wildlife in a fraction, α, of the total area of interest is censused. This approach leads to the estimator:

$$\hat{N} = \hat{N}'/\alpha \quad (2)$$

where α is the proportion of the total coveredf area, $\hat{N}'$ is the count for the covered area, and $\hat{N}$ is the estimate for the

Table 2. Types of bias that affect aerial surveys of Florida manatees (*Trichechus manatus latirostris*).

Visibility bias[a] (= sightability or observability bias): Proportion of the target species within the survey area that is not observed (Gasaway et al. 1985; Packard et al. 1985; Pollock and Kendall 1987; Samuel et al. 1987; Lancia et al. 1994).

- Perception bias (= observer bias): Proportion of groups of the target species that is visible in the transect but is not observed (Marsh and Sinclair 1989).
- Availability bias: Proportion of groups of the target species that is present on the transect but not visible (Marsh and Sinclair 1989).

Sampling bias: Proportion of entire area of interest in which the survey actually occurs (Lancia et al. 1994).

- Absence bias: Proportion of the target species that is not present in the survey area and for which the count is not corrected (this paper).

[a] Authors who used these terms are listed after each definition.

total area. Although for many species the sampling fraction can be determined with reasonable accuracy, manatees present a greater challenge because of the many types of water bodies they inhabit—from residential canals to large bays—and the strong seasonal pattern of their movements and habitat requirements. Most manatee biologists tend to assume that their counts represent complete coverage of the area in which the survey takes place and do not attempt to estimate a sampling fraction. However, even the statewide synoptic manatee surveys do not cover all potential manatee habitat.

The statewide synoptic survey is conducted immediately after cold fronts to minimize bias caused by absence of manatees from the sample areas. Absence bias is the proportion of manatees that are not present in the survey area at the time of the survey. Manatees may be in a different warm-water aggregation site or somewhere between different sites. Absence bias affects the expected value of the estimate and is more strongly related to temporal variability than visibility bias. It can be controlled to some extent by timing surveys to coincide with periods of high manatee aggregation and with knowledge of manatee movements. Absence bias is of considerable concern in surveys of manatees in aggregation sites in winter. Because the severity and pattern of winter cold fronts differ across years, the manatee distributions among and between aggregation sites may differ (*Packard 1985). To obtain a statewide estimate, surveys for manatees must take place at all major aggregation sites in a relatively short period to avoid double-counting (counting the same manatees twice in different sites) and when most of the population is clumped at aggregation sites, not dispersed between sites.

Factors That Cause Bias

Several factors are known to relate to the effectiveness of aerial counts of manatees. These factors are in one of three categories: environmental, behavioral, and survey-related. Most of the environmental and behavioral factors influence all three sources of bias (perception, availability, and absence) in manatee counts, making it difficult to sort out what, where, and when bias correction is needed (Table 3). Most survey-related factors, such as height and speed of the plane, time of day, and survey dates, can be controlled by the sampling protocol (Table 3). Some of the environmental factors, such as water temperature, cloud cover, and surface condition can be controlled to some extent by appropriate timing of the survey; however, few of the factors related to manatee behavior can be controlled through survey methods (Table 3). All environmental and behavioral factors of visibility bias can vary considerably across survey sites, and the development of visibility models for manatees in each major aggregation site is essential.

The current method of compensating for variability in environmental conditions and manatee behavior is variable survey effort: the greater the difficulty in counting manatees because of water turbidity or manatee submergence, the longer the pilot is directed by the observer to circle a particular site. This was described as the variable effort recount (VER) method by Lefebvre and Kochman (1991). Because this procedure has not been standardized, differences may be considerable among observers in how long they circle individuals or groups until they are satisfied that they obtained the best (highest) possible count. Moreover, survey effort is not allocated objectively and consistently across surveys; observers decide spontaneously how to allocate effort in each individual survey. Thus, the estimation of the sampling fraction is difficult and differs across surveys. A standardized procedure by which observers evaluate environmental conditions also does not exist, although many observers record a subjective ranking of sea state (Beaufort scale), cloud cover, glare, water clarity, air temperature, wind direction, and wind speed at the start of each survey (Ackerman 1995).

Control of Bias

The problem of bias can be solved with three approaches. The best is the development of a sampling design and estimation procedure that results in unbiased estimates. One attempts to identify sources of bias that can be controlled in the design of the sampling scheme, for example, by replication, stratification, and proper selection of when and where to sample (*Packard 1985). Standardization of survey procedures primarily reduces perception bias (Table 3). A second approach is the estimation of the amount of bias in the estimate and application of correction factors, essentially by combining equations (1) and (2):

$$\hat{N} = C/\alpha\beta \qquad (3)$$

so that bias from problems with visibility and sampling are corrected (Lancia et al. 1994). The difficulties with this approach for manatees are that the degree of bias changes with conditions, potentially requiring a large number of correction factors, and that complete enumeration is rarely, if ever, possible.

A third approach is the calibration of a population index by using ratio estimation or double sampling (Eberhardt and Simmons 1987). This approach is based on the assumption that a relation between an index value and the true population density is known or can be estimated. The index value is usually obtained with lower sampling intensity and therefore is of lower accuracy than the estimate of the true population density.

Table 3. Factors of visibility bias in aerial surveys of Florida manatees (*Trichechus manatus latirostris*).

Factors	Perception bias	Availability bias	Absence bias	Controllable with sampling protocol
Environmental factors				
Water turbidity	X	X		
Water depth	X	X		
Distribution of food resources		X	X	
Background of bottom	X	X		
Water temperature		X	X	X
Cloud cover/light	X	X		X
Surface conditions	X	X		X
Tides		X	X	X
Behavioral factors				
Group size	X	X		
Propensity to aggregate	X	X		X
Surfacing/diving patterns	X	X		
Diurnal activities	X	X	X	
Local spatial movements	X	X		
Seasonal spatial movements			X	X
Size (age, sex)	X	X	X	
Response to disturbance	X	X	X	
Survey related factors				
Number of observers				X
Experience of observers/pilot				X
Height of plane				X
Speed of plane				X
Time of day		X		X
Length of flight				X
Survey dates			X	X
Number of surveys			X	X
Flight path	X		X	X

Manatee population sizes are generally believed to be underestimated from aerial-survey counts (*Hartman 1974; *Eberhardt 1982; *Packard 1985), largely because of availability bias. As a result, survey effort has been geared to maximize counts rather than to standardize counts. However, maximum counts of unknown accuracy are inferior to an index that accurately portrays the population-size trend. More attention should be paid to the identification of optimal survey conditions that minimize visibility bias and to the development of survey protocols that incorporate information on environmental conditions. The geographic (aggregation sites versus non-aggregation sites) and temporal (winter versus warm seasons) stratification of survey effort should be designed to optimize site-specific conditions.

Perception Bias

Counts from two independent observers can be used in a Petersen estimate (Seber 1982; Pollock and Kendall 1987; Marsh and Sinclair 1989) to determine observer variation and to estimate the population size of individuals with non-zero detection probabilities. The differences among observers in the designation of calves and manatee activity should also be established.

Tests of different types of flight paths should be conducted. Results obtained by the variable effort recount method could be compared with those obtained in simultaneous surveys in which the number and location of circles are fixed and with surveys with straight flight lines (no circling). Straight flight lines provide information on the error in sighting of groups, whereas tests of circling effort provide information on the error of counting individuals. A stopping rule could be developed, so that observers can standardize their circling efforts. Variance component models can be developed for repeated, fixed-effort surveys to determine the most important factors of variability in counts, such as survey dates, cold fronts, and survey units (Packard et al. 1989, Lefebvre and Kochman 1991).

Availability Bias

The effect of environmental and behavioral factors on counts of manatees can be tested by double-sampling strategies, i.e., from counts on the ground or from a boat, radiotelemetry, and counts from airships conducted simultaneously with routine aerial surveys (Ackerman 1995). The detection probability of manatees can be estimated by the ratio of aerial survey counts to counts on the ground, counts from a boat, or counts from an airship or by the proportion of radio-tagged manatees seen from the air to all tagged manatees in the survey area. Problems with the use of radio-tagged manatees for double-sampling experiments are that the radio tags are variably visible, which differs from the tagged manatee's detection probability (Packard et al. 1989; Ackerman 1995) and that an adequate sample of tagged manatees is probable only in winter when the distribution of the manatees is highly clumped. This results in uncertainty of whether the tagged manatee was actually sighted; one may simply know that the tag belongs to one of the members of a group. In a strict statistical sense, estimation of availability bias is dependent on the ability to estimate the true population size by an alternative procedure. If the estimate from the alternative procedure is consistently biased with respect to the survey estimate or count, it still may provide information about the population-size trend.

The use of airships (Ackerman 1995) or some other stationary observation platform to obtain close-to-exact counts of manatees may be useful for developing models of detection probabilities. This approach requires measuring (or ranking) environmental and behavioral factors at various sites (or at the same site on different dates) and determining proportions of manatees not seen during routine surveys. Resultant models of detection probability based on the most influential factors may be constructed by regression techniques (Gasaway et al. 1985; Samuel et al. 1987). Environmental (e.g., depth, turbidity, and temperature) and behavioral (e.g., resting, feeding) factors are treated as covariates that are tied to strata or sighted groups. A theoretical example of the relation among survey effort, water clarity, and percentage of present manatees that are seen (Fig. 2) illustrates how information about an environmental variable (water clarity) allows correction of manatee counts if effort was measured or standardized. Correction factors may also be based on direct observation of tagged individuals from an airship to determine the proportion of timed intervals that individuals are visible, given different environmental and behavioral factors. Other new technologies should be explored, such as time-depth recorders and infrared multispectral photography, that may be useful for obtaining finer measurements of behavioral and environmental factors.

Although Packard et al. (1986) did not specifically identify availability bias as a type of visibility bias, their sight-resight index was intended for the correction of short-term

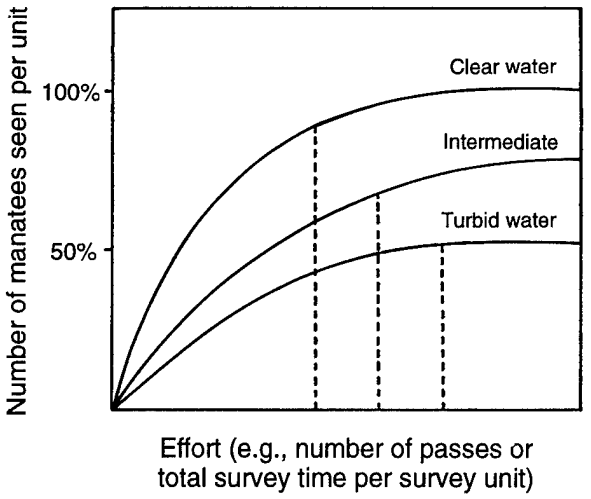


Fig. 2. Theoretical relation of aerial survey effort with counts of Florida manatees (*Trichechus manatus latirostris*) in clear, intermediately clear, and turbid water. Establishing such relations at important aggregation sites or in different survey strata may allow a determination of minimum effort for obtaining accurate counts or of correction factors if conditions do not permit accurate counts.

changes in visibility that result from the appearance and disappearance of manatees because of obstructions to viewing (what we define as availability bias). Lefebvre and Kochman (1991) rejected use of the sight-resight index (based on capture-recapture methods) for this purpose because of problems with the accurate re-identification of individual manatees in successive passes over a survey unit and because manatees in aggregation sites tend to be captured (resighted) in groups (i.e., their capture probabilities are not independent).

Absence Bias

To quantify absence bias, regions should be identified that encompass aggregations in winter with little short-term probability of exchange of individuals with other such regions. On the Atlantic Coast, manatees aggregate in three major areas or regions during cold periods in winter: Blue Spring, the upper Indian River, and Riviera Beach to Port Everglades. On the Gulf Coast of Florida, four regions can be distinguished: Crystal River, Tampa Bay, Fort Myers, and Naples to the Everglades. During cold periods in winter, most of Florida's manatee population may reasonably be expected to be in these regions and absence bias is therefore minimized. (A relatively small number of manatees use industrial effluents in northeastern Florida and in southeastern Georgia. These regions could be added to the statewide survey, depending on the survey objectives and funding in a given year.) The survey regions should be stratified so that survey effort is proportional to anticipated or known manatee densities and distribution. Survey methods can differ

among strata, e.g., multiple circling in small units in high-density strata and single passes or transects in larger units of low-density strata. The sampling fraction in each stratum should be determined.

Packard and Mulholland (*1983) were optimistic that an index of manatee abundance in winter aggregation sites could be statistically compared among years by an analysis of covariance or by some other regression technique. However, they concluded that survey data available to them at the time were not suitable for such a comparison. Also, they were not able to identify a set of conditions that would predict optimal conditions for obtaining maximum counts in each survey site. More recent count data from surveys by the Florida Power and Light Company were analyzed with additional temperature covariates to determine population-size trends after correction for differences in winter severity across years (Garrott et al. 1995).

The potential of obtaining consistent, relatively unbiased estimates of abundance from warm-season surveys should be investigated (Ackerman 1995). Weather and water conditions may be considerably better in some survey regions during the non-winter months, and problems with counting large groups would be avoided. A protocol should be developed for surveys in non-aggregation areas, so that trends in both types of season and regions can be compared over years. However, such surveys should not be attempted unless statistical power analysis suggests that population sizes and precision of the estimates are sufficient to determine trends over a reasonable time period (Gerrodette 1987; Taylor and Gerrodette 1993).

Recommendations

The interaction of numerous factors affects our ability to accurately census or estimate manatee populations with data from aerial surveys (Fig. 3). To determine manatee trends in abundance and, ultimately, to estimate total manatee abundance, several strategies should be employed: development of a protocol for a statewide

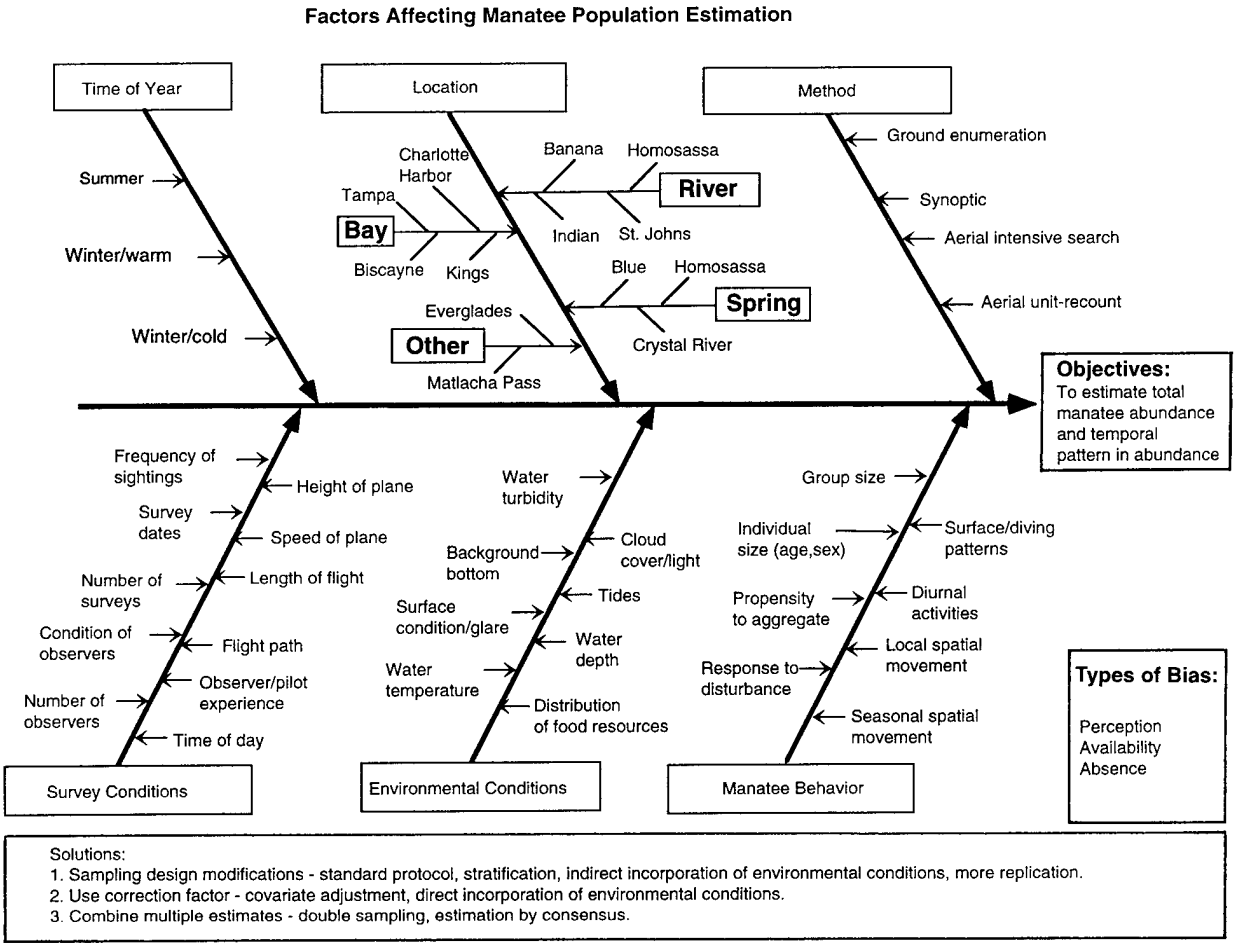


Fig. 3. Interrelation of factors of estimation of population sizes of Florida manatees (*Trichechus manatus latirostris*) based on aerial surveys.

survey of aggregation sites, development of a sampling protocol for surveys during warm seasons, and development of correction factors for biased counts.

Because part of a protocol for a statewide survey is dependent on the results of experiments on bias, these experiments should be initiated as soon as possible. Depending on the results of investigations into the effects of covariates such as water temperature, cloud cover, or glare on counts, some covariates may be removed from the survey; a tolerable range of survey conditions could be established. Availability bias related to manatee behavior and environmental conditions must be measured by direct observation from appropriate platforms or in experiments with double-sampling, so that correction factors can be developed. Perception bias can be determined by using two independent observers. Absence bias can be controlled by identifying regions in which manatees aggregate during cold periods in winter, and stratifying these regions so that survey effort is proportional to manatee density and distribution in the survey areas. After experiments are conducted to determine the best census conditions and other, less-controllable factors are modeled to determine their influence on visibility bias, the final protocol can be developed for a statewide survey of aggregation sites. The final protocol must be clearly defined to allow reasonable comparisons across areas and years and must be easily repeatable from year to year. Alternatively, detection probabilities can be estimated at specific aggregation sites every year by developing sightability models for each site.

A protocol should also be developed for surveys in warm seasons, to provide additional information on the manatee population-size trend. In the early stages of protocol development, resulting estimates should be analyzed to determine whether trends can be detected, and, if so, the number of surveys per year and total number of years required to detect trends with the degree of confidence required to permit timely response by managers.

A multi-agency, aerial-survey working group should be established to ensure that research needs of survey design, survey technique, and correction for survey bias are logically and efficiently addressed (Table 4). This group should meet periodically to review the progress of aerial-survey research and must keep abreast of progress in other areas of manatee population research, particularly mortality patterns (Ackerman et al. 1995) and the use of capture-recapture data from recognizable manatees to estimate survival rates (O'Shea and Langtimm 1995). The use of survival rates to establish trends and the potential development of population-size estimation procedures with capture-recapture data may ultimately replace the aerial surveys for all but manatee distribution information.

Acknowledgments

We are grateful to T. J. O'Shea for encouragement and for providing this opportunity to review the development and current status of manatee aerial-survey methods. We thank P. M. Rose and the Florida Department of Natural Resources for cooperation and support of the 1987 Manatee Aerial Survey Technical Meeting. Participants in the 1987 Manatee Aerial Survey Technical Meeting and the 1992 Technical Workshop on Manatee Population Biology contributed many of the ideas presented in this paper: D. P. DeMaster, J. D. Nichols, M. A. O'Connell, J. E. Reynolds, III, M. D. Samuel, and B. L. Weigle. I. E. Beeler and R. Muller also provided useful advice. J. Vorhees skillfully coordinated the 1987 Manatee Aerial Survey Technical Meeting. H. Marsh reviewed an early draft of the manuscript and made many

Table 4. Areas of survey design, technique, and bias correction that must be further researched to improve aerial surveys of Florida manatees (*Trichechus manatus latirostris*). Establishment of a multi-agency aerial survey group is an important first step of setting research priorities, assigning responsibilities for tasks to organizations, and evaluating progress.

Survey design	Survey technique	Survey bias
Stratification by habitat type (bays, lagoons, rivers, canals, complex coastlines)	Tandem observers	Test assumption that absence bias can be controlled by timing of surveys
Stratification by habitat use (primary and secondary units)	Recorders	Double sampling experiments (radio tags, airships)
Replication (temporal and spatial)	GPS	Correction factors
Total counts versus sampling (aggregation site versus non-aggregation site)	Photography	Models
	Proportion of calves	Determine sampling fraction
	Environmental data	

helpful suggestions. J. P. Reid provided helpful information on manatee distribution in winter.

Cited References[3]

Ackerman, B. B. 1995. Aerial surveys of manatees: a summary and progress report. Pages 13–33 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Ackerman, B. B., S. D. Wright, R. K. Bonde, D. K. Odell, and D. J. Banowetz. 1995. Trends and patterns in mortality of manatees in Florida, 1974–1992. Pages 223–258 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

*Brownell, R. L., Jr., K. Ralls, and R. Reeves. 1981. Report of the West Indian manatee workshop. Pages 3–16 *in* *R. L. Brownell, Jr. and K. Ralls, editors. The West Indian manatee in Florida. Proceedings of a workshop held in Orlando, Fla., 27–29 March 1978. Florida Department of Natural Resources, Tallahassee. 154 pp.

*Eberhardt, L. L. 1982. Censusing manatees. Manatee Population Research Report Number 1, Technical Report 81, Florida Cooperative Fish and Wildlife Research Unit, University of Florida, Gainesville. 18 pp.

Eberhardt, L. L., and M. A. Simmons. 1987. Calibrating population indices by double sampling. Journal of Wildlife Management 51:665–675.

Garrott, R. A., B. B. Ackerman, J. R. Cary, D. M. Heisey, J. E. Reynolds, III, and J. R. Wilcox. 1995. Assessment of trends in sizes of mantaee populations at several Florida aggregation sites. Pages 34–55 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Gasaway, W. C., S. D. Dubois, and S. J. Harbo. 1985. Biases in aerial transect surveys for moose during May and June. Journal of Wildlife Management 49:777–784.

Gerrodette, T. 1987. A power analysis for detecting trends. Ecology 68:1364–1372.

*Hartman, D. S. 1974. Distribution, status, and conservation of the manatee in the United States. Document Number PB 81-140725, National Technical Information Service, Springfield, Va. 246 pp.

Irvine, A. B. 1982. West Indian manatee. Pages 241–242 *in* D. E. Davis, editor. CRC Handbook of Census Methods for Terrestrial Vertebrates. CRC Press, Inc., Boca Raton, Fla. 397 pp.

Irvine, A. B., and H. W. Campbell. 1978. Aerial census of the West Indian manatee, *Trichechus manatus*, in the southeastern United States. Journal of Mammalogy 59(3):613–617.

Kinnaird, M. F. 1985. Aerial census of manatees in northeastern Florida. Biological Conservation 32:59–79.

Lancia, R. A., J. D. Nichols, and K. H. Pollock. 1994. Estimating the number of animals in wildlife populations. Pages 215–253 *in* T. A. Bookhout, editor. Research and management techniques for wildlife and habitat. The Wildlife Society, Bethesda, Md. 740 pp.

Lefebvre, L. W., and H. I. Kochman. 1991. An evaluation of aerial survey replicate count methodology to determine trends in manatee abundance. Wildlife Society Bulletin 19:298–309.

Lefebvre, L. W., T. J. O'Shea, G. B. Rathbun, and R. C. Best. 1989. Distribution, status, and biogeography of the West Indian manatee. Pages 567–610 *in* C. A. Woods, editor. Biogeography of the West Indies past, present, and future. Sandhill Crane Press, Inc., Gainesville, Fla. 878 pp.

Marsh, H. 1995. Fixed-width aerial transects for determining dugong population sizes and distribution patterns. Pages 56–62 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Marsh, H., and D. F. Sinclair. 1989. Correcting for visibility bias in strip transect aerial surveys of aquatic fauna. Journal of Wildlife Management 53:1017–1024.

*McGehee, M. A. 1982. Manatees (*Trichechus manatus*): abundance and distribution in and around several Florida power plant effluents during the winter of 1981–1982. Florida Power and Light Company, Contract Report 31534-86419. 67 pp.

O'Shea, T. J. 1988. The past, present, and future of manatees in the southeastern United States: realities, misunderstandings, and enigmas. Pages 184–204 *in* R. R. Odom, K. A. Riddleberger, and J. C. Ozier, editors. Proceedings of the Third Southeastern Nongame and Endangered Wildlife Symposium. Georgia Department of Natural Resources, Game and Fish Division, Social Circle. 253 pp.

O'Shea, T. J., and C. A. Langtimm. 1995. Estimation of survival of adult Florida manatees in the Crystal River, at Blue Spring, and on the Atlantic Coast. Pages 194–222 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

*Packard, J. M. 1985. Development of manatee aerial survey techniques. Manatee Population Research Report 7, Technical Report 8-7. Florida Cooperative Fish and Wildlife Research Unit, University of Florida, Gainesville. 68 pp.

*Packard, J. M., and R. Mulholland. 1983. Analysis of manatee aerial surveys: A compilation and preliminary analysis of winter aerial surveys conducted in Florida between 1977 and 1982. Manatee Population Research Report 2, Technical Report 8-2. Florida Cooperative Fish and Wildlife Research Unit, University of Florida, Gainesville. 119 pp.

Packard, J. M., R. C. Summers, and L. B. Barnes. 1985. Variation of visibility bias during aerial surveys of manatees. Journal of Wildlife Management 49:347–351.

Packard, J. M., D. B. Siniff, and J. A. Cornell. 1986. Use of replicate counts to improve indices of trends in manatee abundance. Wildlife Society Bulletin 14:265–275.

Packard, J. M., R. K. Frohlich, J. E. Reynolds, III, and J. R. Wilcox. 1989. Manatee response to interruption of a thermal effluent. Journal of Wildlife Management 53:692–700.

Pollock, K. H., and W. L. Kendall. 1987. Visibility bias in aerial surveys: a review of estimation procedures. Journal of Wildlife Management 51:502–509.

[3] An asterisk denotes unpublished material.

Powell, J. A., and G. B. Rathbun. 1984. Distribution and abundance of manatees along the northern coast of the Gulf of Mexico. Northeast Gulf Science 7:1–28.

*Raymond, P. W. 1981. Manatees (*Trichechus manatus*): abundance and distribution in and around several Florida power plant effluents. Florida Power and Light Company, Contract Report 31534-82511. 62 pp.

Reid, J. P., G. B. Rathbun, and J. R. Wilcox. 1991. Distribution patterns of individually identifiable West Indian manatees (*Trichechus manatus*) in Florida. Marine Mammal Science 7:180–190.

*Reynolds, J. E., III. 1989. Distribution and abundance of the West Indian manatee (*Trichechus manatus*) around selected Florida power plants following winter cold fronts: 1988–1989. Florida Power and Light Company, Contract Report B87806-00039. 48 pp.

*Reynolds, J. E., III. 1990. Distribution and abundance of the West Indian manatee (*Trichechus manatus*) around selected Florida power plants following winter cold fronts: 1989–1990. Florida Power and Light Company, Contract Report B89806-00264. 41 pp.

*Reynolds, J. E., III. 1991. Distribution and abundance of the West Indian manatee (*Trichechus manatus*) around selected Florida power plants following winter cold fronts: 1990–1991. Florida Power and Light Company, Contract Report B89806-00264. 39 pp.

Reynolds, J. E., III, and J. R. Wilcox. 1985. Abundance of West Indian manatees (*Trichechus manatus*) around selected Florida power plants following winter cold fronts, 1982–1983. Bulletin of Marine Science 36:413–422.

Reynolds, J. E., III, and J. R. Wilcox. 1986. Distribution and abundance of the West Indian manatee, *Trichechus manatus*, around selected Florida power plants following winter cold fronts: 1984–1985. Biological Conservation 38:103–113.

*Rose, P. M., and S. P. McCutcheon. 1980. Manatees (*Trichechus manatus*): abundance and distribution in and around several Florida power plant effluents. Florida Power and Light Company, Contract Report 31534-86626. 128 pp.

Samuel, M. D., E. O. Garton, M. W. Schlegel, and R. C. Carson. 1987. Visibility bias during aerial surveys of elk in north-central Idaho. Journal of Wildlife Management 51:622–630.

Seber, G. A. F. 1982. The estimation of animal abundance. Charles Griffin, London. 624 pp.

Shane, S. H. 1983. Abundance, distribution, and movements of manatees (*Trichechus manatus*) in Brevard County, Florida. Bulletin of Marine Science 33:1–9.

Taylor, B. L., and T. Gerrodette. 1993. The uses of statistical power in conservation biology: the vaquita and northern spotted owl. Conservation Biology 7:489–500.

*U.S. Fish and Wildlife Service. 1989. Florida manatee (*Trichechus manatus latirostris*) recovery plan. Prepared by the Florida Manatee Recovery Team for the U.S. Fish and Wildlife Service, Atlanta, Ga. 98 pp.

The Life History, Pattern of Breeding, and Population Dynamics of the Dugong

by

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Abstract. The literature and recent unpublished data on the breeding cycle and life history of the dugong (*Dugong dugon*) are summarized. The studies were based on the analysis of carcasses from animals accidentally drowned in shark nets or killed by native hunters in northern Australia and in Papua New Guinea. Age was estimated by counting the dentinal growth-layer groups in the tusks, the deposition rate deduced from the seasonal pattern of growth-layer group deposition. The maximum estimated age was 73 years, and the minimum pre-reproductive period was 9 or 10 years in both sexes. The pre-reproductive period was variable and ranged to 15–17 years in some animals. Neither males nor females were continuously in breeding condition and breeding was diffusely seasonal. A single calf was usually born after an estimated gestation period of about 13 months. Calves suckled for at least 18 months. Estimates of mean interbirth interval based on pregnancy rates and placental scar counts ranged from 3 to 7 years in various samples. Variation between years was marked in the proportions of breeding males and females. Reliable data on age-specific fecundity or mortality are not available. Population simulations indicated that, with even the most optimistic combination of life history parameters and a low rate of mortality, a dugong population probably does not increase at more than about 5% or 6%/year.

Key words: Dugong, *Dugong dugon*, life history, reproduction, age determination, population dynamics.

The life history of the dugong (*Dugong dugon*) has been studied in northern Australia and in southern Papua New Guinea as part of the development of conservation and management of this species. However, data from known-age animals are not available. No longitudinal information comparable to that about wild Florida manatees (*Trichechus manatus latirostris*; O'Shea and Hartley 1995; O'Shea and Langtimm 1995; Rathbun et al. 1995) is available about dugongs. In addition, unlike manatees, dugongs have rarely been maintained in captivity and have never bred in captivity. All information has been obtained from the analysis of carcasses of animals that were either killed in native fisheries (Bertram and Bertram 1973; Nietschmann 1984; Hudson 1986) or opportunistically collected when animals incidentally drowned in shark nets set for the protection of bathers (Heinsohn 1972).

In this paper, I summarize the current understanding of dugong life history and breeding ecology to provide a comparative perspective of these features of manatee biology. My assessment is based on previously published accounts (Marsh 1980, 1986; Marsh et al. 1984a, 1984b, 1984c) and my emphasis is on aspects of dugong life history that are relevant to the parallel research on manatees in Florida.

Life-history Parameters

Sex Ratio

Dugongs from a native fishery at Numbulwar (Northern Territory, Australia) sampled by Bertram and Bertram (1973) had a preponderance of females (88:143). In contrast, a sex ratio close to parity is indicated by other large samples from native fisheries (267:237, Western Islands of the Torres Strait, Australia, Nietschmann 1984; 218:235, Daru near the Papua New Guinean coast in the central Torres Strait, Hudson 1986) and from incidentally drowned animals in shark

nets at Townsville, northern Queensland, Australia (44:45, Marsh et al. 1984c).

Maximum Age

The absolute ages of 75 (Mitchell 1976) and 160 (Marsh 1980; H. Marsh, James Cook University, unpublished data) dugongs from various locations in northern Australia and of 96 dugongs from Daru (H. Marsh and B. Hudson, James Cook University, unpublished data) were estimated. The ages were estimated from the number of dentinal growth-layer groups in the tusks (Fig. 1); the seasonal layer deposition indicates that one growth-layer group is deposited per year (Marsh 1980). Estimated minimum ages (≤34.5 years) are available only of adult male dugongs because their tusks erupt and wear after puberty (Marsh 1980). Some more-than-40-year-old females also have erupted and worn tusks so that their ages are underestimated because of wear. The estimated age of the oldest examined female was 73 years (H. Marsh, James Cook University, unpublished data). However, less than 1.5% of females whose absolute ages were estimated were older than 60 years.

Age at Attainment of Sexual Maturity

Females

Dentinal-layer counts and reproductive organs are available from 47 females from Townsville and Mornington Island (Queensland, Australia) and from 28 females from Daru. These data are appropriate for estimating the range of ages at which sexual maturity occurs but are insufficient for estimating the age at which 50% of the females are mature or for quantifying age-related changes in fecundity.

The ovaries and uteruses of all less-than-8-year-old females were small and undeveloped. Those of two 8-year-old and four 9-year-old animals from Townsville showed some enlargement that suggested approaching maturity; macroscopic follicles were present in the ovaries of two of the animals (Marsh et al. 1984c).

The most accepted definition of sexual maturity in females is that the animal has ovulated at least once. The youngest female with corpora lutea or corpora albicantia in the ovaries was a 9.5-year-old nulliparous female from Townsville. All 10-year-old or older females from Townsville were parous and had one or more placental scars in the uterus (Marsh et al. 1984a, 1984c). However, data from Mornington Island and Daru suggested that the age at which females bear their first calves is variable; three females from Mornington Island were still nulliparous at 15–17 years (Table 1). Two of the animals were sexually mature because their ovaries contained small numbers of corpora lutea or corpora albicantia (Marsh et al. 1984c). One 18-year-old female from Daru had recently had her first calf.

Males

What constitutes sexual maturity in males is complex. Attempts to estimate the age of sexual maturity in male dugongs have been hampered by the asynchronous, discontinuous pattern of male sexual activity (Marsh et al. 1984b); difficulties with distinguishing the testicular histology of pubertal males (those approaching first spermiogenesis) from that of mature males with recrudescent testes (Marsh et al. 1984b); and small sample sizes in the pubertal age range. The data suggested a pre-reproductive

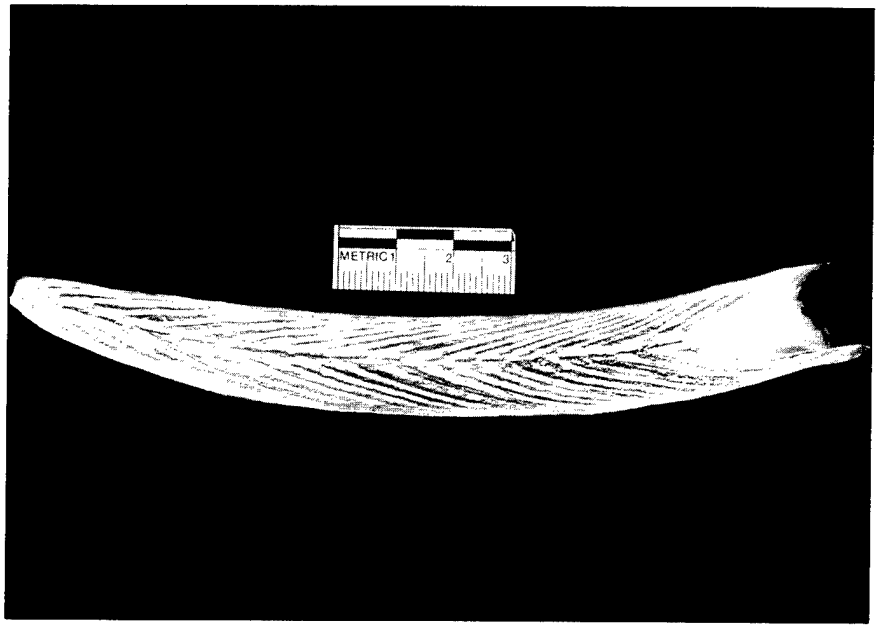


Fig. 1. A longitudinally bisected tusk of a female dugong (*Dugong dugon*) prepared for age determination. One dark band and one light band are laid down each year, indicating that this animal was 21 years old when it died.

Table 1. Pre-reproductive periods of female dugongs (*Dugong dugon*) from various areas.

Location	Youngest female with placental scar	Oldest female without placental scar	Source of data
Townsville	10	9.5	Marsh et al. (1984c)
Mornington Island	14.5	17.5	Marsh et al. (1984c)
Daru	13	12[a]	Marsh (1986)

[a] One 18-year-old female had recently given birth to her first calf.

period similar to that of females. Most male dugongs from Townsville were sexually mature when they were about 9 or 10 years old, and all 12-year-old or older males from Townsville had erupting or erupted tusks. However, some dugongs from Mornington Island and Daru that were as old as 16 years were immature and their tusks had not erupted (Table 2).

Size at Sexual Maturity

Marsh (1980) developed growth curves of male and female dugongs. The range of body lengths of dugongs of a particular age is considerable, and body length as an indicator of age is unsatisfactory except for young animals. Similarly, the size at which dugongs mature sexually is variable of animals of both sexes. The data of Marsh et al. (1984c) suggested that less-than-2.2-m-long male and female dugongs from northern Australia were immature, whereas those longer than 2.5 m were probably mature. Dugongs with body lengths between 2.2 and 2.5 m may be either immature or mature. There is some evidence (Marsh 1980) that the asymptotic body length of females is slightly greater than that of males.

Size at Birth

Nine fetal and nine postnatal dugongs had body lengths between 100 and 130 cm. The data are insufficient for the 50% interpolation method of estimating size at birth recommended by Perrin and Reilly (1984). Accordingly, I estimated the mean birth length as 115 cm from the lengths of the postnatal animals. With this method, size at birth tends to be overestimated (Perrin and Reilly 1984); however, three fetuses were longer than 115 cm.

Gestation Period

I estimated a gestation period of 13.9 months with the method of Huggett and Widdas (1951) and Laws (1959) and data on the body lengths and dates of deaths of 26 fetuses from Daru (Fig. 2). As a result of the small sample size and the diffusely seasonal breeding pattern of the dugong, the 95% confidence interval for this estimate was so imprecise, it was meaningless. However, the estimated mean was in good agreement with the estimated 12–14 month gestation period of captive Florida manatees. (*[1]Odell et al. 1992; Qi Jingfen 1984).

Length of Lactation

Data on length of lactation are sparse, especially because of the ban on taking females with attendant calves in the Daru fishery. A calf of an estimated age of 1.5 years (on the basis of dentinal-layer counts) and its presumed mother who was still lactating were caught in a shark net. This suggested that lactation can last at least 1.5 years (Marsh et al. 1984c), even though dugongs start eating seagrass soon after birth (Marsh et al. 1982). Pregnancy can occur during lactation. I noted one lactating female with a 41-cm-long fetus at necropsy (Marsh 1989).

Litter Size

One fetus was found in each of the 34 pregnant females that scientists examined in recent years. Reports of the occasional occurrence of twin fetuses (Norris 1960; Jarman 1966; Thomas 1966; Bertram and Bertram 1968) are

[1] An asterisk denotes unpublished material.

Table 2. Pre-reproductive periods of male dugongs (*Dugong dugon*) from various areas.

Location	Youngest male with mature testes	Oldest male with immature testes	Oldest male with unerupted tusks	Source of data
Townsville	9	6	10.5	Marsh et al. (1984c)
Mornington Island	15	15.5	15.5	Marsh et al. (1984c)
Daru	11	16	18	Marsh (1986)

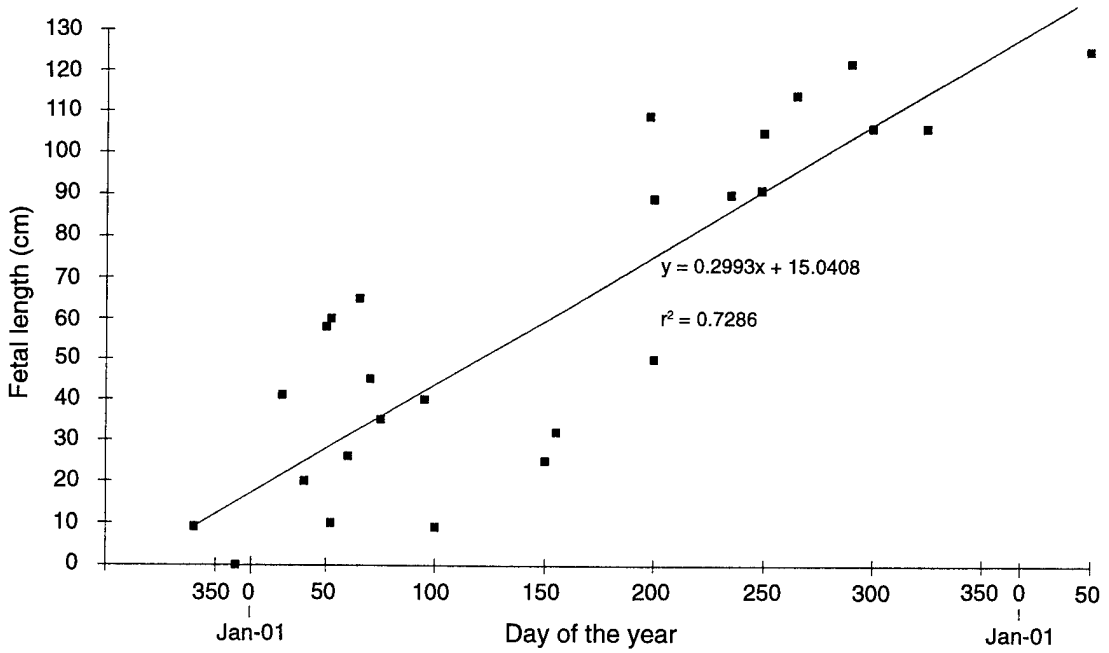


Fig. 2. The relation between fetal length and day of the year (January 1 is day 1) in dugongs (*Dugong dugon*) from Daru in the Torres Strait. Data from H. Marsh and B. Hudson (James Cook University, unpublished data).

vague and unsubstantiated. The mean litter size must be close to one as in Florida manatees whose twin calves account for a low proportion of the total births (Marmontel 1995; O'Shea and Hartley 1995; Rathbun et al. 1995).

Pregnancy Rate and Interbirth Interval

The annual pregnancy rate is usually estimated as the percentage of mature pregnant females (including those pregnant and lactating) divided by the length of gestation in years (Perrin and Reilly 1984). The interbirth interval is the reciprocal of the annual pregnancy rate. Calculation of the annual pregnancy rate requires accurate knowledge of the length of the gestation period. Accordingly, I used the apparent pregnancy rate (proportion of pregnant females uncorrected for the length of gestation) in the following discussion and three estimates of the gestation period (12, 13, and 14 months) in the estimates of interbirth intervals based on pregnancy rates.

Apparent pregnancy rates of three series of dugong carcasses are available: 86 mature-sized females from the native fishery at Numbulwar (Bertram and Bertram 1973), 18 mature females from the Townsville shark nets (Marsh et al. 1984c), and 168 mature females from the native fishery in Daru (H. Marsh and B. Hudson, James Cook University, unpublished data). The females from Townsville and Daru were classified as mature by the appearances of their ovaries.

The probability of detecting a pregnancy increases as gestation progresses because of the size of the fetus, and some small embryos may have been overlooked, especially in examinations in the field. Accordingly, I estimated the pregnant proportion based on only confirmed pregnancies (which tends to provide an underestimated pregnancy rate) and on possible pregnancies from females with corpora lutea in their ovaries. This tends to provide an overestimated pregnancy rate because not all corpora lutea are associated with pregnancy (Marsh et al. 1984a). Irrespective of the gestation period used in the model or whether the pregnancy rate was based on confirmed or possible pregnancies, all estimated interbirth intervals are long, ranging from about 3 to 7 years (Table 3). These estimates are generally higher than those of manatees (Marmontel 1995; O'Shea and Hartley 1995; Rathbun et al. 1995; Reid et al. 1995). The biases in the dugong samples on which these estimates are based are unquantified. However, the sample from Daru was probably biased in favor of pregnant females. These were regarded as a delicacy (Hudson 1986), and there was a ban against taking females with young calves (*Hudson 1981). Thus, the estimated pregnancy rates of the Daru sample are probably high.

A maximum of nine placental scars has been counted in the uterus of a dugong (Marsh et al. 1984a). The interbirth interval can also be estimated by regressing the number of placental scars against age of parous dugongs if persistence of the scar is assumed. These estimates also suggested that the interbirth interval was long: 6.6 years in Townsville dugongs and 4 years in Mornington Island

Table 3. Estimates of the interbirth interval of various dugong (*Dugong dugon*) populations based on the annual pregnancy rate and three possible gestation periods of 12, 13, and 14 months. Estimates are based on confirmed pregnancies (a) and all possible pregnancies (b).

Location	Number of mature females	Estimated interbirth interval for three possible gestation periods (± *S.E.*) 12 months	13 months	14 months	Source of data
Numbulwar	86[a]	3.07 ± 0.47[a]	3.32 ± 0.55[a]	3.58 ± 0.62[a]	Bertram and Bertram (1973)
		2.69 ± 0.38[b]	2.91 ± 0.43[b]	3.14 ± 0.49[b]	
Townsville	18	4.50 ± 1.98	4.88 ± 2.26	5.25 ± 2.55	Marsh et al. (1984c)
Daru	168	5.79 ± 0.98[a]	6.28 ± 1.11[a]	6.76 ± 1.25[a]	H. Marsh and B. Hudson (James Cook University, unpublished data)
		4.94 ± 0.76[b]	5.35 ± 0.86[b]	5.76 ± 0.97[b]	

dugongs (Marsh et al. 1984c). The sample sizes on which these estimates are based are too small for meaningful associated confidence intervals. The difference in the mean ages of the dugongs from Townsville with one and two placental scars is also 6.6 years. Placental scars do not persist in manatees and cannot be used to estimate the number of parities (Marmontel 1995).

Evidence from Daru suggested marked temporal fluctuations in the apparent pregnancy rate. Hudson (1986) presented anecdotal evidence that none of the 35 females caught between October 1976 and July 1977 was pregnant. Carcasses were collected during the succeeding 4 years (1978–82). The proportion of mature females that was pregnant increased monotonically from 0.09 to 0.35 during this time (Table 4). The difference between years was significant (Table 4) and was paralleled by a significant increase in the proportion of males with active testes between 1978 and 1981 (Table 5), suggesting that a common factor was affecting female and male reproduction during this period. Anecdotal reports (Johannes and MacFarlane 1991) suggested a major die-back of seagrasses in the Torres Strait in the mid-1970's, and Nietschmann (1984) reported that seagrasses were overgrazed in the Torres Strait during 1976–77. Nietschmann and Nietschmann (1981) observed that wati dangal (lean dugongs with poor-tasting meat) were quite common in the Torres Strait during this period.

Incidence of Breeding

The samples from Townsville (Marsh et al. 1984c) and Daru (H. Marsh and B. Hudson, James Cook University, unpublished data) indicated that neither male nor female dugongs are continuously in breeding condition. The ovaries of non-pregnant females probably contain follicles or corpora lutea in the second half of the year. Sterile cycles seem to be common (Marsh et al. 1984a) and may occur also in Florida manatees (Marmontel 1995, Rathbun et al. 1995).

Mature male dugongs do not continuously produce spermatozoa (Marsh et al. 1984b). Histological examination of the testes of 41 pubertal and mature males from northern Queensland and 141 mature male dugongs from Daru showed that more than half the males in each sample were infertile at the time of sampling. Some of these males had regressed testes (sensu Marsh et al. 1984b), suggesting long-term or permanent sterility (Marsh et al. 1984b). Animals with developed testes (fully spermatogenic or recrudescent testes sensu Marsh et al. 1984c) were a significantly higher proportion of the sample from Daru

Table 4. Differences between years (July 1978–June 1982) in the apparent pregnancy rate of dugongs (*Dugong dugon*) sampled at the Daru fishery in Papua New Guinea. Data from H. Marsh and B. Hudson (James Cook University, unpublished data).

Year[a]	Number of mature females	Apparent pregnancy rate ± *S.E.* Confirmed pregnancies	All possible pregnancies
1978–79	75	0.093 ± 0.034[b]	0.107 ± 0.036[c]
1979–80	47	0.191 ± 0.057[b]	0.255 ± 0.064[c]
1980–81	29	0.241 ± 0.079[b]	0.276 ± 0.083[c]
1981–82	17	0.353 ± 0.116[b]	0.353 ± 0.116[c]

[a] 1 July through 30 June.

[b] Difference between years $G = 8.0001$, 3 df, $P = 0.046$.

[c] Difference between years $G = 8.677$, 3 df, $P = 0.034$.

Table 5. The numbers (%) of mature male dugongs (*Dugong dugon*) with active and inactive testes between February and May and between June and January, sampled at the Daru fishery each year between July and June 1978–1981 (H. Marsh and B. Hudson, James Cook University, Townsville, Australia, unpublished data). Animals with regressed testes were omitted from the table because they may have been permanently sterile (Marsh et al. 1984b).

	February–May		June–January	
Year	Active testes	Inactive testes	Active testes	Inactive testes
1978–79[a]	5 (20)	20 (80)	12 (71)	5 (29)
1979–80	7 (37)	12 (63)	25 (83)	5 (17)
1980–81	6 (46)	7 (54)	14 (93)	1 (7)

[a] The effects of year, season, and testicular activity were not independent ($G_7 = 42.92$, $P < 0.001$); the effect of year was independent of season and of testicular activity ($G_5 = 10.07$, $P = 0.074$); testicular activity was dependent on season ($G_1 = 32.86$, $P < 0.001$).

between June and January than between February and May (Table 5). This seasonal pattern of gonadal activity overlaps that in females. Spermatogenesis also decreased in male manatees in Florida in winter (Hernandez et al. 1995), and the behavior of mating herds also revealed seasonal shifts in frequency (Rathbun et al. 1995).

Births also seem to be diffusely seasonal in dugongs in northern Australia. In the Townsville-Cairns area, dugongs give birth from August–September through November (Marsh et al. 1984c). Dugongs with near-term fetuses (>110 cm body length) were sampled at Daru between July and February (Fig. 2). Seasonal parity has been reported of Florida manatees (Marmontel 1995; O'Shea and Hartley 1995; Rathbun et al. 1995).

Natural Mortality

Reliable data on natural mortality in dugongs are not available. An age-frequency distribution can provide life-table information and hence survivorship curves, but only when it is drawn from a population with a stable age distribution and a known rate of change (Caughley 1977). The age-frequency data from dugongs at Townsville and Daru are not suitable for this analysis. The rates of population change were not known, and the assumption that the populations were stable was not valid. The sample from Townsville was obtained as a result of a massive increase in mortality from the introduction of shark nets. The sample from the Daru fishery was obtained during a time of rapidly changing harvest levels (Hudson 1986) and was not representative because of the ban on taking females with attendant calves. An additional problem was that minimum-age estimates are available only of mature male dugongs because of the loss of growth layers when the tusks wear (Marsh 1980). Admitting these limitations, a crude estimate of the mortality rate calculated from the age-frequency distribution of females drowned in the Townsville shark nets (Marsh 1980) was 0.08 with a 95% confidence interval of 0.06–0.10 (H. Marsh, James Cook University, unpublished data).

In the absence of reliable natural mortality schedules of dugongs, Marsh (1986) constructed a simple population model by using two mortality schedules based on those developed for population models of another paenungulate, the African elephant (*Loxodonta africana*), by Hanks and McIntosh (1973). This model was extended to three mortality schedules (Table 6). The typically U-shaped mammalian mortality curve (Caughley 1966) was modeled as a step function with levels that corresponded to four different age groups.

Population Dynamics

For each mortality schedule, I constructed population models to determine the annual rate of increase of stable dugong populations for various combinations of pre-reproductive periods and interbirth intervals, chosen to span the range of estimates of pre-reproductive periods and interbirth intervals obtained from carcass analysis (Tables 1 and 3 unpublished data).

The models were based on six simplifying assumptions: (1) the reproduction rate is independent of age during the reproductive part of the female's life span, (2) females cease to bear calves at age 50 or 60 (this age has a minimal effect on the results; Fig. 3), (3) no females live

Table 6. Mortality schedules used for the population models of dugongs (*Dugong dugon*). Mortality is expressed as % of population in various age categories dying per year.

	Age in years			
	0–4	5–45	45–55	55–60
Low mortality	5	1	5	50
Medium mortality	10	2	5	50
High mortality	20	4	5	50

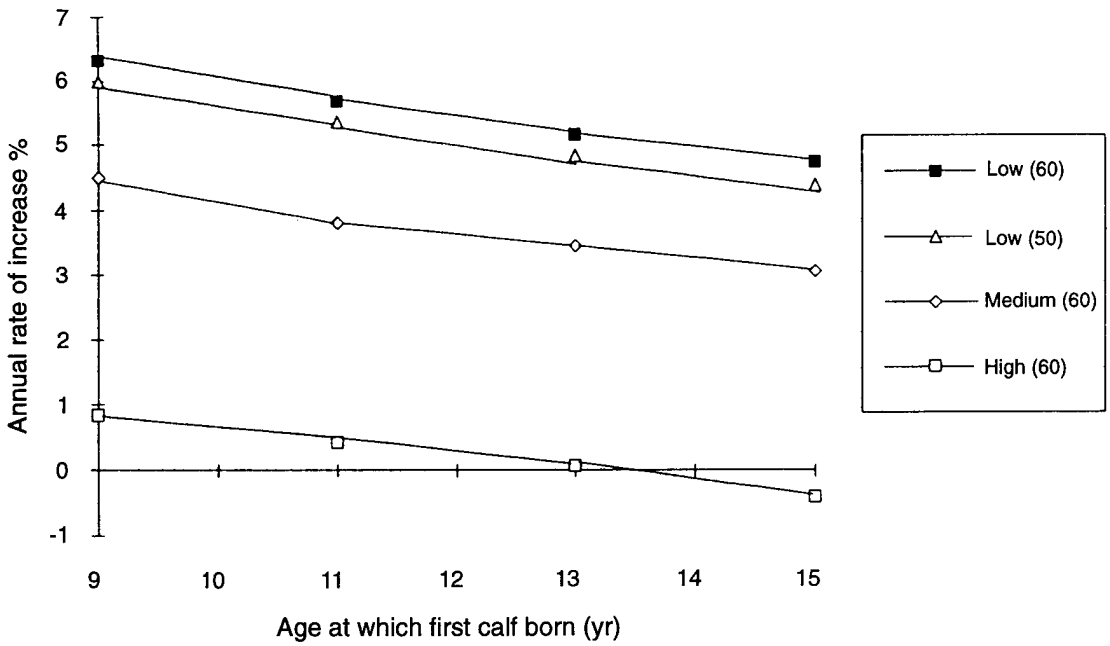


Fig. 3. The effects of the mortality schedules defined in Table 6 and age at which the first calf is born at the annual rate of increase of a dugong (*Dugon dugon*) population with a mean interbirth interval of 3 years. The two graphs of the low mortality schedule show the effect of changing the age at which females bear their last calves at ages 50 to 60. For the medium and high mortality schedules, the graphs are based on the assumption that females bear their last calves at age 60.

beyond age 60 (only 1.5% of females of which absolute age estimates are available were older than 60 years), (4) the sex ratio at birth is 1:1, (5) immigration and emigration do not occur, and (6) the anthropogenic mortality is zero.

Each asymptotic rate of increase was determined by executing the appropriate Leslie matrix model over a 100-year period with an approximate initial stable age distribution that was determined from an analogous continuous model (Pollard 1973). The resultant asymptotic rates of increase were confirmed by using them to modify the conditions of the simulation model.

The models indicated that the expected maximum asymptotic annual rate of increase of an unharvested dugong population is only 6.3% even with the most optimistic combination of life-history parameters derived from the carcass samples and a schedule of low mortality. If the parameters suggested by the Daru sample apply (pre-reproductive period 12 years, interbirth interval 6 years), the estimated annual rate of increase is only 2.4%. The simulations of Marsh et al. (1984c) and Marsh (James Cook University, unpublished data) also indicate the sensitivity of the models to changes in survivorship, particularly adult survivorship, and interbirth interval (Fig. 3; Table 7). The models are less sensitive to changes in the age at first reproduction (Table 7). These patterns are consistent with those predicted by Eberhardt and Siniff (1977) in marine mammals and by Packard (*1985) and Eberhardt and O'Shea (1995) in manatees.

Implications for Conservation

Despite the limited sample sizes, the analyses of specimens from dugong carcasses from various locations in northern Australia and Papua New Guinea indicated that the dugong is a long-lived mammal with a low reproduction rate. The data suggested plasticity in the age and size at which dugongs mature sexually, but the causes of such variation are not known. Neither mature males nor females are continuously in breeding condition, and breeding is diffusely seasonal (Marsh et al. 1984a, 1984b, 1984c). The data from Daru suggested considerable differences between years in the proportions of breeding males and

Table 7. Annual rate of increase of a stable dugong (*Dugong dugon*) population at various combinations of pre-reproductive period and interbirth interval; the assumed mortality schedule is age 0–4 years (5%), 5–45 years (1%), 46–55 years (5%), 56–60 years (50%), and females are assumed to reproduce until they die.

Mean pre-reproductive period (year)	Mean interbirth interval		
	3	5	7
9	6.3	3.7	2.2
11	5.6	3.3	2.0
13	5.1	3.0	1.7
15	4.7	2.7	1.5

females. Anecdotal evidence links these fluctuations in breeding with changes in food availability.

Goodman (1981) pointed out that large mammals have a particular life table; survival is high, fecundity is low, and sexual maturity is usually late. The dugong is an even more extreme example of this life-history strategy than the Florida manatee (Eberhardt and O'Shea 1995; Marmontel 1995). If dugongs are to be conserved, survivorship must be high and anthropogenic mortality, low.

As explained by Marsh (1995), the range of the dugong in Australia extends over a vast area in which all causes of anthropogenic mortality cannot be prevented. Such prevention is unacceptable because it would not allow traditional hunting. A more practical approach is to provide a high level of protection in areas that support large numbers of dugongs. This protection must extend to the seagrass habitat and to the dugongs. Such a policy of zonal ecosystem management exists in the Great Barrier Reef Marine Park (*Great Barrier Reef Park Authority 1983, 1985) and is being extended to other regions by the Australian Government's Oceans 2000 program to establish a national system of protected marine areas.

Cited References[2]

Bertram, C. K. R., and G. C. L. Bertram. 1968. The Sirenia as aquatic meat producing herbivores. Symposium of the Zoological Society of London 21:385–391.

Bertram, G. C. L., and C. K. R. Bertram. 1973. The modern Sirenia: their distribution and status. Biological Journal of the Linnean Society 5:297–338.

Caughley, G. 1966. Mortality patterns in mammals. Ecology 47:906–918.

Caughley, G. 1977. Analysis of vertebrate populations. John Wiley and Sons, London. 234 pp.

Eberhardt, L. L., and T. J. O'Shea. 1995. Integration of manatee life-history data and population modeling. Pages 269–279 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Eberhardt, L. L., and D. B. Siniff. 1977. Population dynamics and marine mammal management. Journal of the Fisheries Research Board of Canada 34:325–428.

Goodman, D. 1981. Life history analysis of large mammals. Pages 415–436 *in* C. W. Fowler and T. D. Smith, editors. Dynamics of large mammal populations. John Wiley and Sons, New York. 477 pp.

*Great Barrier Reef Marine Park Authority. 1983. Cairns section zoning plan and Cormorant Pass section zoning plan. Great Barrier Reef Marine Park Authority, Townsville, Australia. 55 pp.

*Great Barrier Reef Marine Park Authority. 1985. Far northern section zoning plan. Great Barrier Reef Marine Park Authority, Townsville, Australia. 42 pp.

Hanks, J., and J. A. E. McIntosh. 1973. Population dynamics of the African elephant (*Loxodonta africana*). Journal of Zoology 169:29–38.

Heinsohn, G. E. 1972. A study of dugongs (*Dugong dugon*) in northern Queensland, Australia. Biological Conservation 4:205–213.

Hernandez, P., J. E. Reynolds, III, H. Marsh, and M. Marmontel. 1995. Age and seasonality in spermatogenesis of Florida manatees. Pages 84–97 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

*Hudson, B. E. T. 1981. The dugong conservation, management and public education program in Papua New Guinea: working with people to conserve their dugong resources. Pages 123–141 *in* H. Marsh, editor. The dugong. Proceedings of a seminar/workshop held at James Cook University 8–13 May 1979. 400 pp.

Hudson, B. E. T. 1986. The hunting of dugong at Daru, Papua New Guinea, during 1978–1982. Community management and education initiatives. Pages 77–94 *in* A. K. Haines, G. C. Williams, and D. Coates, editors. Torres Strait Fisheries Seminar, Port Moresby, February 1985. Australian Government Publishing Service, Canberra.

Huggett, A. St. G., and W. F. Widdas. 1951. The relationship between mammalian foetal weight and conception age. Journal of Physiology 114:306–317.

Jarman, P. J. 1966. The status of the dugong (*Dugong dugon* Müller): Kenya 1961. East African Wildlife Journal 4:82–88.

Johannes, R. E., and W. MacFarlane. 1991. Traditional fishing in the Torres Strait Islands. Australian Government Publishing Service, Canberra. 268 pp.

Laws, R. M. 1959. The foetal growth of whales with special reference to the fin whale, *Balaenoptera physalus* Linn. Discovery Reports 29:281–308.

Marmontel, M. 1995. Age and reproduction in female Florida manatees. Pages 98–119 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Marsh, H. 1980. Age determination of the dugong (*Dugong dugon* Müller) in northern Australia and its biological implications. Reports of the International Whaling Commission, Special Issue 3:181–201.

Marsh, H. 1986. The status of the dugong in Torres Strait. Pages 53–76 *in* A. K. Haines, G. C. Williams, and D. Coates, editors. Torres Strait Fisheries Seminar, Port Moresby. February 1985. Australian Government Publishing Service, Canberra.

Marsh, H. 1989. Mass stranding of dugongs by a tropical cyclone. Marine Mammal Science 5:75–84.

Marsh, H. 1995. Fixed-width aerial transects for determining dugong population sizes and distribution patterns. Pages 56–62 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival,

[2] An asterisk denotes unpublished material.

editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Marsh, H., P. W. Channells, G. E. Heinsohn, and J. Morrissey. 1982. Analysis of stomach contents of dugongs from Queensland. Australian Wildlife Research 9:55–67.

Marsh, H., G. E. Heinsohn, and P. W. Channells. 1984a. Changes in the ovaries and uterus of the dugong, *Dugong dugon* (Sirenia: Dugongidae) with age and reproductive activity. Australian Journal of Zoology 32:743–766.

Marsh, H., G. E. Heinsohn, and T. D. Glover. 1984b. Changes in the male reproductive organs of the dugong, *Dugong dugon* (Sirenia: Dugongidae) with age and reproductive activity. Australian Journal of Zoology 32:721–742.

Marsh, H., G. E. Heinsohn, and L. M. Marsh. 1984c. Breeding cycle, life history, and population dynamics of the dugong, *Dugong dugon* (Sirenia: Dugongidae). Australian Journal of Zoology 32:767–785.

Mitchell, J. 1976. Age determination in the dugong, *Dugong dugon* (Müller). Biological Conservation 9:25–28.

Nietschmann, B. 1984. Hunting and ecology of dugongs and green turtles in Torres Strait. National Geographic Society Research Reports 17:625–651.

Nietschmann, B., and J. Nietschmann. 1981. Good dugong, bad dugong; good turtle, bad turtle. Natural History 90:54–62.

Norris, C. E. 1960. The distribution of the dugong in Ceylon. Loris 296–300.

Odell, D. K., G. D. Bossart, M. T. Lowe, and T. D. Hopkins. 1992. Reproduction of the West Indian manatee in captivity. Pages 192–193 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

O'Shea, T. J., and W. C. Hartley. 1995. Reproduction and early-age survival of manatees at Blue Spring, upper St. Johns River, Florida. Pages 157–170 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

O'Shea, T. J., and C. A. Langtimm. 1995. Estimation of survival of adult Florida manatees in the Crystal River, at Blue Spring, and on the Atlantic Coast. Pages 194–222 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

*Packard, J. M. 1985. Preliminary assessment of uncertainty involved in modeling manatee populations. Manatee Population Research Report Number 9, Technical Report Number 8-9, Florida Cooperative Fish and Wildlife Research Unit, University of Florida, Gainesville. 19 pp.

Perrin, W. F., and S. B. Reilly. 1984. Reproductive parameters of dolphins and small whales of the family Delphinidae. Reports of the International Whaling Commission (Special Issue) 6:97–125.

Pollard, J. H. 1973. Mathematical models for the growth of human populations. Cambridge University Press. 186 pp.

Qi Jingfen. 1984. Breeding of the West Indian manatee (*Trichechus manatus* Linn) in captivity. Acta Theriologica Sinica 4:27–33.

Rathbun, G. B., J. P. Reid, R. K. Bonde, and J. A. Powell. 1995. Reproduction in free-ranging Florida manatees. Pages 135–156 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Reid, J. P., R. K. Bonde, and T. J. O'Shea. 1995. Reproduction and mortality of radio-tagged and recognizable manatees on the Atlantic Coast of Florida. Pages 171–191 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Thomas, D. 1966. Natural history of dugongs in Rameswaram waters. Madras Journal of Fisheries 2:80–82.

Age and Seasonality in Spermatogenesis of Florida Manatees

by

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Abstract. A histological study of the testes and epididymides of the Florida manatee (*Trichechus manatus latirostris*) was made to assess reproductive status. Testes or epididymides of 67 animals were examined for presence and abundance of sperm. In addition, qualitative and quantitative examinations of the seminiferous tubules from 31 manatees, ranging in length from 98 to 320 cm (total length), revealed 10 stages in the spermatogenic cycle. The shortest manatee in which spermiogenesis occurred was a 237-cm-long, 2-year-old. Males as short as 252 cm had fully spermatogenic testes, and one 255-cm-long individual was 2–3 years old. Spermatogenesis was not continuous and was significantly affected by season. In winter (December through February), sperm were found in either the testes or epididymides of only 13% of the recovered manatees that measured 241 to 280 cm, and

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in 25% of those longer than 280 cm. In contrast, 75% of the 241- to 280-cm-long manatees and 93% of the greater-than-280-cm-long animals recovered in non-winter months (March through November) had mature sperm. Of the manatees recovered in winter, none was fully spermatogenic and most had regressed seminiferous tubules (characterized by immature cell stages and reduced diameters), suggesting reduction, if not cessation, in the ability to impregnate females.

Key words: Florida manatees, reproduction, spermatogenesis, testes, *Trichechus manatus latirostris.*

In contrast to the dugong (*Dugong dugon*) for which excellent data on reproduction in males (at the gross and microscopic levels) have been available for some time (Marsh et al. 1984), relatively little effort has been focused on the reproductive tracts from male Florida manatees (*Trichechus manatus latirostris*). Observations of behavior revealed that mating may occur year-round but may be seasonally depressed during winter (Hartman 1979; Rathbun et al. 1995), but the reproductive status of males, in terms of spermatogenic activity, has not been examined by season or by age and size of the animals.

A preliminary description of reproductive tracts in male manatees (*[3]Odell et al. 1981) revealed that testicular weight increased exponentially with body length in 275 to 290-cm-long animals; this observation led the authors to the conjecture that sexual maturity in male manatees occurred at a body length of 275 cm or greater, corresponding to estimated ages of 9–10 years. The figure of 9 to 10 years was based on the growth of some captive-born manatees of known age. In contrast, Hartman (1979) suggested, based on behavior of wild manatees, that sexual maturity occurs at about 3–5 years of age.

Odell et al. (*1981) noted that even large manatee carcasses recovered in winter had relatively small testes that were brown and from which no evidence of sperm could be found in smears. Conversely, testes from carcasses with comparable body lengths that were recovered in seasons other than winter were larger and white; however, smears were not available from these carcasses. Odell et al. (*1981) suggested a seasonal cycle in testicular activity and significantly less activity in winter.

With routine histological techniques and a recent technique for aging manatees (*Marmontel et al. 1990), we describe the reproductive status of male manatees, including some of known age that were recovered by the manatee-carcass-salvage network (*Bonde et al. 1983). The data provide information about age at onset of sexual maturity, variability in that age, and seasonality of spermatogenic activity. These data are useful for an understanding of the life history and population dynamics of manatees.

[3] An asterisk denotes unpublished material.

Materials and Methods

Tissues from reproductive tracts of 68 male manatees were obtained between April 1975 and February 1985 through a carcass-salvage network (*Bonde et al. 1983). At necropsy, collected data included body length and condition of the animal prior to death (reflected by quantitative or qualitative assessment of blubber or body-fat thickness). Animals recovered throughout the year were included in this study. Gonads or epididymides from all 67 manatees were examined for the presence of sperm. Tissues from 31 of the animals were of sufficient quality (i.e., had minimal autolysis) to permit analysis of seminiferous tubules for precise stages in the spermatogenic cycle. Manatees were arbitrarily separated into three size categories: 98- to 240-cm length, 241- to 280-cm length, and 281- to 320-cm length. The lower limit of the final size category corresponds approximately to the length at which Odell et al. (*1981) found that testicular weight increased exponentially, and the upper limit corresponds to the length of the largest animals in this sample.

Although testicular weights of some animals were provided, records and notes at necropsies were unclear about whether the weight was for one or both testes or whether the epididymis had been completely trimmed. Therefore, we did not use testicular weights but focused on the histological determination of sexual maturity.

Ages were estimated from counts of growth-layer groups in the dome region of the tympano-periotic complex (*Marmontel et al. 1990). An age of 1 was used to designate an animal 1–2 years of age, 2 indicated an animal 2–3 years old, and so on. Bone resorption or other changes in the layers precluded accurate age determination of some old manatees.

During necropsy, samples from the epididymides or testes were excised for histological examination and fixed in 10% buffered formalin. Although whole testes were occasionally preserved, often only one piece was excised. The precise locations from which these samples were taken was generally not noted and was presumably not consistent. Fixed tissues were dehydrated in an ethanol series, cleared in xylene, embedded in Paraplast, and sectioned at 6 μm. Sections of testis were stained with hematoxylin and eosin (H and E). Epididymides and testes were also stained with Putt's stain (Appendix) to

detect the presence of sperm. No testes were serially sectioned.

Many of the 67 manatees assessed for the presence of sperm had seminiferous tubules that were severely autolyzed. In specimens with good quality of the preserved tissues, seminiferous tubules were assessed in two ways. Diameters of 50 seminiferous tubules were measured at 400× with an ocular micrometer. The same tubules were then analyzed with phase analysis, in which a numerical value was assigned to each tubule based on certain cellular associations in the seminiferous epithelium. Each section from the testes typically contained at least 50 round seminiferous tubules. In rare cases when only small sections were available, two or more separate pieces from the testes were examined to locate 50 round tubules. If consecutive sections through the same piece of tissue had been used, biased data may have been collected because consecutive sections probably included the same plane through the seminiferous tubule.

A series of 10 phases was recorded after the same criteria as Marsh et al. (1984). Phases −4 to 0 (Fig. 1) represent seminiferous tubules in which spermatogenesis was either arrested or incomplete and Phase −4 suggest total inactivity. Phases 0 through +5 represent active spermiogenesis as round spermatids mature into spermatozoa (Fig. 2). The mean seminiferous tubule phase of any given animal (termed the *testicular stage*) was used for comparisons among animals. A manatee was considered fully spermatogenic if the testicular stage was a positive number (i.e., the mean tubule phase was between 0 and +5). Testes at this stage were undergoing active spermiogenesis, characterized by a distinct cellular organization of the seminiferous epithelium (Marsh et al. 1984). With similar categories of Marsh et al. (1984), 31 manatees were placed in three reproduction categories: 29% immature; 29% mature in resting or intermediate state, recrudescent (undergoing spermiogenesis) or prepubescent; and 42% fully spermatogenic (undergoing spermatogenesis). The term *fully spermatogenic* is used here to imply a stage at which most seminiferous tubules were undergoing spermiogenesis, during which spermatozoa were produced (Marsh et al. 1984).

Data were examined for normality and found not to conform to necessary assumptions to justify the use of parametric statistics. Nonparametric statistics were used for comparisons of reproduction among seasons and size classes and for correlation analyses. The Kruskal-Wallis test was used to determine significant differences in testicular histology and tubule diameter among the three size categories of the carcasses, and between carcasses that were recovered in winter and carcasses that were recovered in seasons other than winter. Spearman's rank correlation test was used to determine significant correlations between testicular stage and animal length and between testicular stage and diameter of seminiferous tubules. The latter was tested to determine a fast and simple method by which reproductive status can be determined from histological samples. A probability value of 0.01 was chosen to represent significant results from all analyses.

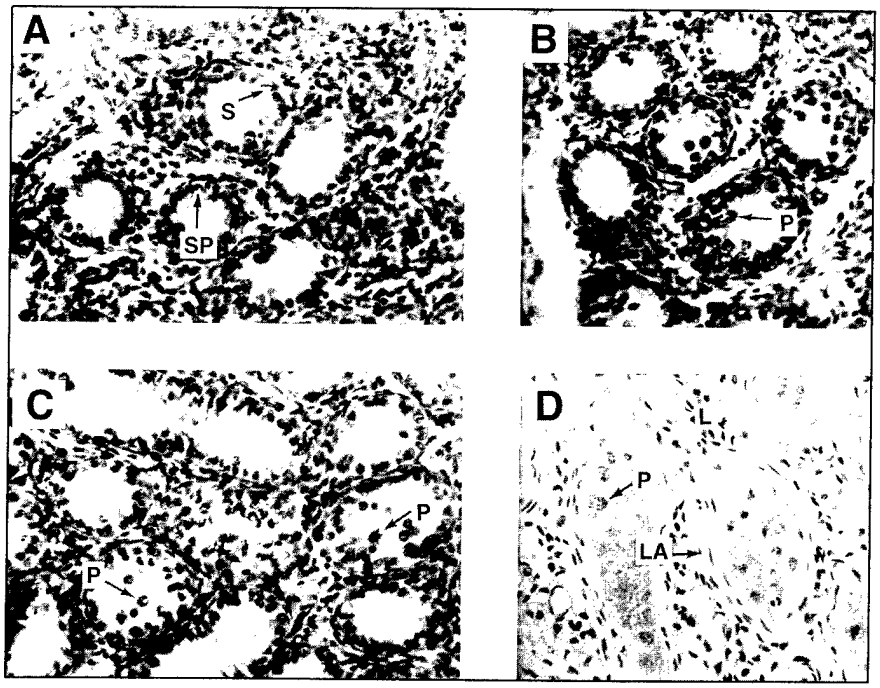


Fig. 1. Early and regressed phases of spermatogenesis in Florida manatees *(Trichechus manatus latirostris)*. (A) Phase −4, the most immature stage, is characterized by Sertoli cell nuclei (S) and spermatogonia (SP) lining the periphery of the seminiferous tubule. (B) Phase −3, similar to Phase −4 with a few primary spermatocytes (P). (C) Phase −2, like the previous phases but with numerous primary spermatocytes. Seminiferous tubules at this phase may be open or closed. (D) Regressed tubule in Phase −3. This condition is characterized by a few primary spermatocytes, increased diameter of the lamina propia (LA), decreased tubule diameter and increased cross-sectional area of interstitial tissue (note Leydig cells, L). All samples were stained with hematoxylin and eosin and photographed at 100X.

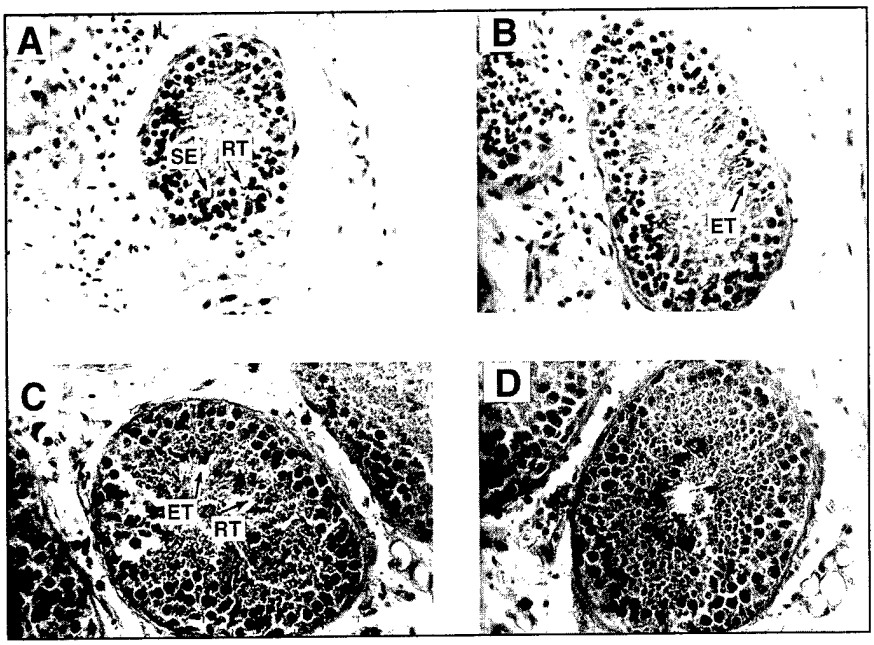


Fig. 2. Several seminiferous tubules from Florida manatees (*Trichechus manatus latirostris)* undergoing spermiogenesis. Diameters of seminiferous tubules are larger than in Fig. 1. (A) Phase 0. Primary and secondary (SE) spermatocytes and round spermatids (RT) are present. (B) Phase +2. During this phase, spermatogonia and Sertoli cell nuclei line the basement membrane. Primary and secondary spermatocytes are organized into layers with elongating spermatids (ET) along the lumen. (C) Phase +4. This phase includes round (RT) and elongating (ET) spermatids. (D) Phase +5. Round spermatids and spermatozoa line the tubule lumen. All samples were stained with hematoxylin and eosin and photographed at 100X.

Results

Staged Testes

Different cellular associations of the seminiferous epithelium characterized the different phases. Phase –4, the least active phase, was represented by essentially solid tubules lined with spermatogonia and occasional Sertoli cells. The underlying lamina propria was relatively thick (5–10 μm) during this phase. The next phase, –3, included tubules with small numbers of primary spermatocytes in addition to already mentioned cell types. Phase –2 tubules had numerous primary spermatocytes. The lumen of the tubule became evident during Phase –1, at which time the different cells of the seminiferous epithelium became organized into layers that included some secondary spermatocytes. Phase 0 tubules contained a few rounded spermatids in addition to the already named cell types.

Tubules assigned to Phases 1 through 5 were found in animals undergoing spermiogenesis, during which the haploid spermatids transformed into spermatozoa (Fig. 2). Tubules in Phase 1 had Sertoli cells with basal nuclei and spermatogonia lining the periphery of the tubules and primary and secondary spermatocytes and round spermatids organized into layers. Phase 2 tubules contained spermatids beginning to elongate and becoming associated with Sertoli cells. Phase 3 tubules were characterized by well-organized spermatid bundles associated with Sertoli cells and maturation divisions among primary and secondary spermatocytes. In contrast to Phase 3, two generations of spermatids (round and elongating) were present in Phase 4. Sperm (with tails) lined the entire lumen of tubules in Phase 5. Phase 6, identified by Marsh et al. (1984), represented by spent tubules at the end of a period of sexual activity, was not identified in this study.

Testicular stage and diameter of seminiferous tubules strongly correlated (Fig. 3; $n = 31$; Spearman's rank correlation test; $r = 0.815$). A higher correlation existed between diameter of seminiferous tubules and age (Fig. 4; $n = 26$; Spearman's rank correlation test; $r = 0.770$) than between testicular stage and age (Fig. 5; $n = 18$; Spearman's rank correlation test; $r = 0.487$). Increases in diameter of seminiferous tubules and testicular stage were sharp in animals that were longer than approximately 250 cm (Figs. 6 and 7).

The tubule diameter (Fig. 6; $n = 31$; $P = 0.0001$), testicular stage (Fig. 7; $n = 31$; $P = 0.0008$), and presence of sperm in the testis or epididymis (Fig. 8; $n = 29$, $P = 0.0012$) of manatees differed by size class. Testicular stage ($P = 0.05$, $n = 11$) or diameters of tubules ($P = 0.016$, $n = 17$) did not differ by size category during winter months because regressed testes were histologically indistinguishable from immature testes.

Lack of testicular weights made it impossible to differentiate between mature resting (i.e., reproductively quiescent) and prepubescent animals.

Immature Manatees

Nine 98- to 235-cm-long manatees fit characteristics ascribed to immature animals (Table 1). Where age was known, these animals ranged from 0–2 years old. Testicular stage was always negative and approached or was equal

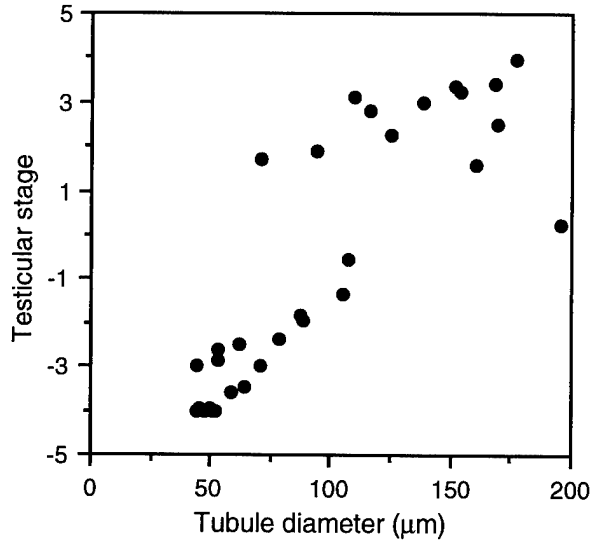


Fig. 3. Correlation between mean diameter of seminiferous tubules and testicular stage in the Florida manatee (*Trichechus manatus latirostris; n* = 31).

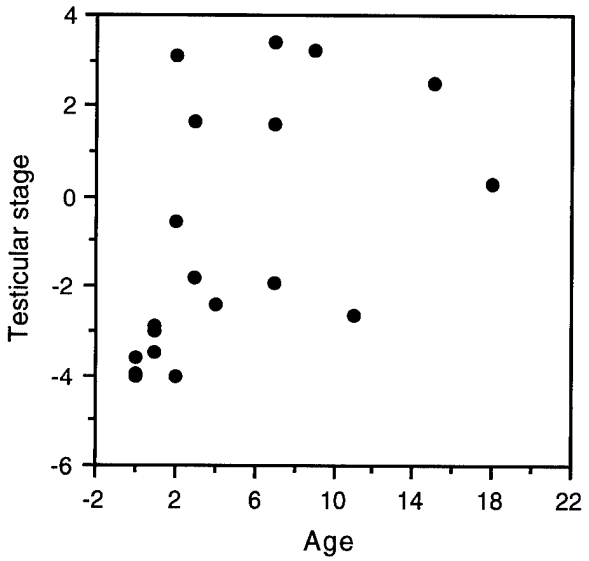


Fig. 5. Relation between age and testicular stage in Florida manatees (*Trichechus manatus latirostris)* sampled during all seasons (*n* = 18).

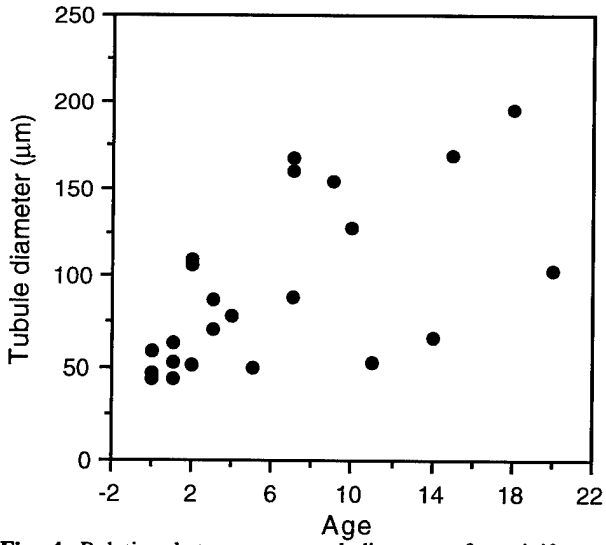


Fig. 4. Relation between age and diameter of seminiferous tubules in the Florida manatee (*Trichechus manatus latirostris; n* = 26).

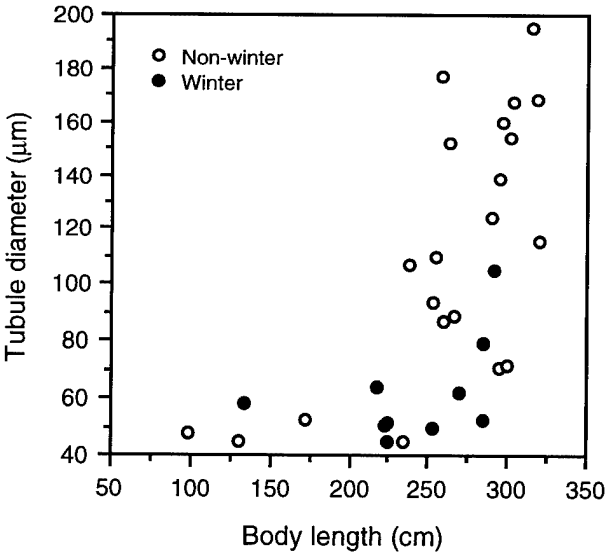


Fig. 6. Relation between body length and mean diameter of seminiferous tubules in the Florida manatee (*Trichechus manatus latirostris*; *n* = 31).

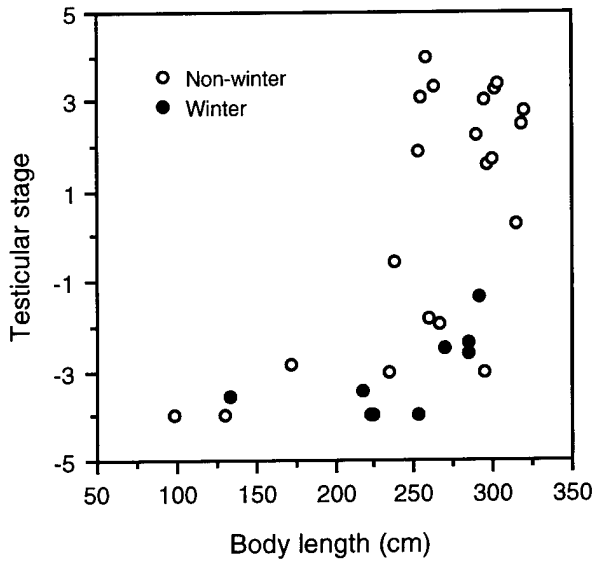


Fig. 7. Relation between body length and testicular stage in the Florida manatee (*Trichechus manatus latirostris*; $n = 31$).

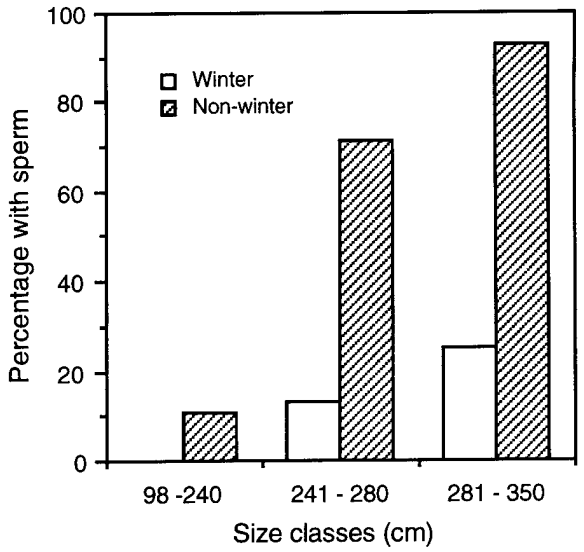


Fig. 8. Percentage of Florida manatees (*Trichechus manatus latirostris*) with sperm in the testes or epididymides. Note that, for the smallest age class, 10% represents only a single animal ($n = 29$).

Table 1. Life history data of male Florida manatees (*Trichechus manatus latirostris*) with a total body length of 98–240 cm ($n = 21$). Tubule diameter (in μm) represents a mean of 50 measurements. Sperm density represents the observed highest density in tissues of a particular manatee. 0 = no sperm; 1 = sparse sperm; 2 = moderate density; 3 = very dense sperm. Putt's (1951) stain, which is specific for spermatids and spermatozoa, was used to identify sperm in the epididymides. Months 12, 1, and 2 represent winter; 3–5 represent spring; 6–8 represent summer; and 9–11 represent fall. The testicular stage is the mean phase of 50 evaluated seminiferous tubules/animal; the phases range from –4 to 5.

Total body length (cm)	Specimen field number	Tubule diameter	Sperm density	Age (year)	Month of death	Testicular stage
98	M-293	47.60	0	0	05	–4.00
117	M-213		0	0	12	
119	M-178		0	0	12	
130	M-403	44.84	0	0	09	–3.98
133	M-135	58.68	0	0	02	–3.58
146	M-75-5		0	0	04	
172	M-79-1	52.75	0	1	01	–2.86
175	M-144		0	0	04	
177	M-76-3		0		01	
190	M-244		0	1	06	
205	M-79-26		0	0	12	
209	M-388		0	0	05	
218	M-154	63.62	0	1	02	–3.46
219	M-314		0		11	
219	M-82-8		0		02	
222	M-81-66	50.30	0		12	–4.00
225	M-82-16	44.44	0	0	02	–4.00
225	M-79-9	51.62	0	2	02	–4.00
228	M-137		0	2	02	
235	M-79-24	44.40	0	1	11	–3.00
237	M-308	107.20	1	2	08	–0.56

to –4. Seminiferous tubules were narrow (44–64 μm) containing only spermatogonia, Sertoli cells, and primary spermatocytes resting on a thick lamina propria (i.e., no spermatids or spermatozoa were present). Intertubular tissue was extensive among these largely solid tubules.

Prepubescent or Recrudescent Manatees

Nine 237- to 295-cm-long and 2 to 11-year-old manatees (when age was determined) were placed in this category (Tables 1–3). Mean diameter of the seminiferous tubules was between 50 and 107 μm, and the lamina propria seemed to be thinner than in immature manatees. In addition to the cell types in immature animals, secondary spermatocytes and a few round spermatids were included in the seminiferous epithelium. Testicular stage was always negative, although the value approached zero in at least one individual (M-308[4]). This 237-cm-long, 2-year-old individual was the most precocious of the examined manatees; he already had some sperm in his testes.

[4] Identification numbers of manatees are provided when known for completeness of information.

Fully Spermatogenic Manatees

Animals were considered fully spermatogenic when the testicular stage was between 0 and +5. Active spermiogenesis occurred in thirteen 252 to 320-cm-long, 2 to 18-year-old manatees (Tables 2 and 3). Average tubular diameters were 71–195 μm. Cross-sectional area of interstitial tissue (which includes Leydig cells) was reduced in fully spermatogenic animals (Fig. 2). Although testicular tissue of the oldest male in this study (M-235; 25 years old) was not available, a moderate amount of sperm was in the epididymis (Table 3).

Seasonality of Changes in Testicular Histology

Several important factors of potential reproduction differed by season. Mean testicular stage (Kruskal-Wallis test; $n = 31$; $P = 0.009$) and the presence of sperm in the epididymis or testes (Kruskal-Wallis test; $n = 67$; $P = 0.007$) differed by season in which manatees were recovered. Most of the differences seemed to reflect changes in testicular histology in winter, when regressed seminiferous tubules, containing mostly immature cell stages, were typical, even in testes obtained from large animals.

Table 2. Life history data of male Florida manatees (*Trichechus manatus latirostris)* with a total body length of 241–280 cm ($n = 24$). Tubule diameter (in μm) represents a mean of 50 measurements. Months 12, 1, and 2 represent winter; 3–5 represent spring; 6–8 represent summer; and 9–11 represent fall. The testicular stage is the mean phase of 50 evaluated seminiferous tubules/animal; the phases range from –4 to 5. Eight manatees died in December, January, or February (winter). One of them (13%) produced sperm. Twelve of 16 (75%) produced sperm in non-winter seasons.

Total body length (cm)	Specimen field number	Tubule diameter	Sperm density	Age (year)	Month of death	Testicular stage
241	M-219		0	2	01	
244	M-220		0	1	01	
247	M-55		1		02	
252	M-428	50.00	0	9	02	–3.96
252	M-82-34	93.40	1		04	1.90
252	M-217		0	4	01	
255	M-78-42	109.50	2	2	11	3.10
256	M-153		3	4	05	
257	M-78-35	176.60	2		09	3.96
258	M-82-20		0		02	
260	M-275	86.90	0	3	03	–1.80
263	M-79-23	151.70	1	4	10	3.34
263	M-239		0		08	
267	M-280	88.60	0	7	04	–1.94
267	M-77-16		0	2	05	
270	M-258	61.60	0		01	–2.50
271	M-223		0	7	02	
271	M-79-7		1		03	
271	M-79-18		3	20	08	
273	M-174		3	5	10	
274	M-108		1	5	03	
277	M-166		3	3	08	
278	M-76-28		1	7	11	
279	M-156		3	6	06	

Table 3. Life history data of male Florida manatees (*Trichechus manatus latirostris*) with total body length of more than 281 cm ($n = 22$). Tubule diameter (in μm) represents a mean of 50 measurements. Months 12, 1, and 2 represent winter; 3–5 represent spring; 6–8 represent summer; and 9–11 represent fall. The testicular stage is the mean phase of 50 evaluated seminiferous tubules/animal; the phases range from –4 to 5. Eight manatees died in December, January, or February (winter). Two of them (25%) produced sperm. Thirteen of 14 (93%) produced sperm in nonwinter seasons.

Total body length (cm)	Specimen field number	Tubule diameter	Sperm density	Age (year)	Month of death	Testicular stage
284	M-83-2	79.00	0	4	01	–2.38
285	M-78-8	52.85	0	11	02	–2.62
288	M-82-29		1	11	03	
290	M-74-2	124.80	2		06	2.26
291	M-78-15		0	10	02	
292	M-78-29		1	10	06	
292	M-353		2	14	12	
292	MSW-4	105.40	2		01	–1.34
295	M-210	71.00	0		10	–3.00
295	G-75-76	138.00	1		10	3.00
297	M-208	160.20	2	7	10	1.60
297	M-80-27		0		12	
299	M-209	71.25	3	3	10	1.68
301	M-381	153.60	1	9	03	3.24
303	M-391	167.60	1	7	09	3.40
312	M-78-10		0	20	02	
314	M-255	195.30	2	18	11	0.26
318	M-235		2	25	05	
318	M-299	168.90	2	15	06	2.48
320	M-146		2	>12	04	
320	M-82-30	115.50	2		03	2.78
320	M-81-11		0		01	

The presence of sperm in the reproductive tracts of 67 manatees was examined. In the smallest size class (98–240 cm), sperm was present in 11% (1 of 9) of the carcasses recovered in a season other than winter, and in none of the 12 carcasses recovered in winter (Table 1). In the second size class (241–280 cm), sperm was present in 13% (1 of 8) of the carcasses recovered in winter and in 75% (12 of 16) of the carcasses recovered in seasons other than winter (Table 2). In the largest size class (281–320 cm), sperm was present in 93% (13 of 14) of the carcasses recovered in seasons other than winter but in only 25% (2 of 8) of the carcasses recovered in winter (Fig. 8; Table 3). Manatees with sperm in the testes or epididymides were 237–320 cm long and 2–25 years old.

Of the 31 manatees whose testes were quantitatively assessed, none (0 of 9) in the first size class (98- to 240-cm length) was fully spermatogenic; however, 44% (4 of 9) of the 241- to 280-cm-long carcasses and 69% (9 of 13) of the 281 to 320-cm-long carcasses were fully spermatogenic (Fig. 9; Tables 1–3). Among the carcasses that were longer than 241 cm, none of 5 recovered between December and February, 60% (3 of 5) recovered between March and May, 67% (2 of 3) recovered between June and August, and 89% (8 of 9) recovered between September and November were fully spermatogenic (Tables 2 and 3).

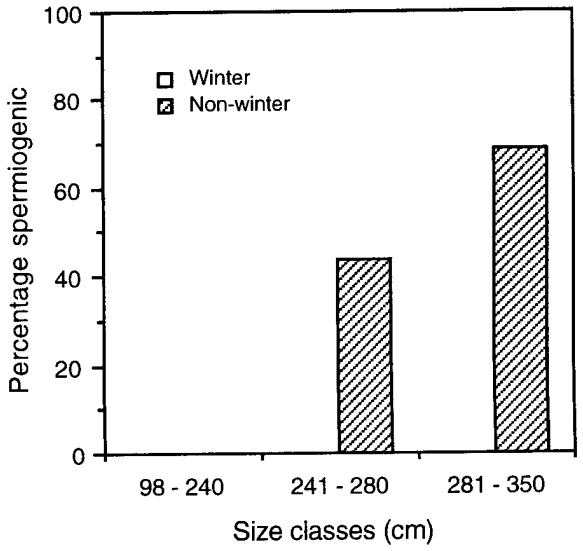


Fig. 9. Percentage of fully spermatogenic Florida manatees (*Trichechus manatus latirostris*) in each size class.

Discussion

Odell et al. (*1981) predicted that male manatees became reproductively active at a length of about 275 cm (at an estimated age of 9–10 years based on growth of some captive-born animals), when testicular weight increased exponentially. Our results showed that males may be capable of impregnating females at a much smaller size and younger age. Increases in diameter of seminiferous tubules and testicular stage at a body length as short as 237 cm and at an age as young as 2 years were notable (Figs. 5 and 6). Whether the sperm from such young males can impregnate females is not known.

The possibility of early successful reproduction, as supported by histological evidence, corroborates observations of behavior by Hartman (1979), who suggested that reproduction began in male manatees between 3 and 5 years of age, and more recent observations of Rathbun et al. (1995), who noted the presence of free-ranging males (whose ages were known) of even younger ages in herds of males pursuing presumably estrous females in the Crystal River. The dynamics of these herds suggest no clear pattern of participation by males on the basis of size or age (Rathbun et al. 1995). In controlled breeding of captive animals, keeping small male manatees, considered immature (based on their size or age), with females may not prevent pregnancy. Odell (Sea World of Florida, Orlando, Florida, personal communication) noted that captive, about 2-year-old male California sea lions (*Zalophus californianus*) successfully mated and produced offspring and that similar matings occur in the wild with unknown results.

In manatees, total length seemed to be a better, but still imprecise, predictor of reproduction than age. Onset of spermatogenic activity in mammals in general may be more closely related to somatic development of the individual than to age (Johnson et al. 1970). The dependence of sexual maturity on attainment of critical body mass in some mammals has been suggested (Laws 1956). In our study, testicular activity, as gleaned from phase in the spermatogenic cycle and diameter of seminiferous tubules, increased profoundly when the manatee reached a length of approximately 250 cm, although this size did not correspond to a particular age (Fig. 10; $n = 26$). Several examples illustrated the point that size is not a good predictor of age: one 9-year-old manatee (M-428) was only 252 cm long, but a 2-year-old manatee (M-78–42) was already 255 cm long; two 3-year-old manatees (M-209 and M-275) were 299 cm and 260 cm long; a 20-year-old manatee (M-79–18) was only 271 cm long, whereas two 3-year-olds (M-166 and M-209) were longer than 270 cm.

Seasonal changes in testicular activity in our study concur with findings of Odell et al. (*1981), who assessed

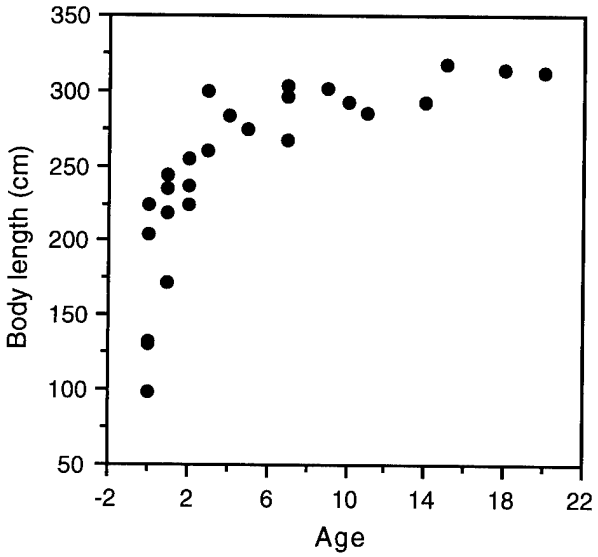


Fig. 10. Relation between age of male Florida manatees (*Trichechus manatus latirostris*) and total body length ($n = 26$).

testicular weight and appearance and suggested that activity was high in summer and fall and low in winter. Our observations (e.g., presence of regressed seminiferous tubules, characterized by immature cell stages and reduced diameters) suggested diminution, if not cessation, of spermiogenesis in winter. Although some larger manatees (13% from 241–280 cm long, and 25% >281 cm; Tables 2 and 3) recovered in winter had some sperm in the testes or epididymides, none was fully spermatogenic.

Seasonal effects seem to be an important factor of potential reproduction in male manatees. This is evidenced by the fact that no fully spermatogenic manatees were observed during winter. Only one (M-210) of 21 longer-than-270-cm carcasses recovered in seasons other than winter lacked sperm in the gonads or epididymis. This animal was an unusual case because it died in an emaciated condition in the Chesapeake Bay (outside the range of Florida manatees). In other-than-winter months, healthy male manatees longer than 250 cm may well undergo spermatogenesis, and in any healthy individual longer than 270 cm, spermatogenesis is almost certain.

Cessation of spermatogenic activity in winter was identified in other taxonomic orders of mammals. These changes in the capability of males to reproduce may be due to varying lengths of photoperiod (Millar and Glover 1973; Grocock and Clarke 1975) that affect circulating levels of gonadotrophins and testicular hormones. Seasonal reproduction in ringed seals (*Phoca hispida*) was due to pulses in secretion of hypothalamic gonadotrophin that released hormones that were influenced by several cues including photoperiod, nutrition, and social

stimuli (Ryg et al. 1991). These environmental factors, stress from the onset of cold weather, and the resulting need for hurried, often-lengthy migrations may play a similarly prominent role in the control of spermatogenesis in the manatee. Although insufficient nutrition cannot be ruled out as a cause of cessation of spermatogenesis in some manatees, at least one large manatee that died in winter (M-78–15; 291 cm) had no sperm but extensive body fat. This animal, presumed well nourished and healthy, died from a collision with a boat. This example may suggest that seasonal effect on spermatogenesis is not entirely due to nutritional stress during winter.

Only limited seasonality of spermatogenic activity occurred in male dugongs near Australia (Marsh et al. 1984; Marsh 1995). Although some individuals had not continuously produced sperm throughout the year, the influence of season on the capability to reproduce was less clear in these animals than in manatees in Florida where seasonal effects strongly correlated with spermatogenic activity. If one assumes that seasonal effects on reproduction are due, at least in part, to changes in temperature, the difference between dugongs and manatees may reflect that the sampled dugongs were from the northern regions of Australia and southern Papua New Guinea where seasonal changes in water temperature are less marked than in waters occupied by manatees in Florida. The examined dugongs may not have undergone the types of environmental, nutritional, or energetic stresses associated with changes in temperature experienced by Florida manatees in winter. To isolate and evaluate the importance of seasonal changes in temperature on spermatogenesis, an examination of West Indian manatees would be helpful outside Florida (i.e., in countries bordering the Caribbean Sea) where water temperatures are consistently warm. Similarly, an examination of testes of dugongs in cooler parts of the species' range (e.g., Moreton Bay) may be helpful to determine whether spermatogenesis in these animals is influenced by seasonal change in water temperature.

De Jong and Zweers (1980) confirmed monophyly of the paenungulate Orders Hyracoidea, Sirenia, and Proboscidea. Results from studies of seasonal effects on spermatogenic activity among the paenungulates failed to provide information that may unite the group by the physiology of reproduction. Whereas Laws (1969) found that the diameter of the seminiferous tubules of African elephants (*Loxodonta africana*) is affected by seasons, Short et al. (1967) did not identify marked seasonal changes in androgen concentration in these elephants. Seasonal effects on spermatogenesis were not shown in all hyraxes (Order Hyracoidea) (Glover and Sale 1968; Millar and Glover 1973). Animals far from the equator showed marked seasonality in their capabilities to reproduce, whereas in the tropics, as seen in the dugongs, hyraxes had no well defined breeding season. Animals at lower latitudes may be incapable of detecting strong-enough changes in photoperiod to affect seasonal changes in spermatogenesis. Alternatively, either temperature or nutritional value of foods may play a vital role in seasonal reproduction (Millar and Glover 1973). Moreover, as described by Marsh et al. (1984) in dugongs, male hyraxes in the tropics do not undergo coordinated spermatogenic activity (i.e., not all members of the population undergo spermatogenesis simultaneously). As in most eutherian mammals, manatees share a similar spermatogenic cycle as that seen in elephants, hyraxes, and dugongs, but unlike in most other examined paenungulates, the capability to reproduce (as defined by presence of sperm and testicular stage) correlates with season in manatees (at least in Florida).

Whereas dugongs and manatees differ in the degree to which their spermatogenic capability is affected by seasons, the species are comparable in body length at which sexual maturity may occur. Dugongs as short as 219 cm may exhibit spermatogenesis (Marsh et al. 1984), whereas spermatogenesis occurs in manatees as short as 237 cm. However, manatees reach a larger maximum size than dugongs. Age at sexual maturity differs considerably between the two species; the youngest mature male dugong was 9 years old (Marsh et al. 1984), and the youngest mature male manatees were only 2 years old. The difference may reflect species-specific differences in life history. Alternatively, age at sexual maturity in Florida manatees may have dropped, possibly because of faster growth from changing population parameters and resource availability, whereas the examined dugong populations may be stable and occupy more stable habitats. Age, but not body size at sexual maturity, dropped in Antarctic fin whales (*Balaenoptera physalus*), presumably because of exploitation of mysticetes and subsequent greater availability of food (Gambell 1985); in other words, body size, not age, is the cue for sexual maturity.

As noted earlier, spermatogenic activity diminishes in winter in many mammalian groups; however, some species in the Order Chiroptera are able to store viable sperm throughout winter (Asdell 1946). Five manatees in this study (M-108, M-209, M-255, M-353, and MSW-4) had little if any sperm in the testes but had abundant sperm in the epididymides. This suggested that manatees may be able to store sperm in the epididymis after completing a spermatogenic cycle. Because the viability of stored sperm is not known, the importance of this phenomenon remains unknown. Because we did not serially section and examine whole testes, spermiogenesis may have occurred in tissues we did not examine. In dugongs,

abundant spermatozoa were found only in epididymides of animals at the height of spermiogenesis (Marsh et al. 1984).

Testicond mammals (mammals without scrota) include species in the Orders Hyracoidea, Proboscidea, Edentata, Cetacea, Sirenia, and Insectivora. Spermatogenesis proceeds as usual in testicond mammals without apparent detriment from abdominal temperature (Carrick and Setchell 1977). Although lower temperature seems to be more important for sperm storage than production in most cases, a mechanism for maintaining the epididymides at a cooler temperature in most testicond mammals is not known (*Bedford 1977). Recent anatomical evidence suggested that cetaceans have a vascular counter-current exchange that may serve to cool the testes and epididymides (Rommel et al. 1992). A similar vascular arrangement, if present, may explain viable sperm storage in the epididymides of manatees.

In conclusion, observations of manatee testes and epididymides suggested near cessation of spermatogenesis in winter, an apparent peak in spermatogenic activity in late summer and fall, and initiation of spermiogenesis in manatees as short as 237 cm long and as young as 2 years. This type of information provides important life-history data, and could influence the captive maintenance of manatees. Future tissue analysis should be made a priority, particularly to determine whether age at sexual maturity or timing of spermatogenesis change over time. In addition to examining seminiferous tubules, future researchers should include measuring hormone levels in blood, feces, or urine. Testosterone plays a central role in controlling the spermatogenic cycle (Sharpe et al. 1990). Although testosterone levels are affected by stress, a direct measure of testosterone level and an assessment of the relation between testicular stage and testosterone level may be informative. Finally, entire testes, especially of recovered carcasses in winter, should be serially sectioned and examined to determine whether spermatogenic activity occurs at a consistent level throughout the gonad.

Acknowledgments

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Cited References[5]

Asdell, S. A. 1946. Patterns of mammalian reproduction. Comstock Publishing Company, New York. 437 pp.

*Bedford, J. M. 1977. Evolution of the scrotum: The epididymis as the prime mover. Pages 171–182 *in* J. H. Calaby and C. H. Tyndale-Biscoe, editors. Reproduction and evolution: Proceedings of the Fourth International Symposium on Comparative Biology of Reproduction. Australian Academy of Science, Canberra.

*Bonde, R. K., T. J. O'Shea, and C. A. Beck. 1983. A manual of procedures for the salvage and necropsy of carcasses of the West Indian manatee (*Trichechus manatus*). National Technical Information Service. Springfield, Va. PB83-255273. 175 pp.

Carrick, F. N., and B. P. Setchell. 1977. The evolution of the scrotum. Pages 165–170 *in* J. H. Calaby and C. H. Tyndale-Biscoe, editors. Reproduction and evolution: Proceedings of the Fourth International Symposium on Comparative Biology of Reproduction. Australian Academy of Science, Canberra.

De Jong, W. W., and A. Zweers. 1980. Study of eye lens protein confirms relationship of manatee with hyraxes and elephants. Acta Amazonica 10:897–902.

Gambell, R. 1985. Fin whale *Balaenoptera physalus* (Linnaeus, 1758). Pages 171–192 *in* S. H. Ridgway and R. J. Harrison, editors. Handbook of marine mammals, volume 3: the sirenians and baleen whales. Academic Press, New York.

Glover, T. D., and J. B. Sale. 1968. The reproductive system of male rock hyrax (*Procavia* and *Heterohyrax*). Journal of Zoology 156:351–362.

Grocock, C. A., and J. R. Clarke. 1975. Spermatogenesis in mature and regressed testes of the vole (*Microtus agrestis*). Journal of Reproduction and Fertility 43:461–470.

Hartman, D. S. 1979. Ecology and behavior of the manatee (*Trichechus manatus*) in Florida. Special Publication 5, American Society of Mammalogists, Lawrence, Kans. 153 pp.

Johnson, A. D., W. R. Gomes, and N. L. Vandemark. 1970. The testis. Volume 1: development, anatomy, and physiology. Academic Press, New York. 684 pp.

Laws, R. M. 1956. Growth and sexual maturity in aquatic mammals. Nature 178:193–194.

Laws, R. M. 1969. Aspects of reproduction in the African elephant (*Loxodonta africana*). Journal of Reproduction and Fertility Supplement 6:193–217.

*Marmontel, M., T. J. O'Shea, and S. R. Humphrey. 1990. An evaluation of bone growth-layer counts as an age-determina-

[5] An asterisk denotes unpublished material.

tion technique in Florida manatees. Document PB 91-103564, National Technical Information Service, Springfield, Va. 94 pp.

Marsh, H. 1995. The life history, pattern of breeding, and population dynamics of the dugong. Pages 75–83 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Marsh, H., G. E. Heinsohn, and T. D. Glover. 1984. Changes in the male reproductive organs of the dugong, *Dugong dugon* (Sirenia: Dugongidae), with age and reproductive activity. Australia Journal of Zoology 32:721–742.

Millar, R. P., and T. D. Glover. 1973. Regulation of seasonal sexual activity in an ascrotal mammal, the rock hyrax, *Procavia capensis*. Journal of Reproduction and Fertility Supplement 19:203–220.

*Odell, D. K., D. J. Forrester, and E. D. Asper. 1981. A preliminary analysis of organ weights and sexual maturity in the West Indian manatee (*Trichechus manatus*). Pages 52–65 *in* R. J. Brownell, Jr., and K. Ralls, editors. The West Indian manatee in Florida. Workshop proceedings, Orlando, Fla., 27–29 March 1978. Special Publication of the Fla. Department of Natural Resources, Tallahassee.

Putt, F. A. 1951. A modified Ziehl-Neelsen method for demonstration of leprosy bacilli and other acid-fast organisms. American Journal of Clinical Pathology 21(1):92–95.

Rathbun, G. B., J. P. Reid, R. K. Bonde, and J. A. Powell. 1995. Reproduction in free-ranging Florida manatees. Pages 135–156 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Rommel, S. A., D. A. Pabst, W. A. McLellan, J. G. Mead, and C. W. Potter. 1992. Anatomical evidence for a countercurrent heat exchanger associated with dolphin testes. The Anatomical Record 232:150–156.

Ryg, M., T. G. Smith, and N. A. Ritsland. 1991. Seasonal and developmental changes of reproductive organs of male ringed seals (*Phoca hispida*) in the Svalbard area. Journal of Zoology 224:93–100.

Sharpe, R. M., S. Maddocks, and J. B. Kerr. 1990. Cell-cell interactions in the control of spermatogenesis as studied using Leydig cell destruction and testosterone replacement. American Journal of Anatomy 188:3–20.

Short, R. V., T. Mann, and M. F. Hay. 1967. Male reproductive organs of the African elephant, *Loxodonta africana*. Journal of Reproduction and Fertility 13:517–536.

Appendix. Citation, recipe, and results of Putt's stain (Putt 1951).

Required reagents

A. H_2O-90 mL, methanol 10 mL, phenol, 5 magenta-III.
B. Sat. aq sol. lithium carbonate.
C. 0.5% acetic acid in 95% alc.
D. 0.5% meth. blue in abs. alc.

Procedure:

1. water
2. A - 5 min
3. B - 1 min
4. C - 3–5 min until sections pale pink
5. Abs. alc. wash
6. D - 1 min
7. Abs. alc. - 2 changes (30 s each)
8. neutral mountant

Results: Spermatids and spermatozoa - magenta
Other tissue - light blue

Age and Reproduction in Female Florida Manatees

by

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Abstract. Data from the carcasses of 821 female Florida manatees (*Trichechus manatus latirostris*) recovered between 1976 and 1991 were analyzed in this study. Age and information on reproduction of 275 specimens were available. Estimates of ages were based on counts of growth-layer groups in the dome portion of the tympano-periotic bone complex. Bone resorption in specimens older than 20 years may affect the interpretation of the depositional patterns. The estimated age of the oldest female in the sample was 59 years. Reproduction status was determined from field records and from histological examination. Females mature sexually when they are 3 years old (between 3 and 4 years of age) and probably first reproduce when they are 4 years old. Forty-six percent of the females in the sample for which information on reproduction was available were considered mature; of these, 40% were reproducing. Three schedules (conservative, intermediate, and optimistic) are presented for each estimated reproduction parameter. The intermediate values better represent reality and are used throughout the text. At any one time, 33% of the mature females are pregnant. This translates into an average period of 3.0 years between births. Age-specific fecundity remains relatively unchanged (0.24) from age of first parturition throughout life. Reproduction patterns in older females are not clear because of the scarcity of old-age specimens.

Key words: *Trichechus manatus latirostris*, reproduction, age determination, fecundity.

Florida manatees (*Trichechus manatus latirostris*) are listed as endangered because of anthropogenic mortality and habitat alteration (*[2]U.S. Fish and Wildlife Service 1989). The recovery plan (*U.S. Fish and Wildlife Service 1989) calls for the development of population models to assist with establishing criteria to remove the manatee from endangered status. Demographic parameters for modeling include age structure, sex ratio, and age-specific fecundity and mortality, estimation of which depends on the accurate aging of individuals (Caughley 1977), and an age-determination technique had to be developed to allow the estimation of some of these parameters in Florida manatees.

Data in this study originally were from carcasses of female manatees recovered in Florida and adjacent states by cooperating members of the southeastern United States Stranding Network between April 1976 and December 1991. The specimens were measured and processed according to standard procedures (*Bonde et al. 1983).

I collected biological data from this large sample of manatee carcasses and matched them with estimates in newly derived age classes to determine age-related aspects of reproduction. During necropsies, various institutions (*Bonde et al. 1983; Ackerman et al. 1995) collected tissue specimens for eventual use in studies of aging and reproduction. Whenever the state of decomposition permitted, a cause of death was determined from each carcass. Because I wanted to estimate fecundity (calculated as live young born to a female), I examined original necropsy data sheets for specimens in the dependent-calf category for indications of premature deaths. I reviewed carcass size, level of healing of the umbilicus, floatability of lung tissue, and presence or absence of meconium in the digestive tract. Twenty-two specimens were aborted or stillborn calves and were not included in my analyses. The revised data set included 821 females; the ages of 511 were estimated by growth-layer-group counts (Table 1).

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[2] An asterisk denotes unpublished material.

Table 1. Reproduction status of female Florida manatees (*Trichechus manatus latirostris*) collected between 1976 and 1991 in the southeastern United States.

Reproduction status		Total number	Number aged	Number not aged
Immature		248	132	116
	Pregnant	47	33	14
Mature (n = 212)	Lactating	38	27	11
	Resting	127	83	44
Status unknown		361	236	125
Total		821	511	310

Age Determination

Dentinal growth-layer counts are widely used for age determination in cetaceans (*Perrin and Myrick 1980) and dugongs (*Dugong dugon*; *Marsh 1980, 1995) but cannot be used for manatees because of the indeterminate number of teeth and lifelong horizontal tooth replacements (Domning and Hayek 1984). The record of layers in teeth becomes incomplete after the first cheek teeth are replaced. Because of this problem, I determined the feasibility of estimating age with analysis of other hard structures. This method, which was recently developed, is the count of growth-layer groups in the dome portion of the tympano-periotic bone complex (*Marmontel et al. 1990). The technique consists of decalcifying a slab of bone and obtaining 40-µm thick sections by using a freezing microtome and subsequently staining the sections with hematoxylin. The method was validated in the examinations of 16 known-age, minimum known-age, or tetracycline-marked individuals that revealed one growth-layer group per year (Fig. 1).

The process of bone resorption begins to interfere with the estimation of age at about age 15–20, when some of the layers may be obliterated. The bone was affected by resorption, allowing the assignment of only a minimum age in 32 cases, representing 22% of the adult females for which ear bones were available (n = 143). Under these circumstances, a best-estimate approach was taken by examining the structure of the bone, the extent and degree of resorption, and the distances between visible layers. Initially, the first-year zone (represented by a change in the structure of the bone) was identified or, if that was not visible, the first growth line. Then all subsequent visible growth lines were counted. Interrupted lines were followed along the microscopic slide whenever possible. When large areas were affected by resorption, the number of missed lines was estimated on the basis of the average distance between growth-layer groups; taken into consideration was that the first 3–6 growth-layer groups are wider than subsequent groups. Possible minimum and maximum ages were assigned, and the midpoint was used as the estimated age. Five readings of each earbone specimen were taken. With one exception, all females who were 21 years old or older were classified by this method.

Age Composition and Longevity

The frequency distribution of ages of the females in the carcass sample was highly skewed (Fig. 2). The average age of sexually mature females for which information on reproduction status was available (n = 143; Fig. 3) was 12.6 years. This was similar to a value of 12.9 years obtained under the assumption that all 5-year-old or older females are mature (n = 208) and from known mature specimens in age class 3 (between 3- and 4-year-old individuals; n = 2) and age class 4 (between 4- and 5-year-old individuals; n = 7).

Manatees may reach age 60. The highest estimated age was of a 362-cm-long total length (TL) female (M-157[3])—a victim of a boat strike—whose carcass was found in June 1979. This female was more than 51 years old; the best estimate was 59 years (age class ~59). A specimen (KDL-8745) that drowned in a shrimper's net in Georgia in September 1987 was about 39 years old. The Florida manatee that has been held longest in captivity (Snooty) is alive at 44 years old in 1992, and one captive female has continued to reproduce throughout her 35-year captivity in the Miami Seaquarium (D. K. Odell, Sea World of Florida, personal communication). These estimated maximum ages also correlate with an estimated life span of 73 years in dugongs (Marsh 1995) and with estimated longevity from statistical analysis of survival (O'Shea and Langtimm 1995). Although longevity in manatees may be high, only 19 (3.7%) of the examined females were older than 25 years (n = 511).

Reproduction

The age at which individuals begin reproducing is an important point in the life history. Age at sexual maturation, age at first parturition, and age-specific fecundity are valuable biological parameters for population modeling and,

[3] The identification numbers of manatees are provided for completeness of information.

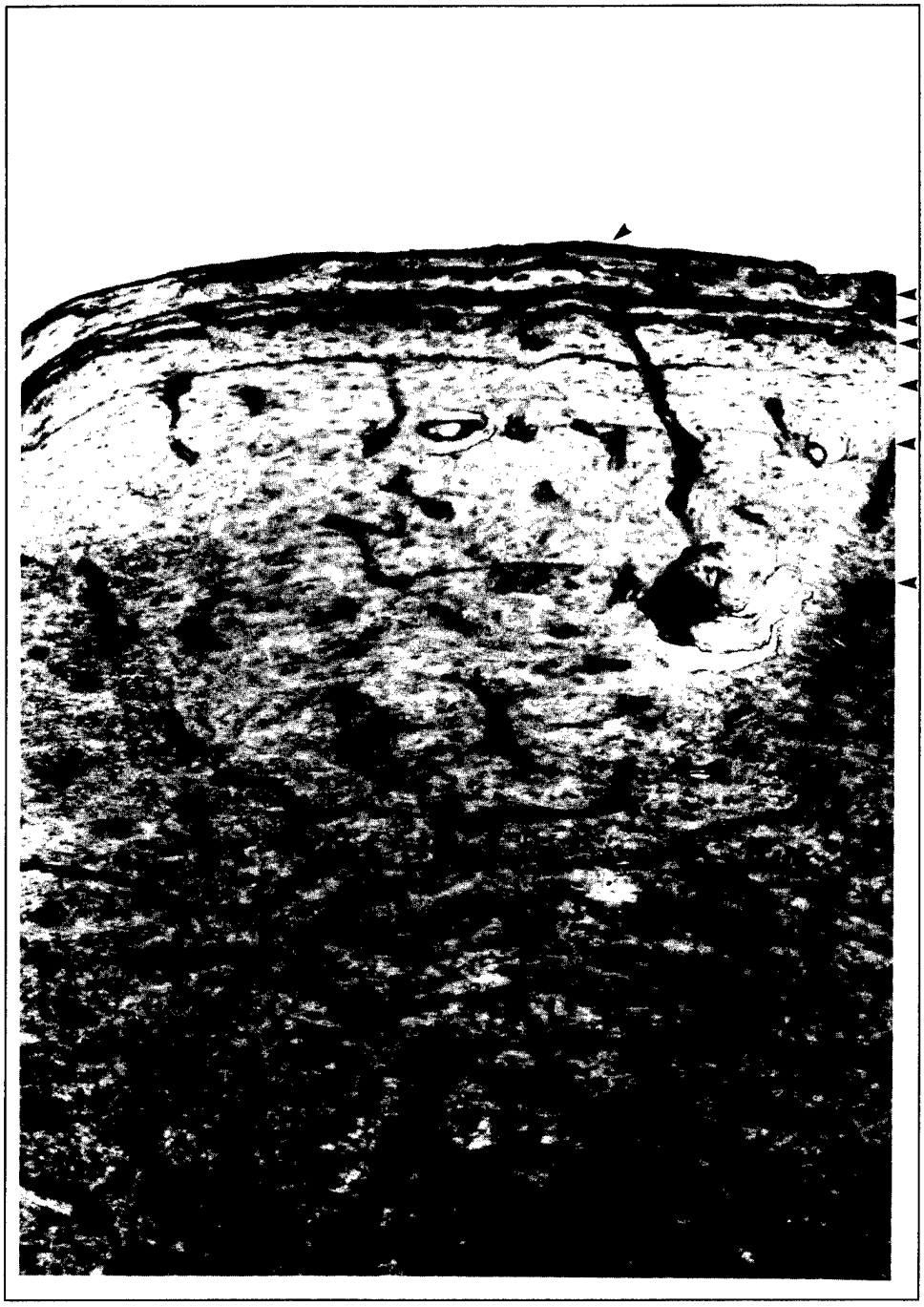


Fig. 1. Photomicrograph of the ear bone of a female Florida manatee (*Trichechus manatus latirostris*) carcass (BS-36, KDL-8827, Felicity), used in the validation of the age-estimation technique. This was a resident female from Blue Spring, upper St. John's River, Florida, born in May 1980, whose carcass was found in April 1988. The *arrows* point to the adhesion lines that correspond with growth-layer groups. The first arrow represents the first-year zone.

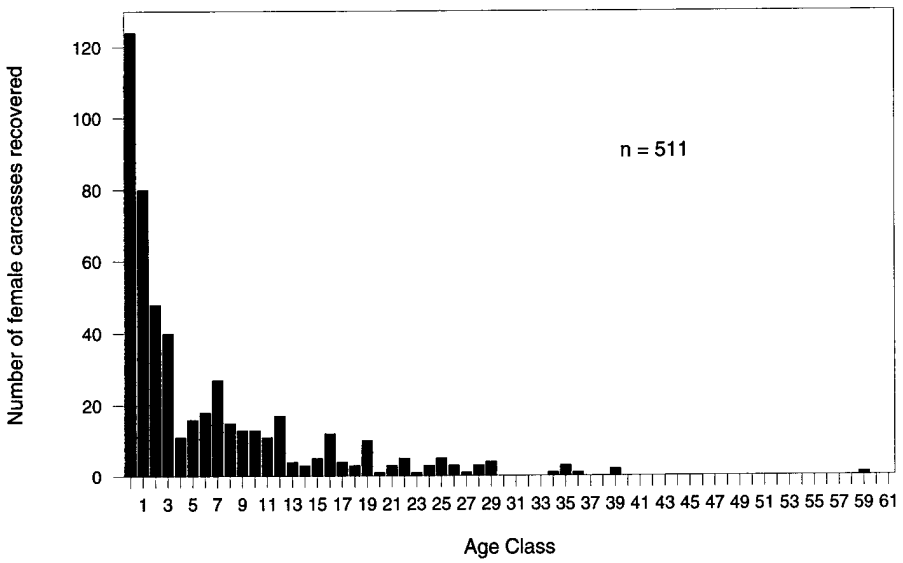


Fig. 2. Frequency distribution of age classes of 511 female Florida manatees (*Trichechus manatus latirostris*) whose carcasses were recovered in the southeastern United States between April 1976 and December 1991.

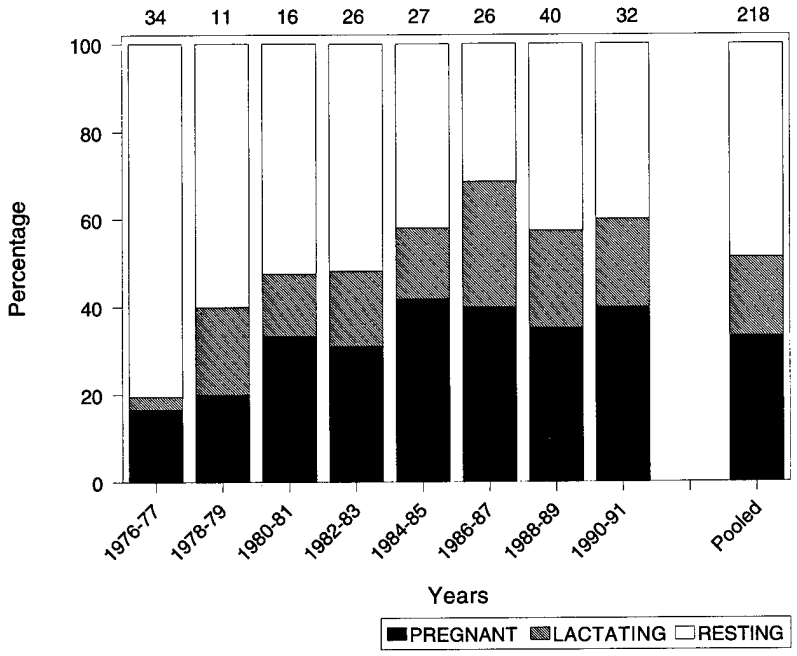


Fig. 3. Reproduction status (pregnant, lactating, or resting by 2-year interval) of mature female Florida manatees (*Trichechus manatus latirostris*) whose carcasses were recovered in the southeastern United States, 1976–1991.

coupled with mortality, influence the ability of a population to replace itself.

Data on reproduction were obtained from the macroscopic and microscopic examination of reproductive tracts of 77 carcasses of females ranging from 115 to 375 cm TL and from the review of 460 necropsy sheets with information compiled over the years by various field investigators. Information on age and reproduction condition of 275 females (132 immature and 143 mature females; Table 1) was available. Determination of sexual maturity involved examining follicular development and identifying the presence of corpora lutea or albicantia in the ovaries, which indicate previous ovulation (Mossman and Duke 1973).

The rate of ovulation may be used as a parameter for modeling reproduction if each ovulation results in one corpus luteum and all corpora albicantia remain throughout life, representing a permanent record of the number of times a female ovulated (Perrin and Donovan 1984). One must also know whether all ovulations resulted in pregnancies and, if not, which proportion did not. Similar to dugongs (Marsh et al. 1984; Marsh 1995), manatees are polyovular (Fig. 4) and produce an average of 36.3 corpora lutea/ovary/pregnancy. If the corpus luteum produces only small amounts of progesterone, multiple corpora lutea may be necessary to reach sufficiently high progesterone levels for gestation (Marmontel 1988). Furthermore, corpora albicantia do not remain visible for life and are resorbed at an unknown rate (Marmontel 1988). Females may become pregnant when they first ovulate, but not every ovulation results in fertilization, and the actual pregnancy rate is therefore probably lower than the ovulation rate. Furthermore, the number of corpora varies among individuals, and the ovulation rate may change with age. Therefore, the first-time-ovulators method (DeMaster 1984) cannot be used as an index of sexual maturity, and the corpora albicantia counts do not reflect the number of ovulations.

Another technique for determining the number of pregnancies in other species is the counting of placental scars (Laws 1967; Seber 1973; Martin et al. 1976; Lindström 1981). Whereas in the related dugong the scars persist for at least several years and their number increases with age (Marsh et al. 1984), in manatees these structures probably neither remain visible for long periods nor persist throughout life (Fig. 5; Marmontel 1988). The number of placental



Fig. 4. The ovary of a mature female Florida manatee (*Trichechus manatus latirostris*), showing multiple corpora lutea (*arrows*). Numerous smaller structures are follicles.

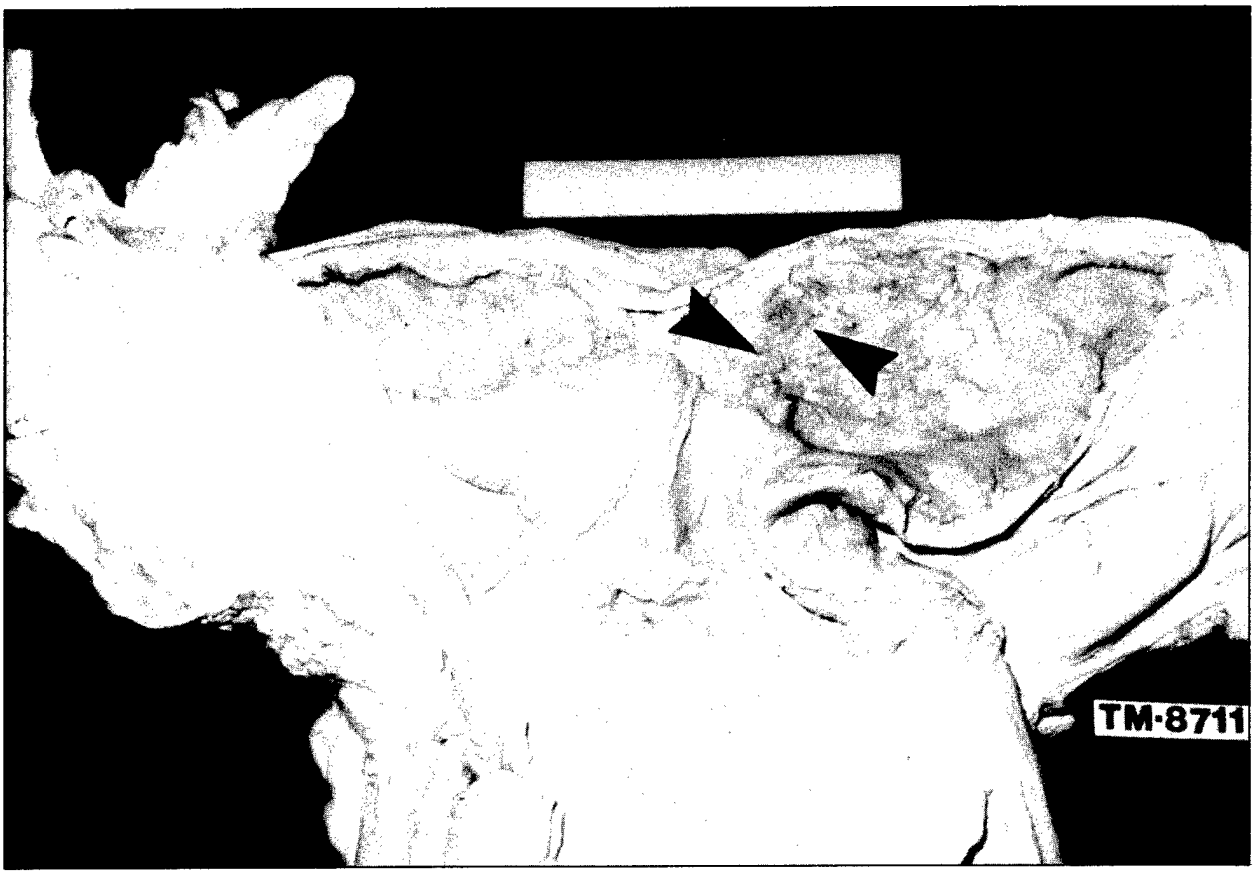


Fig. 5. Detail of reproductive tract of a lactating 329 cm TL female Florida manatee (*Trichechus manatus latirostris*; M-87–11) with one placental scar (*arrows*) in the uterine horn.

scars in manatees does not increase with TL or age of the animal, and the maximum count at any one time was four in a 307-cm-long female (M-82-28, age unknown). Only one placental scar was found in each uterine horn of a 355-cm-long female (M-85-23, age unknown). The estimated age of a known animal from the Crystal River (UF 24989, CR09F, Dihedral, M-422) was 28 years old. She gave birth to a calf in 1979 (Rathbun et al. 1990) and was 375 cm long when she died in 1985. The absence of placental scars in her uterus indicated that scars may be resorbed and disappear some time after 6 years. Therefore, placental scar counts cannot be used to estimate the number of parities in Florida manatees.

Attainment of Sexual Maturity

Age at Sexual Maturation

The determination of age of sexual maturation is usually made by three criteria: first ovulation, first conception, and first lactation (Perrin and Donovan 1984). An assessment of reproductive condition (mature versus immature) can be obtained in the field from the size of the female (although females can be of intermediate sizes for which this method is not reliable) and from the size, appearance, and vascularization of the uterus and ovaries. The presence of one or more corpora lutea, a fetus, and milk are macroscopic indications of mature, pregnant, and lactating animals. These three conditions may also be histologically identified or confirmed (Table 2).

Some female manatees in the wild attained sexual maturity at age 3, but sample sizes were not large enough to calculate a mean age of sexual maturity—defined as the age at which 50% of the females are mature (DeMaster 1978). A similar value of 3.2 was calculated as the mean age at sexual maturity of wild manatees in the Crystal River (Rathbun et al. 1995), and manatees at Blue Spring may also become sexually mature as early as age 3 (O'Shea and Hartley 1995). All salvaged carcasses of 5-year-old or older females for which information on reproduction was available were sexually mature (n = 143). The presence of corpora lutea in nulliparous females indicated that female manatees may undergo several ovulations before they first conceive (Marmontel 1988). This may partially explain the high percentage of free-ranging, living females that were pursued by herds of males but were not seen with accompanying calves in the

Table 2. Histological characteristics of ovaries, uteri, and mammary glands of female Florida manatees (*Trichechus manatus latirostris*) in different stages of reproduction. CA = corpus albicans, CL = corpus luteum, LGF = large Graafian follicle, PS = placental scar.

Stage	Ovaries	Uterus	Mammary gland
Immature, prepubescent	Pinkish, smooth and flattened surface Numerous small follicles on the surface	Glands undeveloped	Inactive
Immature, maturing	Several LGF	Early proliferative endometrium	Inactive
Sexually mature, nulliparous	Follicular: several LGF, may have CL	Proliferative endometrium, no PS	Inactive
Ovulating	Luteal: LGF, CL	Secretory endometrium, with or without PS. Not pregnant	Inactive
Parous	Follicular or luteal	Secretory endometrium	Inactive
Lactating	Luteal: no LGF, several CL	Secretory endometrium	Active
Resting	Resting: no LGF, no CL, some CA	Involuting endometrial glands. PS present or absent	Inactive

following season (Rathbun et al. 1995). Based on observations of these herds with females and calves in the Crystal River, Hartman (1979) was the first to suggest the occurrence of pseudo-estrus in manatees.

Some manatees may conceive as early as age 3, as demonstrated by the carcasses of seven 3-year-old reproductive females (Table 3). These observations are corroborated by observations of living animals in the field by Rathbun et al. (1995) and O'Shea and Hartley (1995). A dilated cervix, enlarged uterine horns, and quiescent ovaries found during the necropsy of a 3-year-old female (KDL-8852, 283 cm TL) suggested a recent abortion. Another 3-year-old female (SWF-Tm-9008-B, 302 cm TL) died in captivity as a result of pregnancy complications and retention of a dead, full-term fetus. The carcass of another 3-year-old female (M-195, 276 cm TL) had one placental scar in each of its uterine horns; according to age and body size, probably at least one of the pregnancies marked by the scars was not carried to term. One placental scar in each uterine horn was also found in the carcass of a 4-year-old female (M-199, 294 cm TL), but whether she carried both pregnancies to term could not be determined. The conditions of the described incomplete pregnancies indicated that not all young females are able to carry a pregnancy to term because of either anatomical or physiological constraints. Unsuccessful reproduction cycles before full development of the anatomical structures occur in other mammals (Buechner et al. 1966; Newson 1966; Sowls 1966; Sikes 1971; Martin 1981; Bryden and Harrison 1986; Porton et al. 1987). The large proportion of young females may partially explain the increased percentage of perinatal deaths in recent years (Ackerman et al. 1995). If more young females are conceiving but not delivering and nursing offspring, a higher early-age mortality may be expected. However, a higher mortality of young may tend to decrease the interval between births because of a shortening of the lactation anestrus.

Table 3. Total length (TL) of carcasses of female Florida manatees (*Trichechus manatus latirostris*) identified as having been in age class 3 and as having been mature.

Identification	TL (cm)	Year of death	Coast
NM 527926	254.0	1978	East
M-195	276.0	1980	East
UF 20598	277.0	1985	East
NM 530312	281.0	1978	East
KDL-8852	283.0	1988	East
KDL-8849	285.0	1988	East
SWF-TM-9008B	302.0	1990	West

The minimum age at first parity should be about 1 year after the age of maturation if the gestation period lasts approximately 12–14 months (Hartman 1979; Rathbun and Powell 1982; *Odell et al. 1992; O'Shea and Hartley 1995; Rathbun et al. 1995). In fact, the estimated age of the youngest pregnant female (UCF-9021, 283 cm TL) whose death was not related to pregnancy or parturition was 4 years.

A reduction in the age of sexual maturity is believed to represent a density-dependent response that results in a net reproduction rate greater than zero in populations under increasing exploitation (Smith 1983; Fowler 1984). The number of recovered manatee carcasses has steadily increased since 1974 (Ackerman et al. 1995), and earlier studies revealed that sexual maturity is reached at older ages than reported here (Hartman 1979; *Odell et al. 1981; Rathbun and Powell 1982). However, these earlier studies were based on much smaller sample sizes. In this study, mature 3-year-old females were collected as early as in 1978, and the data did not support changes in the age at sexual maturation during the time of analysis. Likewise, a comparison of ages at attainment of sexual maturity on the

two coasts of the Florida peninsula would be premature. Six of the seven reproductive, 3-year-old females were recovered on the eastern coast between 1978 and 1985; the seventh was found on the western coast in 1990.

Body Length at Sexual Maturation

Knowledge of the body length at sexual maturity in marine mammals allows an evaluation of animals for which the only available age-related datum is length (Perrin and Reilly 1984). The smallest female classified as mature based on field examination was 254 cm TL and her estimated age was 3 years. The average length of the seven youngest (3-year-old) mature females was 279.7 cm TL (SD = 14.2; range = 254–302 cm). A 257-cm-long female (KDL-8811, age unknown) was lactating. The average TL of the five 3-year-old immature females was 254.8 cm (SD = 13.6; range = 242–272 cm). These data are supported by the relation between body size and the area of germinal epithelium of the manatee ovary (as verified in dugongs by Marsh et al. 1984). In manatees, the area of germinal epithelium increases gradually until animals reach about 280 cm TL, when a sudden increase occurs, probably from the presence of the corpora of ovulation or from pregnancy (Marmontel 1988). This value is also comparable to the size of females at maturity (260 cm) derived by Odell et al. (*1981) based on ovary weights. According to life-history theory, long-lived animals have a delayed age of sexual maturation (Eisenberg 1981). However, some large mammals (bears, lions, whales) mature earlier than expected (Stearns 1992). That may be explained by the rapid growth and maturity of animals on high planes of nutrition and may explain the adult size of some manatees at age 3.

Reproduction Traits of Mature Females

Approximately 46% (212 of 460) of the dead females whose reproductive tracts were examined in the field or in the laboratory were classified as having been mature. Forty percent (85 of 212) of them were either pregnant or lactating at the time of death.

Reproduction Schedules

Estimates of reproduction parameters were first calculated based on a conservative schedule, containing solely the confirmed pregnant or lactating females. Alternative schedules were then calculated to provide a range of reproduction values. Females that according to comments on data sheets had recently calved or given birth within a few weeks were included in the intermediate schedule of estimates of fecundity and pregnancy rates. When a female was noted as possibly lactating (based on size of mammae or proximity of a small calf), she was added to the portion of lactating females of the sample in the intermediate schedule. Rich superficial vascularization and enlargement of the uterus are indicators of the onset of pregnancy in cetaceans (Benirschke and Marsh 1984; Collet and Robineau 1988). Females recorded in necropsy sheets as possibly having recently given birth were so classified because of enlarged and vascularized reproductive organs but without mention of a placental scar for confirmation. Therefore, those females could have been pregnant with very small fetuses. A great deal of the uncertain classifications of these females could be attributed to the condition of the carcasses. In an optimistic schedule, I also included pregnant females from the last two categories. No additional lactating females were added to the optimistic schedule because all were previously included in the intermediate schedule. The conservative schedule is believed to err by exclusion of some females that were reproductive and were not so classified; it also renders low estimates of the reproduction parameters. On the other hand, the optimistic schedule may inflate the estimates by assigning females to reproduction categories by subjective assessment of their conditions. Therefore, the intermediate schedule is believed to be the most realistic.

Resting Females

Not all females had been reproducing. Nine (19%, ages 7–23) of the dead 47 mature, histologically examined females had been neither pregnant nor lactating and did not present signs of ovarian activity (i.e., no large Graafian follicle, no corpora lutea or corpora albicantia). Another 18 (38%) were not pregnant or lactating but had active ovaries (follicular or luteal). Again, based on the histological sample, 43% were reproductive, which was close to the value of the overall sample of 40% (85 of 212). In the larger sample in the intermediate schedule (n = 261), a similarly high percentage (48.6%) of females was in the resting category (not pregnant, not lactating; Fig. 3). Ovarian activity was not necessarily assessed in all cases; the resting category probably included some pregnant or lactating females whose reproduction status was masked by decomposition. In addition, some small embryos may have been missed during necropsies (Fig. 6).

Incidence and Seasonality of Pregnancy and Lactation

The probability of detecting a fetus during gross necropsy increases with the proximity to term, simply because of fetal size. Most pregnancies (72%) in carcasses were detected during either winter or spring (Fig. 7). Fetuses in salvaged carcasses of females (n = 43), aborted fetuses (n = 14), stillborn calves (n = 29), and calves that died soon after birth (n = 40) were largest during March–July (Fig. 8). Although pregnancy occurs year-round, the data indicated that most calves are born in spring and in early summer. Relatively few large, near-term fetuses were found in fall and winter (Fig. 8).

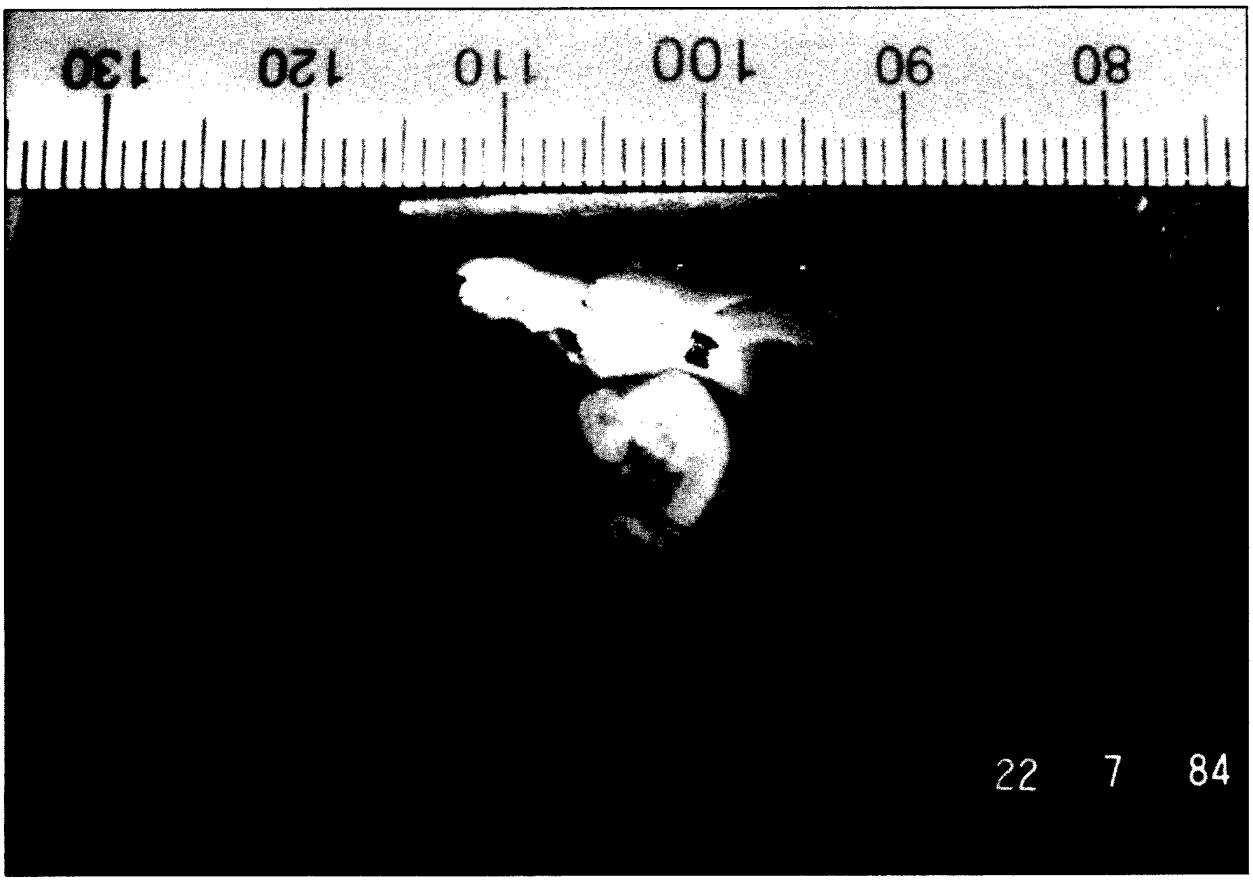


Fig. 6. Small 1.2 cm TL embryo collected from the carcass of a female Florida manatee (*Trichechus manatus latirostris*; M-395; SWF-Tm-8424-B). Undiscovered embryos because of small size or state of decomposition may bias estimates of reproduction rates. *Photo by C. Beck.*

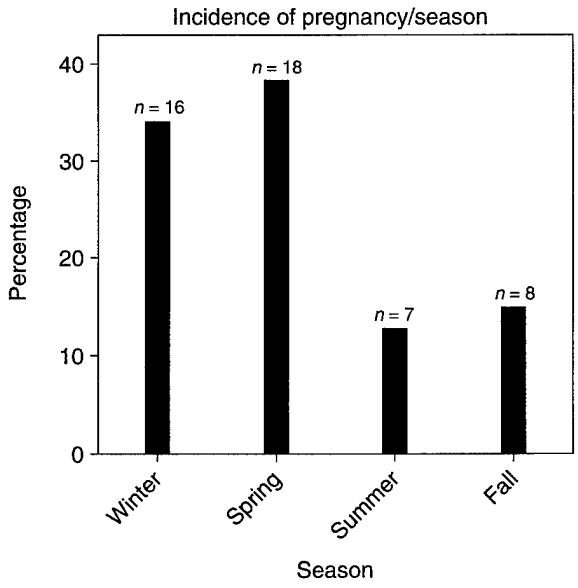


Fig. 7. Pregnancy rate by season (winter through fall) of female Florida manatees (*Trichechus manatus latirostris*) whose carcasses were collected in the southeastern United States, 1976–1991.

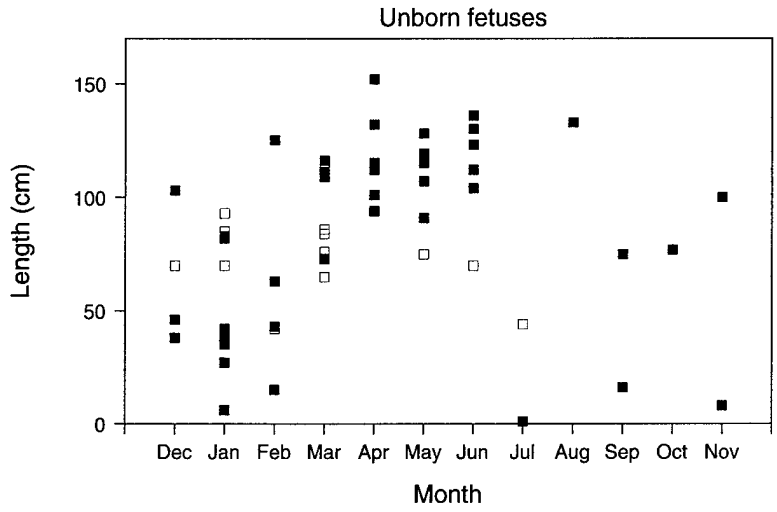


Fig. 8A. Length distribution of fetuses from dead female manatees (*closed squares*) and aborted fetuses (*open squares*).

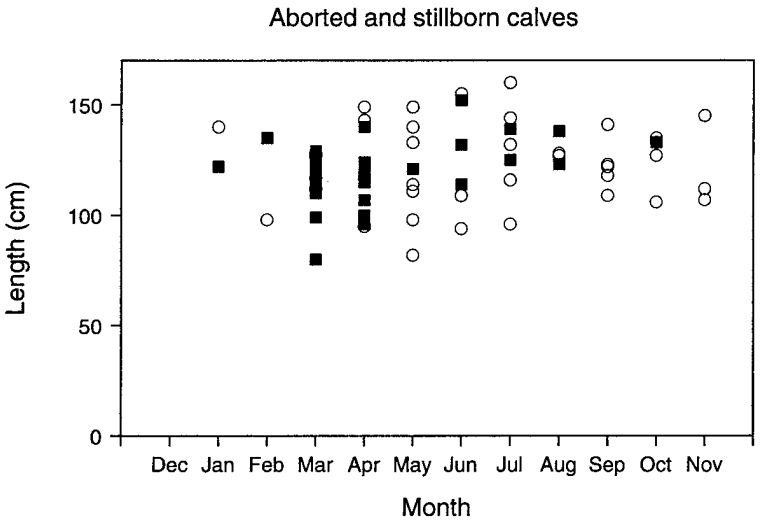


Fig. 8B. Length distribution of aborted and stillborn calves (*closed squares*), and calves that died soon after birth (*open circles*), collected in the southeastern United States (1976–1991) by month.

The lengths of unborn and aborted fetuses differed by season ($F = 9.18$, $df = 3$, $P = 0.0001$). The lengths of fetuses did not differ among warm months ($F = 0.55$, $df = 1$, $P = 0.4606$) and among cold months ($F = 0.04$, $df = 1$, $P = 0.8353$); however, the difference was significant between warm (unweighted mean of 99.4 cm) and cold months (unweighted mean of 56.8 cm; $F = 18.06$, $df = 1$, $P = 0.0001$). Irvine and Campbell (1978) reported that the number of young seen during aerial surveys was lower in winter than in summer, supporting the concept of a tendency toward parturition in spring. Apparent seasonality in numbers of observations of females pursued by herds of males and the general absence of successful births in winter in warm-water refuges during more than 15 winters of field work at the Crystal River (Rathbun et al. 1995) and at Blue Spring (O'Shea and Hartley 1995) further support this conclusion. Furthermore, Hernandez et al. (1995) indicated virtual cessation of spermatogenesis in winter. Seasonal or diffusely seasonal reproduction in Amazonian manatees (*Trichechus inunguis*; Best 1982) and in dugongs (Marsh et al. 1984) was also suggested. Milder spring and summer temperatures than winter temperatures may reduce the energetic stress on lactating females and newborn calves and favor greater survival of the calf. Breeding and giving birth in spring and summer may be an advantage for adult fe-

Table 4. Conservative reproduction schedule: reproductive condition of adult female Florida manatees (*Trichechus manatus latirostris*) collected as carcasses in the southeastern United States, 1976–1991; numbers in parentheses represent proportion of the total. The number of carcasses of pregnant females includes females that had been simultaneously pregnant and lactating.

Year	Total	Resting	Pregnant	Lactating
1976–77	34	29 (0.853)	4 (0.118)	1 (0.029)
1978–79	11	9 (0.818)	2 (0.182)	0
1980–81	16	11 (0.687)	4 (0.250)	1 (0.062)
1982–83	26	15 (0.577)	6 (0.231)	5 (0.192)
1984–85	27	13 (0.481)	9 (0.333)	5 (0.185)
1986–87	26	11 (0.423)	6 (0.231)	9 (0.346)
1988–89	40	23 (0.575)	8 (0.200)	9 (0.225)
1990–91	32	16 (0.500)	8 (0.250)	8 (0.250)
Pooled	212	127 (0.599)	47 (0.222)	38 (0.179)

males and young. Vitamin A and protein for ovulation are found in green vegetation (Hart and Guilbert 1933; Miller et al. 1942), and young manatees find nutritious spring and summer forage when they start to ingest vegetation at a few weeks of age (Husar 1977). A seasonal reproduction pattern associated with rainfall and consequent availability of vegetation has also been shown in elephants (Elephantidae) and in other equatorial species (Smith and Buss 1973; Buss 1990).

The mature sample of only confirmed cases ($n = 212$) included 22% pregnant and 17.9% lactating females (Table 4), which is comparable to 18.4% reproducing females (39.9 reproducing × 46.1 mature) in the overall sample ($n = 460$). These numbers must be cautiously interpreted because of biases if the carcass sample is not representative of all females in the population. These percentages may have been underestimated; several females were classified in necropsy records as possibly pregnant, possibly lactating, having recently calved/aborted, and having possibly recently calved or otherwise had enlarged reproductive organs. The presence of milk was also not recorded, except in two cases when it was noted as absent.

Alternatives to the conservative schedule (Tables 5 and 6) were also calculated to provide a range of reproduction values. According to the intermediate schedule (Table 5), the proportion of pregnant females was 33.3%, and the proportion of lactating females was 18% ($n = 261$; Fig. 3). The estimated proportion of reproducing females was therefore 23.6% (46.1 × 51.3), a value that conforms with Rathbun and Powell's (1982) estimate based on data from aerial surveys and carcass analysis. The proportion of pregnant females is approximately 20% higher in the optimistic schedule than in the intermediate schedule (Table 6). The conservative schedule is believed to be wrong because of the exclusion of some reproductive females that were incorrectly classified and thereby caused low values of reproduction parameters. Estimates in the optimistic schedule may be inflated because it included females placed in reproduction categories by subjective evaluations of their condition.

Table 5. Intermediate reproduction schedule: reproductive condition of adult female Florida manatees (*Trichechus manatus latirostris*) collected as carcasses in the southeastern United States, 1976–1991; numbers in parentheses represent proportion of the total. The number of carcasses of pregnant females includes females that had been simultaneously pregnant and lactating.

Year	Total	Resting	Pregnant	Lactating
1976–77	36	29 (0.805)	6 (0.167)	1 (0.028)
1978–79	15	9 (0.600)	3 (0.200)	3 (0.200)
1980–81	21	11 (0.524)	7 (0.333)	3 (0.143)
1982–83	29	15 (0.517)	9 (0.310)	5 (0.172)
1984–85	31	13 (0.419)	13 (0.419)	5 (0.161)
1986–87	35	11 (0.314)	14 (0.400)	10 (0.286)
1988–89	54	23 (0.426)	19 (0.352)	12 (0.222)
1990–91	40	16 (0.400)	16 (0.400)	8 (0.200)
Pooled	261	127 (0.486)	87 (0.333)	47 (0.180)

Table 6. Optimistic reproductive schedule: reproductive condition of adult female Florida manatees (*Trichechus manatus latirostris*) collected as carcasses in the southeastern United States, 1976–1991; numbers in parentheses represent proportion of the total. The number of carcasses of pregnant females includes females that had been simultaneously pregnant and lactating.

Year	Total	Resting	Pregnant	Lactating
1976–77	39	29 (0.743)	9 (0.231)	1 (0.256)
1978–79	15	9 (0.600)	3 (0.200)	3 (0.200)
1980–81	22	11 (0.500)	8 (0.364)	3 (0.136)
1982–83	32	15 (0.469)	12 (0.375)	5 (0.156)
1984–85	36	13 (0.361)	18 (0.500)	5 (0.139)
1986–87	37	11 (0.297)	16 (0.432)	10 (0.270)
1988–89	60	23 (0.383)	25 (0.417)	12 (0.200)
1990–91	46	16 (0.348)	22 (0.478)	8 (0.174)
Pooled	287	127 (0.442)	113 (0.394)	47 (0.164)

Therefore, I interpret the intermediate schedule as the most realistic.

Pregnant, lactating females were recorded only twice (0.9% of the sample of sexually mature females). However, both fetuses were large, suggesting that milk was present for nursing the new infants, not that the female had become pregnant while nursing an earlier calf. When one of these two carcasses (M-021, 299.7 cm TL, age unknown) was recovered in April 1976, a 152-cm fetus protruded from its genital aperture; when the other carcass (M-155, 355 cm, age ~25 years) was found in June 1979, it carried a 123-cm fetus. This further implies that female manatees cannot give birth more frequently than every 2 years if the calf survives to independence.

Manatees usually give birth to single calves but may have twins (O'Shea and Hartley 1995; Rathbun et al. 1995). Each of two carcasses simultaneously carried two fetuses at necropsies (M-331, 375 cm TL, age ~29; M-389; 313 cm TL, age 7; Fig. 9), corresponding to 4% of all detected pregnancies in the carcass sample. Circumstantial evidence suggested three other cases of twinning. Three pairs of dead young or near-term fetuses were found at the same time in the same location (M-190, female perinatal young, 103 cm TL; M-191, female perinatal young, 110 cm TL; MSE-8915, female, 132 cm TL; MSE-8914, male, ~130-cm; MSW-187, female, 83 cm TL; KDL-8906, male, 85 cm TL). The proportion of twins in the carcass sample (4%) was similar to the proportion reported by Laws (1967) in African elephants (*Loxodonta africana*) but slightly higher than the percentage observed in nursing manatee young in a larger sample in the wild (O'Shea and Hartley 1995; Rathbun et al. 1995) and higher than the norm in uniparous mammals (Slijper 1966; Laws 1967). The death of one or both twins near birth may explain the discrepancy between observed samples in the field and carcass samples. Twinning has also been reported in the Antillean subspecies (*T. m. manatus*; Gumilla 1745; Charnock-Wilson 1968).

Size at birth

The lengths and the sex of fetuses and carcasses of small young were determined. Information was recorded that facilitated the classifications as unborn fetuses removed from the female at necropsy, aborted fetuses in prenatal developmental stages, and stillborn or born-alive calves. A distinction between live and stillborn births was based on the inability of the lung tissue of stillborn animals to float, indicating the absence of air in the lungs because the animal had never breathed. Born-alive calves were judged to have died soon after birth based on meconium in the gastrointestinal tracts and on unhealed umbilici. The largest unborn fetus was recorded in April 1976 and measured 152 cm TL or 50.7% of its mother's (M-021) body length. The largest newborn (with an attached umbilical cord) was 160.0 cm TL. Based on lengths of stillborn calves and calves born alive but dying soon after birth ($n = 69$; Table 7), length at birth ranged from 80 to 160 cm with a mean of 122 cm (SD = 17.1).

Age-specific Fecundity and Senescence

Age-specific fecundity was calculated as the number of female births/female/year (Caughley 1977) with the formula

$$m_x = B_x/2f_x$$

where f_x is the number of sampled mature females and B_x is the number of females classified as pregnant or lactating. Because manatees give birth less frequently than once a year, the number of lactating females was adjusted by an arbitrary factor of 0.4 to account for dead females that may have been in the first year of the lactation period. This value was chosen as being intermediate between the possibilities of one half and one third of the lactating females recently

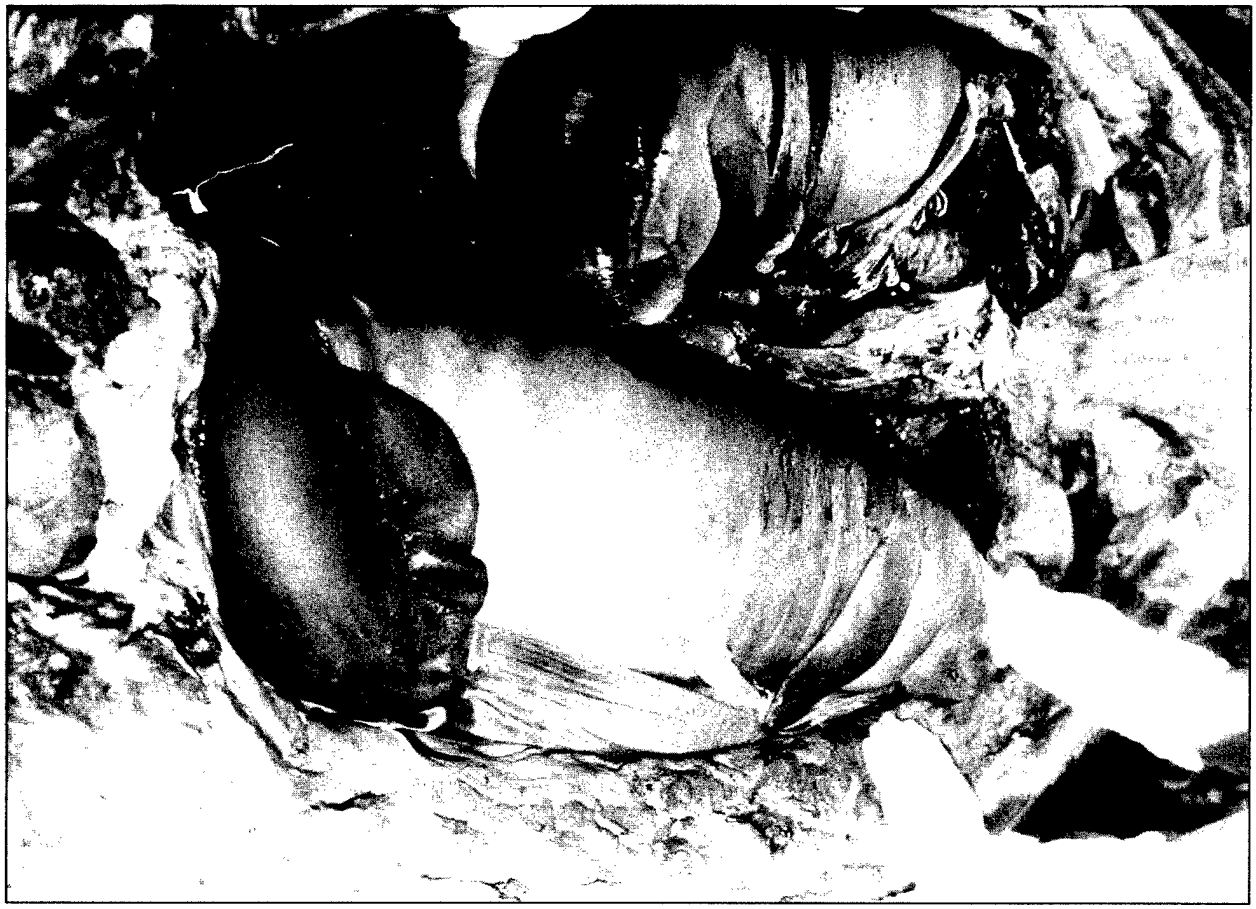


Fig. 9. Twin, near-term fetuses found during the necropsy of a female Florida manatee (*Trichechus manatus latirostris*; M-331), estimated age class 29. Both fetuses were female and measured 132 and 135 cm TL. *Photo by C. Beck.*

having given birth. Because the range of values by year was wide, the data were grouped in 2-year intervals to produce a smoother curve and more comparable sample sizes (Table 8).

Age-specific fecundity increased from zero (age class 0) to 0.27 at age of first parturition (age classes 4–5) and remained at a level of approximately 0.24 in the intermediate schedule (age classes 4 through 29; Fig. 10). Values in age class 3 were included in this schedule (4 females with indication of pregnancy or parturition; see Age at Sexual Maturation) that were not included in the calculation of mean age-specific fecundity. Values did not differ across the age classes in either schedule (Table 9). The mean age-specific fecundity was 0.19 and 0.27 in the conservative and optimistic schedules (Table 8). In most mammals, the fecundity rises from puberty and levels to a plateau (Caughley 1977). Fecundity is seemingly constant throughout the life of a female manatee. Nevertheless, Caughley (1977) pointed out that deviations from a constant rate in adult fecundity can only be detected in large samples.

Table 7. Morphometrics of unborn and newborn Florida manatee (*Trichechus manatus latirostris*) carcasses that were collected in the southeastern United States, 1976–1991.

	Length (cm)					Weight (kg)				
Stage	Minimum	Maximum	Mean	Standard deviation	*n*	Minimum	Maximum	Mean	Standard deviation	*n*
Unborn fetus	1.0	152.0	83.5	42.3	43	1.0	45.0	18.8	17.0	19
Aborted fetus	42.0	112.0	75.3	18.1	42	1.4	32.0	12.5	12.6	7
Stillborn calf	80.0	152.0	121.0	15.3	29	9.0	35.0	24.1	8.1	9
Live birth	82.0	160.0	122.7	18.5	40	8.0	47.6	25.8	9.8	24

Table 8. Age-specific fecundity and standard error (SE) of carcasses of female Florida manatees (*Trichechus manatus latirostris*; age classes 2–3 through 38–39) in three reproduction schedules, collected in the southeastern United States, 1976–1991. *Blanks* indicate no data.

	Schedule					
	Conservative		Intermediate		Optimistic	
Age classes	Mean	SE	Mean	SE	Mean	SE
2–3			0.183	0.032	0.183	0.032
4–5	0.150	0.045	0.267	0.037	0.285	0.035
6–7	0.145	0.016	0.219	0.013	0.228	0.013
8–9	0.174	0.016	0.211	0.015	0.256	0.014
10–11	0.115	0.016	0.180	0.015	0.233	0.014
12–13	0.150	0.025	0.173	0.025	0.212	0.024
14–15	0.314	0.066	0.314	0.066	0.355	0.053
16–17	0.200	0.036	0.225	0.035	0.225	0.035
18–19	0.175	0.047	0.240	0.043	0.264	0.040
20–21	0.175	0.095	0.175	0.095	0.314	0.066
22–23	0.000	0.000	0.125	0.041	0.125	0.041
24–25	0.240	0.085	0.271	0.063	0.271	0.063
26–27	0.500	0.500	0.500	0.500	0.500	0.500
28–29	0.125	0.083	0.200	0.080	0.250	0.072
30–31						
32–33						
34–35	0.100	0.150	0.233	0.141	0.233	0.141
36–37						
38–39	0.200	0.160	0.350	0.238	0.350	0.238
Average AC 4–29	0.189		0.238		0.271	

No peak was identifiable in the potential reproduction or decline of reproduction with age. However, sample sizes in the older age classes were small. Senescence has only been documented in a few species such as humans (Asdell 1964), other large primates (Graham 1986), some cetaceans (Perrin et al. 1977; Marsh and Kasuya 1984), and elephants (Laws et al. 1975). In cetaceans, senescent ovaries are described as lacking follicles, corpora lutea, and young or partially regressed corpora albicantia (Perrin and Donovan 1984). Close gross examination of 11 and histological processing of 37 reproductive tracts from mature female manatees did not reveal signs of senescence. Changes in ovulation rates—also indicative of senescence—cannot be detected in manatees because of the polyovular condition of their ovaries. Fluid-filled ovarian cysts are associated with inactive ovaries in dugongs (Marsh et al. 1984). However, in manatees

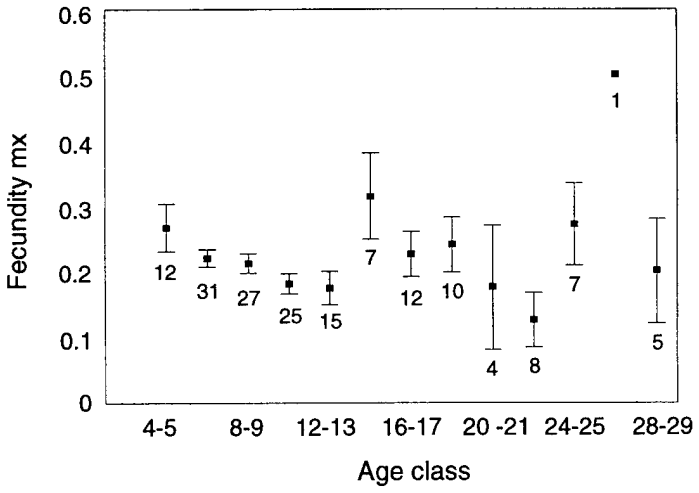


Fig. 10. Age-specific fecundity (female births/female/year) by 2-year age-class intervals in a sample of female Florida manatees (*Trichechus manatus latirostris*) whose carcasses were salvaged. *Squares* represent fecundity values, *bars* represent standard error, and *numbers below bars* represent sample size.

Table 9. Age-specific fecundity of Florida manatee (*Trichechus manatus latirostris*) carcasses in the conservative, intermediate and optimistic reproduction schedules. Mean in age classes 4 through 29 was calculated. Chi-square goodness-of-fit tests were used to test for differences in fecundity among the three reproduction schedules.

Schedule	Mean	χ^2	*df*	*p*
Conservative	0.189	11.994	12	0.446
Intermediate	0.238	6.759	12	0.873
Optimistic	0.271	7.297	12	0.837

these cysts were always associated with active ovaries, pregnancy, or recent birthing. An extremely large female (UF 24989, M-422, CR09F, 375 cm TL, 1,650 kg) at an estimated age of 28 years had four fluid-filled cysts and few regressed corpora albicantia in the ovaries; the generally smooth ovarian surface seemed to be exhausted of follicles. Nevertheless, 16 corpora lutea in the right ovary and 8 in the left ovary indicated that she was still ovulating. Other observations also revealed that manatees remain reproductive into old age. Juliet, brought to the Miami Seaquarium as an unknown-aged adult in 1958, is still reproductive after 34 years in captivity (D. K. Odell, Sea World of Florida, personal communication). Another female (M-331, 375 cm TL, estimated age ~29 years) was carrying twins when she died as a result of a collision with a boat in April 1983. A female (KDL-8867, 332 cm, estimated age ~35 years) had given birth a few weeks before her carcass was found and was lactating. A well nourished female (KDL-8745, age ~39 years) had recently given birth and was lactating when she drowned in a shrimper's net. Based on only these two old reproductive females, minimum estimates of the coefficient of female fertility (*B*, or maximum length of breeding period; Braham 1984) are 0.55–0.60 of the life span, given an assumed maximum life span of 60 years.

Annual Pregnancy Rates

The pregnancy rate was expressed as the proportion of pregnant females in the sample of sexually mature females. Data were grouped in 2-year intervals between 1976 and 1991. More than half of the mature females were reproducing (including simultaneously pregnant and lactating females) in the intermediate schedule. The proportion of pregnant females (Fig. 3) varied from 16.7 (1976–77) to 41.9% (1984–85; Table 5). No temporal trends in the probability of female pregnancy grouped in 2-year or 1-year intervals in the conservative schedule (Table 4) could be detected from 1976–91 by logistic regression ($P = 0.1$ for 8 biannual periods and 16 individual years). A trend toward increase was detected ($P = 0.0001$) in the intermediate and optimistic schedules when reproduction data were grouped by 2-year intervals (Tables 5, 6). If the period 1976–77 is excluded from the analysis because of uncertainty about the representativeness of the sample, a trend is still present in data grouped biannually ($P = 0.0388$) and in 14 individual years $P = 0.005$).

Annual pregnancy rates were calculated from the quotient of the proportion of pregnant females and the gestation period in years (Perrin and Reilly 1984). The calculation rested on the assumptions that the distribution of the reproduction condition in the sample reflected that in the actual population, biases from seasonal birthing did not exist, and no pregnancies were undetected (Perrin et al. 1977). Some or all of the assumptions may have been violated because sick and non-reproductive females may die at a greater rate than healthy animals, birthing is seasonally diffuse, and some pregnancies went undetected for reasons such as decomposition, examiner's inexperience, or early pregnancy stage. The variance in the annual pregnancy rates was calculated as

$$\mathrm{APR} * [(1-\mathrm{APR})/n]$$

(Perrin and Reilly 1984). The estimated annual pregnancy rates spanned a two-fold increase (0.190 to 0.394) by schedule (conservative, intermediate, or optimistic) and by gestation period (Tables 10–12). The range of the estimated gestation length was selected based on studies in the field and on studies of captive manatees (Odell et al. 1995, Rathbun et al. 1995); 12 months was the most probable length (*Dekker 1977; Rathbun et al. 1995). The percentage of reproductive females was lowest during 1976–77. This low value was probably due to a time-sampling effect; 1977 began with a severe winter, and an unusually high number of carcasses was recorded (*Irvine et al. 1981). Some of these were not thoroughly examined and many were badly decomposed. In addition, expert recognition of reproductive conditions may not have been fully developed by the various salvage workers early in the program. Other environmental conditions may have influenced the overall temporal fluctuation in pregnancy rates but are difficult to evaluate with available data. An increase in the annual pregnancy rate is expected in exploited populations such as in cetaceans (Mackintosh 1942; Laws 1961; Fowler 1984), pinnipeds (Bowen et al. 1981), and coyotes (Knowlton 1972). The proportion of reproducing females seemingly almost doubled during 1976–91. If adult mortality was excessive, the reproduction rate may have increased. However, cases of density-dependence often occur in populations at carrying capacity (Fowler 1984) and entail a greater availability of food resources after a reduction in population size. There is no evidence that manatees are at the carrying capacity in Florida. Furthermore, the density-dependence concept is based on a decreased manatee density. Although population-

Table 10. Conservative reproduction schedule: parameters in reproduction based on a gestation period of 12 months (T_G = 1.0), 13 months (T_G = 1.08) and 14 months (T_G = 1.17) of female Florida manatee (*Trichechus manatus latirostris*) carcasses collected in the southeastern United States (1976–1991). APR = annual pregnancy rate, SE = standard error, IB = interval between births, GARR = gross annual recruitment rate.

	Gestation period of 12 months					Gestation period of 13 months					Gestation period of 14 months				
Years	APR	SE	IB	SE	GARR	APR	SE	IB	SE	GARR	APR	SE	IB	SE	GARR
1976–77	0.118	0.009	8.5	0.68	0.027	0.109	0.009	9.2	0.77	0.025	0.101	0.009	9.9	0.87	0.023
1978–79	0.182	0.035	5.5	1.06	0.042	0.168	0.034	5.9	1.21	0.039	0.156	0.033	6.4	1.36	0.036
1980–81	0.250	0.027	4.0	0.43	0.057	0.231	0.026	4.3	0.49	0.053	0.214	0.026	4.7	0.56	0.049
1982–83	0.231	0.016	4.3	0.30	0.053	0.213	0.016	4.7	0.35	0.049	0.197	0.015	5.0	0.39	0.045
1984–85	0.333	0.017	3.0	0.16	0.077	0.308	0.017	3.2	0.18	0.071	0.286	0.017	3.5	0.20	0.066
1986–87	0.231	0.016	4.3	0.30	0.053	0.213	0.016	4.7	0.35	0.049	0.198	0.015	5.0	0.39	0.045
1988–89	0.200	0.010	5.0	0.25	0.046	0.185	0.010	5.4	0.28	0.042	0.171	0.009	5.8	0.32	0.039
1990–91	0.250	0.013	4.0	0.22	0.057	0.231	0.013	4.3	0.25	0.053	0.214	0.013	4.7	0.28	0.049
Mean	0.222		4.5		0.051	0.205		4.9		0.047	0.190		5.3		0.044

Table 11. Intermediate reproduction schedule: parameters in reproduction based on a gestation period of 12 months (T_G = 1.0), 13 months (T_G = 1.08) and 14 months (T_G = 1.17) of female Florida manatee (*Trichechus manatus latirostris*) carcasses collected in the southeastern United States (1976–1991). APR = annual pregnancy rate, SE = standard error, IB = interval between births, GARR = gross annual recruitment rate.

	Gestation period of 12 months					Gestation period of 13 months					Gestation period of 14 months				
Years	APR	SE	IB	SE	GARR	APR	SE	IB	SE	GARR	APR	SE	IB	SE	GARR
1976–77	0.167	0.010	6.0	0.37	0.038	0.154	0.010	6.5	0.42	0.035	0.143	0.010	7.0	0.48	0.033
1978–79	0.200	0.027	5.0	0.67	0.046	0.185	0.026	5.4	0.76	0.042	0.171	0.025	5.8	0.85	0.039
1980–81	0.333	0.022	3.0	0.20	0.077	0.308	0.022	3.2	0.23	0.071	0.286	0.021	3.5	0.26	0.066
1982–83	0.310	0.016	3.2	0.16	0.071	0.286	0.015	3.5	0.19	0.066	0.266	0.015	3.7	0.21	0.061
1984–85	0.419	0.016	2.4	0.09	0.096	0.387	0.016	2.6	0.10	0.089	0.359	0.015	2.8	0.12	0.083
1986–87	0.400	0.014	2.5	0.07	0.092	0.369	0.014	2.7	0.10	0.085	0.343	0.013	2.9	0.11	0.079
1988–89	0.352	0.009	2.8	0.07	0.081	0.345	0.009	3.1	0.08	0.075	0.301	0.009	3.1	0.09	0.069
1990–91	0.400	0.012	2.5	0.08	0.092	0.369	0.012	2.7	0.08	0.085	0.343	0.012	2.9	0.10	0.079
Mean	0.333		3.0		0.077	0.308		3.2		0.071	0.286		3.5		0.066

Table 12. Optimistic reproduction schedule: parameters in reproduction based on a gestation period of 12 months (T_G = 1.0), 13 months (T_G = 1.08) and 14 months (T_G = 1.17) of female Florida manatee (*Trichechus manatus latirostris*) carcasses collected in the southeastern United States (1976–1991). APR = annual pregnancy rate, SE = standard error, IB = interval between births, GARR = gross annual recruitment rate.

	Gestation period of 12 months					Gestation period of 13 months					Gestation period of 14 months				
Years	APR	SE	IB	SE	GARR	APR	SE	IB	SE	GARR	APR	SE	IB	SE	GARR
1976–77	0.231	0.011	4.3	0.20	0.053	0.213	0.010	4.7	0.23	0.049	0.198	0.010	7.0	0.48	0.045
1978–79	0.200	0.027	5.0	0.67	0.046	0.185	0.026	5.4	0.76	0.042	0.171	0.025	5.8	0.85	0.039
1980–81	0.364	0.022	2.7	0.16	0.083	0.336	0.021	3.0	0.19	0.077	0.312	0.021	3.2	0.22	0.071
1982–83	0.375	0.015	2.7	0.11	0.086	0.346	0.015	2.9	0.12	0.080	0.321	0.014	3.1	0.14	0.074
1984–85	0.500	0.014	2.0	0.05	0.115	0.461	0.014	2.2	0.06	0.106	0.428	0.014	2.3	0.07	0.098
1986–87	0.432	0.013	2.3	0.07	0.099	0.399	0.013	2.5	0.08	0.092	0.371	0.013	2.7	0.09	0.085
1988–89	0.417	0.008	2.4	0.05	0.096	0.385	0.008	2.6	0.05	0.088	0.357	0.008	2.8	0.06	0.082
1990–91	0.478	0.011	2.1	0.05	0.110	0.441	0.011	2.3	0.05	0.101	0.410	0.011	2.4	0.06	0.094
Mean	0.394		2.5		0.090	0.363		2.7		0.083	0.337		3.0		0.078

size estimates are unavailable, certain indices indicate the opposite, i.e., the population size may have been increasing in recent years. Trend analysis of the counts of aggregated manatees in power-plant cooling waters during winter, when adjusted for temperature, indicated a significant increase in counts of manatees on the eastern coast (Garrott et al. 1995). The relation between counts and population size is unknown, but this finding does not support a population-size decline. Densities of manatees in at least two other wintering areas, in the Crystal River and Blue Spring, have also remarkably increased since the late 1970's, even though some of those increases may be attributable to immigration from other sites in Florida (O'Shea 1988; Ackerman 1995). Therefore, the difference in the proportion of reproducing females over the years may also reflect the differences in other investigators' abilities to recognize reproduction status, in which case no density-dependence mechanism is at work. Another corroborating factor would be increasing adult-calf ratios in aerial surveys. Future researchers should examine such data.

Intervals Between Births

Intervals between births were calculated as the reciprocal of the pregnancy rate (Perrin and Reilly 1984) and their variances as

$$APR^{-4} * \sigma^2_{APR}$$

The overall value of eight 2-year periods in the intermediate schedule was 3 years if the length of gestation was 12 months (Table 11). Ovulation is physiologically suppressed during lactation, but observations of wild and captive manatees revealed that as soon as young are weaned (or lost), the female may again cycle (Hartman 1979; Odell et al. 1995). At a 1- to 2-year period of calf dependency (Hartman 1979) and a gestation of approximately another year, the value of 3 years is slightly higher than the calculated interval in free-ranging manatees (but with smaller sample sizes) by Rathbun et al. (1995) in the Crystal River, by Reid et al. (1995) on the Atlantic Coast, and by O'Shea and Hartley (1995) at Blue Spring. The Crystal River area of northwestern Florida may represent a particularly favorable area for giving birth and for rearing young, and the rates derived for manatees in that region may not necessarily represent manatees throughout Florida. Birth rates may be influenced by the age and the health of females (a potentially large variable because of non-fatal boat strikes) and factors such as females who do not recycle immediately after young are weaned, ovulations that do not lead to conception, or incomplete pregnancies. Intervals between births are also time-specific and influenced by the variability in pregnancy rates and subject to the biases in sampling. The actual number of offspring is constrained by the mortality in the age classes of the reproductive and pre-reproductive females. It is also constrained by nonlethal injuries or diseases that cause disruptions of the estrous cycle. In a total number of 36 reproduction years ($B = 0.6$) at an interval between births of 3.0 years, a female manatee produces an average of 12 young during her lifetime. At an assumed interval of 2.5 years between parturitions (O'Shea and Hartley 1995; Rathbun et al. 1995; Reid et al. 1995), the potential maximum number of offspring by a female manatee is 14. The calculated numbers of young per lifetime in manatees corresponds well with the norm in mammals (Eisenberg 1981).

Rates of Reproduction

The analysis of the database on salvaged carcasses during April 1976-December 1991 suggested a sex ratio close to 1:1 (Table 13). The average proportion of females in the sample that were mature during 1976–91 (animals for which information on reproduction is available) was 46.1% (212 of 460), and in the sample of specimens of known age and reproduction, 52% (143 of 275).

The gross annual reproduction rate was calculated as the product of the proportion of females in the population, the proportion of mature females, and the annual pregnancy rate (Smith 1983; Perrin and Reilly 1984). It represents the annual rate of the production of calves or a measure of recruitment into the total population (rather than into a specific age class) if no mortality takes place during the time of the estimate (Braham 1984; Perrin and Reilly 1984).

The average recruitment rate ranged from 0.044 to 0.090 in the three schedules; the mean was 0.077 at a gestation length of 12 months in the intermediate schedule (Table 11). This represents an approximate 8% potential increase of the population (birth rate) without mortality of young calves. Because the annual reproduction rate is sensitive to the percentage of mature females and to the annual pregnancy rate, some bias toward a low value may be expected because of violations of the assumption that the sample was representative (because of decomposition or observer-missed pregnancies). Another way to obtain an estimate of the gross reproduction rate would be to equate numbers of lactating females with numbers of calves. This excludes the young that did not survive the neonatal period but includes larger, still dependent young, potentially overestimating the true value of the parameter. The percentage of lactating females in the sample was 0.18. Hence, the real recruitment rate is probably between 8 and 18%. Only with accurate accounting of reproductive females in the population can the uncertainty associated with this estimate be removed. Field studies and aerial surveys provide a similar range of estimates. Rathbun et al. (1995) calculated an average of 13.5% calves in the Crystal River population, which includes first- and second-year young. The average percentage of calves in

Table 13. Sex ratio in different age categories of Florida manatee carcasses (*Trichechus manatus latirostris*) collected in the southeastern United States, 1976–1991; chi-square tests of even distribution of age categories, adjusted for continuity ($df = 1$).

Category	Females	Males	Ratio	χ^2	P
Unborn fetuses	14	24	0.58	0.857	0.355
Stillborn or aborted calves	21	20	1.05	0.0	1.0
Dependent calves (age classes 0–1)	508	605	0.84	4.062	0.044
Subadults (age classes 2–3)	87	80	1.09	0.075	0.784
Adults (age classes 4–59)	210	227	0.95	0.258	0.612

aerial censuses during a 15-year period was 9.56% (*Reynolds 1992), where calves were defined as less than half the length of a closely associated animal.

Low reproduction and long life span are not unique to manatees, but are part of the life-history strategies of some birds (Amadon 1964, Mertz 1971), many species of whales (Ridgway and Harrison 1985), several herbivores (Verheyen 1954; Goddard 1970; Laws et al. 1975), and a few carnivorous mammals (Ridgway and Harrison 1981; Nowak 1991). Some requisites associated with low rates of reproduction include a stable environment, approximately permanent geographic ranges, and freedom from ongoing forms of mortality such as predators. Slowly reproducing species are not good colonizers and could not recover quickly after a population crash or a massive destruction (Mertz 1971).

Antillean Manatee

In addition to the larger sample, 13 ear bones from dead females recovered in Puerto Rico were made available by the Caribbean Stranding Network. These included animals from 142 to 300 cm TL. Information on reproduction from one large female (NEP-ST-164) supported the conclusion that they reproduce into old age. This specimen had recently been pregnant and died in May 1991. Her estimated age was 25 years.

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Cited References[4]

Ackerman, B. B. 1995. Aerial surveys of manatees: a summary and progress report. Pages 13–33 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Ackerman, B. B., S. D. Wright, R. K. Bonde, D. K. Odell, and D. J. Banowetz. 1995. Trends and patterns in mortality of manatees in Florida, 1974–1992. Pages 223–258 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Amadon, D. 1964. The evolution of low reproductive rates in birds. Evolution 18:105–110.

Asdell, S. A. 1964. Patterns in mammalian reproduction. Second edition. Comstock Publishing Associates, Ithaca, New York. 670 pp.

Benirschke, K., and H. Marsh. 1984. Anatomic and pathologic observations of female reproductive organs in the short-finned pilot whale, *Globicephala macrorhynchus*. Pages 451–456 *in* W. F. Perrin, R. L. Brownell, Jr., and D. P. DeMaster, editors. Reproduction in whales, dolphins and porpoises. Reports of the International Whaling Commission (Special Issue 6), Cambridge, England.

[4] An asterisk denotes unpublished material.

Best, R. C. 1982. Seasonal breeding in the Amazonian manatee, *Trichechus inunguis* (Mammalia: Sirenia). Biotropica 14(1):76–78.

*Bonde, R. K., T. J. O'Shea, and C.A. Beck. 1983. A manual of procedures for the salvage and necropsy of carcasses of the West Indian manatee (*Trichechus manatus latirostris*). National Technical Information Service, Springfield, Va. Document PB 83-255273. 175 pp.

Bowen, W. D., C. K. Capstick, and D. E. Sergeant. 1981. Temporal changes in the reproductive potential of female harp seals (*Pagophilus groenlandicus*). Canadian Journal of Fisheries and Aquatic Science 38:495–503.

Braham, H. W. 1984. Review of reproduction in the white whale, *Delphinapterus leucas*, narwhal, *Monodon monoceros*, and Irrawaddy dolphin, *Orcaella brevirostris*, with comments on stock assessment. Pages 81–89 *in* W. F. Perrin, R. L. Brownell, Jr., and D. P. DeMaster, editors. Reproduction in whales, dolphins and porpoises. Reports of the International Whaling Commission (Special Issue 6), Cambridge, England.

Bryden, M. M., and R. J. Harrison. 1986. Gonads and reproduction. Pages 149–159 *in* M. M. Bryden and R. J. Harrison, editors. Research on dolphins. Clarendon Press, New York.

Buechner, H. K., J. A. Morrison, and W. Leuthold. 1966. Reproduction in Uganda kob with special reference to behavior. Pages 69–88 *in* I. W. Rowlands, editor. Comparative biology of reproduction in mammals. Symposia of the Zoological Society of London, 15. Academic Press, London.

Buss, I. O. 1990. Elephant life—fifteen years of high population density. Iowa State University Press, Ames. 191 pp.

Caughley, G. 1977. Analysis of vertebrate populations. John Wiley & Sons, New York. 234 pp.

Charnock-Wilson, J. 1968. The manatee in British Honduras. Oryx 9:293–294.

Collet, A., and D. Robineau. 1988. Data on the genital tract and reproduction in Commerson's dolphin, *Cephalorhynchus commersonii* (Lacépède, 1804), from the Kerguelen Islands. Pages 119–141 *in* R. L. Brownell, Jr. and G. P. Donovan, editors. Biology of the genus *Cephalorhynchus*. Reports of the International Whaling Commission (Special Issue 9), Cambridge, England.

Dekker, D. 1977. Manatee (*Trichechus manatus manatus*) born at Artis Zoo, Amsterdam. International Zoo News 24:30–31.

DeMaster, D. 1978. Calculation of the average age of sexual maturity in marine mammals. Journal of Fisheries Research Board of Canada 35:912–915.

DeMaster, D. 1984. Review of techniques used to estimate the average age at attaining sexual maturity in marine mammals. Pages 175–185 *in* W. F. Perrin, R. L. Brownell, Jr., D. P. DeMaster, editors. Reproduction in whales, dolphins and porpoises. Reports of the International Whaling Commission (Special Issue 6), Cambridge, England.

Domning, D. P., and L. A. C. Hayek. 1984. Horizontal tooth replacement in the Amazonian manatee (*Trichechus inunguis*). Mammalia 48(1):105–127.

Eisenberg, J. F. 1981. The mammalian radiations—an analysis of trends in evolution, adaptation, and behavior. The University of Chicago Press, Chicago, Ill. 610 pp.

Fowler, C. W. 1984. Density dependence in cetacean populations. Pages 373–379 *in* W. F. Perrin, R. L. Brownell, Jr., and D. P. DeMaster, editors. Reproduction in whales, dolphins and porpoises. Reports of the International Whaling Commission (Special issue 6), Cambridge, England. 495 pp.

Garrott, R. A., B. B. Ackerman, J. R. Cary, D. M. Heisey, J. E. Reynolds, III, and J. R. Wilcox. 1995. Assessment of trends in sizes of manatee populations at several Florida aggregation sites. Pages 34–55 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Goddard, J. 1970. Age criteria and vital statistics of a black rhino population. East African Wildlife Journal 8:105–121.

Graham, C. E. 1986. Endocrinology of reproductive senescence. Pages 93–99 *in* W. R. Dukelow, and J. Erwin, editors. Reproduction and development. Comparative primate biology, volume 3. Alan R. Liss, Inc., New York. 497 pp.

Gumilla, J. 1745. El Orinoco ilustrado, y defendido, historia natural, civil, y geographica de este gran rio, y de sus caudalosas vertientes. Volume 1:226–230.

Hart, G. H., and H. R. Guilbert. 1933. Vitamin-A deficiency as related to reproduction in range cattle. University of California Experimental Station Bulletin 560:1–30.

Hartman, D. S. 1979. Ecology and behavior of the manatee (*Trichechus manatus*) in Florida. The American Society of Mammalogists, Special Publication 5. 153 pp.

Hernandez, P., J. E. Reynolds, III, H. Marsh, and M. Marmontel. 1995. Age and seasonality in spermatogenesis of Florida manatees. Pages 84–97 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Husar, S. L. 1977. The West Indian manatee (*Trichechus manatus*). U.S. Fish and Wildlife Service Wildlife Research Report 7. 22 pp.

Irvine, A. B., and H. W. Campbell. 1978. Aerial census of the West Indian manatee, *Trichechus manatus*, in the southeastern United States. Journal of Mammalogy 59(3):613–617.

*Irvine, A. B., D. K. Odell, and H. W. Campbell. 1981. Manatee mortality in the southeastern United States from 1974 through 1977. Pages 67–75 *in* *R. L. Brownell, Jr. and K. Ralls, editors. 1981. The West Indian manatee in Florida. Proceedings of a workshop held in Orlando, Fla., 27–29 March 1978. Florida Department of Natural Resources, Tallahassee. 154 pp.

Knowlton, F. F. 1972. Preliminary interpretations of coyote population mechanics with some management implications. Journal of Wildlife Management 36(2):369–382.

Laws, R. 1961. Reproduction, growth and age of southern fin whales. Discovery Reports 32:327–486.

Laws, R. 1967. Occurrence of placental scars in the uterus of the African elephant (*Loxodonta africana*). Journal of Reproduction and Fertility 14:445–449.

Laws, R. M., I. S. C. Parker, and R. C. B. Johnstone. 1975. Elephants and their habitats—the ecology of elephants in north Bunyoro, Uganda. Clarendon Press, Oxford. 376 pp.

Lindström, E. 1981. Reliability of placental scar counts in the red fox (*Vulpes vulpes* L.) with special reference to fading of the scars. Mammal Review 11(4):137–149.

Mackintosh, N. A. 1942. The southern stocks of whalebone whales. Discovery Reports 22:197–300.

Marmontel, M. 1988. The reproductive anatomy of the female manatee *Trichechus manatus latirostris* (Linnaeus 1758) based on gross and histologic observations. M.S. thesis, University of Miami, Coral Gables, Fla. 91 pp.

*Marmontel, M., T. J. O'Shea, and S. R. Humphrey. 1990. An evaluation of bone growth-layer counts as an age determination technique in Florida manatees. National Technical Information Service, Springfield, Va. Document PB 91-103564. 104 pp.

Marsh, H. 1980. Age determination of the dugong (*Dugong dugon* (Muller)) in northern Australia and its biological implications. Pages 181–201 *in* W. F. Perrin, and A. C. Myrick, Jr., editors. Age determination of toothed whales and sirenians. Reports of the International Whaling Commission (Special Issue 3). Cambridge, England.

Marsh, H. 1995. The life history, pattern of breeding, and population dynamics of the dugong. Pages 75–83 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Marsh, H., and T. Kasuya. 1984. Changes in the ovaries of the short-finned pilot whale *Globicephala macrorhynchus*, with age and reproductive activity. Pages 311–335 *in* W. F. Perrin, R. L. Brownell, Jr., and D. P. DeMaster, editors. Reproduction in whales, dolphins and porpoises. Reports of the International Whaling Commission (Special Issue 6), Cambridge, England.

Marsh, H., G. E. Heinsohn, and P. W. Channels. 1984. Changes in the ovaries and uterus of the dugong, *Dugong dugon* (Sirenia: Dugongidae), with age and reproductive activity. Australian Journal of Zoology 32:743–766.

Martin, D. E. 1981. Breeding great apes in captivity. Pages 343–373 *in* C. E. Graham, editor. Reproductive biology of the great apes. Academic Press, New York. 437 pp.

Martin, K. H., R. A. Stehn, and M. E. Richmond. 1976. Reliability of placental scar counts in the prairie vole. Journal of Wildlife Management 40:264–271.

Mertz, D. B. 1971. The mathematical demography of the California condor population. The American Naturalist 105(945):437–453.

Miller, R. H., G. H. Hart, and H. H. Cole. 1942. Fertility in sheep as affected by nutrition during breeding season and pregnancy. University of California Experimental Station Bulletin 672:1–31.

Mossman, H. W., and K. L. Duke. 1973. Comparative morphology of the mammalian ovary. The University of Wisconsin Press, Madison. 461 pp.

Newson, R. M. 1966. Reproduction in the feral coypu (*Myocastor coypus*). Pages 323–334 *in* I. W. Rowlands, editor. Comparative biology of reproduction in mammals. Symposia of the Zoological Society of London, 15. Academic Press, London.

Nowak, R. M. 1991. Walker's mammals of the world. Fifth edition. Volume II. The Johns Hopkins University Press, Baltimore, Md. 1,629 pp.

*Odell, D. K., D. J. Forrester, and E. D. Asper. 1981. A preliminary analysis of organ weights and sexual maturity in the West Indian manatee (*Trichechus manatus*). Pages 52–65 *in* *R. L. Brownell, Jr. and K. Ralls, editors. 1981. The West Indian manatee in Florida. Proceedings of a workshop held in Orlando, Fla., 27–29 March 1978. Florida Department of Natural Resources, Tallahassee, Fla. 154 pp.

Odell, D. K., G. D. Bossart, M. Lowe, and T. Hopkins. 1995. Reproduction of the West Indian manatee in captivity. Pages 192–193 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

O'Shea, T. J. 1988. The past, present, and future of manatees in the southeastern United States: realities, misunderstandings, and enigmas. Pages 184–204 *in* R. R. Odom, K. A. Riddleberger, and J. C. Ozier, editors. Proceedings of the Third Southeastern Nongame and Endangered Wildlife Symposium. Georgia Department of Natural Resources, Game and Fish Division, Social Circle. 235 pp.

O'Shea, T. J., and W. C. Hartley. 1995. Reproduction and early-age survival of manatees at Blue Spring, upper St. Johns River, Florida. Pages 157–170 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

O'Shea, T. J., and C. A. Langtimm. 1995. Estimation of survival of adult Florida manatees in the Crystal River, at Blue Spring, and on the Atlantic Coast. Pages 194–222 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Perrin, W. F., and G. P. Donovan. 1984. Report of the workshop. Pages 1–24 *in* W. F. Perrin, R. L. Brownell, Jr., and D. P. DeMaster, editors. Reproduction in whales, dolphins and porpoises. Reports of the International Whaling Commission (Special Issue 6), Cambridge, England.

Perrin, W. F., D. B. Holts, and R. B. Miller. 1977. Growth and reproduction of the eastern spinner dolphin, a geographical form of *Stenella longirostris* in the eastern tropical Pacific. Fishery Bulletin 75:725–750.

Perrin, W. F., and A. C. Myrick, Jr., editors. 1980. Age determination of toothed whales and sirenians. Reports of the International Whaling Commission (Special Issue 3), Cambridge, England. 229 pp.

Perrin, W. F., and S. B. Reilly. 1984. Reproductive parameters of dolphins and small whales of the family Delphinidae. Pages 97–133 *in* W. F. Perrin, R. L. Brownell, Jr., and D. P. DeMaster, editors. Reproduction in whales, dolphins and porpoises. Reports of the International Whaling Commission (Special Issue 6), Cambridge, England.

Porton, I., D. G. Kleiman, and M. Rodden. 1987. Aseasonality of bush dog reproduction and the influence of social factors on the estrous cycle. Journal of Mammalogy 68:867–871.

Rathbun, G., and J. Powell. 1982. Reproduction in the manatee (*Trichechus manatus*). Abstract. Sixty-second annual meeting of the American Society of Mammalogists, Snowbird, Utah.

Rathbun, G. B., J. P. Reid, and G. Carowan. 1990. Distribution and movement patterns of manatees (*Trichechus manatus*) in northwestern peninsular Florida. Florida Marine Research Publications 48. 33 pp.

Rathbun, G. B., J. P. Reid, R. K. Bonde, and J. A. Powell. 1995. Reproduction in free-ranging Florida manatees. Pages 135–156 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Reid, J. P., R. K. Bonde, and T. J. O'Shea. 1995. Reproduction and mortality of radio-tagged and recognizable manatees on the Atlantic Coast of Florida. Pages 171–191 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

*Reynolds, J. E. 1992. Distribution and abundance of Florida manatees (*Trichechus manatus latirostris*) around selected power plants following winter cold fronts: 1991–1992. Final report to Florida Power and Light Company, B91135-00073. 41 pp.

Ridgway, S. H., and R. Harrison, editors. 1981. Handbook of marine mammals. Volume 1. The walrus, sea lions, fur seals and sea otter. Academic Press, London. 235 pp.

Ridgway, S. H., and R. Harrison, editors. 1985. Handbook of marine mammals. Volume 3. The sirenians and baleen whales. Academic Press, London. 362 pp.

Seber, G. A. F. 1973. The estimation of animal abundance and related parameters. Hafner Press, New York. 506 pp.

Sikes, S. K. 1971. The natural history of the African elephant. Weidenfeld and Nicholson, London. 397 pp.

Slijper, E. J. 1966. Functional morphology of the reproductive system in Cetacea. Pages 279–319 *in* K. Norris, editor. Whales, dolphins and porpoises. University of California, Berkeley and Los Angeles.

Smith, T. D. 1983. Changes in the size of three dolphin (*Stenella* spp.) populations in the eastern tropical Pacific. Fishery Bulletin 81(1):1–13.

Smith, N. S., and I. O. Buss. 1973. Reproductive ecology of the female African elephant. Journal of Wildlife Management 37:524–534.

Sowls, L. K. 1966. Reproduction in the collared peccary (*Tayassu tajacu*). Pages 155–172 *in* I. W. Rowlands, editor. Comparative biology of reproduction in mammals. Symposia of the Zoological Society of London, 15. Academic Press, London. 559 pp.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford. 249 pp.

*U.S. Fish and Wildlife Service. 1989. Florida manatee (*Trichechus manatus latirostris*) recovery plan. Prepared by the Manatee Recovery Team for the U.S. Fish and Wildlife Service, Atlanta, Ga. 98 pp.

Verheyen, R. 1954. Monographie éthologique de l'hippopotame (*Hippopotamus amphibius* Linné). Exploration du Parc National Albert, Institut des Parcs Nationaux du Congo Belge, Bruxelles. 91 pp.

An Automated Photo-identification Catalog for Studies of the Life History of the Florida Manatee

by

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Abstract. Many free-ranging Florida manatees *(Trichechus manatus latirostris)* are scarred from encounters with boats, entanglement in fishing gear, or fungal infections. A computer-based system, the Manatee Individual Identification System, was developed in 1988 to aid with cataloging manatees with distinct features. An IBM PC-compatible 386 computer with a 150-Mbyte hard-disc drive is used with the system. A serial port connects the computer to a videodisc player that displays images on a 30.5 cm NTSB, superfine-pitch color monitor. The foundation of the Manatee Individual Identification System catalog is high-quality photographs. Cataloging criteria are conservative and require manatees to be well photographed. A permanent unique feature must be recognizable in future photographs. Feature codes that describe each scar or mutilation of each individual are created and stored in a features database. A total of 913 manatees were cataloged in the system by 31 December 1991. Deaths of 42 cataloged manatees were recorded. Features of 482 manatees on the Atlantic Coast were coded. Records of sightings (9,796; $\bar{x}$ = 10.7/animal) of all individuals (except of the Blue Spring residents, which are filed in a separate database) were updated through 1991. The number of resightings of cataloged manatees is greatest during December, January, and February when manatees are aggregated in warm-water refugia. Most resightings are annual. The longest interval between initial sighting and first resighting of one individual was 11 years. The photo-identification catalog has been useful for studies of populations that include analyses of movements, reproduction traits, and survival. Suggestions are made for the improvement of the technique.

Key words: Identification, Florida manatee, photo-identification, scars, *Trichechus manatus latirostris*, resightings.

Natural marks and scars have been used to identify individual animals in studies of the behavior and ecology of large mammals (Katona and Whitehead 1981; Darling and McSweeney 1985; Miththapala et al. 1989; Mizroch et al. 1990). Moore (1956) first identified and recorded sightings of uniquely marked Florida manatees (*Trichechus manatus latirostris*), and his technique has been used by others since the late 1960's (Hartman 1979; Powell and Rathbun 1984; Reid et al. 1991; O'Shea and Hartley 1995; Rathbun et al. 1995). In 1982, a statewide catalog of photo-identification of distinctive manatees was assembled (Reid et al. 1991), which incorporated a manually sorted, punched-card system. Codes of unique features were used to access the records of individuals in the system. By 1988, the number of cataloged manatees was unwieldy, and a computer-based system was developed for maintaining the catalog. This system and the characteristics of the resulting database are described in this report.

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Methods

Identification of Manatees

This is the first published description of the identification system. The Manatee Individual Identification System is an interactive videodisc-microcomputer database. Developed by Greyrock Software of Maryland, the system is a Clipper-compiled dBase III application. The data files of the system are stored in DBF format, and modifications to the data files can be done with the system or with dBase. The menu-driven system is user-friendly and offers a rapid method for searching a feature-code database to match new and former photographs of cataloged manatees. Minimum hardware specifications for the system include an IBM PC-compatible 286 microcomputer with 640K RAM, a videodisc player, and a color monitor. The system currently is operated under MS-DOS 5.0 on an 80386, 25 MHz computer with 640K RAM, 150-Mbyte hard-disc drive and with an access time of 17 ms. A serial port connects the computer to a Pioneer LDV-4200 videodisc player that displays photographic images on a Sony PVM-1271Q 30.5-cm color monitor.

The catalog is dependent on high-quality photographs of distinct features of each manatee (Reid et al. 1991). Features may be anywhere on the animal; photos of the tail, dorsum, and lateral aspects of the animal are necessary (Figs. 1–10). Unique features are not common on the ventrum. Corresponding field notes accompany all photographs of scarred individuals and include sketches, exposure numbers, sighting date and location, size class, and reproduction information.

Opportunities for photographing are available when manatees are aggregated in refugia in winter and in areas that are well frequented in summer. During radio-tracking of tagged manatees, accompanying animals also are photographed. Photographs are taken from a boat or from shore when the animals are cruising at or near the surface, resting on the surface, or surfacing to breathe. At some sites, photographs are also taken underwater. At Blue Spring, water clarity is good and the population is

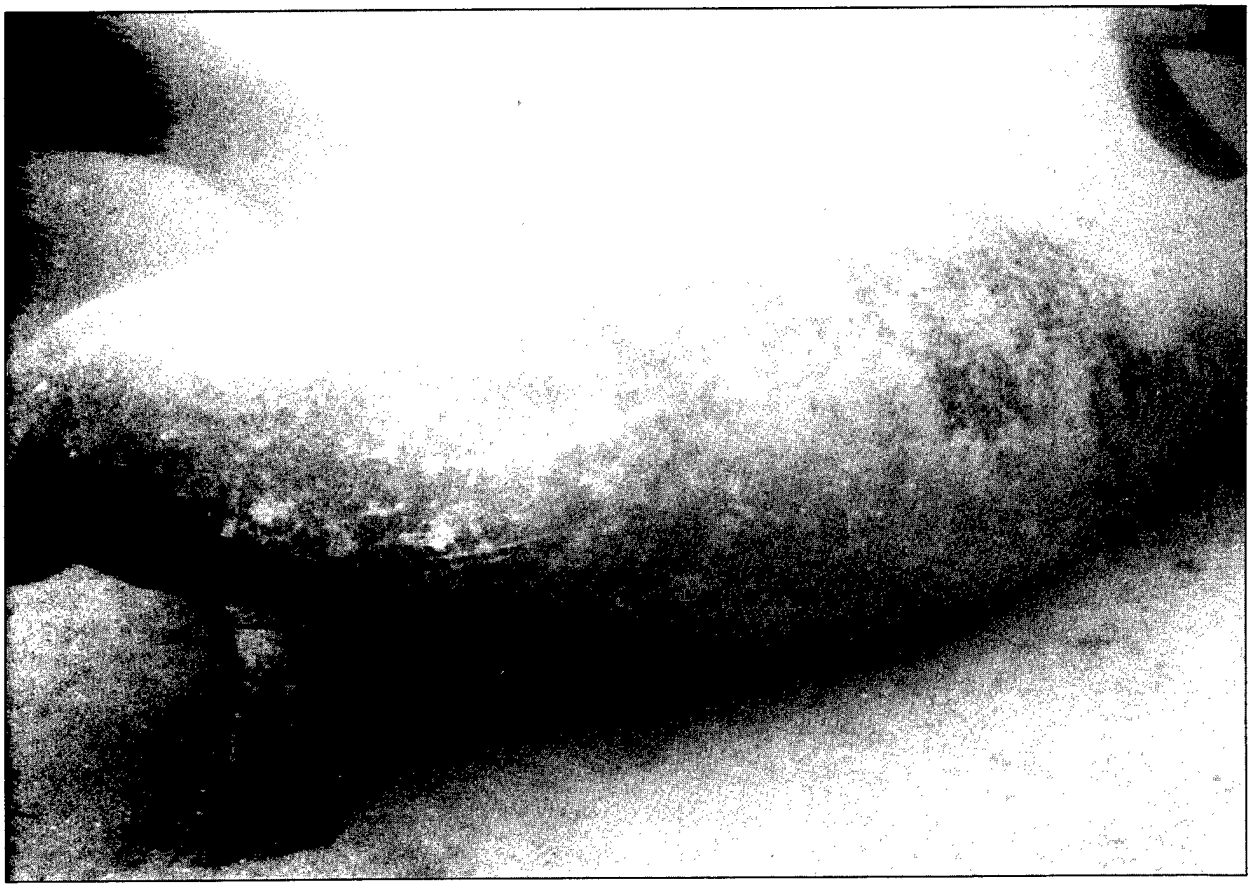


Fig. 1. Cataloged Florida manatee (*Trichechus manatus latirostris*) RB 257; recorded features on the left dorso-lateral trunk. *Photo courtesy of Sirenia Project, National Biological Service.*



Fig. 2. Cataloged Florida manatee (*Trichechus manatus latirostris*) RB 257; recorded features on the right dorso-lateral trunk. *Photo courtesy of Sirenia Project, National Biological Service.*

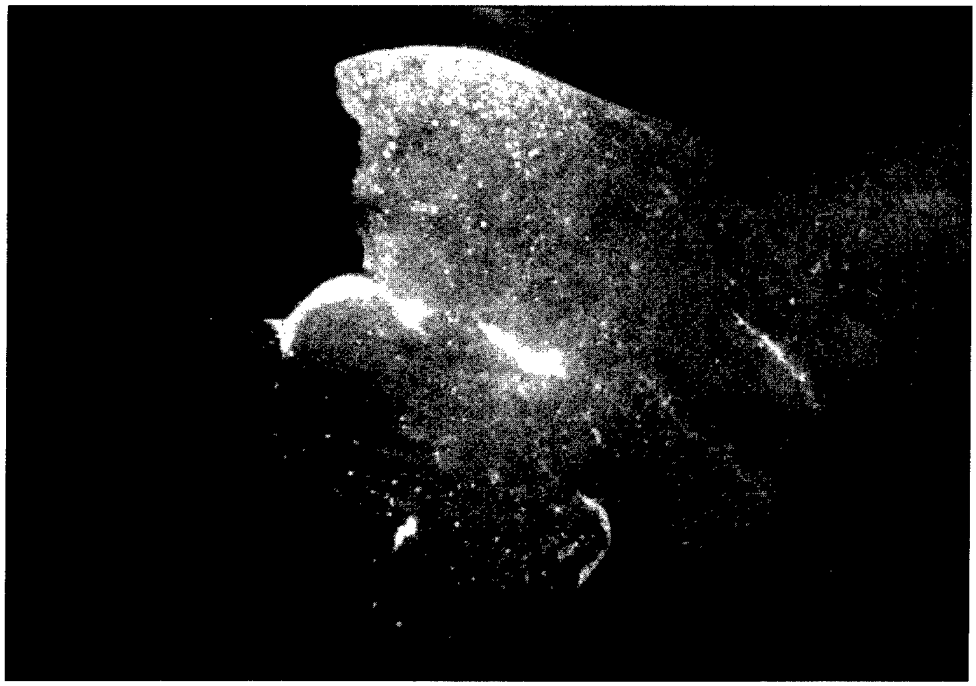


Fig. 3. Cataloged Florida manatee (*Trichechus manatus latirostris*) RB 257; recorded mutilations and scars on the tail. *Photo courtesy of Sirenia Project, National Biological Service.*



Fig. 4. Cataloged Florida manatee (*Trichechus manatus latirostris*) RB 257; recorded tail, taken 2 years after the photograph in Fig. 3. The integrity of the white scars and the mutilation silhouette remained. *Photo courtesy of Sirenia Project, National Biological Service.*



Fig. 5. Cataloged Florida manatee (*Trichechus manatus latirostris*) RB 358 with a unique white blotch scar on the left mid-trunk (feature code = SLB1LWB). *Photo courtesy of Sirenia Project, National Biological Service.*



Fig. 6. Cataloged Florida manatee (*Trichechus manatus latirostris*) CR 202 with a unique series of gray line scars caused by a propeller strike on the dorsal posterior trunk (feature code = SDC4MGL). *Photo courtesy of Sirenia Project, National Biological Service.*

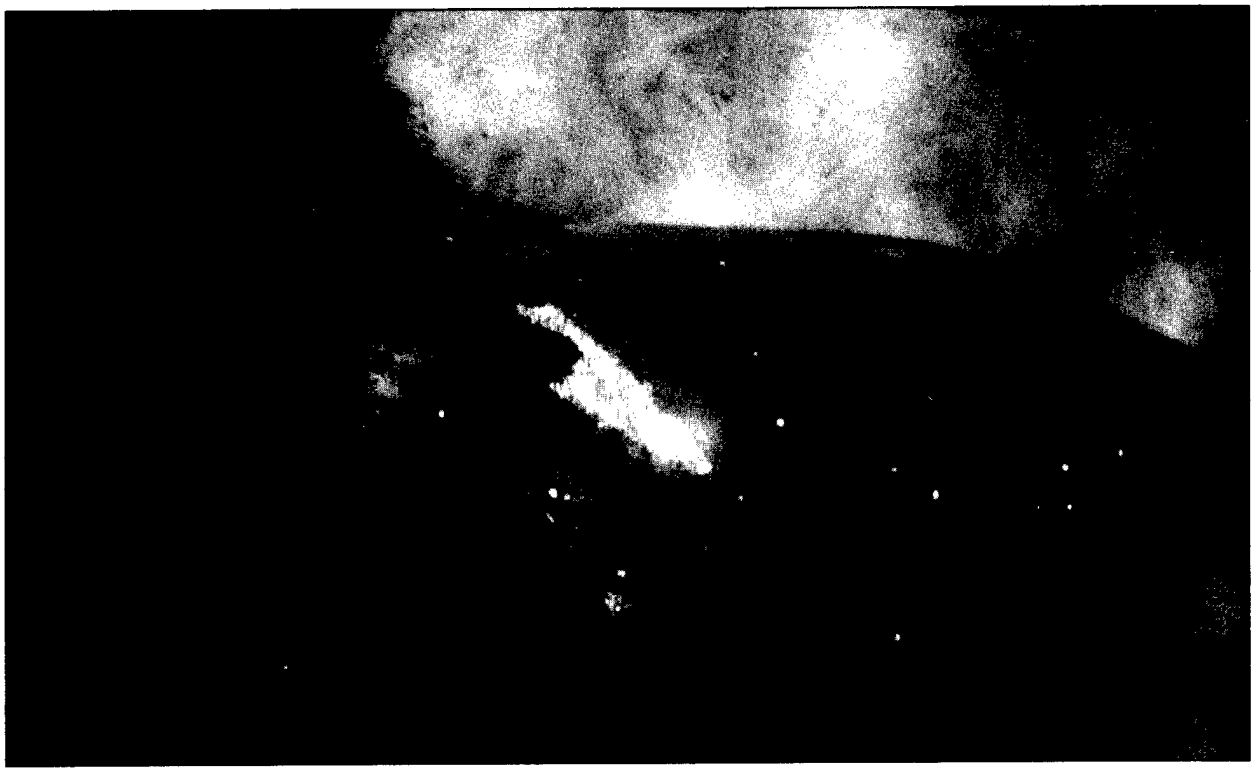


Fig. 7. Cataloged Florida manatee *(Trichechus manatus latirostris)* BC 9 with a white blotch scar with a feature code identical to that of RB 358 (Fig. 5), yet with two unique features. *Photo courtesy of Sirenia Project, National Biological Service.*

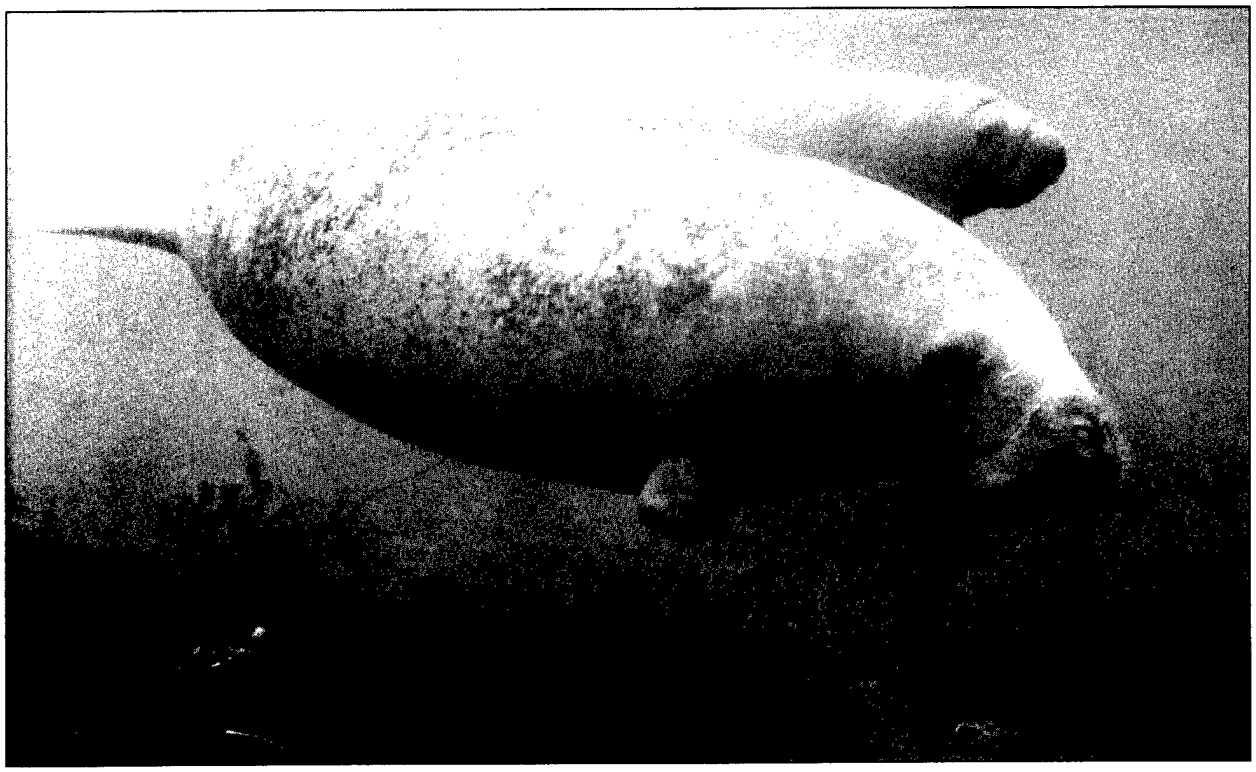


Fig. 8. Cataloged Florida manatee (*Trichechus manatus latirostris*) CR 75 who lost a flipper, probably caused by entanglement in fishing gear (feature code = MRF1L). *Photo courtesy of Sirenia Project, National Biological Service.*

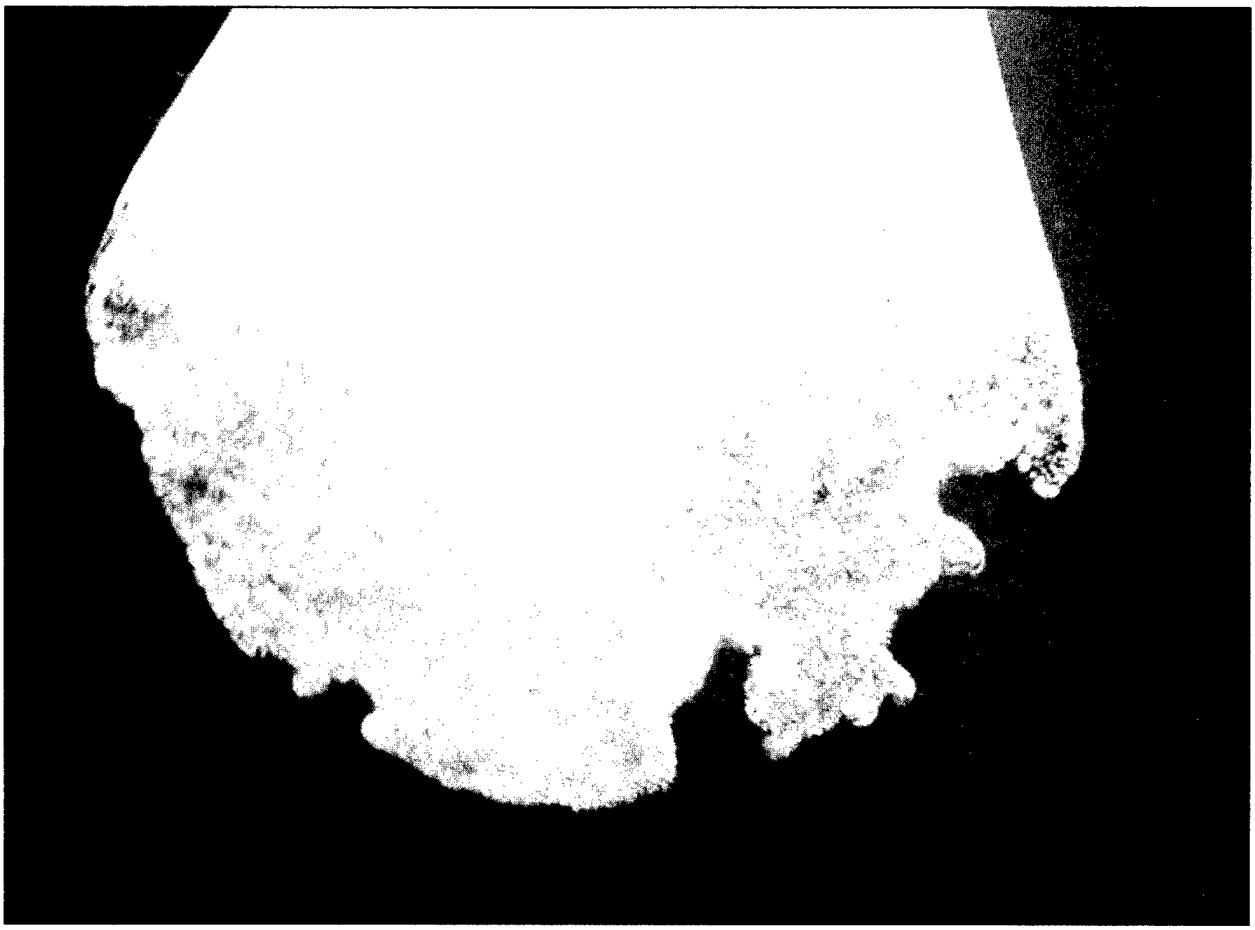


Fig. 9. Cataloged Florida manatee (*Trichechus manatus latirostris*) CR 22 with tail mutilations from fungal lesions (feature codes = MLY2S, MRY4M). *Photo courtesy of Sirenia Project, National Biological Service.*

closely monitored by a single, experienced researcher (O'Shea and Hartley 1995; O'Shea and Langtimm 1995). The water is clear also at Crystal River, where many manatees are habituated to humans, and experienced researchers have photographed manatees underwater for many years (Hartman 1979; Powell and Rathbun 1984; Rathbun et al. 1990, 1995). Manatees in other sites are less intensively monitored, partly because of variable sighting conditions. Aggregation sites in Georgia, and in Jacksonville, Brevard County, Fort Pierce, Port Everglades, Miami, Fort Myers, and Tampa Bay in Florida are in dark, often turbid, water and photographs of manatees are usually taken from shore or from a boat. Water clarity is better at Riviera Beach, where manatees are photographed underwater and from above the surface of the water.

Photographed manatees are only included in the catalog if they meet the following criteria: the manatee has at least one distinct and permanent (healed) scar or mutilation; photographs of the entire body of the manatee (tail, back, and sides) are available; and clear, good-quality photographs depict the features for identification. Manatees currently are cataloged by the first date of a recorded sighting.

When a new individual is entered into the catalog, an identification number is assigned and a composite sketch of all distinct features is drawn from photographs onto a diagrammatic outline of a manatee (Fig. 11). Many manatees have multiple features. Each feature (or pattern of scars) is sketched, coded, and entered as a single record into DBF files. Identity information, feature codes, and sighting records of each manatee are stored in three separate dBase files.

Identity Files

Information about each manatee is stored in the identity files. The identification number prefix is a two-letter code (Table 1) that represents the geographic area where

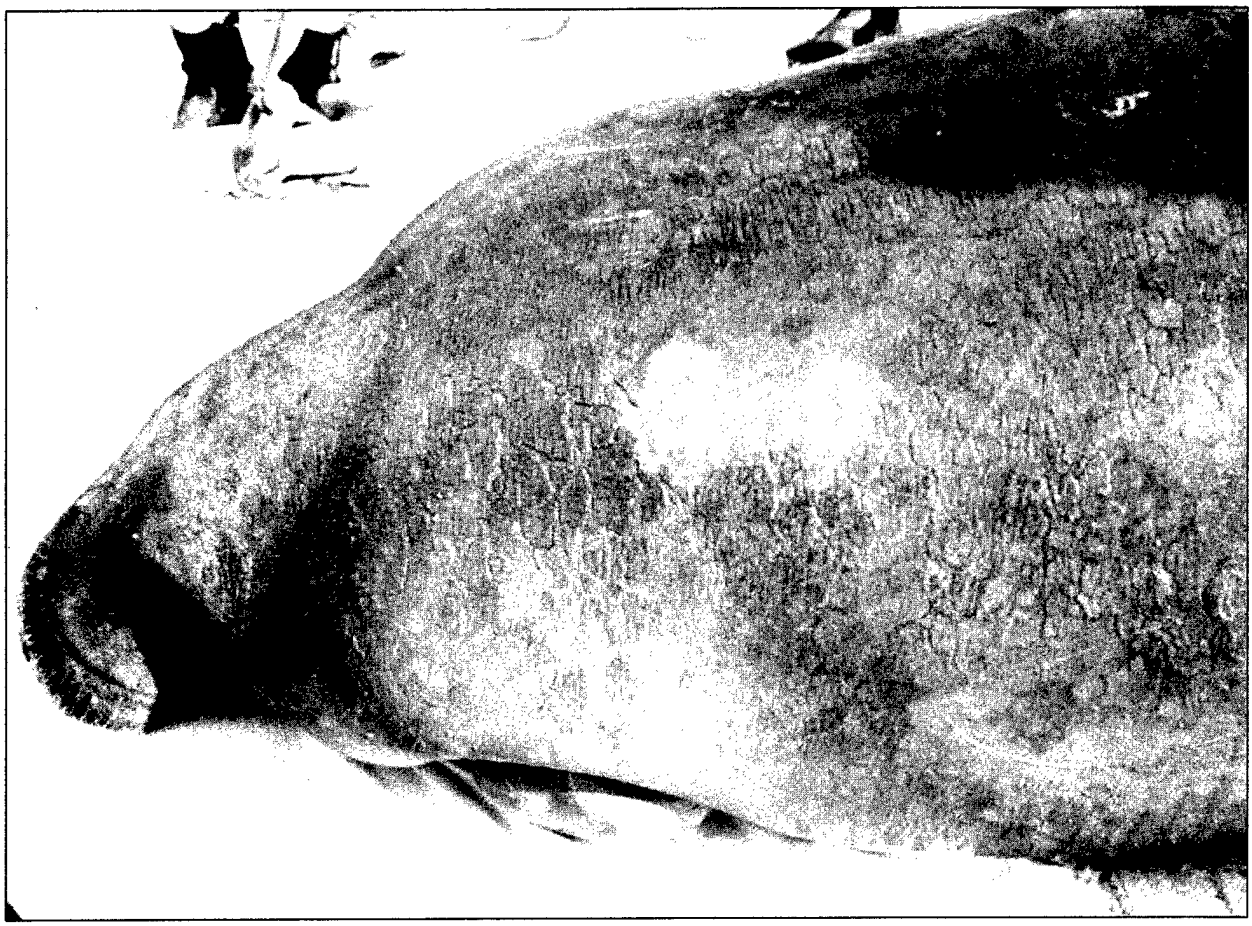


Fig. 10. Rehabilitated Florida manatee (*Trichechus manatus latirostris*) with a freeze brand on the left anterior trunk; photographed just prior to release. *Photo courtesy of Sirenia Project, National Biological Service.*

the manatee has been sighted most commonly followed by a unique number. Names of some individuals also are included. When known, the dates of birth and death of each manatee are listed in this file.

Feature Files

Feature files store the codes that describe the unique features (e.g., scars, mutilations) of each individual. Features are manually coded from photographs, a composite sketch, and field notes. Feature codes are used to describe unique identifying features and the animal's sex and may contain as many as seven characters (Fig. 11). The first character of the code describes the feature type in eight possible choices (e.g., S = scar, M = mutilation). Two of these eight types are one-letter codes without further feature description (K = trunk plain, L = tail plain). Two are two-letter codes for sex (XF = female or XM = male) and the natural medial tail-notch codes (NN = none, NS = small, NM = medium, or NL = large). Because four of the eight possible feature types (scar, mutilation, deformity, freeze brand) can be present on any part of the manatee (although rarely on the venter), the general region is included as the second-character entry of these four types (e.g., R = right side). One of eight position choices (e.g., A = anterior trunk, F = flipper, Y = posterior tail) for the feature in the region is coded as the third character. The remaining characters that make up the complete feature code are the number of marks constituting the feature (1 = single, 2 = two or three, and 4 = four or more), the overall feature size (S = small, M = medium, or L = large), the predominant color (W = white or G = gray), and the overall shape (L = line or B = blotch). Color and shape are not included if the feature type is a mutilation (portions of the flipper or tail missing; Figs. 1–10). As many as five photographs of each individual that best illustrate the most distinct features are archived on a videodisc and can be accessed through the program and displayed on a

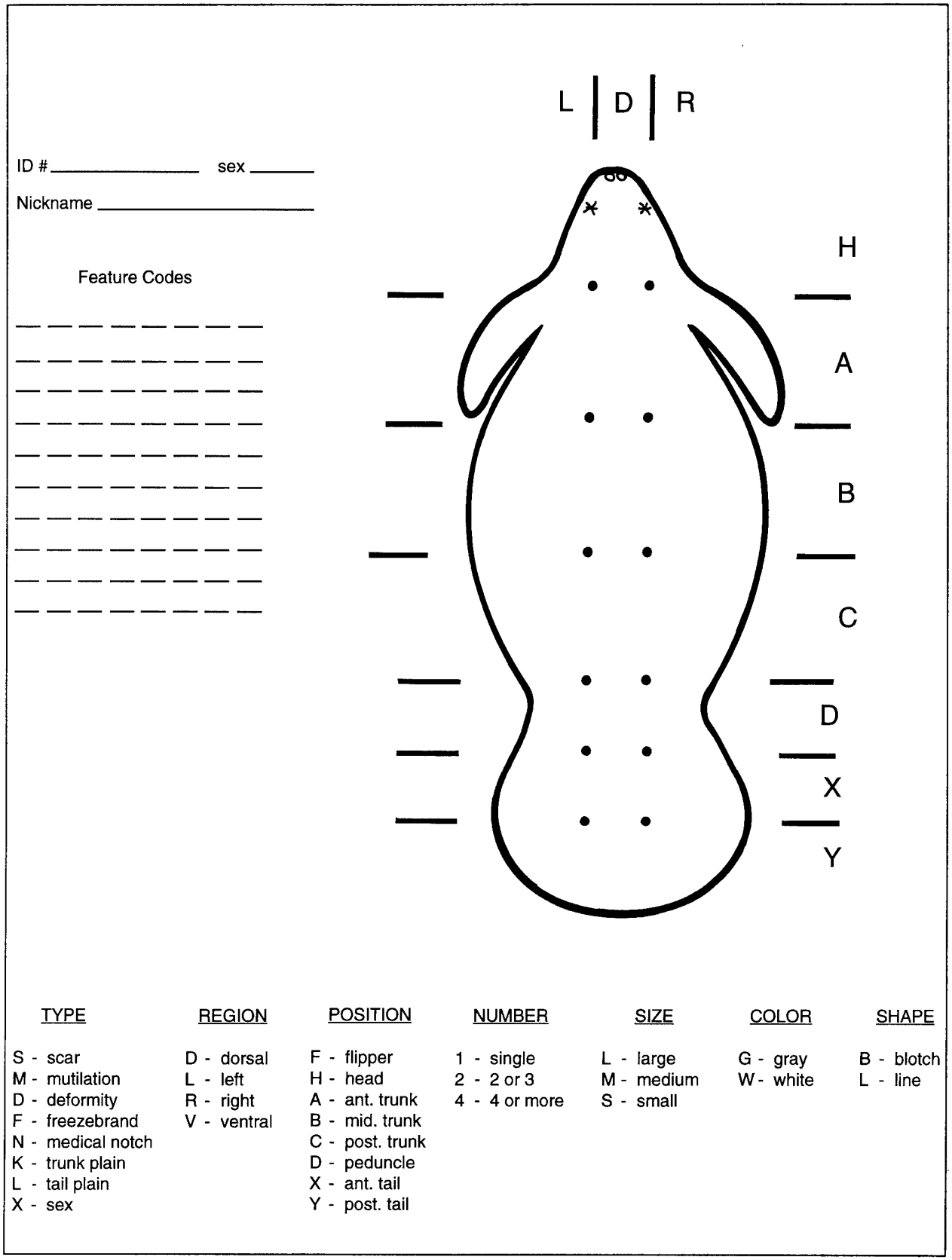


Fig. 11. Form for creating a composite sketch of Florida manatee (*Trichechus manatus latirostris*) features from photographs and for coding each feature prior to entry into the Manatee Individual Identification System catalog.

Table 1. Location codes for the standardization of identification numbers and Florida manatee *(Trichechus manatus latirostris)* sightings in the southeastern United States through December 1991.

East Coast

BC - Brevard County area, Indian and Banana rivers
BS - Blue Spring State Park, St. Johns River
FP - Ft. Pierce power plant, St. Lucie River, Vero Beach
GA - Georgia
JX - Jacksonville area, including industrial plants and Fernandina Beach
MI - Miami area, including Biscayne Bay, Little River, and Miami River
PE - Port Everglades power plant, Ft. Lauderdale, New River
RB - Riviera Beach power plant, Loxahatchee River, Lake Worth, Hobe Sound

West Coast

CR - Crystal River area, including Inglis Lock and Chassahowitzka, Homosassa, Suwannee, and Withlacoochee rivers
FM - Ft. Myers area, including Orange and Caloosahatchee rivers,Charlotte Harbor, Franklin and Moorehaven locks
TB - Tampa Bay area, including TECO power plant and Alafia River

video monitor. A videodisc that can accommodate 54,000 images is used for the Manatee Individual Identification System.

Sighting Files

Sighting files list the date, specific location, and observer of each sighting and are stored in a separate database file. Recorded death dates are also entered in these files. Sighting locations are assigned the same two-letter standardized codes used to prefix identification numbers (Table 1) and indicate the general geographical region of the sighting. The next characters are numerical codes specifically created for locations of frequent sightings. The reproductive status (e.g., pregnant, with calf) or activity (e.g., nursing, with herd of males) at each sighting is included. Size class, based on approximate length, also is entered. A space for comments about other relevant information is provided. These files allow more efficient retrieval and analyses of sightings and histories of reproduction of individuals than manual sorting.

Operation of the Manatee Individual Identification System

After each winter field season, new photographs are presorted prior to searches for matches in the Manatee Individual Identification System. For each designated site, each photographer manually sorts the photographs of individual manatees and arranges these slides by type of feature, thereby separately grouping all photographs of head scars, right trunk scars, tail mutilations, and so on. Matches of individuals in these subcategories are made and pooled before the computer is accessed.

The system can be used for two purposes. First, a direct access portion of the program allows the operator to retrieve the photographs, feature codes, and sighting history of a specific manatee by entering the manatee's identification number or name. Secondly, a search can be made for a match between a newly photographed and a cataloged manatee by entering a feature code of the new individual. The computer then searches the entire database or a specific region of the state and retrieves a list of all cataloged manatees with feature codes like the entered code. The computer screen displays a list of the identification numbers of manatees that are possible matches. As the operator scrolls through this list, features previously sketched onto a manatee outline and a list of all feature codes of that individual are simultaneously displayed. Photographs of each listed manatee on the videodisc are accessed by the videodisc player and simultaneously displayed on another monitor for the operator's comparison with the newly photographed manatee. In this way, the operator can quickly evaluate all possible candidates for a match. In practice, the final verification or elimination of a possible match is made by comparing additional photographic, archived files of each cataloged individual. For matching old photographs with records in the catalog, photographs and information files of deceased, cataloged manatees are maintained in the system.

Results

The Manatee Individual Identification System contains records of 913 manatees that were cataloged through December 1991. The number of new individuals added each year decreased in recent years, although

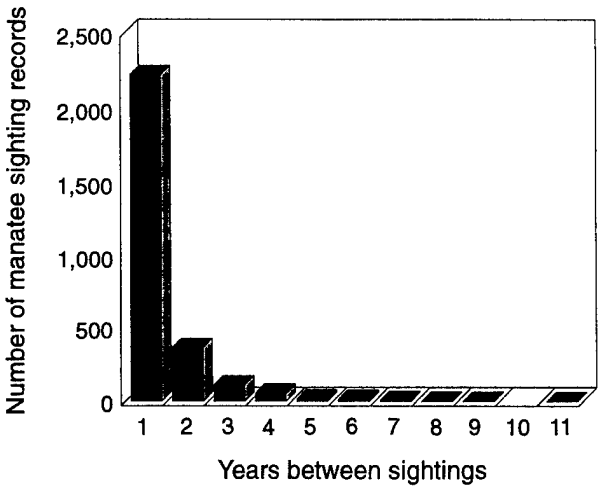


Fig. 12. Yearly intervals between resightings of cataloged Florida manatees (*Trichechus manatus latirostris*), 1975–1991.

nearly 6,000 photographs are now handled annually. Sightings of known individuals steadily increased as photoidentification increased and new manatees were added to the catalog. Most intervals between sightings of living manatees are short, usually a single year. When cataloged, most manatees are resighted every year, usually on more than one occasion (Fig. 12). However, one individual was first resighted after an 11-year interval.

Nine hundred and thirteen individuals are identified in each region (Table 2). Feature codes of 482 manatees (n = 1,865 features, $\bar{x}$ = 3.9/manatee, SD ± 1.9, CV = 48.5%) from seven Atlantic Coast sites (prefixes BC, BS, FP, JX, MI, PE, RB) are entered (Table 1). Feature codes of manatees from some BS sites and from West Coast sites CR, TB, and FM have not yet been created. Nearly all coded features are either scars (n = 950) or mutilations (n = 499), and the remaining codes are categorized as natural medial-tail notches (n = 110), plain (unmarked) trunks (n = 19), plain tails (n = 30), freeze brands (n = 2), congenital deformities (n = 4), or sex (n = 251). Approximately 1,300 photographs of 729 manatees are archived on the videodisc (range = 1–5/individual). The videodisc does not yet include photographs of manatees cataloged since 1988.

Table 2. Number of cataloged Florida manatees (*Trichechus manatus latirostris*) identified by region through December 1991. See Table 1 for key to abbreviations.

East Coast		West Coast	
BC	128	CR	279
BS	51	FM	59
FP	6	TB	25
JX	23		
MI	28		
PE	118		
RB	196		
Totals	550		363

However, sighting histories through 1991 were updated and consist of 9,796 entries ($\bar{x}$ = 10.7/animal; Table 3). Because manatees are more accessible for photography in winter and observer effort is increased at warm-water refugia, the number of sightings is greater in winter than in summer (Fig. 13).

The sex of 295 cataloged manatees is known, although feature codes of 44 of these manatees have not yet been entered. Known females (n = 200) outnumber known males (n = 95) because, at least in part, sex of females can be determined by the close association of a nursing calf with an adult. Direct observation of the genital area, which is difficult and not always possible, is used to identify the sex of males and females without calves.

Manatees with fresh wounds, small features, or incompletely recorded features are categorized as distinct unknowns (DU), and their photographic records are archived in separate files for possible later inclusion in the system. Poor-quality photographs may also cause a manatee's categorization as DU. Nearly 15,000 photographs are of DUs, and most were taken at Atlantic Coast sites. As part of the yearly working files of photographs, the DU files remain arranged by geographic area and are sorted by feature type and location on the animal (e.g., all manatees with head scars photographed in Miami are grouped together). The DU files include the following:

Manatees with photographs of only a portion of the body. For example, a manatee with a photograph of a well-documented tail scar but without a photograph of the trunk would not be cataloged in the system. The photograph is temporarily filed as a DU until complete documentation is made. (However, a tail or trunk photo alone may be sufficient to match the manatee to a previously cataloged animal with full documentation.)

Manatees with fresh wounds and without other distinct, identifying features. Feature codes for fresh wounds are not created until the wounds are healed and the final or near-final size, shape, and coloration of the feature can be ascertained.

Table 3. Number of sightings of cataloged Florida manatees (*Trichechus manatus latirostris*) in each region through December 1991. See Table 1 for key to abbreviations.

Site	Number of sightings	Number of individuals
East Coast		
BC	888	199
BS	106	50
FP	77	47
GA	13	9
JX	89	46
MI	398	52
PE	881	179
RB	851	240
West Coast		
CR	6,203	277
FM	235	57
TB	55	26

Manatees with very small or indistinct features. These cannot be used as the sole identifying feature, although they may aid in discerning differences between manatees with other similar features.

Since the cataloging of individual manatees began, 42 dead manatees with previous sighting histories have been identified. Thirty-seven of these were previously cataloged and five were matched with individuals in the DU files.

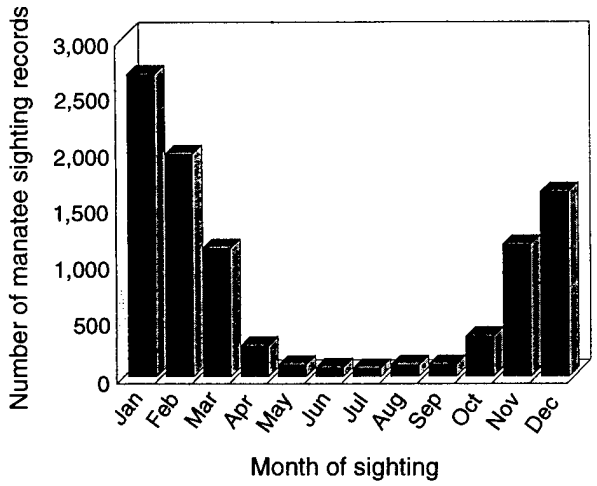


Fig. 13. Sightings of all cataloged Florida manatees (*Trichechus manatus latirostris*) in all areas by month, 1977–1991.

Discussion

A substantial photo-identification database and an automated system for sorting the information are ideally suited for studies of manatee population biology. The photo-identification technique has already resulted in the documentation of complex seasonal movement patterns (Reid et al. 1991), long histories of reproduction of females (O'Shea and Hartley 1995; Rathbun et al. 1995; Reid et al. 1995), and in the estimation of adult survival (O'Shea and Langtimm 1995). The potential for other complex applications also deserves attention by future investigators. For example, use of this database with new advances in statistical approaches may provide further understanding of reproductive traits (Barlow 1990), site fidelity (Hestbeck et al. 1991), survivorship (Lebreton et al. 1992), and perhaps eventually, estimation of population size. Parallel advances in the use of photo-identification to study other marine mammal populations are found in Hammond (1986).

Because of the high potential of the Manatee Individual Identification System and photo-identification database for quantification of important aspects of manatee population dynamics, several attributes of the process need refinement and further development, notably, increasing the efficiency with which individuals are matched or entered into the catalog and investigating the probability of meeting assumptions that are important for certain statistical uses of the data set.

Increasing Cataloging Efficiency

Maintaining current video images of manatees is problematic, partly because of the high cost of frequently remastering the videodisc. The comparison of newer photographs with those already on the videodisc and the determination of the value of replacing old images are time consuming. About 6,000 photographs are handled each year, and frequent replacement of old video images would be inefficient and expensive. The ability to directly capture images from slides without the delay and expense of mastering a new videodisc would allow more frequent updates of the photographic files, including adding images of newly acquired features of known manatees and of newly cataloged manatees. The feasibility of optical disc storage or other technology is being explored.

The enormous size and complexity of the DU photographic collection dictates the need for an alternate sys-

tem of handling these photographs. The DU photographs from some areas date to the early 1970's and probably include dead manatees whose carcasses were not identified; manatees with small features that later were masked by newer features that may be included separately in the DU files or in the Manatee Individual Identification System catalog; manatees with new wounds that healed in such a way that the animals were not recognized as catalogued individuals; manatees whose records are incomplete, for example the marked tail and trunk of the same animal were represented twice; and manatees that have not yet been matched. Most of these photographs are sorted by hand, and matches are undoubtedly missed. All photographs not matched to cataloged manatees remain in the DU binders. Because these photographs are sorted by feature type, matches in the DU files are made, and a manatee may eventually be matched with a cataloged manatee or may be added to the catalog as a new individual when its record is completed. However, files of manatees photographed at different sites or not seen for several years may not be matched because of the overwhelming volume of photographs that must be visually examined. A separate system to more efficiently handle these photographs would be helpful. Field personnel also must be allowed to dedicate more office time to handling photographs.

Photographs are taken opportunistically and depend on the availability of field personnel and weather conditions (prolonged cold periods result in denser aggregations and allow more intensive photography). Standardization of photographic methods and efforts to enumerate and categorize the manatees photographed at each study site are underway. These include total counts of manatees at a site, including the numbers that are marked, unmarked, or not categorized (i.e., not discernable). Instituting sampling methods to improve determination of the number of manatees at each site during a discrete time period may allow the use of the Manatee Individual Identification System catalog for estimating survival or population sizes. This will require additional researchers and testing of new methodologies. A concerted effort to fully document features of each manatee carcass also is essential.

Meeting Important Assumptions

Hammond (1986) noted several problems in studies when the recognition of individual animals is achieved using naturally occurring marks and not by tags or devices placed on the animals by investigators. Two major requisites common to all potential uses of manatee photo-identification databases are the need for permanent and unchanging marks and the need for unique patterns of marks on each animal. Processes of sorting and reviewing images by eye that minimize the potential for errors in identification are also necessary. Some of these problems are probably minimized with the manatee scar catalog and the restrictive criteria before unique identification numbers are assigned. However, they have not yet been directly addressed or quantified. For example, many Florida manatees have scar patterns from multiple accidents (Wright et al. 1995), and living individuals that obtained new patterns over time are regularly recognized. Nonetheless, the amount of information in the original patterns usually is great enough to allow recognition of unique features despite changes and additions. The high rates of resighting each year also minimize the problems with features that accrued between resighting periods and increase the ease of recognition. Hammond (1986) reviewed approaches by other investigators to quantify the probabilities of not recognizing individuals because of changes in marks (e.g., double-tagging methods) and to calculate the probability that patterns of separate individuals are indistinguishable. Similar approaches should be made in future analyses of the manatee photo-identification database.

Furthermore, several other assumptions must be met to satisfy requirements for using manatee photo-identification data with various capture–recapture, statistical models. Treatment of each of these assumptions is beyond the scope of this paper but must be considered in future analyses. O'Shea and Langtimm (1995) characterized aspects of many of these assumptions because they pertain to calculations of survival from the manatee photo-identification database with the Cormack-Jolly-Seber open population models (Pollock et al. 1990). General reviews of the assumptions in various population-size estimations were produced by Hammond (1986), Pollock et al. (1990), Lebreton et al. (1992), Nichols (1992), and references therein. Some of these assumptions are knowledge of how representative the members of the marked population are of the unmarked population and the requirement of equal probabilities of survival and capture among individuals. For manatees, the latter involves equal probabilities of sighting individuals, equal probabilities of photographing markings, and sorting and treatment of photographs by strict guidelines. For certain analyses, problems from heterogeneity in capture probabilities may be minimal if probabilities of capture of Florida manatees are as high as reported (O'Shea and Langtimm 1995). Adult survival rates do not seem to vary greatly with age or between sexes in study areas (O'Shea and Langtimm 1995). More stringent tests of the assumptions must be done for the use of the full range of potential applications of the manatee photo-identification database.

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Cited References

Barlow, J. 1990. A birth-interval model for estimating cetacean reproductive rates from resighting data. Pages 155–160 *in* G. P. Donovan, P. S. Hammond, and S. A. Mizroch, editors. Individual recognition of cetaceans: use of photo-identification and other techniques to estimate population parameters. Report of the International Whaling Commission, Special Issue 12, Cambridge, England.

Darling, J. D., and D. J. McSweeney. 1985. Observations on the migrations of North Pacific humpback whales *(Megaptera novaeangliae)*. Canadian Journal of Zoology 63:308–314.

Hammond, P. S. 1986. Estimating the size of naturally marked whale populations using capture–recapture techniques. Pages 253–282 *in* G. P. Donovan, editor. Behavior of whales in relation to management. Report of the International Whaling Commission, Special Issue 8, Cambridge, England.

Hartman, D. S. 1979. Ecology and behavior of the manatee (*Trichechus manatus*) in Florida. Special Publication 5. American Society of Mammalogists, Lawrence, Kans. 153 pp.

Hestbeck, J. B., J. D. Nichols, and R. A. Malecki. 1991. Estimates of movement and site fidelity using mark-resight data of wintering Canada geese. Ecology 72:523–533.

Katona, S. K., and H. P. Whitehead. 1981. Identifying humpback whales using their natural markings. Polar Record 20:439–444.

Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67–118.

Miththapala, S., J. Seidensticker, L. G. Phillips, S. B. U. Fernando, and J. A. Smallwood. 1989. Identification of individual leopards (*Panthera pardus kotiya*) using spot pattern variation. Journal of Zoology, London 218:527–536.

Mizroch, S. A., J. A. Beard, and M. Lynde. 1990. Computer assisted photo-identification of humpback whales. Pages 63–70 *in* G. P. Donovan, P. S. Hammond, and S. A. Mizroch, editors. Individual recognition of cetaceans: use of photo-identification and other techniques to estimate population parameters. Report of the International Whaling Commission, Special Issue 12, Cambridge, England.

Moore, J. C. 1956. Observations of manatees in aggregations. American Museum Novitiates 1811. 24 pp.

Nichols, J. D. 1992. Capture–recapture models: using marked animals to study population dynamics. BioScience 42:94–102.

O'Shea, T. J., and W. C. Hartley. 1995. Reproduction and early-age survival of manatees at Blue Spring, upper St. Johns River, Florida. Pages 157–170 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

O'Shea, T. J., and C. A. Langtimm. 1995. Estimation of survival of adult Florida manatees in the Crystal River, at Blue Spring, and on the Atlantic Coast. Pages 194–222 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture–recapture experiments. Wildlife Monographs 107:1–97.

Powell, J. A., and G. B. Rathbun. 1984. Distribution and abundance of manatees along the northern coast of the Gulf of Mexico. Northeast Gulf Science 7:1–28.

Rathbun, G. B., J. P. Reid, and G. Carowan. 1990. Distribution and movement patterns of manatees (*Trichechus manatus*) in northwestern peninsular Florida. Florida Marine Research Publications 48:1–33.

Rathbun, G. B., J. P. Reid, R. K. Bonde, and J. A. Powell. 1995. Reproduction in free-ranging Florida manatees. Pages 135–156 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Reid, J. P., G. B. Rathbun, and J. R. Wilcox. 1991. Distribution patterns of individually identifiable West Indian manatees (*Trichechus manatus*) in Florida. Marine Mammal Science 7:180–190.

Reid, J. P., R. K. Bonde, and T. J. O'Shea. 1995. Reproduction and mortality of radio-tagged and recognizable manatees on the Atlantic Coast of Florida. Pages 171–191 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Wright, S. D., B. B. Ackerman, R. K. Bonde, C. A. Beck, and D. J. Banowetz. 1995. Analysis of watercraft-related mortality of manatees in Florida, 1979–1991. Pages 259–268 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Reproduction in Free-ranging Florida Manatees

by

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Abstract. Free-ranging manatees (*Trichechus manatus latirostris*) along the coast of northwestern peninsular Florida aggregate during winter at warm-water springs in the Crystal and Homosassa rivers. Most individuals in these populations are identifiable by distinctive scar patterns. Histories of reproduction were collected during 1976–91 and were used to characterize the population's traits of reproduction. In addition, data from aerial surveys and recovered carcasses were used to further define characteristics of reproduction. The adult and calf sex ratios were not significantly different from 1:1. Herds of manatees exhibiting mating behavior were most frequently sighted in spring, and births rarely occurred during winter, suggesting diffusely seasonal reproduction. The duration of gestation was about 12 months. Litter size was normally one, but about 1.4% of the births were twins. Calf mortality from late pregnancy to initial identification was about 33%. The average period of calf dependence on the mother was 1.2 winter seasons, and the average interval between births was 2.5 winter seasons. Females reached sexual maturity at an average age of 3.2 years. About 36% of calves were recruited into the population. The longest period of reproduction of a female was 22 years, which represents a minimum estimate of the reproductive life. The fecundity (number of first-year calves per number of sexually mature females per year) was 0.4, the crude birth rate (number of first-year calves per total number of individuals, including calves) was 0.11, and the gross birth rate of the population (total number of calves per total number of individuals including calves) was 0.13. The biology of reproduction of the Florida manatee and of the dugong (*Dugong dugon*) is similar except for sexual maturity, which is attained at 9–10 years in the dugong. Sufficient information for most comparisons is not available on other sirenians.

Key words: Crystal River, Florida manatee, *Trichechus manatus latirostris*, reproduction, life history, scar patterns.

The West Indian manatee (*Trichechus manatus*) was listed as endangered under the Endangered Species Act of 1973 (*[4]U.S. Fish and Wildlife Service 1990). The principal reason for this listing was excessive mortality in Florida. In 1974, research into the status of the Florida manatee (*T. m. latirostris*) was initiated by the U.S. Fish and Wildlife Service. Part of this research included carcass recovery (*Bonde et al. 1983) to quantify the causes, extent, and patterns of manatee mortality. Between 1976 and 1981, 367 carcasses were recovered in Florida. Anthropogenic deaths (122) accounted for 33% of the total mortality, and boat strikes (87) were responsible for 71% of the anthropogenic deaths (O'Shea et al. 1985). The number of carcasses recovered each year continues to increase (Ackerman et al. 1995), and so does public concern for the future of the Florida manatee (Reynolds 1995).

The development of techniques to determine the abundance of manatees has been problematic (Packard et al. 1986; Lefebvre and Kochman 1991; Lefebvre et al. 1995). The habits of manatees are generally secretive (Hartman 1979), and the animals typically occur in

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[4] An asterisk denotes unpublished material.

complex and turbid waterways (*Beeler and O'Shea 1988), which complicates censusing. The deficiencies in the understanding of manatee abundance have complicated an interpretation of the significance of the documented mortality to the population (*O'Shea 1988). Similarly, not enough has been known about the biology of reproduction in manatees.

Beginning in winter of 1976–77, the U.S. Fish and Wildlife Service began long-term research on the life history of manatees in the Crystal River. In this paper, we summarize the characteristics of reproduction of identifiable manatees from the southern Big Bend area of Florida (Fig. 1) during a 15-year period. With additional information from aerial surveys and carcass recovery, we developed quantitative estimates of the characteristics of reproduction of free-ranging manatees. These data contribute to a better understanding of the population dynamics of the Florida manatee, especially the significance of the presumably high yearly mortality since the early 1970's.

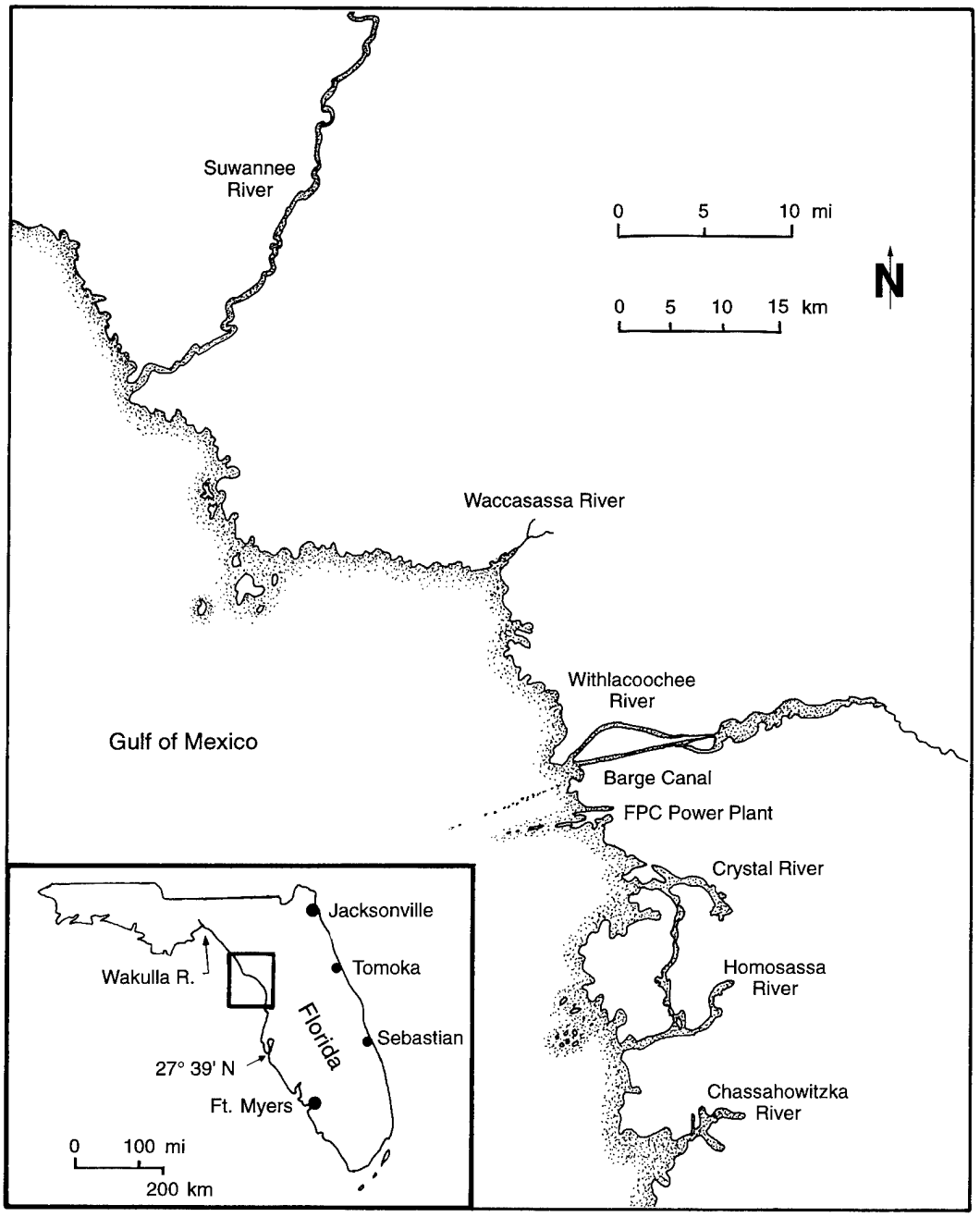


Fig. 1. The southern Big Bend study area of Florida, illustrating the major rivers used by manatees and other important place names.

Methods

Study Sites

The Crystal and Homosassa rivers are about 12 km apart on the southern Big Bend coast in Florida (Fig. 1). The Crystal River flows about 11 km from its spring-fed headwaters in Kings Bay to the Gulf of Mexico, and the Homosassa River flows about 12 km from its spring to the gulf. Artesian springs maintain the water temperatures in winter at the headwaters of these two rivers at about 23° C, well above those of other rivers that are not spring-fed along the southern Big Bend coast (Hartman 1979). Because manatees have a high thermoneutral zone (Irvine 1983), they begin to aggregate in the upper Crystal and Homosassa rivers in late September to escape the cooling waters of the other rivers and of the Gulf of Mexico (Kochman et al. 1985). In March, with the return of warm weather, most of the refuged manatees disperse along the Gulf coast of Florida and move as far north as the Wakulla River on the Panhandle and as far south as Sanibel Island near Fort Myers (Rathbun et al. 1990; Fig. 1). In this vast area, finding and observing the manatees during the summer is nearly impossible because they are so widely dispersed in turbid coastal waters. At least 88% of the individuals return every year to the winter refuges in the Crystal and Homosassa rivers (Rathbun et al. 1990). Because the manatees intersperse between the winter refuges in the Crystal River and in the Homosassa River during and between winters (Rathbun et al. 1990), data on manatees in these two areas are combined.

Identification of Individuals

Boats in Florida often strike manatees, which causes distinctive wound and scar patterns (Beck et al. 1982). Rathbun et al. (1990) estimated that more than 80% of the independent (weaned) individuals in the winter refuges in the Crystal and Homosassa rivers are identifiable from scars and other naturally occurring features. Wounds and scar patterns, however, are dynamic; patterns slowly change as wounds heal and new deformities are accumulated (Powell and Rathbun 1984; Beck and Reid 1995).

Since the late 1960's, the public has been swimming with the refuged manatees in the Crystal River. As a consequence, many of the animals have become habituated to the presence of people, and some actually solicit attention from snorkelers. During winter seasons, we visited both rivers and swam among the manatees, photographing distinctive individuals. We also took photographs of animals from boats. Notes on location, associated manatees, behavior, sex (based on the position of genital openings), and condition of reproduction were recorded on underwater slates. The photographs and data were added to an identification catalog that was updated every year (Powell and Rathbun 1984; Rathbun et al. 1990; Reid et al. 1991; Beck and Reid 1995). Each manatee was assigned a unique identification code, composed of two letters that identify the area where it was first sighted (CR = Crystal River, BS = Blue Spring) and sequential numbers[5] (e.g., CR22, CR208, etc.). Identification numbers of dead manatees were assigned the prefix M (e.g., M-331).

Manatee photographs were cataloged if they could be matched with one or more photographs taken of the same animal during at least two different winter seasons. Each year, numerous photographs of distinctive manatees were put in an unknown file until the yearly catalog update, when they were matched with photographs of previously identified and cataloged individuals. If matching photographs were not found, they were returned to the unknown file for possible future identification. The catalog was further updated each year by combining new with old photographs of an individual. New photographs often showed new scars or changes of old scars. We also updated the catalog by removing photographs of cataloged manatees that had been misidentified. One consequence of the yearly update is that totals and summaries from past analyses must be recalculated. For this reason, some of our data do not agree with data published by Powell and Rathbun (1984) and Rathbun et al. (1990).

Most neonatal calves lacked distinctive features that could be used for recognition. While calves were dependent on their mothers, they were distinguished by association. When weaned, however, they became unidentifiable, unless they were struck by a boat or acquired scars from other sources. As a consequence, the identities of many calves were lost after weaning. From November 1981 through March 1984, we cut one or two small, 1.5-cm-deep nicks into the posterior tail margins of 22 dependent calves. We used a livestock ear-notching tool for this procedure. An effort was made to re-identify these calves when they returned to the winter refugia as independent juveniles. During the three winter seasons during 1981–82 through 1983–84, 6, 4, and 12 dependent calves were tail-nicked in each respective year.

The fidelity of manatees to clearwater sites along the southern Big Bend coast in winter enabled us to observe the same individuals from year to year. Most of our observations were restricted to the 6-month period from October through March, which we call one winter season. Therefore, many of our analyses are inexact because the interval between one winter season to the next may actually include 6–18 months (Fig. 2). We think, however, that with our large sample sizes and the most probable timing of some reproductive events, a one-season period can usually be interpreted as an approximate 12-month period. The frequencies of sightings of individual males and females

[5] Identification numbers of manatees are given for completeness of information.

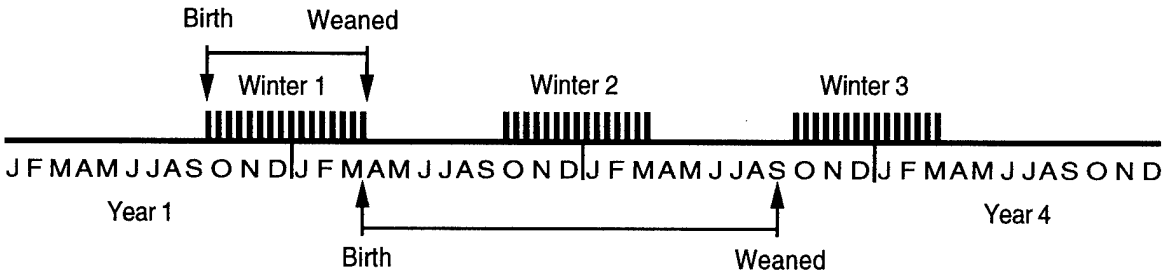


Fig. 2. Schematic illustration of how a "one-season" calf dependence may actually vary from 6 to 18 months. In the minimum (6 month) scenario (above the 4-year time-line), a manatee cow gives birth in late September of year 1 just prior to arriving at a winter refuge for a winter season (first). The female remains in the refuge during the winter, and then weans her calf in late March of year 2, just after dispersing from the refuge. When she returns to the warm-water area (winter 2), she has no calf. In this sequence the actual calf dependence is 6 months, but we would classify it as one season. In the maximum scenario (below the time-line), a female leaves the winter refuge in late March of year 2, and immediately gives birth. She returns to the winter refuge the following winter with a dependent calf, and then weans the calf in September of year 3, just prior to returning to the refuge in winter three. In this case, the calf was again only observed dependent during one season, but in fact it would have been dependent for nearly 18 months.

during the winter seasons were based only on records of individuals that were sighted two or more times during 6 or more years.

The data on individuals that we used for many of our analyses span a 15-year period during winter of 1976–77 through winter of 1990–91. For various analyses, we used subsets of the database. For example, only some reliable records exist for the 1976–77 winter season, and for some analyses, data from this season were therefore omitted. However, data about the reproduction histories from all available years were used but were censored to create a subset of females that were sighted in eight or more continuous winter seasons. To reduce the bias for short intervals between events such as weaning or parturitions, we restricted the censored data set to only sexually mature females that were seen with herds of pursuing males, were visibly pregnant, or were nursing a calf. Reproduction classes of mothers (primiparous or multiparous) were compared for frequency distributions of intervals between births on the basis of two-, three-, and four-seasons. Fecundity in the censored data set was calculated as the reciprocal of the interval.

We also provide descriptions of manatee groups engaged in mating behavior, including anecdotal accounts of composition of these groups and records of their seasonal occurrence. The manatee mating system can be categorized as promiscuous (sensu Wilson 1975). It involves the pursuit of a single female, presumably in estrus, by a herd of as many as 22 or more consorting males for as long as 1 month (Hartman 1979). Copulation has rarely been observed but there may be copulation by the female with more than one male, and male composition in the herd is transient (Hartman 1979). The terminology for these groups has changed. Hartman (1979) described them as *estrous herds*, although not all members of the herd are in estrus. This term was replaced with *mating group* or *mating herd* (Bengtson 1981; *Brownell and Ralls 1981; Powell and Rathbun 1984; Rathbun and O'Shea 1984; Preen 1989; Reynolds and Odell 1991). Because according to editorial policy the term mating herd is also less-than-satisfactory jargon, we refer to such groups as *herds of males* or *herds of consorting males.*

Late pregnancy in free-ranging manatees was visually determined from a distended abdomen seen in profile (Fig. 3). In some cases, the flanks of pregnant females visibly undulated as a result of fetal movements. Female-calf pairs were identified by nursing, close association, and frequent vocalization.

Aerial Surveys

Aerial surveys were conducted almost weekly during the winter seasons from December 1978 through November 1981 and at least biweekly during the non-winter seasons, except in April 1981 when only one survey was conducted. The flight path covered the known distribution of the manatees along the southern Big Bend coast of Florida (Powell and Rathbun 1984). This area included the rivers and nearshore waters from the effluent canal of the Crystal River power plant south through the Homosassa River during the winter months (November–March) and from the Suwannee River south through the Chassahowitzka River during the remaining non-winter months (Fig. 1). A single observer sat in the right front seat of a Cessna 172 aircraft, the right door of which was removed to improve visibility. The location and activity of all sighted manatees were recorded on study-area maps (see Powell and Rathbun [1984] for further details on methods).

Carcass Salvage

The U.S. Fish and Wildlife Service, the Florida Marine Patrol (Department of Natural Resources), and the University of Miami cooperatively salvaged manatee

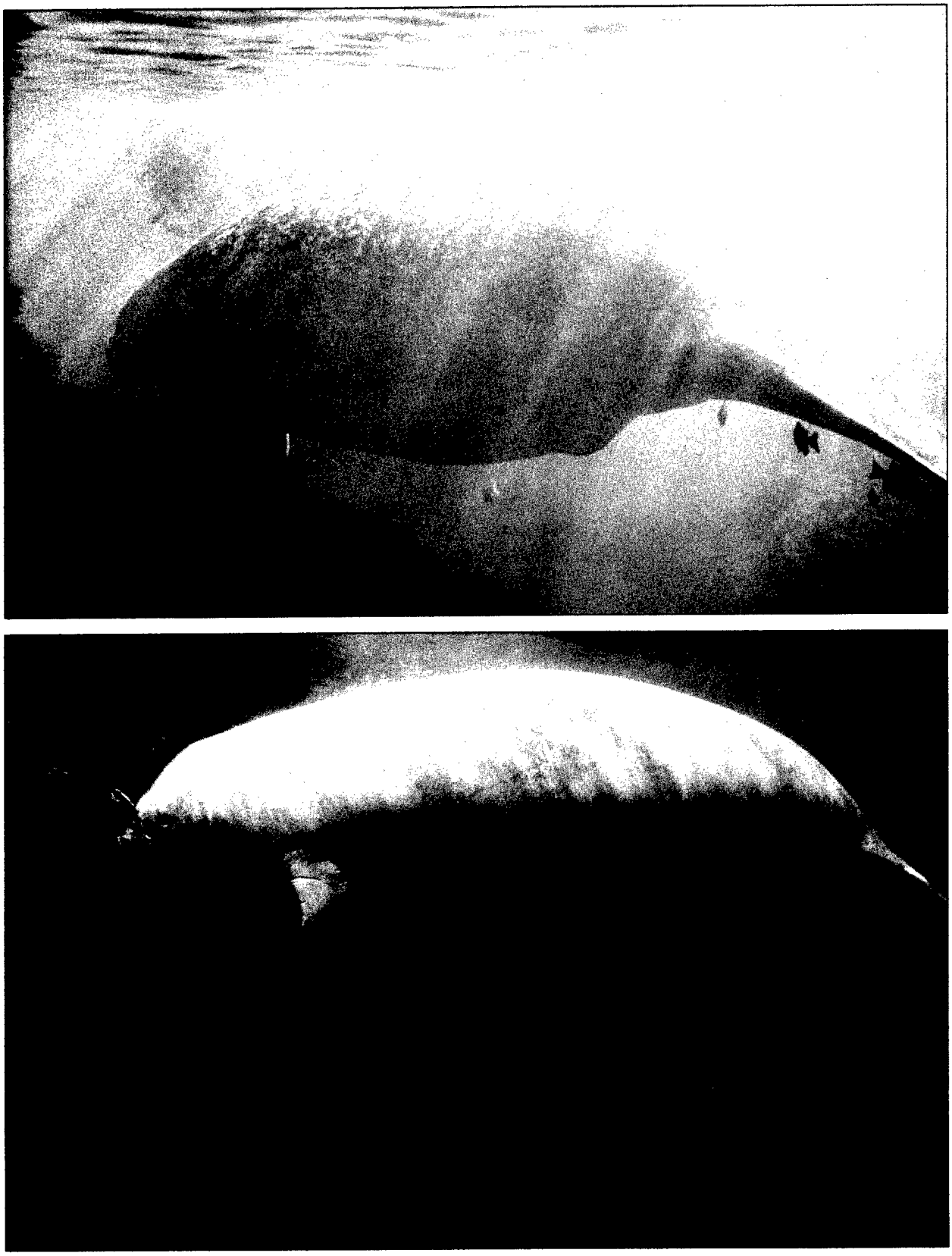


Fig. 3. Lateral views of a visibly pregnant female (CR97, 8 December 1993, Crystal River, Florida) (*top photo*) and an unidentified female that was not visibly pregnant (8 November 1982, Crystal River, Florida) (*bottom photo*). CR97 returned to Crystal River the following winter without a calf. *Photos by J. Reid (top) and G. Rathbun (bottom), U.S. Fish and Wildlife Service.*

carcasses in the southeastern United States from April 1974 through June 1985 (for details see *Bonde et al. 1983; O'Shea et al. 1985; Ackerman et al. 1995). Data we report from salvage records span this time period. Recovered dead manatees were reported and, when the condition of a carcass permitted, a full necropsy was performed that included gathering data on cause of death, morphometrics, and reproductive condition. Manatees were considered adults if they were more than 275 cm total length (TL) and calves if they were less than 150 cm TL (*Odell et al. 1981; O'Shea et al. 1985).

Statistical tests were done with procedures described by Siegel (1956) and Sokal and Rohlf (1969). Calculations were made with the Statistix software program. Probabilities of less than 0.05 were considered significant.

Results

The Manatee Population

The population size of cataloged manatees in the Crystal and Homosassa rivers during the 15-year study was 117 females and 152 males (not significantly different from a 1:1 ratio, $\chi^2 = 2.16$, $df = 1$, $P = 0.14$). During this period, 243 dependent calves in the population were identified.

A yearly average of 61.9 independent females and 69.4 independent males were identified and cataloged during the 14-season period during 1977–78 through 1990–91 (Table 1). The number of males did not significantly differ from the number of females in the population (nonparametric rank sum two-sample test, $P = 0.33$).

Thirty-nine cataloged, adult manatees (18 females, 21 males) were not sighted during the last four winter seasons of the study (1987–88 through 1990–91), but evidence of their emigration from the population or deaths was not found. Three females and two males died. The 39 missing and the 5 dead manatees represent 16.4% of the 269 manatees that were cataloged during the 15-year study.

During the winter seasons, the identifiable females were sighted with a frequency of 0.93, the identifiable males with a frequency of 0.87. For this analysis, only individuals that were sighted two or more times during 6 or more years were used. The return rate to the warm-water refuges was greater by females than by males (nonparametric rank sum two-sample test, $P = 0.004$).

Herds of Males

Nineteen herds of males (Fig. 4) were observed during the 115 aerial surveys along the southern Big Bend coast (see Hartman [1979] and Bengtson [1981] for detailed descriptions of herds). Six of the herds were sighted in the Suwannee River, 1 in the Withlacoochee River, 9 in the Crystal River, 2 in the Homosassa River,

Table 1. Number of identifiable Florida manatees (*Trichechus manatus latirostris*) in the Crystal River and Homosassa River during winter (October–March) seasons. Gross birth rate = number of calves per total individuals. Crude birth rate = number of first-year calves per total number of individuals. Fecundity = number of first-year calves per number of reproductive females. *Blanks* indicate data are not available.

Winter season	Person-days effort	Total independent males	Total independent females	Total first + second year calves	Total individuals	Gross birth rate	Crude birth rate	Total reproductive females	Fecundity rate
1977–78		34	31	8+1	74	0.12	0.11	21	0.38
1978–79		41	37	10+5	93	0.16	0.11	24	0.42
1979–80		39	41	9+2+1	92	0.13	0.10	29	0.31
1980–81	35	53	43	14+2	112	0.14	0.13	30	0.47
1981–82	28	49	59	13+2	123	0.12	0.11	46	0.28
1982–83	41	72	68	15+0	155	0.10	0.10	52	0.29
1983–84	63	80	75	18+4	177	0.12	0.10	59	0.31
1984–85	31	77	71	23+5	176	0.16	0.13	58	0.40
1985–86	31	72	58	16+5	151	0.14	0.11	45	0.36
1986–87	27	87	73	20+4	184	0.13	0.11	61	0.33
1987–88	30	105	82	24+5	216	0.13	0.11	66	0.36
1988–89	31	99	85	21+3	208	0.12	0.10	67	0.31
1989–90	26	85	85	34+3	207	0.18	0.16	74	0.45
1990–91	20	79	58	17+4	158	0.13	0.11	50	0.34
Mean		69.4	61.9			0.13	0.11		0.36
SD		22.6	18.2			0.02	0.02		0.06



Fig. 4. An unidentified female manatee (*upper center*) with three attending males in a mating herd in the headwaters of Homosassa River on 18 March 1985. *Photo by J. Reid, U.S. Fish and Wildlife Service.*

and 1 in the Chassahowitzka River. Although the persistence of each herd was not determined and no correction for multiple sightings of the same herd was possible, we ruled out multiple sightings of the same herds because of the temporal and spatial separation of the sightings.

The mean number of individuals in these herds was 10.2 (SD = 3.7, range = 5–22). The temporal distribution of these sightings (Fig. 5) revealed a peak in mating. The number of herds was significantly greater during April–May than during December–January or October–November. The difference in the number of herds among the six bimonthly periods was significant ($\chi^2 = 14.2$, $df = 5$, $P = 0.01$, MRANK nonparametric multivariate rank test; Sarle 1983).

A large, easily identifiable female (CR22) was observed from shore when she was pursued by males during 3 weeks in March–April 1984. She was first sighted on 13 April 1984 in the discharge canal of the Crystal River power plant. She was resighted on 18 and 19 April 1984 about 14 km farther south in the headwaters of the Crystal River. Finally, on 25 April 1984, she was observed

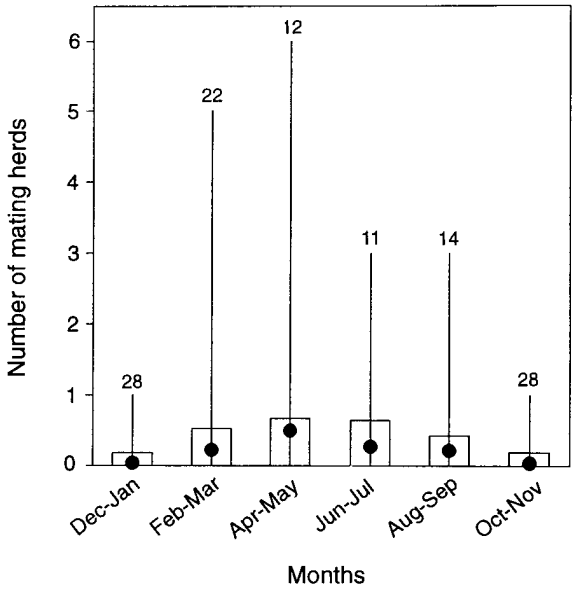


Fig. 5. Temporal distribution of mating herds observed during aerial surveys of the southern Big Bend coast of Florida from December 1978 through November 1981. *Filled circles* = means, *boxes* = standard deviations, *vertical lines* = ranges, and *numbers* = number of aerial surveys/period.

about 20 km south of the Crystal River at the mouth of the Homosassa River. At each respective location, she was accompanied by 12, 9, and 7 manatees. These consorts were mostly, if not all, males (Table 2). Although some of the individuals that accompanied her were seen in the herd at more than one site, the composition of the herd was dynamic over time; no single male was sighted in the herd on all three occasions (Table 2). The participation of the males and their minimum estimated ages were without patterns (Table 2).

Thirty-three females were identified as the subjects of pursuit by herds of males along the southern Big Bend coast during the 15-year study. Seventeen (52%) of the females that were resighted in the winter refuges in the Crystal and Homosassa rivers within 15 months of having been in one of the herds were accompanied by calves. The 48% (12 cases) that appeared at the winter refugia without calves either failed to conceive or lost their calves prepartum or postpartum.

Gestation

Seventeen identifiable females were sighted in separate herds of males, and within 18 months, each was seen with a small calf (not all females in such herds produced calves). Because parturition was never observed, these intervals can only be used as crude approximations of the maximum gestation period (Fig. 6). In one case (CR40 C2; Table 3) the 335-day interval is considered close to the actual gestation because the calf was small when first sighted.

Visual diagnosis of late pregnancy was relatively difficult. Some females consistently appeared pregnant before they gave birth. For example, one female (CR71) always appeared noticeably pregnant before giving birth ($n = 5$), whereas another (CR26) never appeared noticeably pregnant before giving birth ($n = 6$; Table 3). During the eight winter seasons of 1983–84 through 1990–91, 167 calves were born to 78 females. We predicted only 55 (33%) of these births, probably because of the timing of our observations relative to conception, variation in the appearance of pregnancy in different individuals, and neonatal mortality. Fifty-five of 82 cases of females we assessed as pregnant (67%) were sighted with calves in a winter season. If we rarely classified a female as pregnant when she was not, the 27 females without calves indicated a postpartum death rate as high as 0.33.

Table 2. Composition of a herd of Florida manatee (*Trichechus manatus latirostris*) males consorting with female CR22. Minimum age is based on the number of winter seasons between the first identification of a manatee and April 1984. Locations: 13 April 1984 = Crystal River Power Plant effluent; 18 and 19 April 1984 = Headwaters of Crystal River; 25 April 1984 = Homosassa River mouth.

Identification number of male	Minimum age	Date			
		13	18	19	25
17	6	X			
20	6	X			
21	6	X			
91	6				X
94	6		X	X	
100	5	X	X	X	
101	5		X	X	X
114	5		X	X	
128	3			X	
141	4	X			
146	2				X
147	3	X	X		
159	3	X			
161	3	X			
172	4	X			
175	2		X	X	
208	1				X
212	1				X
215	4		X	X	
221	0		X	X	
Number of unidentified males		3	1	1	2
Total		12	9	9	7

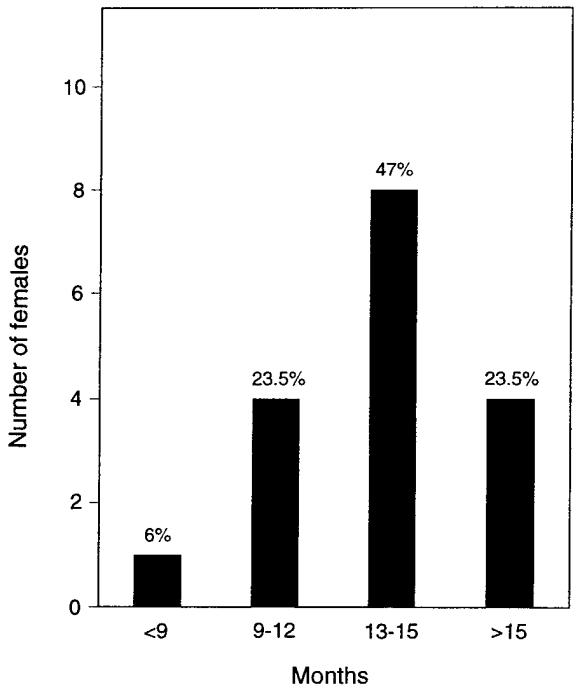


Fig. 6. Frequency distribution of maximum length of gestation periods for 17 females in the southern Big Bend from 1976–1977 through 1990–1991. The gestation periods are based on the time from being seen in a mating herd to the first sighting with a dependent calf within 18 months.

Parturition

Statewide, 53 carcasses of manatee neonates were recovered from April 1974 through June 1985. At necropsy, these calves had inflated lungs, indicating that they probably were born alive. Their average length was 125.3 cm TL (SD = 15.0, range = 95–155 cm). The sex ratio of these calves was 29:24, which is not significantly different from 1:1 (χ^2 = 0.15, df = 1, P = 0.7).

Parturition seems to peak in spring in the southern Big Bend region of Florida. During the eight winter seasons during 1983–84 through 1990–91, 63 of 82 obviously pregnant females (77%) were observed from February through March. The remaining 19 (23%) were seen during October through December. Because females were most noticeably pregnant only near term, these data suggested that most births occurred in spring, soon after the pregnant females left the warm-water refugia. We never witnessed births in the winter refuges, despite the large amounts of time we observed manatees (Table 1). During the entire study, only one citizen reported having observed a possible birth in the refugia (Kings Bay is urbanized). This occurred on 22 February 1986 in a quiet dead-end canal off Kings Bay. In the Crystal River or Homosassa River, we rarely observed females with dependent calves that looked as if they had been born during November through January of the current winter. We identified only three females that possibly gave birth in the winter refuges between mid-February and late March, just as the manatees were dispersing.

Seasonal reproduction is also indicated by the peak in recovered neonatal carcasses along the southern Big Bend coast during February–May (Fig. 7). The number of recovered carcasses during 2 months is significantly different from a uniform distribution (χ^2 = 12.3, df = 5, P = 0.03; Fig. 7). Statewide, the number of births peaks in April–May, but the distribution is not significantly different from a homogeneous distribution (χ^2 = 10.1, df = 5, P = 0.07). However, the three frequency distributions of the neonatal mortalities on the southern Big Bend coast, in the remainder of northern Florida, and in southern Florida (27° 39′ N latitude) significantly differ (χ^2 = 29.2, df = 10, P = 0.001; Fig. 7). The major contributor to this significance is the greater number of deaths of calves along the southern Big Bend coast in February–March versus April–May in the other regions. The frequency distributions of dead calves did not differ between southern Florida and northern Florida excluding the Big Bend (χ^2 = 3.7, df = 5, P = 0.6).

Evidence for twinning in manatees is unequivocal; two sets were born in captivity in Florida (*Odell et al. 1992) and at least two carcasses with twin fetuses were recovered. The statewide carcass recovery included 161 dead adult females (>275 cm TL) from July 1975 through August 1985. Two of them (1.2%) contained twin fetuses. The first (M-331) was a 375-cm-long animal recovered in Jacksonville, Florida, in April 1983. Each of her two female fetuses weighed 39 kg, and their total lengths were 132 and 135 cm. The second (M-389) was collected at Sebastian, Florida, in June 1984. The fetuses in this 313-cm-long female were a 136-cm-long male and a 126-cm-long female. No weights were taken. Both adults contained heavy fat deposits, indicating good physical condition. The first female was killed by a boat strike, the other carcass was badly decomposed and no cause of death was determined. In April 1980, on the Tomoka River, Florida, two dead female calves, 103 and 110 cm long, were recovered. The field record stated, "Circumstantial evidence suggests that M190 and M191 were twins. Size, state of decomposition, and recovery location were nearly identical."

Several probable twin births were observed also in free-ranging manatees. During winter 1980–81, a well-known, identifiable female (CR22) with two small calves of about the same length returned to the headwaters of the Crystal River for the winter. She was observed and photographed numerous times during the winter while she was nursing and interacting with both calves. Each calf was easily identifiable by distinct scars from boat strikes obtained in the Crystal River. They were never

Table 3. Number of births by female Florida manatees (*Trichechus manatus latirostris*) in the Crystal River and Homosassa River during winter seasons (October–March) during 1976–1977 through 1990–1991. Only adult (sexually mature) females that were sighted during winter seasons of 8 or more continuous years are included (censored data); all other females are excluded. An *asterisk*(*) indicates a juvenile female attained sexual maturity as indicated by pregnancy or lactation. B = first winter season after known birth of female; *Slash*(/) = individual was not sighted; *Dash*(-) = individual was sighted without a dependent calf; C = individual was sighted with a dependent calf; *superscript numbers* (C^2) indicate different sequential dependent calves of each mother.

Female identification	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990
09	/	-	-	C^1	-	-	-	-	-	/	/	/	/	/	/
14	/	-	-	-	C^1	-	-	-	-	-	/	/	/	/	/
19	-	C^1	C^1	-	C^2	-	C^3	-	C^4	-	C^5	-	C^6	-	C^7
22	/	-	C^1	-	$C^{2,3}$	-	C^4	C^4	-	/	C^5	C^5	C^6	C^6	-
26	C^1	C^1	-	C^2	-	-	C^3	-	C^4	-	C^5	C^5	C^6	-	-
27	/	-	-	-	-	-	*-	-	C^1	C^1	-	C^2	-	C^3	-
28	-	C^1	-	C^2	-	C^3	-	C^4	-	C^5	-	C^6	-	C^7	C^7
32	/	-	-	*-	C^1	-	-	-	C^2	-	C^3	-	C^4	-	-
33	/	C^1	C^1	-	C^2	-	-	-	C^3	/	C^4	-	C^5	/	C^6
40	/	-	-	C^1	-	-	-	C^2	C^2	/	/	/	/	/	/
41	/	-	-	-	-	*-	-	C^1	C^1	-	C^2	-	C^3	-	C^4
43	/	C^1	C^1	-	C^2	-	C^3	C^3	-	/	-	C^4	/	-	/
46	/	-	C^1	-	C^2	-	C^3	-	C^4	C^4	-	C^5	-	C^6	-
49	-	-	-	-	C^1	-	-	-	C^2	-	-	-	-	C^3	/
54	/	C^1	-	C^2	C^2	C^3	-	C^4	C^5	/	-	-	C^6	-	C^7
60	/	C^1	-	C^2	-	C^3	-	C^4	-	C^5	/	/	-	-	/
61	/	-	-	-	*-	C^1	-	-	C^2	C^2	-	C^3	-	C^4	-
70	/	-	-	C^1	C^1	-	C^2	-	C^3	-	C^4	C^4	C^5	C^5	-
71	-	C^1	C^1	-	C^2	-	-	C^3	-	-	C^4	-	-	C^5	C^5
83	-	-	$C^{1,2}$	C^2	-	C^3	-	C^4	-	C^5	C^5	/	/	/	/
87	/	-	-	-	*-	C^1	-	-	C^2	C^2	-	-	C^3	-	-
93	/	/	/	C^1	-	C^2	-	C^3	-	-	-	C^4	-	C^5	-
97	/	/	C^1	-	C^2	-	C^3	-	-	C^4	-	C^5	-	C^6	-
99	/	/	C^1	-	/	-	C^2	C^2	-	C^3	-	-	C^4	/	/
104	B	-	-	-	*-	C^1	-	-	-	C^2	C^2	-	-	C^3	-
105	-	-	C^1	-	C^2	-	C^3	-	C^4	-	/	-	/	-	/
111	/	/	B	-	-	-	-	*-	-	C^1	C^1	-	-	C^2	-
123	/	/	/	-	-	-	*C^1	C^1	-	C^2	-	C^3	C^3	-	C^4
125	/	/	/	-	-	*C^1	-	C^2	-	C^3	-	C^4	-	C^5	/
130	/	/	/	B	-	-	-	*-	C^1	C^1	-	C^2	C^2	C^3	C^3
134	/	/	-	-	-	-	*-	-	C^1	-	C^2	-	-	-	-
179	/	/	/	-	/	-	C^1	-	C^2	-	-	C^3	-	C^4	-
207	/	/	/	/	/	/	-	C^1	-	C^2	-	-	-	C^3	/
211	/	/	/	/	/	/	C^1	-	C^2	C^2	C^3	-	C^4	-	C^5
227	/	/	/	/	/	/	/	-	C^1	-	C^2	-	C^3	-	-

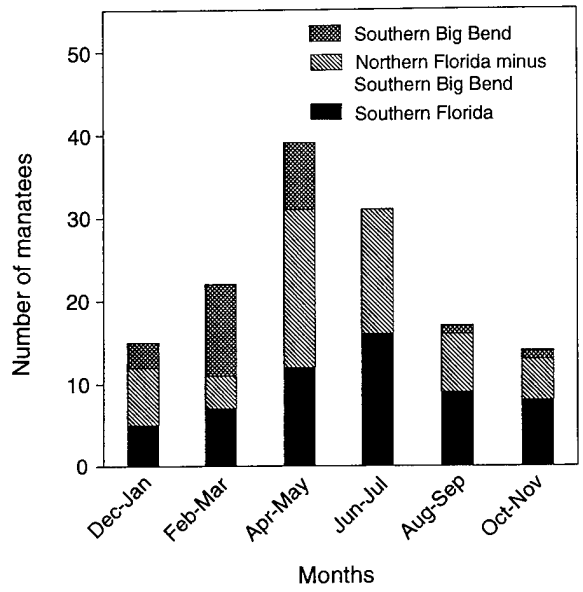


Fig. 7. Temporal distribution of perinatal manatee carcasses (less than 150 cm total length) recovered from the southern Big Bend coast ($n = 24$), northern Florida minus the southern Big Bend coast ($n = 57$), and southern (south of 27° 39′ N Latitude) Florida ($n = 57$) from July 1975 through June 1985.

re-identified in subsequent winters, which suggests that they did not survive a second year. In October 1978, another well-known female (CR83) was sighted with two equal-sized calves, a female and male, in the Crystal River. They were periodically resighted together during winter. While snorkeling on 22 January 1979, we measured the total lengths of the twins. The total length of the female was 142 cm and of the male 140 cm. During the following winter season, the mother returned with only the female calf to the Crystal River; the male was never resighted. During an aerial survey on 13 December 1978, an unidentified female manatee was photographed in the Suwannee River near Manatee Springs with two calves that seemed to be twins. An adult female (CR83) was sighted in the Crystal River on 13 November 1978 and 26 December 1978, making it possible that the sightings were of the same female in the Suwannee River.

At Blue Spring Run on the St Johns River, a female (BS107) returned with twins for the winter during 1991–92 (see photograph in O'Shea and Hartley 1995). Four additional cases of possible twinning in free-ranging Florida manatees have been reported. Two of these (1969–70, Pompano Beach; 19 November 1979, Sand Point Marina, Titusville) were based on photographs of large, unidentified manatees accompanied by two equal-sized calves. The other two cases (10 June 1979, Cocoa; 15 June 1981, St. Petersburg Beach) were based on sightings reported to us by the public.

Calf Dependence

Thirty-three females produced 121 calves that could be used to determine the duration of dependence by calves on their mothers (Table 3). Of 121 calves, 93 (77%) were dependent on their mothers for at least one winter season but for less than two seasons, and 28 (23%) were dependent for at least two but less than three winter seasons (see Fig. 2 for clarification of winter season). In the censored data set, no calf dependencies were longer than two winter seasons, although in the uncensored data one calf's dependence lasted three seasons. The mean duration of dependency from the censored data set was 1.2 winter seasons (SD = 0.42).

Six females of known ages were in the censored data set, and their records began with their first calves (Table 3). These females (CR41, CR61, CR87, CR104, CR111, and CR130) collectively had nine calves that were dependent for one winter season and seven, for two seasons. The 27 other females, which were of unknown ages and thus presumably multiparous when their censored records begin, had 84 calves that were dependent for one season and 21 calves that were dependent for two seasons. These data indicated that calves of younger females tend to be dependent longer than calves of older females ($\chi^2 = 4.4$, $df = 1$, $P = 0.04$).

Thirteen male and 11 female manatee calves were followed from their dependency through at least one winter season after weaning. Six of the females were dependent for one season and five for two seasons. Eleven of the males were dependent for one season, and two for two seasons. However, the duration of dependency did not significantly differ between the sexes (Fisher's exact test, $P = 0.18$).

One female (CR106) with two dependent calves was observed on numerous occasions in the Crystal River during winter of 1980–81. The calves were of such different sizes that they could not have been twins. These were the only observations of subsequent calves nursing at the same time or the possible adoption of a calf.

During winter 1989–90, a female (CR130) was sighted at least six times with her calf. On 23 January, she was nursing her male calf and another male calf. Because this was only observed once, we assumed the second calf was stealing a suckle (Fig. 8).

Recruitment Rate

Based on the uncensored data set, 29 (13 females, 16 males) of 218 calves survived past weaning. The 29 calves were produced by 25 different females; 23 mothers produced only one surviving calf, and each of another three produced two surviving calves (Table 4).



Fig. 8. A manatee calf suckles from its mother's (CR130) right teat on 23 January 1990, while a presumably unrelated calf steals a suckle from the opposite side. *Photo by R. Bonde, U.S. Fish and Wildlife Service.*

The fate of most calves was not determined, mainly because of difficulties with identities after weaning. This complicates the determination of an overall recruitment rate of the population. Eight of the 22 calves that were tail-nicked during 1981–82 through 1983–84 (four females and four males; Table 4) were re-identified at least four seasons after weaning (two, two, and four calves, respectively, from each of the three tagging seasons). Of the four female calves, all survived to sexual maturity, and three produced calves. The remaining 14 notched calves were never sighted as independent animals; they all disappeared or could not be re-identified. These data suggest that at least 36% of calves (33% for females) were actually recruited into the population.

Intervals Between Births

The durations of 99 intervals between births were determined (Fig. 9) from 33 adult females in the censored and further-restricted data set (2 of the 35 females in the censored data produced only one calf and thus had no intervals). The mean interval between calvings was 2.48 winter seasons (SD = 0.77). Intervals were longer in primiparous females than in multiparous females. Six females with calves in the data set were primiparous (Table 3). An additional six females in the uncensored data set for which data were collected during 8 or more continuous years produced two or more calves but were not sexually mature for the entire 8-year period. The frequency distribution of the 1- to 5-year intervals between births in the adults and the frequency distribution of the intervals between births by the juvenile-adults from the censored and uncensored data sets were too sparse for chi-square analysis. Rather than combine seasons, which would have been meaningless, we compared the two-, three-, and four-season frequencies. The two age classes of mothers were significantly different in frequency distributions of two-, three-, or four-season intervals ($\chi^2 = 6.0$, $df = 2$, $P = 0.05$), indicating intervals between births are longer in younger than in older females. This relation, however, may be explained by more postpartum losses of calves by younger mothers, which would result in a seemingly longer interval in the younger females. For example, in the censored data set, four of the ten 4-year intervals were probably attributable to lost calves because we observed the females

Table 4. Histories of reproduction of surviving Florida manatee (*Trichechus manatus latirostris*) calves born to known mothers from the Crystal River and Homosassa River from 1976–1977 through 1990–1991. *Superscript N* indicates the individual was tail-nicked while a dependent calf. C = dependent calf. *Superscript number* indicates dependent-calf identity on Table 3. *Blank* indicates undeterminable. P = visibly pregnant.

Weaned calf	Mother/calf	First sighted	Seasons dependent	Seasons first to last sighting	Date of first reproduction
Females					
104	$71C^{1}$	Feb 1978	2	13	C, Mar 1982
107	$19C^{1}$	Nov 1978	2	9	P, Mar 1982; C, Oct 1984
111	$83C^{2}$	Nov 1978	2	12	P, Nov 1983; C, Dec 1985
130	$70C^{1}$	Feb 1980	2	11	P, Jan 1984; C, Jan 1985
150^{N}	$61C^{1}$	Feb 1982	1	9	C, Dec 1985
151^{N}	$51C^{2}$	Oct 1981	1	9	None
155	$75C^{1}$	Nov 1980	2	4	None
180^{N}	$46C^{3}$	Jan 1983	1	6	C, Jan 1987
225	$99C^{2}$	Jan 1984	1	4	None
238^{N}	$54C^{4}$	Nov 1983	1	7	P, Dec 1987; C, Oct 1989
272	$271C^{1}$	Dec 1989		1	None
321	$227C^{3}$	Nov 1988	1	2	None
324	$202C^{1}$	Dec 1986		4	None
Males					
119	$60C^{2}$	Jul 1979	1	11	
152	$131C^{1}$	Mar 1982	1	8	
167	$49C^{1}$	Sep 1980	1	9	
181^{N}	$158C^{1}$	Nov 1982		8	
183	$26C^{3}$	Nov 1982	1	8	
242^{N}	$110C^{3}$	Jan 1984	1	6	
247^{N}	$71C^{3}$	Oct 1983	1	4	
248	$27C^{1}$	Nov 1984	2	3	
267	$61C^{3}$	Nov 1987	1	3	
269	$97C^{6}$	Nov 1989	1	1	
273	$106C^{3}$	Nov 1983	1	1	
297	$186C^{1}$	Feb 1986	2	4	
306	$33C^{5}$	Dec 1988		2	
314	$33C^{3}$	Dec 1984		4	
320	$171C^{1}$	Nov 1988	1	2	
322^{N}	$28C^{5}$	Sep 1983	1	6	

with herds of consorting males or as obviously pregnant within the 4-year intervals. Similarly, two of 22 3-year intervals probably were attributable to lost calves, but we could not detect these losses.

Calves nursed about as long as they accompanied their mothers, and the durations of lactation and calf dependency were therefore about the same. Six times we observed females with large dependent calves in herds of consorting males, but these calves may soon have been weaned. Six females (CR22, CR26, CR54 twice, CR70, CR211; Table 3) had different dependent calves in subsequent winter seasons, suggesting that lactation and gestation overlapped. The records suggest that gestation and lactation in three of the females (CR22, CR70, CR211) overlapped for 1–6 months, possibly during two pregnancies of one of the females (CR54). Lactation and gestation probably did not overlap in one (CR26) of the five females. If gestation immediately followed lactation but did not overlap with lactation and if the durations of pregnancy and calf dependency each were 12 months, the shortest interval between births that we observed was 2 years.

The temporal separation of nursing and pregnancy explains 9 of 22 three-winter-season intervals between births. The nine calves were nursed longer than one full winter season but less than two full winter seasons. The intervals between births therefore lasted three winter seasons, and the mothers were not pregnant while still nursing calves.

The intervals between births in some females had a pattern. For example, six intervals in one female (CR28)

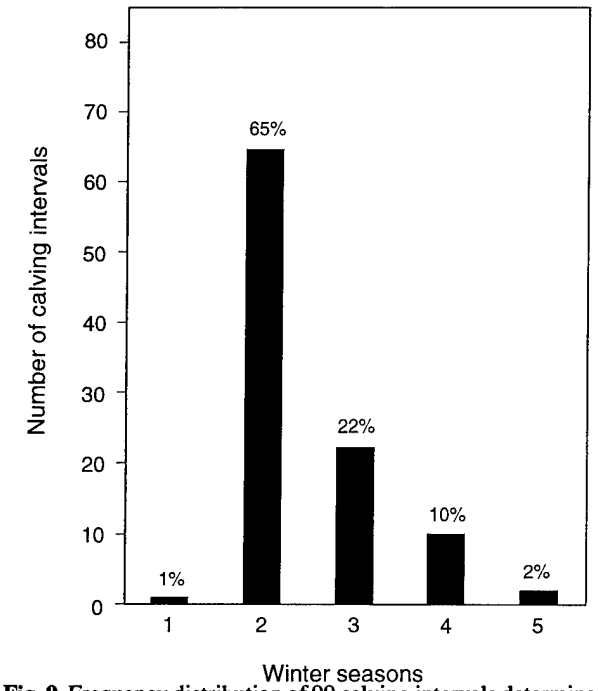


Fig. 9. Frequency distribution of 99 calving intervals determined from 33 females in the censored data set from the southern Big Bend coast during winter seasons, 1976–1977 through 1990–1991.

each lasted 2 years. Four intervals in another female (CR71) each lasted three winter seasons (only one of the calves was dependent for as long as two winter seasons).

Sexual Maturity

Seven female manatees (CR104, CR107, CR111, CR130, CR150, CR180, CR234; Table 4) were observed every winter season from birth to their first successful parturition (except one that was not seen during the third season). The ages at first calf production in these seven were 4, 6, 7, 5, 4, 4, and 6 years. However, four females (CR107, CR111, CR130, and CR238) were obviously pregnant when they were 3.5, 4.0, 5.0, and 5.0 years old. The time lapse between late pregnancy and parturition in two females (CR107 and CR111) suggested fetal or neonatal mortality that was immediately followed by a second pregnancy. If gestation lasts 1 year, the seven females became sexually mature between the ages of 2.5 to 4.0 years (mean = 3.2 years). We were unable to gather information on the age at sexual maturity in males.

Reproductive Life

The identity of one female (CR28) has been maintained from Hartman's (1979) study. She was identified at the Crystal River during winter 1967–68 and was seen with a calf during the following winter, which indicates that she was sexually mature. Her last calf was born during the summer months of 1989; she reproduced during at least 22 years. No data on her were gathered at the Crystal River between Hartman's (1979) study and ours (during 1970–71 through 1974–75), precluding the calculation of this female's rate of reproduction during the entire 22 years.

None of the adult female manatees in the catalog showed unambiguous signs of reproduction cessation. However, one large female (CR09) had a remarkably poor birth rate (0.13; Table 3). She was first identified in the Crystal River during winter 1977–78 and was seen with a calf during winter 1979–80. She was observed every winter from 1980–81 until February 1985, when she was killed by a boat in the Crystal River. During the 4 years before her death, she was seen in three herds of males and appeared to be pregnant twice but never returned to the Crystal River with a calf. At necropsy, she (M-422) was neither pregnant nor lactating, even though she was seen in a herd of males about 12 months before her death. She was in good body condition and had large quantities of fat. In fact, she was obese, being the heaviest manatee on record in Florida (1,620 kg). Her total length (375 cm), however, was not a record. Marmontel (1995) estimated her age at 28 years. This female had active corpora lutea but few regressed corpora albicantia and a smooth ovarian surface as if exhausted of follicles (Marmontel 1995).

A second female (CR39) was obviously pregnant during the 1981–82 and 1982–83 winter seasons in the Crystal River but was not seen with a calf in either of the following winters. She may have been approaching senility. Her carcass (M-382) was found at the Inglis Lock of the Cross Florida Barge Canal about 20 km north of the mouth of the Crystal River on 1 April 1984, but she was too decomposed to determine her reproductive condition or assign a cause of death.

Fecundity

The mean fecundity of manatees in the Crystal River (first-year calves per sexually mature female per year) was 0.36 (SD = 0.06, range = 0.28–0.47), calculated with data from all reproductive females in the population during winter 1977–78 through winter 1990–91 (Table 1). The average rate of the 33 females in the censored (and restricted) data set was 0.403 (SD = 0.102, range = 0.20–0.57). Twinning had a relatively minor effect. The 141 births (143 calves) in the censored data set included at least two sets of twins (1.4% of births; Table 3).

The intervals between births were 2.78 years, based on the arithmetic reciprocals of the fecundity from the population data (Table 1), and 2.48 years based on the restricted and censored data (Table 3).

The average crude birth rate (number of first-year calves per total number of individuals of both sexes including calves per year) during winter 1977–78 through winter 1990–91 was 0.11 (SD = 0.02, range = 0.10–0.16; Table 1). The mean gross birth rate (total number of calves per total number of individuals including calves per year) was 0.13 (SD = 0.02; Table 1).

Discussion

In late 1967, Daniel (Woody) Hartman and James A. Powell (his field assistant) started a 17-month field study of the ecology and behavior of manatees in the Crystal River. Using distinctive scar patterns—a technique first applied to manatees by Moore (1956) in southern Florida—the two researchers identified 63 manatees in the Crystal River during two winter seasons. Only 35 of these identifiable manatees, however, were present in the river during both winter seasons. Based on observations and a certain amount of intuition, Hartman (1979) estimated the basic traits of reproduction of manatees as 13-month gestation; litter size of one, rarely twins; slight birth peak in spring; calf dependence on the mother of 1–2 years; interval between births of 1–2 years; age at sexual maturity of 3–5 years; and longevity of as many as 50 years. The degree of accuracy of his estimates, despite the relatively small number of animals he observed and a study period that was shorter than many of his estimates, attests to his keen understanding of manatees.

The manatee population in the Crystal River has grown since Hartman's study from not only internal recruitment but also from immigration from southwestern Florida. The evidence for immigration comes from studies with radiotracking, resightings of scarred individuals, and the appearance of new adult manatees in the Crystal and Homosassa rivers (Powell and Rathbun 1984; Rathbun et al. 1990; Reid et al. 1991; B. Weigle, Florida Marine Research Institute, personal communication). However, a determination of the number of manatees that immigrate into the southern Big Bend area every year has not been possible. Whether newly identified manatees are immigrants or previously unidentifiable residents with newly acquired scars often can not be determined. Although this bias undoubtedly influences estimates of the rate of growth in the population, it probably did not influence most of our data on reproduction rates.

The identification of individuals by scars has several other potentially important but unavoidable limitations. For example, the unidentifiable individuals in the population (circa 20%; Rathbun et al. 1990) may not be distributed equally across the age classes but are over-represented by newly independent or juvenile animals. However, our observations suggest that juveniles tended to be more habituated to the presence of people and are therefore more easily approached, observed, and identified than some adults. Immigrant adults may be under-represented because they are shyer than the more habituated residents. The influences of these biases on our analysis cannot be determined, but we assume that they are small, especially when independent data are corroborative.

We estimate that the postpartum death rate of calves was about 0.33 of all births. This figure is based on females that were visibly pregnant. Potential, unmeasured biases may again influence our estimate. For example, females that were obviously pregnant may have borne larger than average calves, which may have augmented or lowered the calf mortality. Only continuation of the long-term individual histories can answer this and similar questions.

We present two different estimates for fecundity of manatees in the Crystal River. One is based on a yearly average of identifiable females and calves (0.36; Table 1), the other (0.40) is derived from a censored subset of the former (Table 3) that was further restricted to include only reproductive females that have uninterrupted calf-to-calf cycles. For example, one female (CR83; Table 3) had four calves in the 7 years from 1978 through 1984 at a fecundity of 0.57. Although the estimated fecundity from the censored and restricted data may be the most accurate and, as such, perhaps should be used for population models, comparable data from other manatee populations are still being collected. In the following discussion, we use only the uncensored data for our calculations (Table 1).

Despite the various, briefly described potential biases, we are confident that most of our estimates are reasonably accurate because they often agree closely with independent databases. Marmontel (1995) did an extensive analysis of the reproductive condition of manatee carcasses from throughout the southeastern United States that she aged by counting growth-layer groups in the tympanoperiotic bone. Her estimates of sex ratio, seasonal reproduction, litter size, age at sexual maturity, temporal separation of gestation and lactation, and reproductive life are similar to ours. Only her estimated average interval between births (3.0 years) differed from our estimate (2.5 seasons). The reason for this difference is not known, but as pointed out by Marmontel (1995), probably relates to biases in her methods and data. These include specimens from a wider geographical area (all of Florida), a possible positive correlation between days since conception and determination of pregnancy at necropsy because of decomposition, the influence on the data set of dead females that were not in reproductive condition at death because of illness, and difficulties with accurately reading bone annuli in animals older than 15–20 years.

The U.S. Fish and Wildlife Service and the Florida Park Service have been monitoring the histories of manatees

that aggregate in winter in the Blue Spring Run since the mid-1970's with techniques similar to those we used in the Crystal River area (O'Shea and Hartley 1995). The traits of reproduction of this population are remarkably similar to those we found of manatees in the Southern Big Bend. Sex ratios are 1:1, sexual maturity is attained at 3–6 years, gestation lasts about 12 months, few births occur during winter (1.8% are twins), and the average interval between births is 2.6 years. Because the Blue Spring population of manatees is smaller and more easily monitored, O'Shea and Hartley (1995) were able to estimate calf survival after 3 winters at 63%, which is undoubtedly more precise than our estimate of 36%. At the Crystal River, we had difficulties keeping track of weaned calves, which undoubtedly contributed to our exaggerated rate of loss. Knowing that our estimate of calf loss is high helps resolve the inconsistency with the proportion of females with first-year calves in the Crystal River (0.36) and a growing population (Table 1). This rate of reproduction is similar to the 0.31 rate in manatees at Blue Spring (O'Shea and Hartley 1995), which further collaborates the overall similarity in characteristics of reproduction between these two disjunct populations.

Reid et al. (1995) found similar patterns of reproduction in manatees along the Atlantic Coast, including gestation, birth season, and average interval between births (2.6 years). Even the proportion of females with calves (0.38) compares favorably with that of the manatees in the Crystal River (0.36).

Based on 17 adult females that produced 9 calves in 2 years, Reynolds (1981) estimated a fecundity of 0.26 in manatees in the Blue Lagoon. This is notably lower than our uncensored rate of 0.36 in manatees in the southern Big Bend. This is probably related to Reynolds' (1981) short study period and small, isolated population in the lagoon.

Bengtson (1981) investigated the movements and social behavior of radio-tagged manatees in the St. Johns River but did not estimate reproduction rates or age-specific reproduction. However, he contributed to the understanding of mating behavior. Hartman (1979:100) described the herds of males that pursue females in attempts to mate in the Crystal River: "These groups may remain together for periods ranging from a week to more than a month. As many as 17 bulls once were observed following an estrous cow...juvenile males joined and left the herd constantly, but a nucleus of mature bulls was always present and in persistent pursuit of the cow." He did not, however, provide much quantification of his observations. Females that are the focus of these herds can move distances as long as 160 km in 12 days—as did one female in the St. Johns River (Bengtson 1981)—and a minimum of about 35 km during 3 weeks along the southern Big Bend coast. Bengtson (1981) also presented data on the compositions of three of these herds that support Hartman's (1979) general description, except the nucleus of mature males. Our data (Table 2) and Bengtson's (1981) indicated that these herds routinely include small males that were generally thought of as juveniles based on their total length of less than 275 cm (*Odell et al. 1981). Hernandez et al. (1995), however, showed that even males as short as 252 cm and only 2–3 years old can have fully spermatogenic testes. Even though these smaller males are probably at a disadvantage in physically competing with larger males for access to receptive females, they have the physiological potential of impregnating females. Hartman (1979) also observed intromission achieved by what he described as a juvenile male. More research, however, is needed to determine the specific social and reproductive roles of males in these groups. O'Shea and Hartley (1995) further discuss aspects of mating behavior.

The phenomenon of manatee females remaining in estrus for long periods, traveling great distances, and attracting a large, dynamic group of males, is probably related to an optimal mating strategy by which the female attempts to assemble as many males as possible to increase her choice of mates. The males probably compete with one another to copulate with the receptive female (Rathbun and O'Shea 1984).

Bengtson (1981) observed that some females were attended by herds of males in more than one such event, separated by inactive periods of a few weeks. This observation led him to predict that some estrus periods were pseudo-estrus periods. Marmontel (1995) suggested that females may undergo several ovulations before conception, based on the presence of corpora lutea in ovaries that she examined from nulliparous females. We observed females in herds of males that were not subsequently observed with a calf after sufficient time for gestation, suggesting no pregnancy occurred. Based on Marmontel's (1995) data, these females may have had a pseudo-estrus period, but early failure of pregnancy may explain some of these cases, and misidentification may explain the others. Not all aggregations of manatees engaged in behavior that may be mating are indeed estrous females with males. In the warm-water refugia in Florida, groups of as many as 12 males that intensively cavort for as long as several hours are common (Hartman 1979). These cavorting groups probably represent contests of stamina in which males practice behavior patterns used in mating and possibly establish some sort of rank or hierarchy. Although cavorting herds superficially resemble groups involved in true mating, a close inspection or prolonged observation can reveal the difference. These ambiguities in interpreting observations of manatees in what appear to be groups intent on mating make field determination of pregnancy

and the estimation of gestation difficult and highlight the need for further research on the various behaviors associated with the manatee estrous cycle.

Hartman (1979) and Bengtson (1981) suggested that multiple estrous periods in manatees and the similar pattern in elephants support the paleontological evidence for the common ancestry of elephants and sirenians (Domning et al. 1986). Behavior, and possibly physiology, are relatively labile features in evolutionary time (Wilson 1975). The vast temporal separation between the common ancestor of the elephants and sirenians probably limits the value of comparisons of mating behavior and estrus between living representatives of these two groups for understanding their phylogenetic relationships.

Although manatees have been bred in captivity in the United States since the 1950's, relatively few data were gathered that furthers an understanding of their biology of reproduction (Odell et al. 1995). One aspect of captive reproduction that is of particular interest is the occurrence of adoption, and calves nursing from females other than their mothers (D. K. Odell, Sea World of Florida, personal communication). Should we expect to see these behaviors in free-ranging manatees, or are they the result of artificial containment and crowding? At the Crystal River, despite many years of observation, we documented only one possible case of adoption and one case of a stolen suckle by a presumably unrelated calf (Fig. 8). We think that these two cases represent unique events. Although large aggregations of manatees are common today in Florida, they are actually unusual events in space and time. Only in Florida, which is at the edge of the species' distribution (Lefebvre et al. 1989), do large, persistent resource-based aggregations occur, and they may be a relatively recent phenomenon. As a result of the virtual elimination of purposeful predation by humans in Florida and predation by large carnivores, the concentrations of many manatees became common only in the last 40 years (Moore 1951). These resource-based aggregations were probably not common in prehistoric Florida (Powell and Rathbun 1984), just as they are nearly unheard of in other parts of their distribution. Because concentrated large numbers of manatees, including females and calves, in small areas have probably not been a feature of manatee ecology over evolutionary time, adoption and shared suckling are probably not evolved features but circumstantial accidents.

More is now known about the reproduction biology of the Florida manatee than of any other sirenian. A better understanding of the population dynamics of all sirenians can be achieved by extension of this information to the other taxa and by comparing data among the different species (Marsh 1995). Few data are available on the traits of reproduction of free-ranging west African manatees (*T. senegalensis*) and Amazonian manatees (*T. inunguis*); published material (reviewed by Husar 1977, 1978; Marmontel et al. 1992) suggests that these species are similar to the West Indian manatee (*T. manatus*).

Twinning was one of the first traits of reproduction of manatees reported in the literature; twin fetuses in a *T. manatus* carcass from the Orinoco River in the eighteenth century were documented by Gumilla (1745). Twin births, however, are unusual in manatees, as revealed by our observations (1.4%), by those of O'Shea and Hartley (1995) at Blue Spring (1.79%), and by the examinations of reproduction tracts in carcasses (4%) by Marmontel (1995). Twinning is also rare in most other marine mammals (Perrin et al. 1984; Riedman 1990; Riedman and Estes 1990), including dugongs (Marsh 1995).

The closest modern relatives of manatees are the sea cows (Family Dugongidae). The dugong (*Dugong dugon*) is the only surviving member of this group, and it occurs in tropical and subtropical near-shore waters of the Indo-Pacific (Nishiwaki and Marsh 1985). Most information on the reproduction of dugongs was determined by careful analyses of known-aged carcasses in northern Australia (Marsh et al. 1984a, 1984b, 1984c; Marsh 1995) and by limited observations in the field (Anderson and Birtles 1978; Preen 1989). Most features, such as the durations of gestation, dependence of the calf on its mother, and intervals between births are difficult to determine from carcasses, but estimates for dugongs are similar to estimates for manatees (Marsh 1995). However, female dugongs do not attain sexual maturity until they are 9–10 years old, which is nearly three times the age of sexual maturity in West Indian manatees along the southern Big Bend coast. We do not know why dugongs mature later than manatees, unless the difference relates to food resources, which in general may be of poorer quality and less abundant than those of manatees. Dugongs are largely marine, feeding on submerged marine angiosperms, whereas manatees in Florida consume a much wider selection of plants, including marine and freshwater angiosperms, emergent vegetation, and algae (Best 1981).

Data on reproduction from dugongs (Marsh et al. 1984c), Amazonian manatees (Best 1982), and West Indian manatees (Figs. 3 and 5; Odell et al. 1995) suggest diffuse, seasonal birth peaks in each species. Of particular interest are the proposed explanations of seasonality. Although all relate to seasonal environmental factors, the proximate causes are quite different. Best (1982) suggested that December–July flooding of the Amazon River enables manatees in the region of Manaus, Brazil, to disperse into inundated areas and take advantage of a greater abundance and diversity of nutritious plant foods. These manatees synchronize births with the floods. Marsh et al. (1984c) believed that dugongs breed seasonally during the August–December austral

spring because water temperatures are optimal for seagrass growth, which results in a more nutritious food supply for the dugongs during this time. In Florida, where manatees occur at the edge of their distribution (Lefebvre et al. 1989), low water temperatures during winter are important, but the effects of temperature on manatees are not clear. An indirect influence through the food supply is possible, as Marsh et al. (1984c) suggested in dugongs. We think another, perhaps more important factor, is the physiological stress from hypothermia when water temperatures are below about 13° C. Low temperatures may synchronize parturitions with the warmer summer months in Florida. The risk of parturition in water permits only a small latitude for abnormal occurrences. Cold temperatures may increase the probability of complications at birth that increase calf mortality. However, O'Shea et al. (1985) pointed out that few, if any, moribund hypothermic or dead calves were found during cold weather in Florida. Rather, the newly weaned, subadult age-class is most vulnerable (O'Shea et al. 1985; Ackerman et al. 1995). Lactation is energetically costly (Oftedal 1985) and would be stressful to females during winter. Because gestation is energetically not as demanding as lactation (Oftedal 1985) and because gestation lasts about 12 months in manatees, the avoidance of excessive energetic demands during winter is probably sufficient for the diffusely seasonal pattern of giving birth we observed along the southern Big Bend coast. This explanation is also consistent with the diffusely seasonal reproduction in captive manatees in Florida oceanaria (*Odell et al. 1992), where circulating water systems track ambient air temperatures (D. K. Odell, Sea World of Florida, personal communication). Hernandez et al. (1995) also proposed another possibility: the seasonal occurrence of spermatogenesis during the summer months may dictate or at least contribute to the diffuse birth peak during the summer in manatees in Florida.

When the U.S. Fish and Wildlife Service initiated its research on manatees in Florida in 1974, one of the first activities was the determination of the abundance of manatees in the state with aerial surveys (Irvine and Campbell 1978). Dozens of aerial surveys have now been completed throughout the range of *T. manatus* (*Beeler and O'Shea 1988; Ackerman 1995), and virtually all observers reported the proportion of calves to the total number of sighted manatees (gross birth rate). These rates in the southern Big Bend area (0.11; Table 5) are similar but lower than the rate of known individuals in the same area (0.13). The mean gross birth rate of all manatees in Florida (0.085, SD = 0.03; except in the southern Big Bend) and in manatees outside Florida (0.10, SD = 0.05; Table 5) are lower than the 0.13 (SD = 0.02) rate we determined of known individuals in the Crystal River area (Table 1). Potential biases and errors in aerial survey data are numerous; some relate to survey techniques, such as variation in the number and experience of the observers, different seasons, variable habitats, inconsistent air speed and altitude, and more. Other biases are due to behavior of the manatees, including females having a higher return rate to winter refugia than males, females with dependent calves arriving at winter refugia in advance of most males (Rathbun et al. 1990), calves being difficult to sight when closely associated with their mothers, and females with calves probably being less prone than females and males to wander far from warm-water refugia between winter cold spells.

The basic life-history characteristics of West Indian manatees are similar to many other long-lived marine mammals with relatively low fecundity and high survival rates (Perrin et al. 1984). Based on an initial understanding of the population dynamics of sirenians (Marsh et al. 1984c; *Packard 1985), many biologists were concerned about the future of manatees in Florida (*O'Shea 1988). The recent efforts to develop models with the most current information on reproduction, mortality, and abundance of the manatees (Eberhardt and O'Shea 1995) are essential first steps for generating and implementing management that allows people and manatees to coexist in Florida.

The data that we present in this paper include only some of the basic information for a simple understanding of manatee population dynamics (Eberhardt and O'Shea 1995). Long-term research into basic life history such as age-specific reproduction and mortality must continue. Continued monitoring of the population of manatees in winter in the southern Big Bend region is especially important for determining whether density-dependent effects develop as abundance increases. Only with these additional data can the next generation of population models be developed. Without these powerful tools, no one can predict and plan the future of manatees in Florida.

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Table 5. Crude birth rates (number of calves per total number of individuals including calves) of West Indian manatees (*Trichechus manatus*); data are from aerial surveys reported in the literature. *Blanks* indicate data not available. Order arranged geographically from northeastern Florida along the coastline through Central America and then to the West Indies.

Total number of sightings	Total number of calves	Crude birth rates	Location	Season/year	Source
Eastern Florida					
		0.070	St. Johns River, NE Florida	Jul 1982–Jun 1983	Kinnaird (1985)
151	15	0.099	Brevard Co.	Aug 1977	Leatherwood (1978)
1,139	94	0.083	Banana River	Apr 1977–May 1978	*Irvine et al. (1979)
3,686	326	0.088	Brevard Co.	Jan 1978–Feb 1980	Shane (1983)
	290	0.140	St. Lucie Inlet south to Palm Beach Inlet	Dec 1980–Feb 1981	*Packard (1981)
772	40	0.052	Everglades	Sep 1973–Jun 1976	*Odell (1979)
Southwestern Florida					
335	36	0.101	Tampa Bay	Jun 1979–Feb 1980	*Patton (1980)
554	15	0.027	SW Florida (south of Pasco Co.)	Jul 1979 Sep–Dec 1979	Irvine et al. (1982)
314	26	0.080	Anna Maria south to Venice	Jan–Dec 1985	*Patton (1986)
269	18	0.067	Anna Maria south to Venice	Mar–Dec 1986	*Patton et al. (1987)
Northwestern Florida					
460	50	0.109	Crystal River	Nov–Mar 1977–82	Powell and Rathbun (1984)
		0.110	South Big Bend	Nov–Mar 1981–85	Rathbun et al. (1990)
All of Florida					
Mean and range		0.098 (0.068–0.133)	Various power plants on the eastern coast, St. Johns River, and Fort Myers	Winters 1977–90	*Reynolds (1991)
738 (winter)	71	0.096	Florida (both coasts)	Jan–Feb 1976	Irvine and Campbell (1978)
245 (summer)	34	0.134	Florida (both coasts)	Aug 1976	
		0.117	Combined		
Outside Florida					
295	10	0.034	Q. Roo, Mexico	Jul 1987–Jul 1988	Colmenero and Zárate (1990)
101	9	0.089	Belize	Sep 1977	Bengtson and Magor (1979)
47	5	0.106	Belize	May 1989	O'Shea and Salisbury (1991) (in text)
23	4	0.170	Honduras	Mar 1979, late 1979, May 1980	Rathbun et al. (1983)
70	11	0.157	Panama	May–Dec 1987	Mou Sue et al. (1990)
8	0	0	Haiti	May 1982	Rathbun et al. (1985)
119	14	0.118	Dominican Republic	Feb–Apr 1977 Jun, Aug 1977 Oct–Dec 1977	Belitsky and Belitsky (1980)
226	15	0.066	Puerto Rico	Aug 1976 Jun 1978–Mar 1979	Powell et al. (1981)
523	40	0.076	Puerto Rico	Mar 1984–Mar 1985	*Rathbun et al. (1986)
192	27	0.141	Puerto Rico	Jul 1988–Jan 1989	*Freeman and Quintero (1990)

updated and revised this paper through seemingly endless iterations as more and more data became available.

Cited References[6]

Ackerman, B. B. 1995. Aerial surveys of manatees: a summary and progress report. Pages 13–33 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Ackerman, B. B., S. D. Wright, R. K. Bonde, D. K. Odell, and D. J. Banowetz. 1995. Trends and patterns in mortality of manatees in Florida, 1974–1992. Pages 223–258 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Anderson, P. K., and A. Birtles. 1978. Behaviour and ecology of the dugong, *Dugong dugon* (Sirenia): observations in Shoalwater and Cleveland bays, Queensland. Australian Wildlife Research 5:1–23.

Beck, C. A., and J. P. Reid. 1995. An automated photo-identification catalog for studies of the life history of the Florida manatee. Pages 120–134 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Beck, C. A., R. K. Bonde, and G. B. Rathbun. 1982. Analyses of propeller wounds on manatees in Florida. Journal of Wildlife Management 46:531–535.

*Beeler, I. E., and T. J. O'Shea. 1988. Distribution and mortality of the West Indian manatee (*Trichechus manatus*) in the southeastern United States: a compilation and review of recent information. National Technical Information Service, Springfield, Va. Document PB 88-207980/AS. 613 pp.

Belitsky, D. W., and C. L. Belitsky. 1980. Distribution and abundance of manatees (*Trichechus manatus*) in the Dominican Republic. Biological Conservation 17:313–319.

Bengtson, J. L. 1981. Ecology of manatees (*Trichechus manatus*) in the St. Johns River, Florida. Ph.D. thesis, University of Minnesota, Minneapolis. 126 pp.

Bengtson, J. L., and D. Magor. 1979. A survey of manatees in Belize. Journal of Mammalogy 60:230–232.

Best, R. C. 1981. Foods and feeding habits of wild and captive Sirenia. Mammal Review 11:3–29.

Best, R. C. 1982. Seasonal breeding in the Amazonian manatee, *Trichechus inunguis* (Mammalia: Sirenia). Biotropica 14:76–78.

*Bonde, R. K., T. J. O'Shea, and C. A. Beck. 1983. A manual of procedures for the salvage and necropsy of carcasses of the West Indian manatee (*Trichechus manatus latirostris*). National Technical Information Service, Springfield, Va. Document PB 83-255273. 175 pp.

*Brownell, R. L., Jr., and K, Ralls. 1981. Preface. Pages 1–2 *in* R. L. Brownell, Jr. and K, Ralls, editors. The West Indian manatee in Florida: Proceedings of a workshop held in Orlando, 27–29 March 1978. Florida Department of Natural Resources, Tallahassee. 154 pp.

Colmenero-R., L. C., and B. E. Zárate. 1990. Distribution, status and conservation of the West Indian manatee in Quintana Roo, México. Biological Conservation 52:27–35.

Domning, D. P., C. E. Ray, and M. C. McKenna. 1986. Two new Oligocene Desmostylians and a discussion of Tethytherian systematics. Smithsonian Contributions to Paleobiology Number 59. 56 pp.

Eberhardt, L. L., and T. J. O'Shea. 1995. Integration of manatee life-history data and population modeling. Pages 269–279 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

*Freeman, J., and H. Quintero. 1990. The distribution of West Indian manatees (*Trichechus manatus*) in Puerto Rico. Springfield, Va. National Technical Information Service Report Number PB91-137240. 38 pp.

Gumilla, Father Joseph. 1745. El Orinoco ilustrado, y defendido, historia natural, civil, y geográfica de este gran rio, y de sus caudalosas vertientes. Vd.I, pp. 225–228, plate II. Second edition. Madrid, Spain. 403 pp.

Hartman, D. S. 1979. Ecology and behavior of the manatee (*Trichechus manatus*) in Florida. American Society of Mammalogists Special Publication 5, Lawrence, Kans. 153 pp.

Hernandez, P., J. E. Reynolds, III, H. Marsh, and M. Marmontel. 1995. Age and seasonality in spermatogenesis of Florida manatees. Pages 84–97 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Husar, S. L. 1977. *Trichechus inunguis*. American Society of Mammalogists. Mammalian Species 72:1–4.

Husar, S. L. 1978. *Trichechus senegalensis*. American Society of Mammalogists. Mammalian Species 89:1–3.

Irvine, A. B. 1983. Manatee metabolism and its influence on distribution in Florida. Biological Conservation 25:315–334.

Irvine, A. B., and H. W. Campbell. 1978. Aerial census of the West Indian manatee, *Trichechus manatus*, in the southeastern United States. Journal of Mammalogy 59:613–617.

Irvine, A. B., J. E. Caffin, and H. I. Kochman. 1982. Aerial surveys for manatees and dolphins in western peninsular Florida. Fisheries Bulletin 80:621–629.

*Irvine, A. B., M. D. Scott, and S. H. Shane. 1979. A study of the West Indian manatee, *Trichechus manatus*, in the Banana River and associated waters, Brevard County, Florida. Final report, Contract CC-63426A. John F. Kennedy Space Center, Fla. 49 pp.

Kinnaird, M. F. 1985. Aerial census of manatees in northeastern Florida. Biological Conservation 32:59–79.

Kochman, H. I., G. B. Rathbun, and J. A. Powell. 1985. Temporal and spatial distribution of manatees in Kings Bay, Crystal River, Florida. Journal of Wildlife Management 49:921–924.

Leatherwood, S. 1978. Aerial survey of the bottlenosed dolphin, *Tursiops truncatus*, and the West Indian manatee, *Trichechus manatus*, in the Indian and Banana rivers, Florida. Fisheries Bulletin 77:47–59.

[6] An asterisk denotes unpublished material.

Lefebvre, L. W., and H. I. Kochman. 1991. An evaluation of aerial survey replicate count methodology to determine trends in manatee abundance. Wildlife Society Bulletin 19:298–309.

Lefebvre, L. W., B. B. Ackerman, K. M. Portier, and K. H. Pollock. 1995. Aerial survey as a technique for estimating trends in manatee population size—problems and prospects. Pages 63–72 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Lefebvre, L. W., T. J. O'Shea, G. B. Rathbun, and R. C. Best. 1989. Distribution, status, and biogeography of the West Indian manatee. Pages 567–610 *in* C. A. Woods, editor. Biogeography of the West Indies—past, present, and future. Sandhill Crane Press, Gainesville, Fla.

Marmontel, M. 1995. Age and reproduction in female Florida manatees. Pages 98–119 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Marmontel, M., D. K. Odell, and J. E. Reynolds, III. 1992. Reproductive biology of South American manatees. Pages 295–311 *in* W. C. Hamlett, editor. Reproductive biology of South American vertebrates. Springer-Verlag, New York. 328 pp.

Marsh, H. 1995. The life history, pattern of breeding, and population dynamics of the dugong. Pages 75–83 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Marsh, H., G. E. Heinsohn, and P. W. Channells. 1984a. Changes in the ovaries and uterus of the dugong, *Dugong dugon* (Sirenia: Dugongidae), with age and reproductive activity. Australian Journal of Zoology 32:743–765.

Marsh, H., G. E. Heinsohn, and T. D. Glover. 1984b. Changes in the male reproductive organs of the dugong, *Dugong dugon* (Sirenia: Dugongidae) with age and reproductive activity. Australian Journal of Zoology 32:721–742.

Marsh, H., G. E. Heinsohn, and L. M. Marsh. 1984c. Breeding cycle, life history and population dynamics of the dugong, *Dugong dugon* (Sirenia: Dugongidae). Australian Journal of Zoology 32:767–788.

Mou Sue, L. L., D. H. Chen, R. K. Bonde, and T. J. O'Shea. 1990. Distribution and status of manatees (*Trichechus manatus*) in Panama. Marine Mammal Science 6:234–241.

Moore, J. C. 1951. The range of the Florida manatee. The Quarterly Journal of the Florida Academy of Sciences 14:1–19.

Moore, J. C. 1956. Observations of manatees in aggregations. American Museum Novitates 1811:1–24.

Nishiwaki, M., and H. Marsh. 1985. Dugong (*Dugong dugon*) (Müller, 1776). Pages 1–31 *in* S. H. Ridgway and R. Harrison, editors. Handbook of marine mammals. Volume III: the sirenians and baleen whales. Academic Press, London. 362 pp.

*Odell, D. K. 1979. Distribution and abundance of marine mammals in the waters of the Everglades National Park. National Park Service Biological Series 5:673–678.

Odell, D. K., G. D. Bossart, M. T. Lowe, and T. D. Hopkins. 1995. Reproduction of the West Indian manatee in captivity. Pages 192–193 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

*Odell, D. K., D. J. Forrester, and E. D. Asper. 1981. A preliminary analysis of organ weights and sexual maturity in the West Indian manatee (*Trichechus manatus*). Pages 52–65 *in* R. L. Brownell, Jr., and K. Ralls, editors. The West Indian manatee in Florida. Proceedings of a workshop held 27–29 March, 1978, Orlando, Fla. Florida Department of Natural Resources, Tallahassee.

Oftedal, O. T. 1985. Pregnancy and lactation. Pages 215–238 *in* R. J. Hudson and R. G. White, editors. Bioenergetics of wild herbivores. CRC Press, Boca Raton, Fla.

O'Shea, T. J. 1988. The past, present, and future of manatees in the southeastern United States: realities, misunderstandings, and enigmas. Pages 184–204 *in* R. R. Odom, K. A. Riddleberger, and J. C. Ozier, editors. Proceedings of the Third Southeastern Nongame and Endangered Wildlife Symposium. Georgia Department of Natural Resources, Game and Fish Division, Social Circle. 235 pp.

O'Shea, T. J., and C. A. Salisbury. 1991. Belize—a last stronghold for manatees in the Caribbean. Oryx 25:156–164.

O'Shea, T. J., and W. C. Hartley. 1995. Reproduction and early-age survival of manatees at Blue Spring, upper St. Johns River, Florida. Pages 157–170 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

O'Shea, T. J., C. A. Beck, R. K. Bonde, H. I. Kochman, and D. K. Odell. 1985. An analysis of manatee mortality patterns in Florida, 1976–81. Journal of Wildlife Management 49:1–11.

*Packard, J. M. 1981. Abundance, distribution, and feeding habits of manatees (*Trichechus manatus*) wintering between St. Lucie and Palm Beach inlets, Florida. Final report, Contract 14-16-0004-80-105. U.S. Fish and Wildlife Service, Atlanta, Ga. 142 pp.

*Packard, J. M. 1985. Preliminary assessment of uncertainty involved in modeling manatee populations. Manatee Population Research Report 9. Technical Report Number 8–9, Florida Cooperative Fish and Wildlife Research Unit. University of Florida, Gainesville. 19 pp.

Packard, J. M., D. B. Siniff, and J. A. Cornell. 1986. Use of replicate counts to improve indices of trends in manatee abundance. Wildlife Society Bulletin 14:265–275.

*Patton, G. W. 1980. Studies of the West Indian manatee (*Trichechus manatus*) in Tampa Bay (Florida). Technical report. Mote Marine Laboratory, Sarasota, Fla. 52 pp.

*Patton, G. W. 1986. Studies of the West Indian manatee: Anna Maria to Venice (Florida). Technical report. Mote Marine Laboratory, Sarasota, Fla. 24 pp.

*Patton, G. W., T. A. Kreckman, and J. Sprinkel. 1987. Studies of the West Indian manatee: Anna Maria to Venice (Florida). Technical report. Mote Marine Laboratory, Sarasota, Fla. 37 pp.

Perrin, W. F., R. L. Brownell, Jr., and D. P. DeMaster, editors. 1984. Reproduction in whales, dolphins and porpoises. Reports of the International Whaling Commission. Special Issue 6. 495 pp.

Powell, J. A., and G. B. Rathbun. 1984. Distribution and abundance of manatees along the northern coast of the Gulf of Mexico. Northeast Gulf Science 7:1–28.

Powell, J. A., D. W. Belitsky, and G. B. Rathbun. 1981. Status of the West Indian manatee (*Trichechus manatus*) in Puerto Rico. Journal of Mammalogy 62:642–646.

Preen, A. 1989. Observations of mating behavior in dugongs (*Dugong dugon*). Marine Mammal Science 5:382–387.

Rathbun, G. B., and T. J. O'Shea. 1984. The manatee's simple social life. Pages 300–301 *in* D. Macdonald, editor. The Encyclopedia of Mammals. Facts on File, New York. 895 pp.

Rathbun, G. B., J. A. Powell, and G. Cruz. 1983. Status of the West Indian manatee in Honduras. Biological Conservation 26:301–308.

Rathbun, G. B., C. A. Woods, and J. A. Ottenwalder. 1985. The manatee in Haiti. Oryx 19:234–236.

Rathbun, G. B., J. P. Reid, and G. Carowan. 1990. Distribution and movement patterns of manatees (*Trichechus manatus*) in northwestern peninsular Florida. Florida Marine Research Publications 48:1–33.

*Rathbun, G. B., T. Carr, N. M. Carr, and C. A. Woods. 1986. The distribution of manatees and sea turtles in Puerto Rico, with emphasis on Roosevelt Roads Naval Station. National Technical Information Service. Springfield, Va. Document PB86–1518347AS. 83 pp.

Reid, J. P., R. K. Bonde, and T. J. O'Shea. 1995. Reproduction and mortality of radio-tagged and recognizable manatees on the Atlantic Coast of Florida. Pages 171–191 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Reid, J. P., G. B. Rathbun, and J. R. Wilcox. 1991. Distribution patterns of individually identifiable West Indian manatees (*Trichechus manatus*) in Florida. Marine Mammal Science 7:180–190.

Reynolds, J. E., III. 1981. Aspects of the social behavior and herd structure of a semi-isolated colony of West Indian manatees, *Trichechus manatus*. Mammalia 45:431–451.

*Reynolds, J. E., III. 1991. Distribution and abundance of the West Indian manatee (*Trichechus manatus*) around selected Florida power plants following winter cold fronts: 1990–1991. Final report to Florida Power and Light Company, Juno Beach. 39 pp.

Reynolds, J. E., III. 1995. Florida manatee population biology: research progress, infrastructure, and applications for conservation and management. Pages 6–12 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Reynolds, J. E., III, and D. K. Odell. 1991. Manatees and dugongs. Facts on File, Inc., New York. 192 pp.

Riedman, M. 1990. The pinnipeds—seals, sea lions and walruses. University of California Press, Berkeley. 439 pp.

Riedman, M., and J. A. Estes. 1990. The sea otter (*Enhydra lutris*): behavior, ecology and natural history. U.S. Fish and Wildlife Service Biological Report 90(14). 126 pp.

Sarle, W. S. 1983. The MRANK procedure. Pages 215–228 *in* SAS Institute Inc., editor. SUGI supplemental library user's guide. SAS Institute, Inc., Cary, N.C.

Shane, S. H. 1983. Abundance, distribution, and movements of manatees (*Trichechus manatus*) in Brevard County, Florida. Bulletin of Marine Sciences 33:1–9.

Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York. 312 pp.

Sokal, R. R., and F. J. Rohlf. 1969. Biometry. W. H. Freeman and Company, San Francisco, Calif. 776 pp.

*U.S. Fish and Wildlife Service. 1990. List of endangered and threatened wildlife and plants, 50 CFR 17.11 and 17.12. U.S. Government Printing Office, Washington, D.C. 36 pp.

Wilson, E. O. 1975. Sociobiology—the new synthesis. The Belknap Press, Harvard University, Cambridge, Mass. 697 pp.

Reproduction and Early-age Survival of Manatees at Blue Spring, Upper St. Johns River, Florida

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Abstract. We summarize reproduction of adults and survival of calves and subadult Florida manatees (*Trichechus manatus latirostris*) that were identified in winter at Blue Spring on the upper St. Johns River in Florida. Some records span more than 20 years, but most are from 15-year continuous annual observations during winter 1978–79 through winter 1992–93. Fifty-seven, first-year calves were identified; 55 litter sizes were one, and one consisted of twins (1.79% of all births). Sex ratios of first-year calves did not significantly differ from 1:1. Based on 21 of 35 sighted females (15 individuals) that appeared pregnant and returned with calves during the subsequent winter, we estimated an early (neonatal to about 6 months) calf survival of 0.600. Based on estimations with a minimum-number-known-alive method, calf survival from the first to the second winter was at least 0.822, and subadult survival was 0.903 to the third, 0.958 to the fourth, 1.00 to the fifth, and 1.00 to the sixth winters. Seven females were observed from year of birth to their first winter with a nursing calf; the mean age at parturition to the first calf that survived to the next winter was 5.4 ± 0.98 (SD) years. The estimated ages at first conception ranged from 3 to 6 years. The proportion of adult pregnant females was 0.410/year. Weaning was not observed in winter. Intervals between births averaged 2.60 ± 0.81 years. The pooled proportion of adult females nursing first-winter calves was 0.303; the proportion of adult females nursing calves of any age was 0.407. These values do not significantly differ from those of manatees from the Crystal River or Atlantic Coast study areas. Anecdotal accounts are provided that suggested the existence of a pseudo estrus, an 11 to 13-month gestation, suppression of parturition in winter, and giving birth in quiet backwaters and canals. A female from Blue Spring

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produced at least seven calves during the 22 years since first observed and died giving birth at an estimated age of 29 years.

Key words: Blue Spring, St. Johns River, Florida manatee, *Trichechus manatus latirostris*, early survival, reproduction, life history.

Prior to the 1970's, little accurate information was available on reproduction or early survival in wild populations of manatees. Information on these topics began to be published during the 1970's and early 1980's (Hartman 1979; Bengtson 1981; *[2]Brownell et al. 1981) but was largely anecdotal or based on small data sets. In the absence of other satisfactory means to quickly accumulate data on such traits, the U.S. Fish and Wildlife Service in the late 1970's began to intensify long-term field observations of recognizable Florida manatees (*Trichechus manatus latirostris*) at two clear-water sites where manatees aggregate in winter, Crystal River and Blue Spring. Rathbun et al. (1995) reported results from studies at Crystal River. In this paper, we report aspects of reproduction and early survival of manatees from joint studies by the service and the Florida Park Service at Blue Spring. We compared our results with those from studies at Crystal River and on the Atlantic Coast (Reid et al. 1995) and from studies of carcasses and captive animals (Odell et al. 1995; Marmontel 1995).

Methods

A description and review of the study area, population characteristics, and sampling procedures at Blue Spring were provided by O'Shea and Langtimm (1995). Blue Spring is a clear artesian spring located 240 km upstream (south) from the mouth of the St. Johns River in Volusia County near Orange City, Florida (Fig. 1). The season during which manatees aggregate usually extends from November to late March. Manatees use Blue Spring only as a thermal refuge and must leave it to forage in the St. Johns River. Nearly all manatees at Blue Spring are recognized by unique markings and scar patterns that are recorded by voucher photographs. Individuals are assigned identification numbers (prefix BS) and names. We used identification numbers for reporting our results because investigations on this population have not been terminated, and numbers will be of use to researchers in the future. The clear water and lack of aquatic vegetation allow unobstructed views of the manatees; intensive and repetitive observations are easy because the number of animals is small (total identifications increased because the size of the aggregation increased from 23 during 1978–79 to 74 during 1991–92). The manatees were observed from banks above the spring, from canoes, and from below the water surface (snorkeling observer). Complete censuses were made almost every day during cool weather and have numbered from 59 to 89 censuses/year.

This report is based primarily on research at Blue Spring during winter 1978–79 through winter 1992–93. The spring has been protected from public boating and swimming in winter since the late 1970's, and the number of manatees that frequent the spring each winter has increased from fewer than 30 to more than 70 during our study. Data reported here were collected from November through March each year (unlike in the Crystal River, manatees seldom appear at Blue Spring in October). However, we occasionally reference data from prior winters, from opportune sightings in other seasons, and from anecdotal accounts from year-round studies with telemetry. Information we reference from earlier years of study appeared in Powell and Waldron (*1981); observations during studies with telemetry in 1979 and 1980 were excerpted from Bengtson (1981) and from our unpublished telemetry data from 1981 and 1983. We also made follow-up observations of females (BS 05 and BS 40) who were pursued by three herds of males that Bengtson (1981) tracked by telemetry at various locations in the St. Johns River during summer and early fall 1980. Bengtson (1981) observed three births during radio-tracking in April, May, and August 1980. Beeler and O'Shea (*1988) provided the unpublished summaries of locations of calf carcasses in the St. Johns River during 1974 to 1985, and the Florida Department of Environmental Protection (unpublished data) recorded dates of an additional seven calf carcasses found in the St. Johns River during 1986 through 1992. We present these records with information on mating, gestation, and giving birth.

We followed the techniques, criteria, and definitions described in Rathbun et al. (1995) for recording and calculating information about reproduction. Determination of pregnancy by visible criteria, definition of winter, and application of tail nicks for the identification of calves are identical to those used at the Crystal River (Rathbun et al. 1995). However, Rathbun et al. (1995) estimated parameters in reproduction from a censored data set that was restricted to females sighted for eight or more continuous winter seasons. Because of smaller sample sizes and the potential loss of information, we did not follow this procedure except for calculating intervals between births. We use the term first-winter calf to designate young, suckling manatees born since the previous winter aggregation period. Actual dates of birth were usually not known.

[2] An asterisk denotes unpublished material.

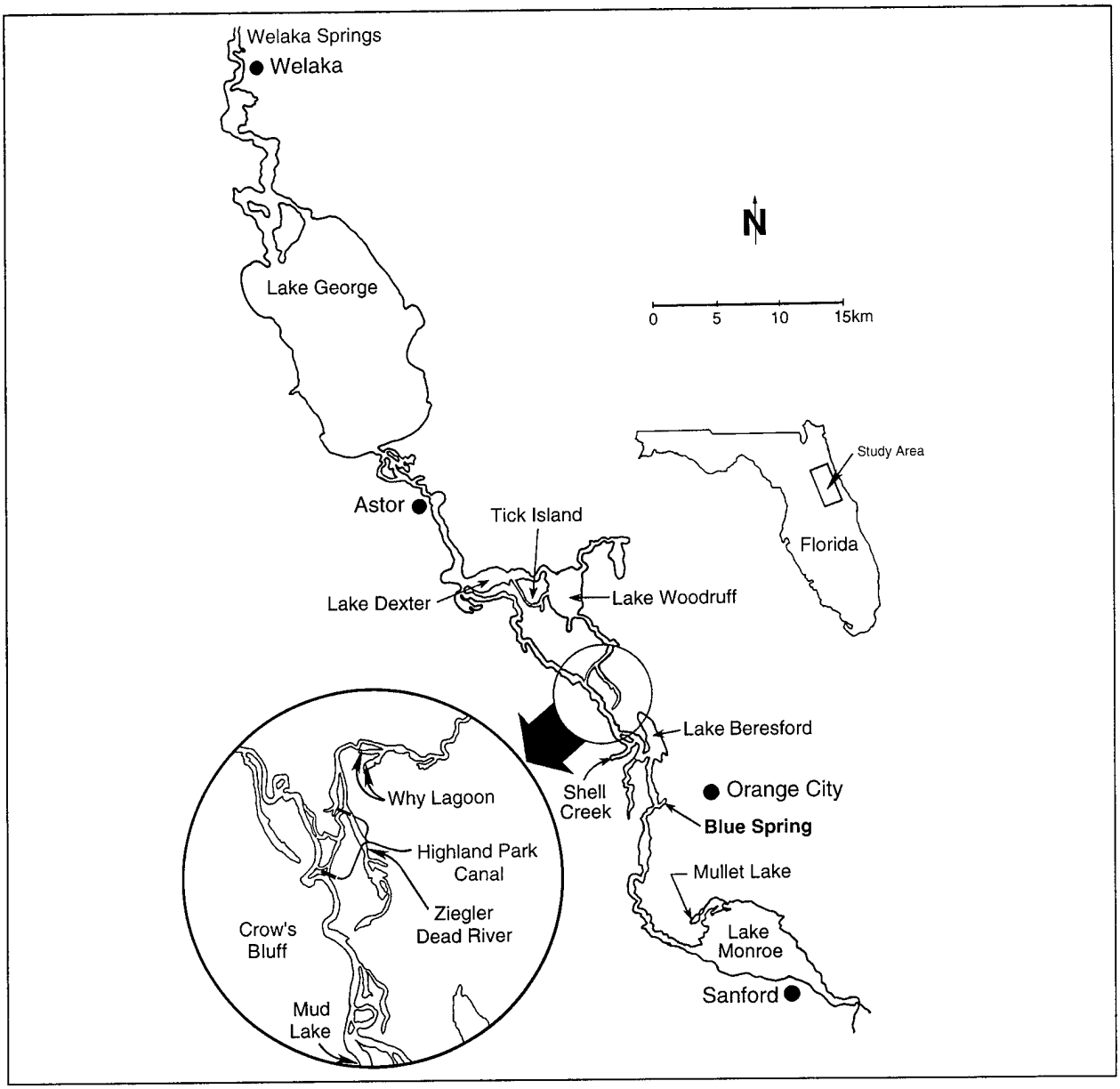


Fig. 1. The St. Johns River and associated backwaters near Blue Spring, Florida, including place names used in this report.

We followed the method of Rathbun et al. (1995) for estimating the proportion of calves that survived from birth to the first winter. We summed records of females that appeared pregnant (swollen and distended as described by Rathbun et al. [1995]; slight bulges were ignored; females that were identified as possibly pregnant were not included in the analyses) in one winter and were observed again in the next winter. The ratio of the number of these females seen with calves in the next winter subsequent to pregnancy and the total number of pregnant females observed the previous winter was considered an index of early-calf survival (roughly covering the period from late pregnancy to about 6 months of age of the calf). We also determined unique markings of each calf (including tail nicks) during the period of dependency on its mother and during subsequent years. Based on these markings, we computed an index of annual survival from winter to winter, beginning with the first winter of life and ending with the sixth winter. Calculations were made with a minimum-number-known-alive-method (Stirling 1971), by which survival was computed as the simple proportion of the total number of calves observed in one winter that was observed alive in the next winter or in any subsequent winter. These are minimum estimates because calves that emigrate to other sites between winters or that may return but are not recognized are assumed to have not survived. We tabulated year of birth and

fate of each calf in each subsequent winter to obtain these estimates. Calculations do not include calves born prior to 1978 and calves of two females (BS 125 and BS 103) who were seldom seen in aggregations in winter at Blue Spring and therefore may not have been subject to the same ecological circumstances as the majority of other females and offspring in the data set. The proportion of adult females pregnant each winter was determined by summing the number of females that appeared pregnant in one winter and the number of females that did not appear pregnant in the same winter but returned to the aggregation site with first-winter calves in the second winter and by dividing this sum by the total number of adult females present in the aggregation the first winter. The total proportion of females reproductive each winter was the quotient of the known lactating and pregnant females and the total number of adult females present in the aggregation that winter. Twins were considered a single birth for calculating these proportions. We used the chi-square statistic to test hypotheses of no differences between proportions (Sokal and Rohlf 1969).

Results

Mating, Gestation, and Parturition

An adult female (BS 05) and her 4-month old calf were attended by a herd of as many as 15 males for 10 days in September 1980. She continued to nurse the calf observed in September 1980 until at least April 1981, and did not give birth again until 1982. We also observed the pursuit of this female by a herd of males in April 1983 during our study with radio-tracking in reaches of the St. Johns River near Welaka. As many as 12 other manatees were with this female from about April 5 until early May. As in September 1980, she was accompanied by a nursing calf (BS 53). However, this calf had been born in 1982 and was older and considerably larger than the accompanying calf in 1980. Subsequent to the 1983 observation near Welaka, the female returned without a calf the next two winters. These observations suggested that the presumed mating did not result in conception.

Two herds of males pursued a female (BS 40) in 1980. The first herd persisted from at least 3 to 14 September 1980 and consisted of eight adult males. The second herd, approximately 3 weeks later, persisted from 4 to 12 October 1980 and consisted of 12 adult males. On 14 November 1981, the female was seen with a small calf at Blue Spring. She was last seen without a calf on 27 August 1981 near Lake Dexter; her transmitter failed on 3 September. The estimated length of gestation may have been as long as 13 months (assuming conception in September 1980 and birth as late as October 1981) or only 11 months (assuming conception in early October 1980 and birth in September 1981, the month after the last sighting without a calf).

On 11 May 1990 a herd of at least seven recognizable adult males passed by Blue Spring in pursuit of a 4-year-old female (BS 73). This individual, however, returned without a new calf and was not judged to be pregnant during winter 1990–91. On numerous other occasions we observed males consorting with females but doubted that such herds were consorting with females in estrus.

Forty-nine births were recorded since 1978 (Table 1). Females did not give birth during November, December, or January in any year. Only one birth occurred in February. One female (BS17) was last seen without a calf at Blue Spring on 2 February 1986 and was pregnant. She was not seen during a subsequent long warm spell but returned on 3 March with a very small suckling calf (BS 78). The calf was alive when we last saw the pair that season on 24 March. However, the mother returned to Blue Spring in the following winter without the calf, which we assumed to have died.

The number of other anecdotal records on timing of births was too small to determine whether giving birth was seasonal other than being suppressed from November through February, although most births were in spring (March, April, and May). Birth dates of three calves were known (25 April, 12 May, and approximately 10 August) from radio-tracking in 1980 (Bengtson 1981). In addition, we made several other observations. One pregnant female (BS 37) left Blue Spring on 21 March 1988 and was again observed on 14 April when she was accompanied by a small calf (BS 95); local residents observed another female (BS 106) giving birth in a canal off the St. Johns River near Astor on 13 April 1993; BS 54 left Blue Spring pregnant on 18 March 1991 and returned with a calf on 9 April. The carcass of a female (BS 36) with a large fetus was recovered on 16 April 1988. Another female (BS 05) with a near-term (143 cm total body length [TL]) fetus died on 6 August 1992. A pregnant female (BS 09) in winter 1982–83 was subsequently observed without a calf in the Why Lagoon off the Highland Park Canal on 15 July 1983 and with a very small calf (BS 62) at the same location on 19 August, indicating a birth in July–August.

The three births in 1980 occurred during warm months in quiet backwaters off the main channel of the St. Johns River. In addition to the birth in April 1993 in the residential canal off the St. Johns near Astor, carcasses of dependent calves were found in the area from April 1974 through December 1992. Carcasses of 10 small, newborn-sized (107 to 150 cm TL) calves were recovered in the St. Johns River system south of Welaka. Locations included the Shell Creek backwater off Mud Lake; a canal off the St. Johns River near Crow's Bluff; the northwest shore of Lake Beresford; Jimmy Cove near Lake Dexter; near Tick Island, Lake Dexter; Welaka Springs; a canal off Ziegler Dead River; a canal off the St. Johns River near Sanford; and a residential

Table 1. Florida manatee (*Trichechus manatus latirostris*) calves observed in aggregations at Blue Spring during winters 1978–1979 through 1992–1993. Winters refer to consecutive winters of life. A = live calves observed at Blue Spring; D = calves that died subsequent to previous winter; U = fate unknown. *Blanks* appear when sex or number of winters dependent was not determined.

Young identification			Number of winters dependent	Year of birth	Winter					
					1	2	3	4	5	6
BS 25	m	Lenny	1	1978	A	A	A	A	A	A
BS 28	m	Floyd	1	1978	A	A	A	A	A	A
BS 29	m	Boomer	1	1979	A	A	A	A	A	A
BS 30	m	Luther	2	1979	A	A	A	A	A	A
BS 35	m	Robin	2	1980	A	A	A	A	A	A
BS 36	f	Felicity	1	1980	A	A	A	A	A	A
BS 37	f	Lucille	2	1980	A	A	A	A	A	A
BS 38	m	Lennon		1980	A	U	U	U	U	U
BS 45	m	Shane	1	1981	A	A	A	A	A	A
BS 46	f	Nora	2	1981	A	A	U	U	U	U
BS 53	m	Philip	1	1982	A	A	A	A	A	A
BS 54	f	Success	2	1982	A	A	A	A	A	A
BS 55	f	Donna	2	1982	A	A	A	A	A	A
BS 62	m	Emmet	1	1983	A	A	U	U	U	U
BS 63	m	Lunatic	2	1983	A	A	A	A	A	A
BS 67	m	Adam West	1	1984	A	A	A	A	A	A
BS 70	m	Porky		1984	A	U	U	U	U	U
BS 71	m	Margarito	1	1984	A	A	A	A	A	A
BS 72	f	Elaine	1	1985	A	U	A	A	A	A
BS 73	f	Lola	2	1985	A	A	A	A	A	A
BS 74		Jolly	1	1985	A	U	U	U	U	U
BS 75	m	Frederick	2	1985	A	A	D			
BS 76	f	Beebe	1	1985	A	U	U	U	U	U
BS 77		Delta	1	1985	A	U	U	U	U	U
BS 78		Kris	0	1986	D					
BS 87	f	Liza	1	1986	A	A	A	D		
BS 91	f	Bubblegum	1	1987	A	U	U	U	U	
BS 92	f	June	1	1987	A	A	A	A	A	A
BS 95		Lufa	0	1988	D					
BS 98	f	Lillith	1	1988	A	A	A	A	A	
BS 99	f	Destiny	2	1988	A	A	A	A	A	
BS 100	m	Phud	1	1988	A	A	A	A	A	
BS 101	m	Lester	1	1988	A	D				
BS 102	f	Dana	2	1988	A	A	A	A	A	
BS 110	m	O'Shea	2	1989	A	A	A	A		
BS 111	m	Luke	1	1989	A	A	A	A		
BS 118	f	Julie	2	1990	A	A	A			
BS 119	m	Loomis	1	1990	A	A	A			
BS 120	f	Lucretia	1	1990	A	A	A			
BS 121	f	Ester	1	1990	A	A	A			
BS 126	m	Chuck	1	1991	A	A				
BS 127	m	Bertram		1991	A	U				
BS 128	m	Bartram	2	1991	A	A				
BS 129	f	Hope	1	1991	A	A				
BS 130	f	Delaine	1	1991	A	A				
BS 131	f	Jessica	1	1991	A	A				
BS 132	m	Murphy	1	1991	A	A				
BS 139	m	Kowabunga		1992	A					
BS 140	f	Precious		1992	A					

canal north of Mullett Lake. All 10 were found during warm months ($n = 3$ in April; $n = 4$ in May; $n = 1$ in July; $n = 1$ in August; $n = 1$ in September), and none was in the main body of the St. Johns River.

One female (BS 08) from Blue Spring gave birth on 25 April 1980 in the quiet backwater of the Ziegler Dead River. The female and the calf stayed in the Ziegler Dead River for several days after birth. On 30 April 1980, at 1230 h, the female was approached by a lone adult male (BS 01) who persistently pushed and thrashed her. The female responded with lunges above the water surface as if trying to break away from the male. The female and 5-day-old calf slowly moved through the shallow (1–2 m) water and spatterdock (*Nuphar luteum*) beds. The male followed closely, often within 1 m and frequently contacted and attempted to mount the female. The male was still accompanying the pair when the observation was terminated at 1630 h. The calf (BS 35) returned to Blue Spring with its mother in the next winter.

Litter Size and Sex Ratio of Calves

Fifty-seven calves were identified at Blue Spring since winter 1970–71, including 49 born to 22 females since winter 1978–79 (Tables 1 and 2). The total included six males identified during winters 1970–71 (1 calf), 1971–72 (1 calf), 1975–76 (3 calves), and 1976–77 (1 calf) and two males (BS 103 and BS 125) that were excluded from analyses. Although litter size at birth was usually not known, all but one of the first-winter calves were singletons. The minimum twinning rate was 1.79% (1 of 56 births). The sex of 21 females and 32 males was determined. The sex of four calves could not be determined. The sex ratio was not significantly different from 1:1 ($\chi^2 = 2.28$, $df = 1$, $P = 0.13$). During the 1970's, all calves ($n = 10$) in the group were males. From 1980 through 1992–93, in contrast, females returned to Blue Spring with 22 male and 21 female calves. A set of male twins was born in 1991.

Early Survival of Calves

Thirty-five pregnancies of 15 females were determined by appearances. These females returned to Blue Spring during winters after each of the observed pregnancies; 21 returned with one calf, indicating an annual calf survival rate of 0.600 from late pregnancy to first winter. Two of the pregnant females were seen with newborn calves (BS 78 and BS 95; Table 1) in March 1986 and April 1988. The calves were assumed to have died prior to the next winter when the females returned without them. Inclusion of these two calves in our analyses raised the estimated minimum survival at birth to 0.657. Many females that returned without their calves to Blue Spring in winters subsequent to giving birth in the preceding spring were pregnant again. Pregnancy was determined of 10 of 14 females who returned to Blue Spring without calves in the subsequent winter; all 10 were pregnant again by the next winter (Table 2).

Thirty-seven of 45 (0.822) calves survived from the first to the second winter (Table 1). The actual survival between the first and the second winter was assumed to be higher. The death of only one calf was verified (BS 101, killed by a boat strike). Four of the seven calves whose fates were unknown (BS 38, BS 70, BS 74, and BS 77) were offspring of females that did not consistently winter at Blue Spring (Table 2) and therefore could have been weaned closer to some other site where manatees aggregate in winter. Only one of the twins (Fig. 2) was alive during the second winter, when it continued to nurse from its mother.

The minimum survival rate between the second and the third winters was 0.903 (28 of 31 calves); one (BS 75) was killed by a boat strike (Table 1). The two calves whose fates could not be determined (BS 46 and BS 62) were the offspring of females that did not consistently winter at Blue Spring. The minimum survival rate from third to fourth winters was 0.958 (23 of 24 calves). One calf was killed by a boat strike. Survival was 1.00 between the fourth and the fifth winters (21 of 21) and between the fifth and sixth winters (17 of 17).

Age at First Reproduction

We estimated the age at first successful reproduction (returning to the spring with a nursing calf) of seven females (Table 3). To the nearest year of ages these females were 4, 5, 5, 5, 6, 6, and 7 years old (mean = 5.4 ± 0.98 [SD]). The youngest ages at which females appeared pregnant were two females between the ages of 3 and 4 (BS 36, BS 102) and one older than 4 but less than 5 (BS 54). However, none of these females returned with a calf in winter after a pregnancy in the preceding spring. The youngest ages at first reproduction based on returns to the spring with first-winter calves were one 3 to 4-year-old female (BS 92), two 4 to 5-year-old females (BS 37 and BS 72), and one 5 to 6-year-old female (BS 55). If the duration of gestation was approximately 1 year, the ages of females at first conception, regardless of outcome, were 3 years ($n = 3$), 4 years ($n = 3$), 5 years ($n = 1$), and 6 years ($n = 1$; Table 3).

Although six of the seven first-born live calves were female, the sex ratio at birth did not deviate significantly from a 1:1 ($\chi^2 = 2.28$, $df = 1$, $P = 0.13$). The age of the female (BS 107) who gave birth to twins was unknown. However, based on size and appearance, she seemed to be about 3 years old when she was first identified in winter 1988–89, 3 years prior to twinning.

Table 2. History of reproduction of all female Florida manatees (*Trichechus manatus latirostris*) observed in aggregations at Blue Spring on the upper St. Johns River, winter 1978–1979 through winter 1992–1993. An *asterisk* (*) indicates a juvenile female attained sexual maturity as indicated by pregnancy or lactation. B = first winter season after known birth of female; *slash* (/) = individual was not present; *dash* (-) = individual was sighted without a dependent calf, pregnancy not determined; VP = individual appeared pregnant; SP = individual pregnant based on presence of calves in the subsequent winter. C = individual accompanied by dependent calf, followed by calf identification number; *subscript number* indicates whether calf was nursing in first or second winter; dead = individual known dead first winter; I = immature, based on continued nursing if not weaned, or absence of previous evidence of pregnancy or giving birth by the mother; IA = assumed immature based on size and appearance.

Female	1978–79	1979–80	1980–81	1981–82	1982–83	1983–84	1984–85	1985–86	1986–87	1987–88	1988–89	1989–90	1990–91	1991–92	1992–93
BS 4	SP	C_1 30	C_2 30	VP	-	SP	C_1 71	VP	-	VP	C_1 98	VP	C_1 119	VP	C_1 139
BS 5	C_1 28	VP	C_1 36	SP	C_1 53	-	VP	C_1 76	-	VP	C_1 100	-	VP	VP	Dead
BS 8	-	VP	C_1 35	C_2 35	VP	SP	C_1 67	-	/	/	/	/	/	/	/
BS 9	VP	C_1 29	VP	C_1 45	VP	C_1 62	SP	C_1 72	Dead						
BS 17	-	VP	VP	SP	C_1 54	C_2 54	-	VP/C_1 78	SP	C_1 91	SP	C_1 110	C_2 110	Dead	
BS 24	C_1 25	VP	C_1 37	C_2 37	VP	C_1 63	C_2 63	SP	C_1 87	VP	C_1 101	SP	C_1 120	VP	VP
BS 36			B	I	I	*VP	VP	C_1 75	C_2 75	VP	Dead				
BS 37			B	I	I	I	*SP	C_1 73	C_2 73	VP	VP	C_1 111	VP	-	VP
BS 39	/	/	C_1 38	/	/	/	/	C_1 74	SP	C_1 92	/	/	/	/	/
BS 40	/	/	VP	C_1 46	C_2 46	SP	C_1 70	/	-	-	-	-	-	-	-
BS 49	/	/	/	SP	C_1 55	C_2 55	SP	C_1 77	-	-	/	Dead			
BS 50	/	/	/	-	/	/	/	/	/	/	/	/	/	/	/
BS 54					B	I	I	I	*VP	SP	C_1 99	C_2 99	VP	C_1 126	-
BS 55					B	I	I	I	I	*SP	C_1 102	C_2 102	VP	C_1 130	-
BS 56	/	/	/	/	-	/	/	/	/	/	C_2 103	/	/	/	/
BS 72								B	/	I	I	*SP	C_1 121	-	/
BS 73								B	I	I	I	I	-	*VP	C_1 140
BS 87									B	I	I	Dead			
BS 92										B	I	I	*SP	C_1 131	-
BS 98											B	I	I	I	I
BS 99											B	I	I	I	I
BS 102											B	I	I	*VP	-
BS 106	/	/	/	/	/	/	/	/	/	/	IA	SP	C_1 118	C_2 118	SP
BS 107	/	/	/	/	/	/	/	/	/	/	IA	IA	VP	C_1 127–8	C_2 128
BS 109	/	/	/	/	/	/	/	/	/	/	-	VP	VP	C_1 129	-
BS 118													B	I	I
BS 120													B	I	I
BS 121													B	I	I
BS 124	/	/	/	/	/	/	/	/	/	/	/	/	C_2 125	Dead	
BS 133	/	/	/	/	/	/	/	/	/	/	/	/		C_1 132	-

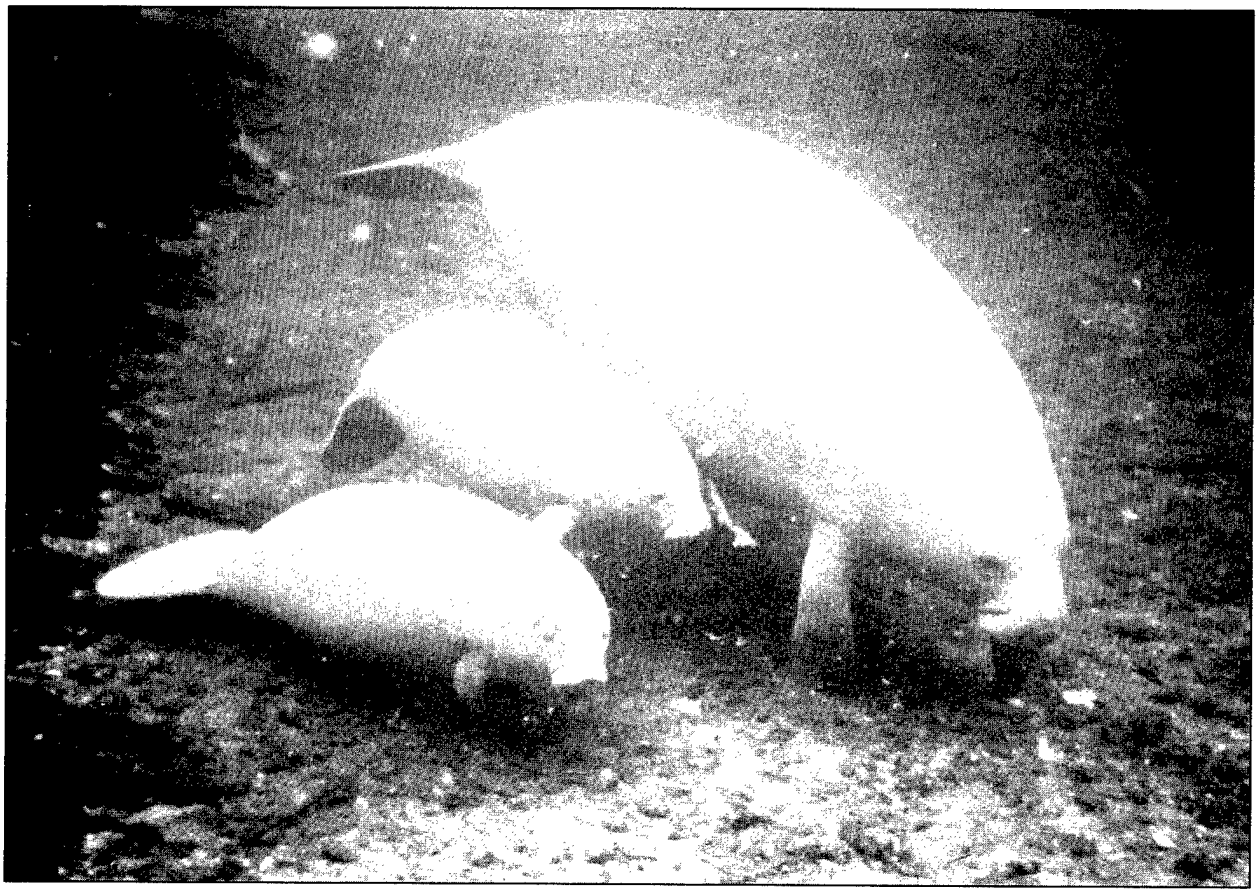


Fig. 2. Florida manatee (*Trichechus manatus latirostris*) female (BS 107) with first-winter twin offspring (BS 127 and BS 128) at Blue Spring, winter 1991–1992. *Photo by T. J. O'Shea.*

Table 3. First pregnancies or births by known-age or approximate known-age female Florida manatees (*Trichechus manatus latirostris*) from Blue Spring on the upper St. Johns River. V = visually detected pregnancy; S = pregnancy determined by appearance with a calf in the subsequent winter. The length of gestation is assumed to be approximately 12 months. Although months of births are usually unknown, births did not occur during November, December, January, and February.

Female	Year/date of birth	First known pregnancy		Estimated age (year)	Probable age at first conception (year)	First nursing calf	
		Basis	Winter			Winter	Estimated age (year)
BS 36	12 May 1980	V	1983–84	3.6	3	1985–86	5.4
BS 37	10 August 1980	S	1984–85	4.3	4	1985–86	5.1
BS 54	1982	V	1986–87	4.0+	4	1988–89	6.0+
BS 55	1982	S	1987–88	5.0+	5	1988–89	6.0+
BS 72	1985	S	1989–90	4.0+	4	1990–91	5.0+
BS 73	1985	V	1991–92	6.0+	6	1992–93	7.0+
BS 92	1987	S	1990–91	3.0+	3	1991–92	4.0+
BS 102	1988	V	1991–92	3.0+	3		

Intervals Between Births and Duration of Dependency of Calves

We calculated a mean interval between births of 2.60 ± 0.81 years (winter seasons; n = 12 females; Table 2). The mean duration of 25 intervals between births in seven females with 9 to 18-year histories in the restricted subset of the data was 2.60 ± 0.87 years.

The duration of dependency on mothers was determined of 42 calves whose fates were known and dependency did not end with the death of the calf. The dependency of 28 (66.7%) calves lasted one winter, whereas the dependency of 14 (33.3%) calves lasted two winters. The length of dependency was not related to the sex of calves ($\chi^2 = 0.44$, $df = 1$, $P = 0.507$): the dependencies of 14 males and 12 females lasted 1 year, and the dependencies of 6 males and 8 females lasted 2 years. Periods of dependency of six calves that were the first-born offspring were 1, 1, 2, 2, 2, and 2 winter seasons. We did not observe weaning, loss, permanent separation, or death of calves during winter months (November through February); all females that were accompanied by nursing calves at the onset of winter continued to be accompanied by their calves at the break-up of the aggregation period in spring.

Proportion of Reproductive Females and Longevity of Reproduction

A high proportion of the females at Blue Spring reproduced each year (Table 4). Sample sizes were small (6–15) each year, and proportions widely fluctuated from year to year. However, based on the total number from all years, the pooled average proportion of adult females that nursed first-winter calves during winters 1978–79 through 1992–93 was 0.303 (46 calves of 152 records of mature females). The proportion of lactating females (nursed either a first- or second-year calf) was 0.407 (62 of 152 records of mature females). The proportion of pregnant females was 0.410, based on 57 of 139 records in the period excluding 1992–93 (records are not complete for this statistic until births of 1992–1993 are observed in 1993–94). Overall, the proportion of females that reproduced each year through winter 1991–92 was 0.834; the sum of the proportion of pregnant females and the proportion of females who were nursing first-year calves was 0.727.

One female (BS 05; Fig. 3) first observed in winter 1970–71 was accompanied by a calf when seen again in 1971–72. No records were kept in 1972–73 or 1973–74,

Table 4. Annual reproductive status of female Florida manatees (*Trichechus manatus latirostris*) in the aggregation site at Blue Spring on the upper St. Johns River. *Dashes* appear where data are incomplete on pregnancy status based on presence of calves the subsequent winter. The case of twins is computed as a single calving.

Winter	Number adult females	Number diagnosed pregnant	Number pregnant based on return	Number pregnancy status unknown	Number nursing first winter calf	Number nursing second winter calf	Proportion pregnant	Proportion lactating	Proportion nursing first winter calf	Proportion reproductive
1978–79	6	1	1	2	2	0	0.333	0.333	0.333	0.666
1979–80	6	3	1	0	2	0	0.666	0.333	0.333	0.999
1980–81	8	3	0	0	4	1	0.375	0.625	0.500	1.000
1981–82	9	1	3	1	2	2	0.444	0.444	0.222	0.888
1982–83	9	3	0	2	3	1	0.333	0.444	0.333	0.777
1983–84	9	1	3	1	2	2	0.444	0.444	0.222	0.888
1984–85	10	2	3	1	3	1	0.500	0.400	0.300	0.900
1985–86	10	2	1	1	6	0	0.300	0.600	0.600	0.900
1986–87	10	1	2	4	1	2	0.300	0.300	0.100	0.600
1987–88	11	5	2	2	2	0	0.636	0.182	0.182	0.818
1988–89	10	1	1	2	5	1	0.222	0.600	0.500	0.800
1989–90	11	2	3	2	2	2	0.455	0.364	0.182	0.819
1990–91	15	6	1	2	4	2	0.466	0.400	0.267	0.866
1991–92	15	5	0	3	6	1	0.333	0.467	0.400	0.800
1992–93	13	2	1	7	2	1	—	0.230	0.154	—
Pooled (through 1991–92)	139	36	21	23	44	15	0.410	0.424	0.317	0.834
Pooled (through 1992–93)	152	38	—	—	46	16	—	0.407	0.303	—

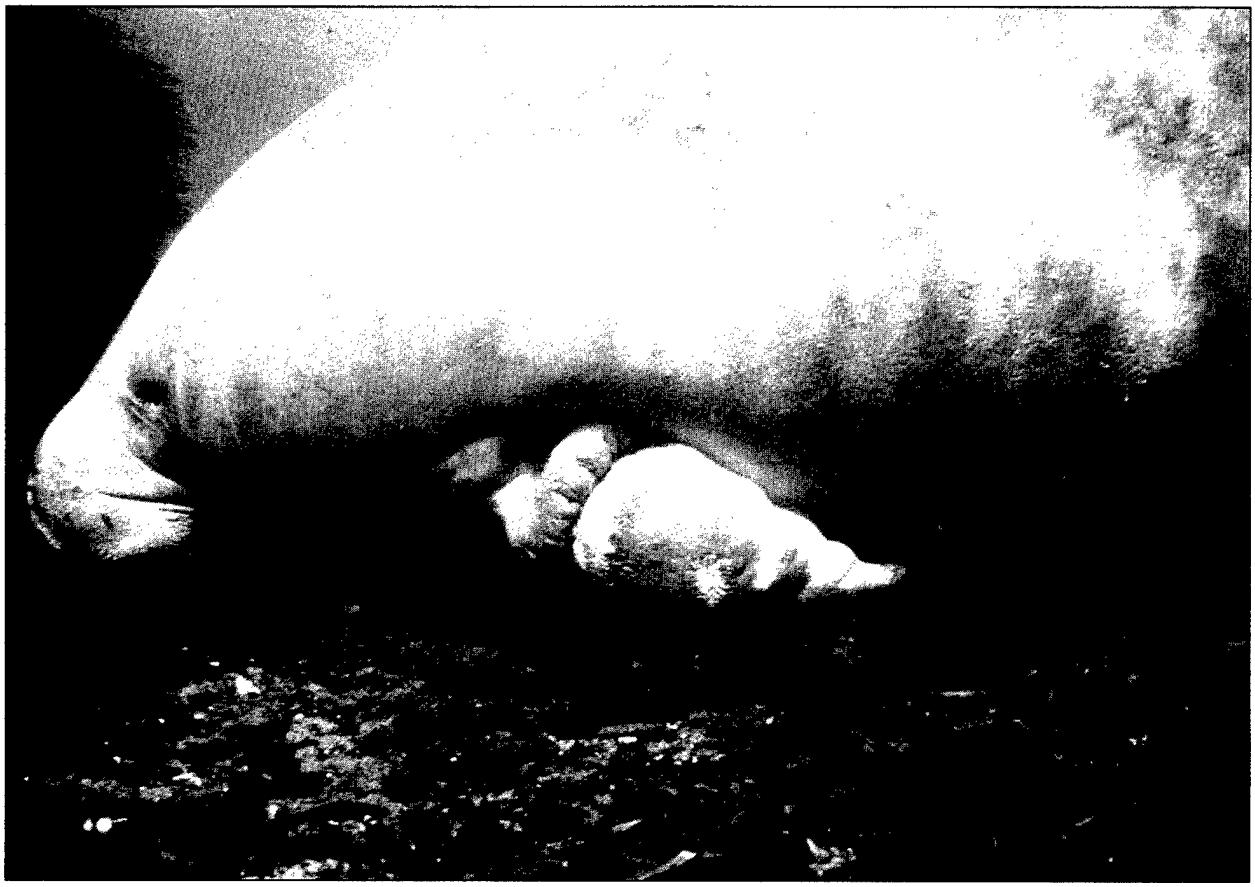


Fig. 3. Phoebe (BS 05), an adult female Florida manatee (*Trichechus manatus latirostris*) recognizable from a deformed flipper and dorsal- and tail-scar patterns. She was first identified from film footage taken by Jacques Costeau at Blue Spring in winter 1970–1971. She had at least seven offspring during a 22-year period and died while pregnant in 1992 at a weight of 1,216 kg. *Photo by T. J. O'Shea.*

but this individual was subsequently observed at Blue Spring in every winter during 1974–75 through 1991–92. She had six calves during the 18 consecutive years. Including her nursing calf in 1971–72, she produced five males and two females. None of the six calves recorded during the 18 consecutive years was dependent longer than one winter season. The female was found in distress and brought to a captive rehabilitation facility on 6 August 1992. She died on the same day from complications of a late-term pregnancy. She was pregnant with a 143-cm TL, 49.9-kg, near-term fetus (which also died). At death, the female was 365 cm TL and 1,216 kg. Her estimated age was 29 years based on growth-layer-group counts in the dome portion of the periotic bone (Marmontel 1993). No other female at Blue Spring was observed for as many winters as this female. She reproduced during at least 22 years (1970–71 through 1991–92).

The observations of some other females also were fairly lengthy. One female (BS 04) was observed from 1974–75 (at an unknown age) through 1992–93 (no records were kept in 1976–77). She returned to Blue Spring with five calves during her 19-year history and was accompanied by a first-winter calf in winter 1992–93. Another female (BS 40) was first identified at an unknown age at Blue Spring in winter 1974–75 but was not observed again until 1980–81. Since winter 1980–81, she was seen at Blue Spring each winter through 1992–93 except in 1985–86 (although in 4 of the 12 winters she was present early but left by mid-winter). This individual, however, has not been pregnant or nursing a calf since 1984–85 (perhaps having entered a phase of reproductive senescence) and was only known to produce two calves during her entire history (Table 2).

Discussion

Much information from our observations of the reproduction of recognizable females at Blue Spring is similar to that obtained in other studies. Rathbun et al. (1995) noted a mean age of 5.1 ± 1.21 years at first successful reproduction by seven female manatees in the Crystal River, an age equivalent to those of the seven females we observed at Blue

Spring (5.4 ± 0.98 years). We noted an average interval between births of 2.60 ± 0.81 years at Blue Spring, whereas Rathbun et al. (1995) calculated an interval of 2.48 ± 0.77 based on a larger data set from the Crystal River. Reid et al. (1995) computed a mean interval between births of 2.6 years based on 11 intervals from ten identifiable individuals on the Atlantic Coast. We estimated that female manatees at Blue Spring became sexually mature when they—like conspecifics in the Crystal River (Rathbun et al. 1995)—were as young as 3 and 4 years old. Based on findings from anatomical studies of carcasses, Marmontel (1995) also estimated that females at their earliest pregnancies were 3 and 4 years old and noted that all salvaged carcasses of females that were 5 years old or older were sexually mature.

The proportion of reproducing females was high at Blue Spring. We noted a pooled proportion (through 1991–92) of 0.41 of the adult females that were pregnant and a proportion of 0.42 that were lactating, indicating that a proportion of 0.83 of the adult females were either pregnant or nursing a calf. The proportion of females nursing first-year calves (through 1992–93) was 0.30. The proportions of females nursing first-year calves were higher in the Crystal River (0.36) and on the Atlantic Coast (0.38), but sample sizes were larger in these two study areas (Rathbun et al. 1995; Reid et al. 1995), and the pooled proportions of females nursing first-year calves were not significantly different ($\chi^2 = 3.16$, $df = 2$, $P = 0.21$, mean proportion 0.362) among the three study areas. The proportion of lactating females (first- and second-year calves) at Blue Spring (0.407) was essentially identical to those on the Atlantic Coast (0.420) and in the Crystal River (0.422; $\chi^2 = 0.07$, $df = 2$, $P = 0.97$, mean proportion 0.420). These proportions are higher than those calculated from findings from examinations of reproductive tracts of salvaged carcasses from throughout the range (0.333 pregnant and 0.180 lactating; Marmontel 1995). Higher rates of pregnancy and lactation from observations on living animals confirmed Marmontel's (1995) caution that such rates based on carcass examinations could be biased downwards because of sampling problems (incomplete necropsies, decomposition of carcasses, and perhaps over-representation of unhealthy, senescent, or otherwise non-reproducing females in carcass samples). Unlike the carcass-based data set, which is accumulated year-round, however, observations from longitudinal studies are seasonally biased. Births and weaning, for example, seemed to be suppressed during winter at Blue Spring. Live-animal data sets may be biased upwards if the sex of reproductively active females is documented with greater frequency because of the presence of calves (O'Shea and Langtimm 1995). However, because the proportions of lactating females do not differ among the three study areas, despite differences in intensity of sampling and sampling conditions (O'Shea and Langtimm 1995), we suspect this bias is minimal. Although the number of observed adult females in any one year was small at Blue Spring, observations were more intensive and repetitive there than in other study areas. The lactation status of all females was determined at Blue Spring, and proportions were equivalent to those in the Crystal River and Atlantic Coast study areas.

Our finding of the non-occurrence of births in winter is also concordant with information from studies in the Crystal River and studies of carcasses (Marmontel 1995; Rathbun et al. 1995). Information on the tendency of suppressed weaning of calves during winter is emerging. In addition to our findings of an absence of weaning in winter at Blue Spring, Reid et al. (1995) noted only one of seven calves was weaned during studies with radiotracking on the Atlantic Coast during November through February. Suppression of weaning during November–February is clearly adaptive (particularly in northern Florida) because cool temperatures during these months impose the most serious energetic stress on manatees (Irvine 1983), and manatees in the weaning age and size classes are most susceptible to mortality in winter (O'Shea et al. 1985; Marmontel 1993; Ackerman et al. 1995). Continued nursing in winter supplements the diet of calves with energy-rich milk, and continued close association with mothers presumably confers on calves the benefits of the adult females' experience in avoiding temperature extremes and finding profitable sources of food. The absence of a pattern of one- or two-winter dependencies according to sex of the calf is consistent with findings on the Crystal River (Rathbun et al. 1995). The proportion of calves that was dependent for two winter periods also did not significantly differ ($\chi^2 = 2.01$, $df = 2$, $P = 0.37$, mean proportion 0.250) among the Blue Spring (0.333; 14 of 42 calves), Crystal River (0.231; 28 of 121 calves; Rathbun et al. 1995), and Atlantic Coast (0.216; 8 of 37 calves; Reid et al. 1995) study sites. Sample sizes of period of dependency by age of female at Blue Spring were too small for statistical analysis but, as in manatees in the Crystal River (Rathbun et al. 1995), a tendency of nursing first-born calves longer than 2 winters may exist in manatees at Blue Spring (four of six cases). If so, energy expenditure may explain the trend. Lactation in first-time reproducing females may pose demands on continued growth in body size (O'Shea and Reep [1990] recorded growth beyond ages at first reproduction in manatees at Blue Spring), and these dual demands may require a longer period of lactation.

Other aspects of reproduction in manatees that were identified in our studies are also similar to findings by others. These include the apparent existence of a pseudoestrus (Hartman 1979; Marmontel 1995; Rathbun et al. 1995), an approximately 1-year gestation (Rathbun et al.

1995; Reid et al. 1995), a seeming preference for giving birth in quiet waters and canals (Rathbun et al. 1995; Reid et al. 1995), and a low incidence of twinning and 1:1 sex ratios of calves (Marmontel 1995; Rathbun et al. 1995). In general, the high concordance of nearly all aspects of reproduction in manatees among study areas is remarkable because of the long distances between these areas and the contrasting habitats and environmental conditions, particularly in winter. These contrasts include the dark, tannin-stained freshwater conditions that dominate the range of the Blue Spring group, which must enter cold water to forage in winter; the ready availability of freshwater vegetation to the aggregation of manatees in winter in the Crystal River (in summer, some of these manatees foraged in estuaries and rivers of the largely uninhabited Big Bend Coast of the Gulf of Mexico); and the seagrass-dominated habitats of the group on the Atlantic Coast (many of these manatees make long migrations and frequent intensively urbanized settings). The ranges of manatees studied at Blue Spring and on the Atlantic Coast overlap, and some interchange occurs between these two aggregations (Reid et al. 1991). However, Crystal River and Blue Spring are as widely separated by water as possible in the range of manatees in Florida and are on opposite sides of the peninsula, precluding significant interchange. Perhaps this concordance of reproductive traits of manatees among study areas indicates that manatees in Florida are convergent on a maximum level of reproduction, unrestrained by density-dependent mechanisms. We recommend the continuation of longitudinal studies at these sites to document shifts in traits of reproduction, to increase sample sizes, and to improve an understanding of patterns of variation.

Survival of calves between late pregnancies in one winter to their appearances with mothers in subsequent winters was also remarkably similar between the Blue Spring (0.60) and Crystal River (0.67) sites, where the number of observations (55 of 82 cases) was substantially higher (Rathbun et al. 1995). Our data show higher annual survival of calves after the first winter at Blue Spring; by the third winter, rates essentially matched those of adults (O'Shea and Langtimm 1995). Comparable data from other studies about the survival of calves beyond the first winter are not available. Rathbun et al. (1995) noted that only 36% of 22 calves that were tail-nicked while dependent were re-identified at least three seasons after weaning in the Crystal River. This is almost half of the survival we observed at Blue Spring by similar criteria (22 of 33 or 67%; Table 1) and is probably attributable to difficulties in re-identifying animals under the observation conditions in the Crystal River rather than higher subadult mortality (in the Crystal River, larger areas must be searched, greater numbers of manatees must be distinguished, and the rate of scarring on calves that facilitates recognition is probably lower).

Mortality factors that contribute to the lower survival of manatees during their early years are largely unknown, but the numbers of dead in the very young perinatal category have been increasing (Ackerman et al. 1995) and are a substantial fraction of the total (Marmontel 1995). Most explanations for these perinatal deaths have been largely speculative and include possible orphaning because of disturbance or death of mothers by human activities, increasing proportions of younger females in the population that may be unsuccessful in first attempts at giving birth or nursing, or pollution or disease (*U.S. Marine Mammal Commission 1993). In reality, early mortality is probably caused by multiple sources, including a variety of natural causes.

We speculate that some perinatal deaths may be due to behavior of males. Hartman (1979:101–102) aptly described the intense and "unrelenting pursuit" of females by herds of "bulls," including "violent jackknife(s)" and "frenzied embraces," and also noted that these pursuits are sometimes of females with calves. Our observations of males that pursued females with calves, including the case of the lone male and the female with a 5-day-old calf, are concordant with those of Hartman (1979). This leads us to speculate that some fraction of the largely unexplained cases of perinatal mortality may result from such pursuits. One may envision young calves being left behind or lost as females try to elude pursuing males, calves that are stressed from trying to keep up with their mothers and having their nursing patterns interrupted, or calves that are physically injured or drowned during the intense pursuits of females by males. Calves may also die if males interrupt females during parturition. Perinatal deaths would be to the advantage of males (akin to the evolutionary male mating strategy involving infanticide known of a variety of mammals; Hausfater and Hrdy 1984) if females become estrous soon after the deaths of their calves. The latter is evidenced by the high incidence of pregnancy we noted among females that had lost calves between successive winters and Hartman's (1979) observations of a female in estrus 10–15 days after the loss of a calf at birth. Because of the low probability that the killed calves are offspring of the pursuing males—considering the relatively promiscuous mating system described by Hartman (1979)—the fitness of such males are enhanced. Movement patterns of male manatees in the St. Johns River have generally been described as patrolling circuits in search of estrous females during warm months (Bengtson 1981), and greater rates and wider ranges of travel were also suggested of male manatees on the Gulf Coast

(Rathbun et al. 1990). Although loss of very young calves would be least costly to females because of the relatively low energetic investment at that stage, the seeming preference by females for giving birth in quiet canals and backwaters away from main channels of travel may function to avoid roving males. We did not observe separation or loss of calves at Blue Spring during winter, when breeding condition of males is suppressed (Hernandez et al. 1995). Mating strategies are an important topic in modern behavioral and evolutionary ecology (Clutton-Brock 1988, Clutton-Brock and Parker 1992), but in manatees have not been well studied or interpreted according to contemporary theory. Future research in this field should be encouraged.

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Cited References[3]

Ackerman, B. B., S. D. Wright, R. K. Bonde, D. K. Odell, and D. J. Banowetz. 1995. Trends and patterns in mortality of manatees in Florida, 1974–1992. Pages 223–258 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

*Beeler, I. E., and T. J. O'Shea. 1988. Distribution and mortality of the West Indian manatee (*Trichechus manatus*) in the southeastern United States: a compilation and review of recent information. National Technical Information Service, Springfield, Va. Document PB 88-207980/AS. 613 pp.

Bengtson, J. L. 1981. Ecology of manatees (*Trichechus manatus*) in the St. Johns River, Florida. Ph.D. thesis, University of Minnesota, Minneapolis. 126 pp.

*Brownell, R. L., Jr., and K. Ralls, editors. 1981. The West Indian manatee in Florida. Proceedings of a workshop held in Orlando, Florida, 27–29 March 1978. Florida Department of Natural Resources, Tallahassee. 154 pp.

Clutton-Brock, T. H., editor. 1988. Reproductive success: studies of individual variation in contrasting breeding systems. University of Chicago Press, Chicago, Ill. 538 pp.

Clutton-Brock, T. H., and G. A. Parker. 1992. Potential reproductive rates and the operation of sexual selection. Quarterly Review of Biology 67:437–456.

Hartman, D. S. 1979. Ecology and behavior of the manatee (*Trichechus manatus*) in Florida. American Society of Mammalogists Special Publications 5, Lawrence, Kans. 153 pp.

Hausfater, G., and S. B. Hrdy, editors. 1984. Infanticide: comparative and evolutionary perspectives. Aldine Publishing Company, New York. 598 pp.

Hernandez, P., J. E. Reynolds, III, H. Marsh, and M. Marmontel. 1995. Age and seasonality in spermatogenesis of Florida manatees. Pages 84–97 *in* T. J. O'Shea, B. B. Ackerman, and H F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Irvine, A. B. 1983. Manatee metabolism and its influence on distribution in Florida. Biological Conservation 25:315–334.

Marmontel, M. 1995. Age and reproduction in female Florida manatees. Pages 98–119 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Marmontel, M. 1993. Age determination and population biology of the Florida manatee, *Trichechus manatus latirostris*. Ph.D. dissertation, University of Florida, Gainesville. 408 pp.

Odell, D. K., G. D. Bossart, M. T. Lowe, and T. D. Hopkins. 1995. Reproduction of the West Indian manatee in captivity. Pages 192–193 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

O'Shea, T. J., and C. A. Langtimm. 1995. Estimation of survival of adult Florida manatees in the Crystal River, at Blue Spring, and on the Atlantic Coast. Pages 194–222 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

O'Shea, T. J., and R. L. Reep. 1990. Encephalization quotients and life-history traits in the Sirenia. Journal of Mammalogy 71:534–543.

O'Shea, T. J., C. A. Beck, R. K. Bonde, H. I. Kochman, and D. K. Odell. 1985. An analysis of manatee mortality patterns in Florida, 1976–1981. Journal of Wildlife Management 49:1–11.

*Powell, J. A., and J. C. Waldron. 1981. The manatee population in Blue Spring, Volusia County, Florida. Pages 33–40 *in* *R. L. Brownell, Jr. and K. Ralls, editors. 1981. The West

[3] An asterisk denotes unpublished material.

Indian manatee in Florida. Proceedings of a workshop held in Orlando, Fla., 27–29 March 1978. Florida Department of Natural Resources, Tallahassee. 154 pp.

Rathbun, G. B., J. P. Reid, and G. Carowan. 1990. Distribution and movement patterns of manatees (*Trichechus manatus*) in northwestern peninsular Florida. Florida Marine Research Publications 48:1–33.

Rathbun, G. B., J. P. Reid, R. K. Bonde, and J. A. Powell. 1995. Reproduction in free-ranging Florida manatees. Pages 135–156 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Reid, J. P., R. K. Bonde, and T. J. O'Shea. 1995. Reproduction and mortality of radio-tagged and recognizable manatees on the Atlantic Coast of Florida. Pages 171–191 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Reid, J. P., G. B. Rathbun, and J. R. Wilcox. 1991. Distribution patterns of individually identifiable West Indian manatees (*Trichechus manatus*) in Florida. Marine Mammal Science 7:180–190.

Sokal, R. R., and F. J. Rohlf. 1969. Biometry. W. H. Freeman and Co., San Francisco, Calif. 776 pp.

Stirling, I. 1971. Population dynamics of the Weddell seal (*Leptonychotes weddelli*) in McMurdo Sound, Antarctica, 1966–68. Pages 141–161 *in* W. H. Burt, editor. Antarctic Pinnipedia. Antarctic Research Series 18. American Geophysical Union, Washington, D.C.

*U.S. Marine Mammal Commission. 1993. Annual report to Congress, 1992. U.S. Marine Mammal Commission, Washington, D.C. 226 pp.

Reproduction and Mortality of Radio-tagged and Recognizable Manatees on the Atlantic Coast of Florida

by

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Abstract. We used radio-tagging (conventional and satellite-based) and photo-identification to study aspects of Florida manatee (*Trichechus manatus latirostris*) reproduction and mortality along the Atlantic Coast of Florida. Fifty-five manatees were tagged during 1986–91 from Georgia to the Biscayne Bay; most were initially tagged in Brevard County, Florida. Tag loss was common and affected the continuity of observations during studies, but our attachment system allowed frequent tag replacement. The duration of continuous transmitter deployment ranged from 1 to 578 days; 34 manatees were monitored during 217 multiple bouts. Termination of deployments was marked by the recovery of the tag after separation at designed weak links, tag replacement with a new unit by snorkelers, loss of the tethered transmitter, loss of signal, or death of the tagged manatee. Observations of tagged females revealed one gestation period, five births, periods of dependence by young, weaning episodes, intervals between births, and sizes of reproductive females. Eighteen females produced 22 calves. Birth dates and locations of five calves were determined. Births occurred between the months of May and September in quiet canals or boat basins. Two of the births were preceded by moves by the females of more than 100 km. Six tagged manatees died. Two deaths were due to anthropogenic causes; the causes of death of the remaining dead manatees were not determined. Reproduction was also studied on the basis of photo-identification records of 185 females collected during 1978 through winter 1991–92. The pooled proportion of females accompanied by young in each winter was 0.42. Calf dependencies on mothers ranged from 1 to 2 years. Eleven intervals between successive births were determined from an abbreviated data set. The average duration of the intervals was 2.6 years. Data on reproduction are concordant with information from studies of manatees elsewhere in Florida.

Key words: Florida manatees, mortality, photo-identification, reproduction, satellite telemetry, tag loss, telemetry.

Information on the life history of the Florida manatee (*Trichechus manatus latirostris*) from field studies in the Crystal River on the northwestern coast of peninsular Florida (Rathbun et al. 1990, 1995) and from Blue Spring on the upper St. Johns River (O'Shea and Hartley 1995) has slowly accumulated. About half the manatee population in the southeastern United States resides along the Atlantic Coast of Florida (Ackerman 1995), but few data on the life history of free-ranging individuals from this region are available. This information would be valuable for evaluating the representativeness of reproduction parameters derived from observations in the Crystal River and at Blue Spring and from carcass examinations (Marmontel 1995) and for determining aspects of manatee population dynamics on the Atlantic Coast. Previous researchers who used scars and other markings to obtain more limited information on manatee ecology along the Atlantic Coast include Moore (1956),

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Shane (1983, 1984), and Packard (*[3]1981). These researchers focused primarily on short-term aggregations of manatees in winter, whereas we made year-round observations during several years.

Two techniques for gathering life-history information from other free-ranging marine mammals are radio-tagging and photo-identification (Hammond et al. 1990; Siniff and Ralls 1991). Techniques for monitoring manatees in saltwater habitats by radio-tagging (*Rathbun et al. 1987a, 1990; *Reid and O'Shea 1989) are used primarily for determining movements and habitat use for the development of conservation (*U.S. Fish and Wildlife Service 1989; O'Shea and Kochman 1990; Reynolds and Haddad 1990). Results from these studies have not been evaluated for utility in providing life-history information. This has been partly due to the unique problem of tag loss intentionally associated with tag design that results in monitoring that is briefer than the duration of certain life-history traits of interest in these long-lived animals. Photo-identification techniques, in contrast, have been successfully used on manatees in Florida for many years (Beck and Reid 1995; O'Shea and Hartley 1995; Rathbun et al. 1995), but previously published results about manatees on the Atlantic Coast were only about site fidelity and resightings among locations (Reid et al. 1991). We therefore used a radio-tagging system to provide a general description of movements and a detailed account of information on tag loss, reproduction, and mortality of manatees on the Atlantic Coast, and photo-identification records to provide the first summary of reproduction of female manatees in this region.

Methods

Radio-tagging

The study was initiated in May 1986 and is ongoing. This report is a summary of data collected through 31 December 1991. Techniques of tagging manatees varied. Thirty of 55 manatees were captured and temporarily restrained with nets, 11 were tagged by snorkelers without restraint, 13 were captive, rehabilitated animals that were released near original points of rescue, and one was rescued and released on site on the same day. Tagged manatees were assigned a sequential number with a prefix to indicate the approximate tagging location. Because the study is ongoing, we use the numbers in the text to designate observations pertinent to a specific individual manatee. Capture nets were from 15 to 150 m long and from 3.6 to 6.7 m deep and were fabricated from 20-cm stretched mesh of number-54 black nylon twine. Most manatees were baited to capture sites with fresh water from hoses (Fig. 1) near shore (municipal drinking water from hoses is a common attractant of manatees in urbanized saltwater habitats in Florida). A net was then pulled across the entrance to the capture area and the manatees were pursed in the net. Netted individuals were hauled to shore where they were manually restrained in shallow water or on a gently sloping beach. During the period of restraint, which averaged 29.8 minutes (SD = 10.5, range = 15–62, n = 30), each manatee was measured, photographed, and fitted with a radio-tag assembly. Some manatees were marked by taking a small nick of skin from the tail margin to enhance future identification (Rathbun et al. 1995). No harmful effects of capture and handling procedures were observed in subsequent tracking (O'Shea et al. 1985a). For previous studies of radio-tagged manatees in Florida the animals were tagged in aggregation sites in winter, primarily in January, and were rarely if ever tagged again (Bengtson 1981; Rathbun et al. 1990; L.W. Lefebvre, National Biological Service, Gainesville, Florida, and R. K. Frohlich, Florida Department of Environmental Protection, Tallahassee, Florida, unpublished data). Our work departs from previous studies because freshwater bait stations and the emphasis on retagging and on transmitter replacement by swimmers allowed year-round capture and tagging (Fig. 2).

Manatees were tagged with a belt and a tethered floating transmitter assembly (Fig. 3). More detailed descriptions and procedures of tag construction are provided by Rathbun et al. (*1987a, *1987b, 1990); descriptions of additional refinements were provided by Reid and O'Shea (*1989). The current tag hardware includes threaded chain connectors at the proximal and distal ends of the tether. Connectors allow replacement of tags by a swimmer who quietly approaches the animals and uses small wrenches to change transmitters in floating housings at the surface or by a shallow free-diving person who replaces the tether and tag assemblies at the belt. Some manatees are extremely tolerant of swimmers, and entire belts can sometimes be fitted without restraint; others are extremely wary, and tag changes can be made only with great stealth at the distal end of the tether assembly.

The tethered floating transmitter assembly is attached to a belt fitted around the peduncle at the base of the manatee's tail. Belts were constructed in advance of tagging to fit an array of potential peduncle girths and were color-coded and engraved with identification numbers. A bear-claw buckle on each belt permitted the tag to be quickly fastened to a manatee. Corrodible nuts and bolts in the belt's construction allowed the complete

[3] An asterisk denotes unpublished material.

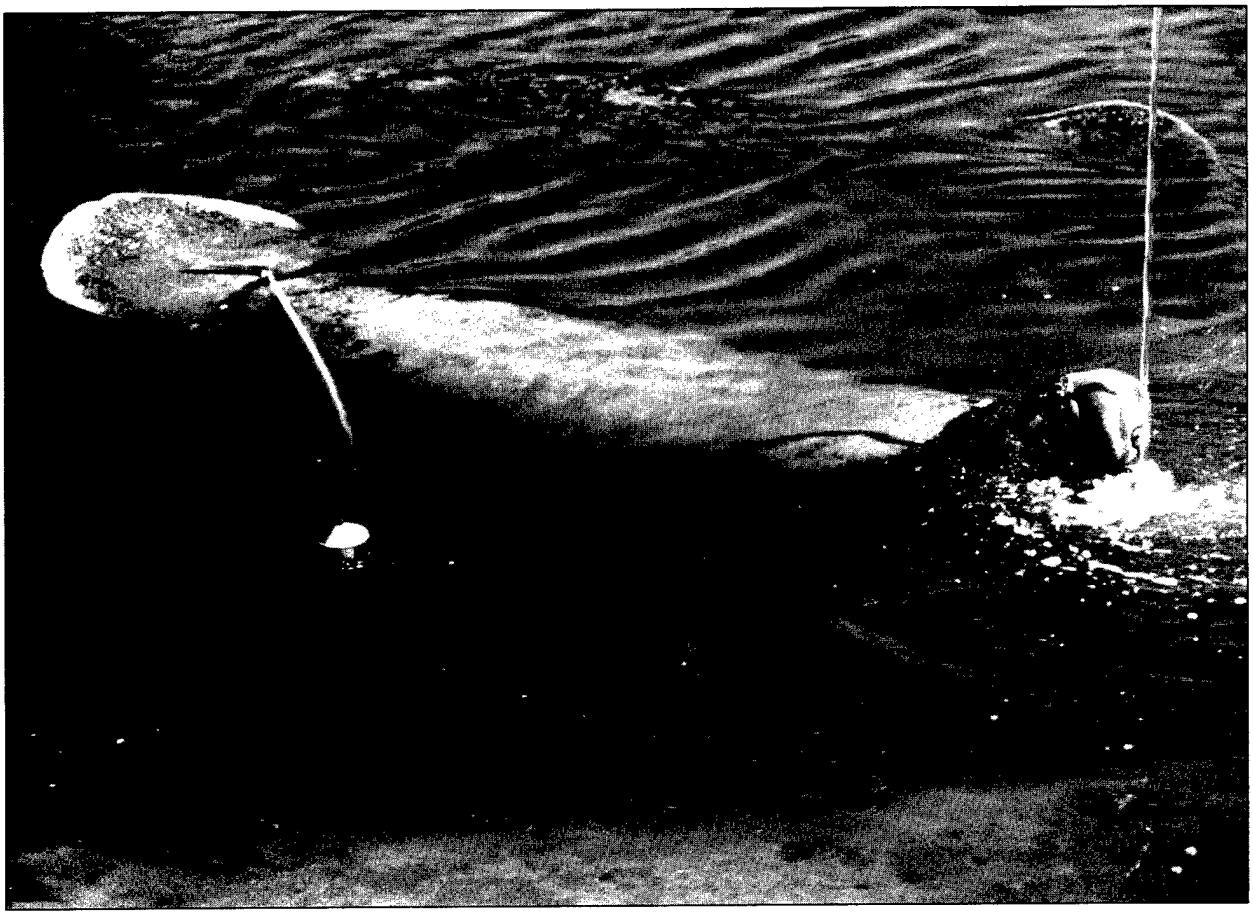


Fig. 1. A radio-tagged adult female Florida manatee (*Trichechus manatus latirostris*) drinking fresh water from a hose at a capture site on Banana Creek, Merritt Island National Wildlife Refuge, Florida. The floating transmitter housing contains a satellite-monitored PTT. *Photo by J. Reid.*

assembly to eventually drop off. Belts were designed to remain on the manatees for 2–3 years, but we found a wide variation that was probably caused by differences in materials, individual behavior, and salinity and temperature of the water.

Small (9.0 cm long and 1.7 cm in diameter) ultrasonic transmitters or pingers were incorporated into some belts. This allowed us to use a sonic receiver and directional hydrophone to relocate belted animals that had lost floating radio tags. This was particularly useful during attempts to reattach radio tags. Ultrasonic transmitters emit signals at 75 kHz, above the range of manatee hearing (Bullock et al. 1982), and were also incorporated into some transmitter housings to assist with the recovery of malfunctioning or detached and submerged transmitters.

Belts and buoyant transmitters were joined by stiff nylon tethers (10-mm diameter rods). Tether lengths ranged from 130 to 200 cm depending on the size of the animal and characteristics of the tracking environment. Each tether had a machined groove near the proximal connecting link that reduced the rod diameter, providing a weak link for tag detachment. Groove depths were varied such that smaller animals were fitted with tethers of lesser breaking-strength thresholds than larger animals.

Two types of radio-transmitters were used: very high frequency (VHF) radio-transmitters and platform transmitter terminals (PTTs). VHF transmitters in this study operated at specific frequencies in the 164-MHz band. We used directional antennas and portable receivers tuned to the VHF signal to radio-track and locate manatees in the field. Locations were determined visually or by triangulation. PTTs emit binary-encoded data via an ultra-high frequency (UHF) signal (401.650 MHz) that is received by equipment on orbiting satellites. These satellites are part of the U.S. National Oceanic and Atmospheric Administration's Polar Orbiting Environ-

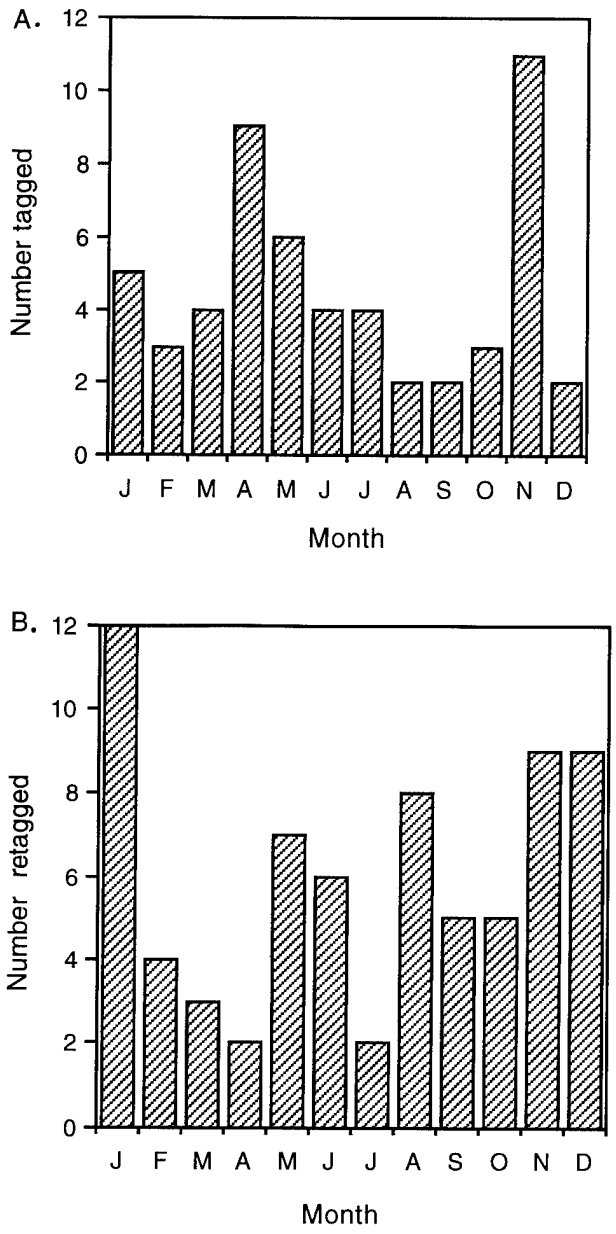


Fig. 2. Frequency distribution of initial radio-tagging and retagging by month, 1986–1991. All Atlantic Coast tagging sites were combined. (A) Number of Florida manatees (*Trichechus manatus latirostris*) that had radio-tags (belt and transmitter) applied for the first time. (B) Number of episodes in which previously tagged individuals missing transmitters were relocated and retagged with a new transmitter or belt. Some individuals were retagged more than once. Transmitter replacements are not included with the number of retaggings.

mental Satellite Program. Receiving equipment on board is operated in a bilateral agreement with France's Centre National d'Etudes Spatiales, and data processing is provided by Service Argos, Inc. As the satellites pass over, on-board receiving equipment uses Doppler shifts in frequency to compute locations and to transmit location and sensor data to receiving stations on earth. Data are rebroadcast through telecommunications satellites to processing centers. From that point, the information can be downloaded via telephone links to personal computers within a few hours or less of the last satellite pass over the manatee. Data from Service Argos are also received monthly on computer diskette. Data received through the satellite link include PTT identification number, location date and time, latitude and longitude, and an accuracy code (best accuracy is one standard deviation within 150 m). Also transmitted are sensor data including transmitter temperature and activity (amount of tipping) and, on newer units, a low-voltage indicator. We usually received two to six locations daily by satellite, providing frequent location updates and minimizing the need for extensive searches in the field. The development and use of PTTs for tracking manatees are described in more detail by Mate et al. (*1986, *1987), Reid and O'Shea (*1989), and Rathbun et al. (1990). Detailed technical descriptions of satellite telemetry systems are provided by Fancy et al. (1988) and Harris et al. (1990).

We used two types of transmitter and housing configurations to track manatees. Both styles were buoyant and attached to the distal end of the tether. The smaller of the two included a single VHF transmitter installed in 33-cm-long, 6-cm-diameter housings. The tag design used most often incorporated a PTT that transmitted to satellites, a back-up VHF transmitter that allowed supplemental localization and observation in the field, and an ultrasonic transmitter that allowed localization of the animal underwater or of the PTT units after detachment and submergence. PTT housings were 39 × 9-cm-diameter cylinders. Both types floated vertically at the surface and had quarter-wave whip antennas mounted on top (antennas on PTTs were tuned for the UHF signal but were also used for transmitting VHF signals). VHF transmitters in housings were 860 g in weight, whereas combined PTT-VHF tags weighed approximately 2,410 g. Battery life was approximately 2 years for VHF transmitters and approximately 8.5 months for PTTs (6.5 months on new units placed into service after spring 1991). Transmitter housings were color coded and marked with large identifying letters and engravings.

The number of tagged manatees was summarized by year to indicate the availability for discovery through

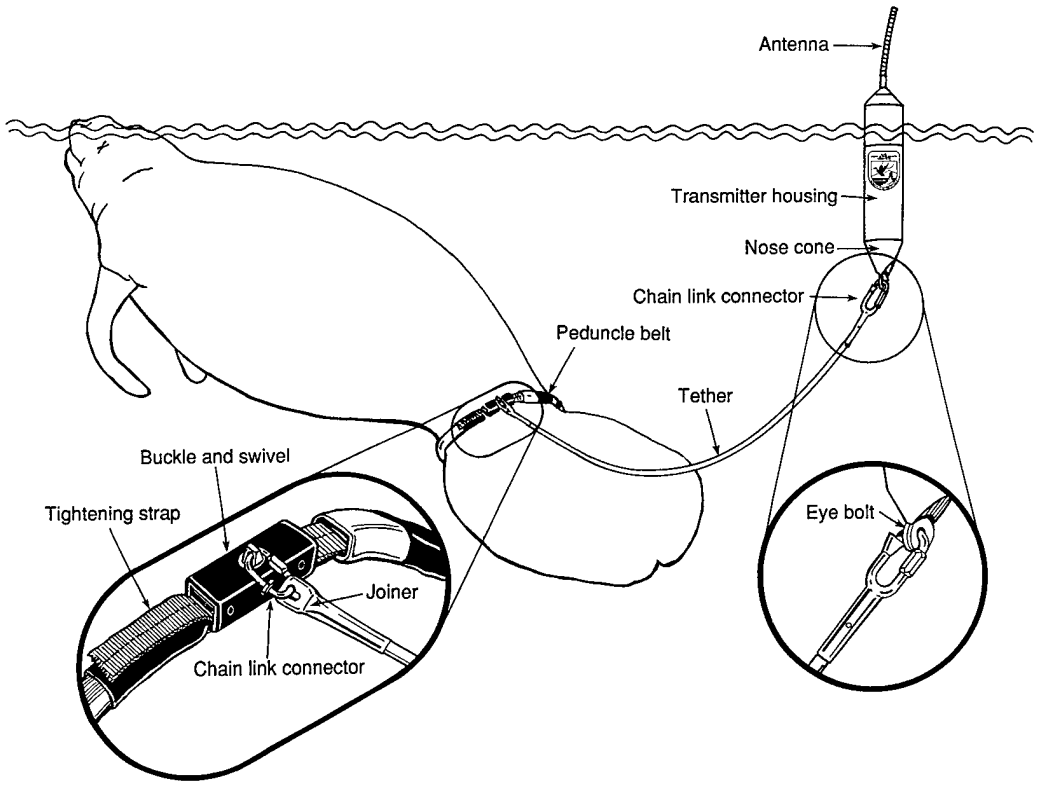


Fig. 3. Radio-tag assembly used on Florida manatees (*Trichechus manatus latirostris*; after *Rathbun et al. 1990). The transmitter housing and belt are attached to a stiff nylon tether by threaded chain connectors. The transmitter housing contains a satellite-monitored PTT, a VHF radio-transmitter, and an ultrasonic transmitter.

the carcass retrieval program (Ackerman et al. 1995) or resightings. For each year, we totaled the number of manatees tracked with floating transmitters and the known number of manatees wearing only belts (based on sightings in that year or in subsequent years) and calculated the proportion of this total that consisted of carcasses recovered during that year. However, the basis for calculating these proportions is uncertain because of possible undiscovered deaths and because some surviving animals probably had belts but were not resighted.

Photo-identification

The photo-identification system in this study was described by Reid et al. (1991) and Beck and Reid (1995). Slide photography was used to record the identities of females. Particular attention was given to documenting the presence or absence of calves with those females. We determined the following aspects of reproduction by compilation of sighting records of females: proportion of females identified with calves each winter, intervals between births, and numbers of winters of dependency by calves on their mothers. No information was available on age at first reproduction from photo-identification or telemetry studies of manatees on the Atlantic Coast. Terminology and criteria used by Rathbun et al. (1995) were followed as closely as feasible for defining reproduction traits. Seasons were defined as three-month periods beginning with January, February, and March (the winter season). Most photo-identification records (88%) were obtained in the fall and winter seasons (fall = 17%; winter = 71%; spring = 7%; summer = 5%) when manatees tend to aggregate at industrial warm-water discharge sites. Records outside of the fall and winter periods were excluded from analysis to allow comparisons with similar data from other study areas (O'Shea and Hartley 1995; Rathbun et al. 1995). How-

ever, all sightings were used to define intervals between births, based on consecutive seasons between the last sighting of a previous calf and the first sighting of a new calf.

Analyses of reproduction histories are based on sighting data through the fall 1991–winter 1992 seasons, as compiled in March 1993. A few photographic records date from 1978 (Shane 1983), but most observations were made in 1982 or later. A total of 447 manatees from the Atlantic Coast (excluding Blue Spring) have been included in the manatee identification catalog during this period: 61 males, 185 females, and 201 of undetermined sex. Most photo-identification records on the Atlantic Coast are taken from the surface where external genitalia are seldom visible, and therefore gender for females is easier to determine based on the presence of calves (Beck and Reid 1995).

Because many females were sighted in only some years and often were missed during one or more years between sightings, an abbreviated subset of all sighting records was created to calculate some reproduction parameters. This subset includes records of 59 sexually mature females that were sighted for at least three consecutive fall-winter seasons. As with Rathbun et al. (1995), sexually mature females were defined as females that were seen as independent from mothers for at least 3 years or were sighted with their own young. However, this censored data set differs in definition from that of Rathbun et al. (1995), who used a criterion of at least 8 consecutive years of sightings. From the censored data set we calculated the duration of dependency by calves as the presence of the calf within 1 year or during 2 years, bracketed by sightings of the female without the calf. A 1-year dependency required that a female was seen in 3 consecutive years with a calf noted in the middle year. A 2-year dependency required a similar arrangement during 4 consecutive years.

We present most results as tabulations of original data or as summary statistics (arithmetic mean ± standard deviation, range). The percentages of females with calves in sighting records between the Crystal River and the Atlantic Coast study groups were compared with a paired (by year) t test on arcsine-transformed proportions. The arcsine transformation was used to correct the non-normal distributions and unequal variances often associated with proportions and percentages. These percentages were based on our tabulations and those of Rathbun et al. (1995), beginning 1981–82 and ending 1990–91. Data from prior years were excluded because of smaller sample sizes on the Atlantic Coast. For these analyses, observations of females with calves included nursing females with first- and second-year calves. The proportion of females with calves in the photo-identification sample was compared with that of the radio-tagged sample with a chi-square test of independence in a 2 by 2 contingency table. For all statistical tests, $P \leq 0.05$ was considered significant.

Results

Monitoring with Radio-tracking

Numbers of Tagged Manatees and Ranges of Movement

Fifty-five manatees (37 females and 18 males) were radio-tagged since 1986 (Table 1). Initial tagging locations ranged from Kings Bay, Georgia, in the north to Biscayne Bay in southern Florida (Fig. 4). Most (34) were tagged in Brevard County, 18 in the Banana River, and 16 in the Indian River or in the adjacent Banana Creek (Fig. 5). Tagging locations of 11 manatees were north and 10 were south of Brevard County. Twenty-one manatees were tracked solely with VHF transmitters, and 34 were tracked with only PTTs or combinations of PTTs and VHF transmitters.

Many tagged manatees ranged long distances from initial tagging locations. Seasonal migrations from northern summer-use areas to southern warm-water sites resulted in a large study area; some individuals moved between Georgia and the Biscayne Bay in southeastern Florida (Fig. 6). In addition to seasonal migrations, some manatees traveled between distant sites during one season. One female (TNC-01), for example, traveled repeatedly between Brevard County and Georgia, including three trips in a single year, and made annual moves south to aggregation sites in winter in southeastern Florida (Fig. 6). Others did not range far from the general area of initial tagging. Five of the 10 manatees tagged in southern Florida (south of Brevard County) did not travel outside of southern Florida. Some individuals made only local movements, traveling less than 30 km between summer- and winter-use areas (Fig. 7).

Tag Loss

Although we tracked some manatees with only one deployment of a transmitter, replacing transmitters was common for various reasons, including low battery life or electronics malfunctions. Manatees that broke free of the transmitter at the tether weak-link were often re-tagged again at a later date. As a result, 34 individuals were monitored over multiple transmitter deployments. Each transmitter deployment is called a tagging bout (Table 1). An extreme case was an adult female manatee (TBC-03), tracked for 26 bouts during nearly 5 years. A total of 239 tagging bouts with a mean of 4.35 bouts/individual (±5.34, range = 1–26) was recorded. These

Table 1. Identification number, name, sex, and size at capture of radio-tagged Florida manatees (*Trichechus manatus latirostris*) tracked on the Atlantic Coast through 31 December 1991. Number of tagging bouts included sequential bouts without intervals between bouts. The sum of the total number of days of tracking and total number of days between bouts equals the total number of days a manatee is tagged (> symbol indicates tracked past 31 December 1991).

ID number	Name	Sex	Total length at capture	Number of bouts	Days tracked	Days between bouts	Total days tagged
TBC-01	Dixie	F	310	4	330	450	780
TBC-02	Trixie	F	270	1	41		41
TBC-03	Moon	F	277	26	>1,219	599	>1,818
TBC-04	Eclipse	F	260	3	248	8	256
TBC-05	Gyro	F	267	3	319	231	550
TBC-06	Moe	M	260	6	852	477	1,329
TBC-07	Bill	M	270	1	65		65
TBC-08	Angela	F	325	1	53		53
TBC-09	C-Cow	F	305	23	>1,148	511	>1,659
TBC-10	Fran	F	310	1	66		66
TBC-11	Gloria	F	300	1	58		58
TBC-12	Heike	F	295	2	59	0	59
TBC-13	Irene	F	260	3	234	0	234
TBC-14	Jerome	M	275	1	132		132
TBC-15	Karen	F	280	6	281	658	939
TBC-16	Larry	M	285	1	4		4
TBC-17	Madonna	F	350	1	37		37
TBC-18	Leroy	M	280	3	96	310	406
TBC-19	Sharon	F	315	1	10		10
TBC-20	Ruth	F	270	15	671	242	913
TBC-21	Willie	M	280	4	161	522	683
TBC-22	Magoo	M	248	2	316	0	316
TBC-23	Hillary	F	273	12	>589	713	>1,302
TBC-24	Betty	F	285	17	>832	168	>1,000
TBC-25	D-Cow	M	225	5	563	26	589
TBC-26	Pee Wee	F	270	6	>675	100	>775
TBC-27	Mel	M	240	3	530	3	533
TBC-28	Liberty	F	222	1	157		157
TBC-29	Casey	M	210	10	>431	57	>488
TBC-30	Maria	F	280	1	119		119
TBC-31	Freddie	F	300	4	>376	50	>426
TBC-32	Tomasina	F	~335	3	>58	165	>223
TBC-33	Ernie	M	280	1	72		72
TBC-34	Miley	M	219	1	>169		>169
TNC-01	Diane	F	330	8	754	871	1,625
TNC-02	Jesse	M	305	1	52		52
TNC-03	Tammy	F	315	1	77		77
TNC-04	Pat	F	310	1	56		56
TNC-05	Roseanne	F	340	1	133		133
TNC-06	Nancy	F	250	3	188	680	868
TNC-07	Whitie	M	250	1	138		138
TNC-08	George	M	275	1	61		61
TGA-01	Mary	F	330	3	285	0	285
TJX-01	Connie	F	270	3	205	26	231
TJX-02	Patience	F	284	2	243	0	243
TPE-01	Spot	F	315	11	>459	605	>1,064
TPE-02	Fireball	F	~325	5	165	47	212
TPE-03	Sickle	F	335	7	>265	477	>742
TPE-04	Susan	F	304	5	442	71	513
TFP-01	Hutch	M	305	1	11		11
TFP-02	Ross	M	288	5	>419	0	>419
TFP-03	Natalie	F	310	2	106	20	126
TFP-04	Sophia	F	~330	1	52		52
TFP-05	Lani	F	~335	2	>141	2	>143
TMI-01	Bob	M	303	2	92	0	92
Total				239	15,315	8,089	23,404
			Mean	4.35	278.5	237.9	425.5
			SD	5.34	283.9	272.0	465.5
			Range	1–26	4–>1,219	0–871	4–1,818

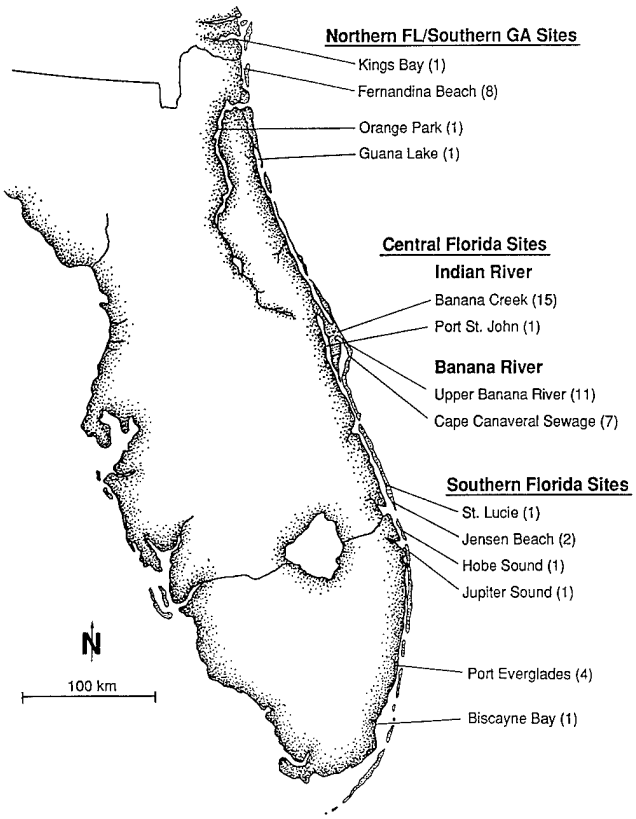


Fig. 4. Sites where Florida manatees (*Trichechus manatus latirostris*) were radio-tagged and the number of tagged manatees ($n = 55$) at each location in parentheses. Most tagging sites were in central Florida.

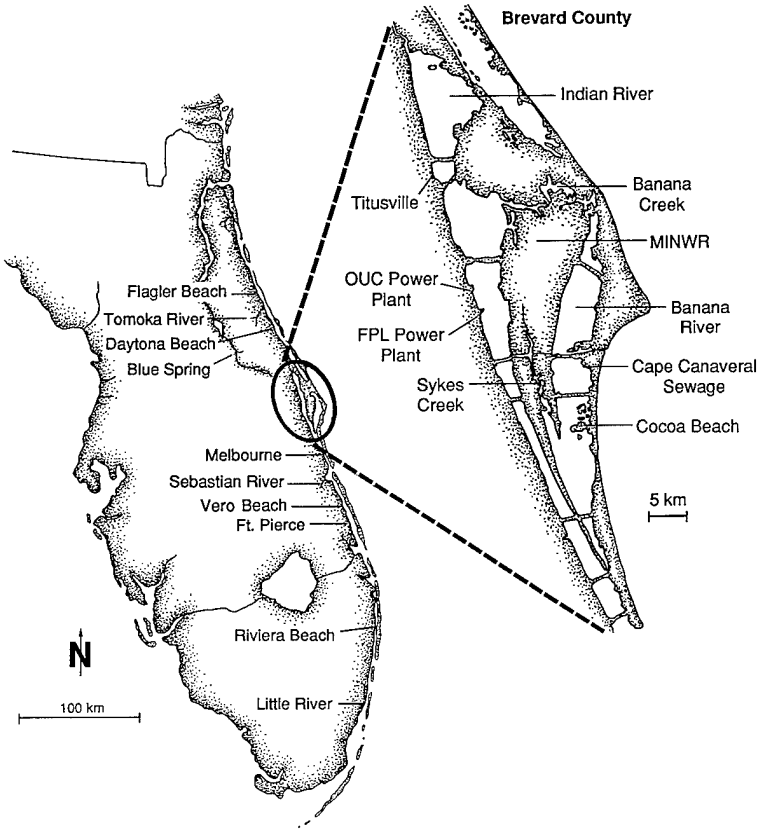


Fig. 5. Place names mentioned in the text and important areas used by Florida manatees (*Trichechus manatus latirostris*) along the Atlantic Coast.

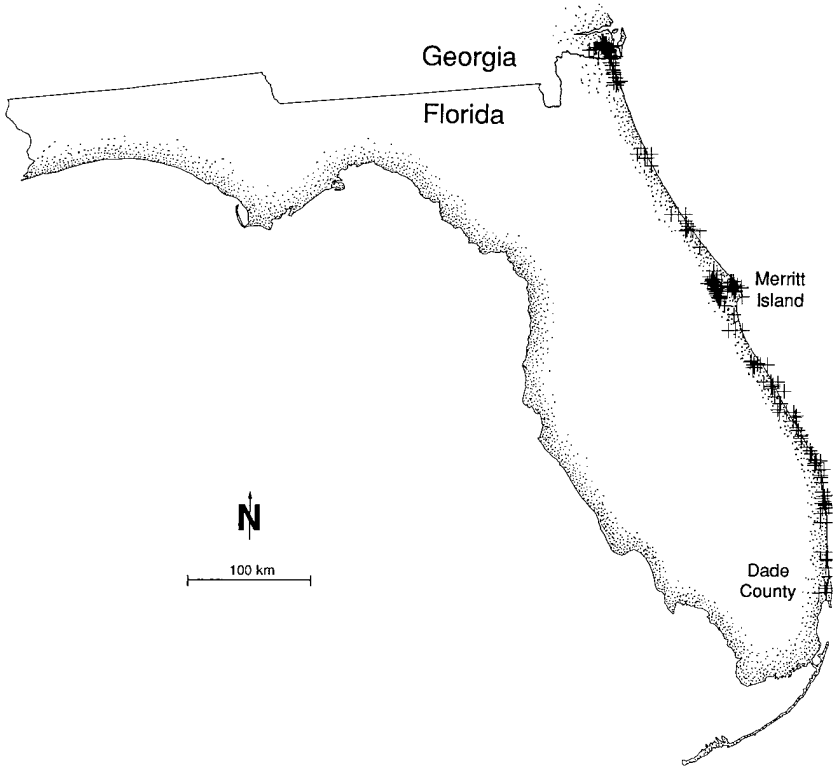


Fig. 6. Cumulative satellite-determined locations (n = 524) of an adult female Florida manatee (*Trichechus manatus latirostris*) between November 1987 and July 1988. Locations of this female (TNC-01) ranged from Port Everglades in southern Florida to Kings Bay, Georgia.

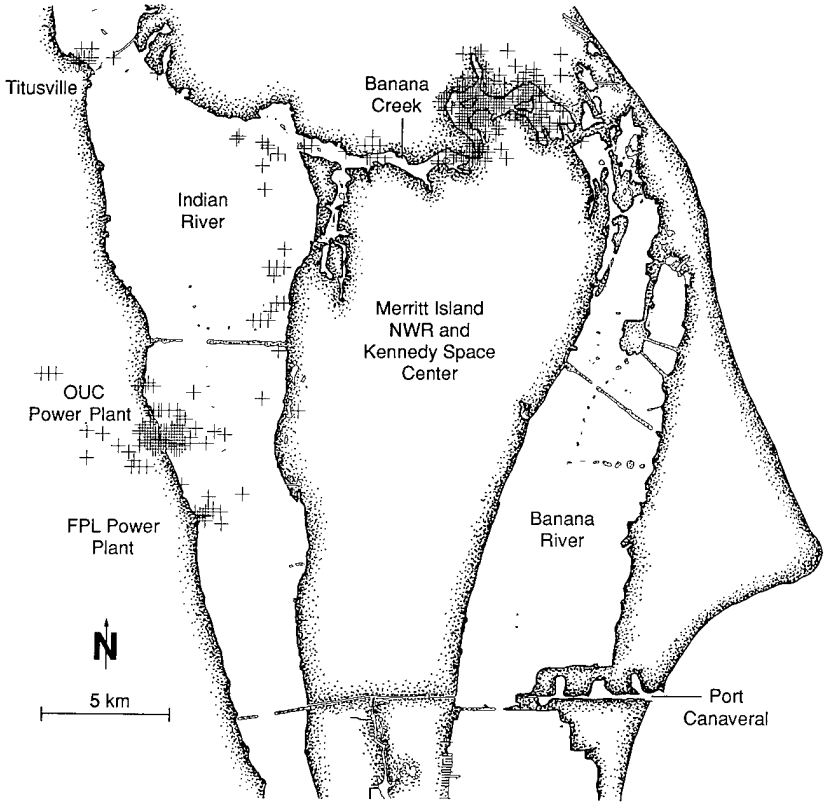


Fig. 7. Total number of plotted locations (n = 417) of a female Florida manatee (*Trichechus manatus latirostris*) in Brevard County, Florida, between January and August 1987. This individual (TBC-05) used the Indian River power plants during cold weather and the upper Banana Creek and Titusville areas during warm weather.

counts included consecutive bouts when transmitters on manatees were replaced without loss of contact. Because many manatees were tracked continuously during consecutive bouts, many tracking periods were longer than the tagging bouts.

Tagging-bout lengths ranged from less than 24 hours to 578 days and had high coefficients of variation. The mean bout length was 64 ± 69.1 days. The mean bout lengths of the VHF transmitters (65 ± 77.3 days) and PTTs (63 ± 56.1 days) were nearly equal. The maximum length of 139 deployments of VHF transmitters was 578 days (19.2 months), and the longest of 100 PTT deployments was 250 days (8.3 months), which was near the maximum battery life of PTTs.

The termination of tagging bouts was marked by the recovery or loss of the tether and transmitter, recovery or loss of the entire tag assembly, replacement with a new transmitter or belt and transmitter, loss of signal, or death of the tagged manatee (Table 2). Transmitter recovery caused by designed failure of the tether weak-link was the predominant reason of termination of tagging bouts (Table 2). Weak-link breaks were caused by transmitter-tether entanglement on dock pilings, out-drives of moored boats, or woody vegetation near shore. Weak-link breaks also occurred on four occasions when well-intentioned or curious people pulled the transmitter and tether free from the manatee. Once an alligator (*Alligator mississippiensis*) seized and pulled a transmitter off a manatee in Banana Creek and carried the housing over an earthen dike. Alligator teeth marks were found also on other transmitter housings, especially on those of tagged manatees that frequented the upper Banana River or Banana Creek in Brevard County. Predation on floating transmitters by alligators may have accounted for the loss of signals from several individuals in these areas. Tag detachment was caused primarily by circumstances beyond our control rather than failure of the tag design. Three of the tagging bouts were terminated by the deaths of the tagged manatees. These tag attachments did not contribute to the manatee's deaths.

We replaced transmitters 113 times. The maximum number of replacements on a single individual was 13. Damaged or malfunctioning transmitters were replaced to continue tracking. Replacements included substitution of new or refurbished VHF transmitters or PTTs of units that approached the end of battery life, had malfunctioned, or were floating low in the water because of heavy barnacle encrustation.

Intervals (Table 2) associated with belt loss or replacement reflected the cause of termination of an indi-

Table 2. Causes for termination of tracking bouts in telemetry studies of manatees (*Trichechus manatus latirostris*) on the Atlantic Coast of Florida, 1986–1991. Frequency of occurrence and mean and maximum tagging bout durations in days are given for each termination cause. Both PTT and VHF transmitters are included.

Cause of termination	Duration of bouts		
	n	Mean	Maximum
Recovered dead manatees wearing transmitter	3	72	90
Recovered transmitter	71	50	193
Weak-link broken, undetermined cause	56	49	193
Weak-link broken by human	4	33	77
Weak-link broken by alligator	1	65	65
Other breakage at transmitter housing or tether; eye bolt, tether	1	155	155
Other breakage at belt; swivel failed	3	88	183
Connector unscrewed/detached by human	3	6	10
Boat strike to transmitter housing	3	48	66
Recovered tag (belt broken)	7	91	183
Replaced transmitter	113	74	578
Low battery	11	146	250
Malfunctioning housing; missing antenna, leaked, barnacles	18	110	363
Electronics malfunction; battery failure, poor range	9	60	106
Boat strike	11	59	158
Replace with improved unit	20	19	98
Replace with PTT	44	72	578
Replaced tag (belt worn or swivel failed)	8	48	121
Lost transmitter	16	52	148
Missing at weak-link	15	48	148
Missing at weak-link; assume boat strike	1	110	110
Missing transmitter; manatee not resighted	8	59	119

vidual tagging bout (transmitter deployment) but usually did not reflect the overall life of the belt. Tags were recovered from seven manatees that broke free of the belt assembly after a mean belt life of 237 days (±222, range = 4–589) from initial tagging to recovery. We replaced eight belts because the belts were worn or the swivel failed. These were deployed on manatees an average of 793 ± 380 days (24 months) and a range of 273 to 1,547 days (9 to 50 months) without obvious detrimental effect on the tagged individuals.

The 55 manatees tagged since 1986 carried floating transmitters for a total of 15,318 days (42.5 years). This includes 9,019 days (24.7 years) with VHF transmitters and 6,299 days (17.3 years) with PTTs. Including the intervals between tagging bouts, which total 8,100 days (22.2 years), our efforts spanned 64.2 manatee-years. One individual was tracked for 1,219 days (3.37 years) of the 1,818 day (5-year) period since she was initially tagged. At the other extreme, one female was tagged once for 4 days before the tag assembly broke free at the belt.

Reproduction

Sizes of reproductive females. Twenty-eight of the 37 tagged female manatees were larger than 275 cm total length (TL) at the time of first tagging and were assumed to be sexually mature based on size (Marmontel 1995; O'Shea et al. 1985b). All females that had accompanying calves when tagged were longer than 275 cm except one. One female was 267 cm and was accompanied by a calf at tagging.

Several individuals that were shorter than 275 cm and believed to be immature when initially tagged were later pregnant or gave birth. One female was 270 cm TL at tagging and reproduced 2 years later. Another female was 273 cm TL and was monitored for 3.5 years but was not sighted with a calf. During November 1989, her abdomen was very distended, and we believed that she was in late pregnancy. After transmitter loss in December, she was not observed until 11 months later, when she was tagged again at which time she had no calf. If a birth occurred, the calf probably did not survive. She is not known to have reproduced through December 1991.

A 270-cm TL female (TBC-20) was tagged in April 1988 and pregnant in July 1990 and gave birth in August 1990 (Fig. 8). Based on photographs and field observations of her as a juvenile in May 1987, we believe this was her first calf. The carcass of this female was found in October 1990; the cause of death was not known. The fate of her accompanying calf was undetermined. The carcass of the female measured 308 cm TL, indicating growth in length since originally tagged. However, the difference in lengths could also be influenced by differences in measuring technique or postmortem change. This female was classified as between 7 and 8 years old at death based on postmortem counts of growth-layer groups in the periotic bone (Marmontel 1993).

Of all females that were longer than 275 cm TL at tagging, one (TNC-01) monitored for more than 17 months failed to reproduce. She was tagged in March 1987 at 330 cm TL and tracked continuously until August 1988. She was not accompanied by a calf during this period. She was retagged in December 1989 while a small calf accompanied her. Based on size, we assumed the calf was 6 months old at retagging. If birth occurred in June 1989, a period of 2.25 years or greater without reproduction was indicated. If gestation lasts about 12 months, the interval between births by this female was longer than 1 year, or she failed to reproduce.

Number of produced calves. Eighteen females produced a total of 22 calves. Each of two tagged manatees produced two calves, and one female had three calves. Twinning was not recorded. The sex of 16 young was determined. Ten were males and six were females. The number of tagged adult females observed with calves during the fall-winter seasons each year suggested that a pooled proportion of 0.348 (8/23) adult females nursed calves at this time of year (Table 3).

*Gestation and Parturition.*The estimated gestation duration was from a single female (TBC-09). From May to late July 1989, she was frequently observed with her calf feeding on the grassbeds and resting in the canals of the middle Banana River, her normal use area in summer. We believe she was pursued by a herd of males starting on or about 28 July 1989, when she traveled 13 km north to areas that she rarely visited. Based on Argos location and transmitter tip data, she exhibited high activity in the upper Banana River for 3 days before her radio-transmitter became detached. Although no observations were made during this period, movements outside of normal use areas can occur during mating (Bengtson 1981; Rathbun et al. 1990). She was observed 12 months later with a distended abdomen indicative of pregnancy. Her next calf was born between 15 and 18 September 1990. A maximum gestation period of 417 days (13.9 months) can be calculated from the initial pursuit of her by the males (28 July 1989) and latest possible birth date (17 September 1990). An alternative estimate of the gestation period could reduce this figure by 3 weeks (based on the duration of typical herds of consorting males) to 396 days (13.2 months), although the pursuit of her by the males could have persisted longer than 3 weeks or she could also have been pursued by another herd of males at a later time (as noted in other cases by Bengtson [1981]).

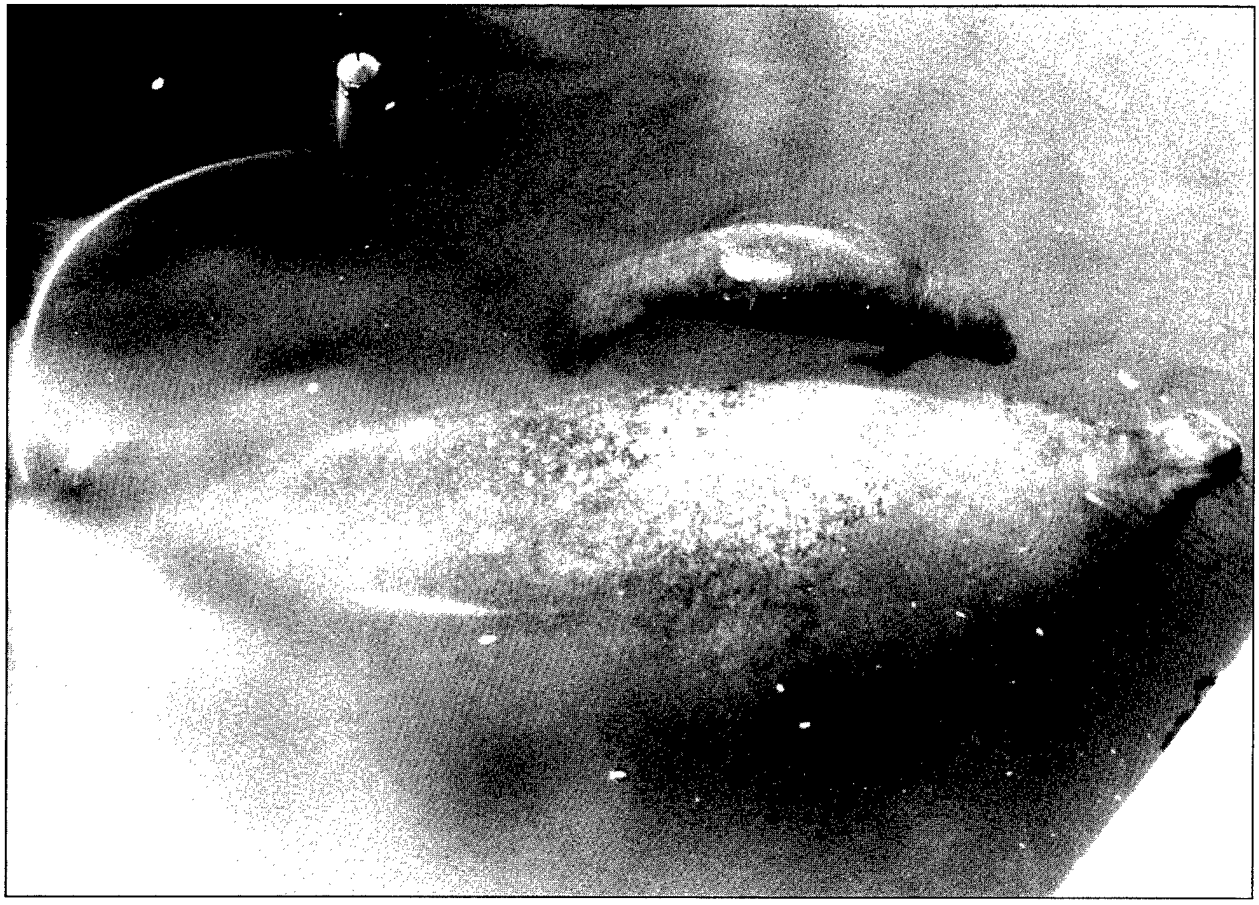


Fig. 8. Tagged female Florida manatee (*Trichechus manatus latirostris*) with newborn calf in Brevard County, Florida. The carcass of this adult female (TBC-20) was found in October 1990. She was between 7 and 8 years old when she died. The cause of death was not known. The calf probably did not survive on its own. *Photo by R. Bonde.*

Table 3. Number of tagged adult female Florida manatees (*Trichechus manatus latirostris*) with first-year and second-year calves in the fall-winter season each year, Atlantic Coast of Florida, 1986–1987 through 1991–1992.

Year	Total number of females	Females without calves	Females with first-year calf	Females with second-year calf	Total number of females with calves
1986–87	2	1	0	1	1
1987–88	3	3	0	0	0
1988–89	4	2	1	1	2
1989–90	4	3	0	1	1
1990–91	4	2	2	0	2
1991–92	6	4	2	0	2
Totals	23	15	5	3	8

Table 4. Details on births of calves to tagged manatees (*Trichechus manatus latirostris*) along the Atlantic Coast of Florida, 1986–1991.

Female-calf ID	Birth date	Birth location	Distance moved to birth location
TBC-09/C[1]	12 Aug 1987	Canal, Banana River, Brevard County	<5 km
TBC-09/C[2]	15–18 Sep 1990	Canal, Vero Beach	98 km
TBC-03/C[2]	30 Jun 1988	Boat basin, Daytona Beach	110 km
TBC-24/C[1]	May/Jun 1990	Canal or adjacent Banana River, Brevard County	<2 km
TBC-20/C[1]	6 Aug 1990	Canal, Sykes Creek, Brevard County	<7 km

Birth dates and approximate locations of births of five calves of four tagged females were determined (Table 4). All calves were born between May and September. Four were born in quiet canals or boat basins. The birth place of the fifth calf was not pinpointed but was either in a quiet residential canal system or in the nearby seagrass beds of the Banana River. Pregnant females moved relatively short distances (<10 km) to birth locations prior to three of these births (Table 4). Birth sites of these three were in or close to the mother's normal use area. Two notable exceptions to this pattern occurred. One female (TBC-03), radio-tracked for most of the previous 1.5 years, had primarily ranged in the canals and grass beds of the Banana River near Cocoa Beach in Brevard County. In June 1988 she traveled into the Indian River and north farther than 140 km to Flagler Beach, our first documentation of any movements by this individual north of Brevard County. On 29 June, she was located in the Daytona Beach Municipal Marina's newly constructed boat basin, 110 km north of Cocoa Beach. On 30 June, she gave birth to a female calf. She remained with the calf in the basin for the next 7 days before traveling 24 km north to the Tomoka River. After at least 8 days there, she swam south with her offspring, arriving in Brevard County on 19 July where she returned to her normal use areas in the Banana River.

A second female (TBC-09) who also made a long-distance move to a birth location traveled less than 5 km for the first of her two recorded parturitions. She traveled more than 100 km south of her summer use area for her second parturition. She regularly made seasonal migrations in fall from Brevard County to an aggregation site at Port Everglades. In four different years, she did not begin this move prior to early November and rarely made lengthy stopovers before arriving at Port Everglades. In 1990, however, she began a similar directed movement on 12 September but stopped in a residential canal near the Vero Beach power plant on 15 September. She was seen with the newborn on 18 September in this canal, where we suspected she gave birth between 15 and 18 September. She remained in this canal or its vicinity until 28 September when she resumed her migration south. Five days later she had traveled past West Palm Beach, when her transmitter was hit by a boat. On 5 October, she was sighted with her calf at a warm-water refuge in Fort Lauderdale. She seemed to have initiated her move south early because of her late-term pregnancy.

Dependence and weaning of calves and intervals between births. Periods of dependence of the calves on their mothers were difficult to determine because of the inopportune tag loss prior to birth or weaning. For example, only 8 of 19 females gave birth or weaned young during tracking periods. Despite these limitations, the estimated minimum dependence included five that were longer than 14 months (Table 5). One of these calves continued to accompany the tagged mother (TBC-09) beyond December 1991 after a dependence of 15.5 months. Another complete period of dependence was approximately 24 months (734 days ± 12 days) of a calf of the same female born on or about 12 August 1987 (Fig. 9) and weaned

Table 5. Period of tracking female manatees (*Trichechus manatus latirostris*) with calves (in months) for which dates of births or weaning were known. Cases with incomplete information on births or weaning and manatees that were observed for 8 months or fewer are not included. Time periods are all discontinuous except for TBC-09/C[1].

Birth (B) or weaning (W) known	Birth and weaning known
TBC-03/C[1]F = 18.5 B	TBC-09/C[1]M = 24.0
TNC-01/C[1]F = 15.5 W	
TBC-09/C[2]F = >15.5	
TPE-04/C[1]M = 14.5 W	

[1,2] Sequential calves produced by tagged females.
>Dependence continued past 31 December 1991.

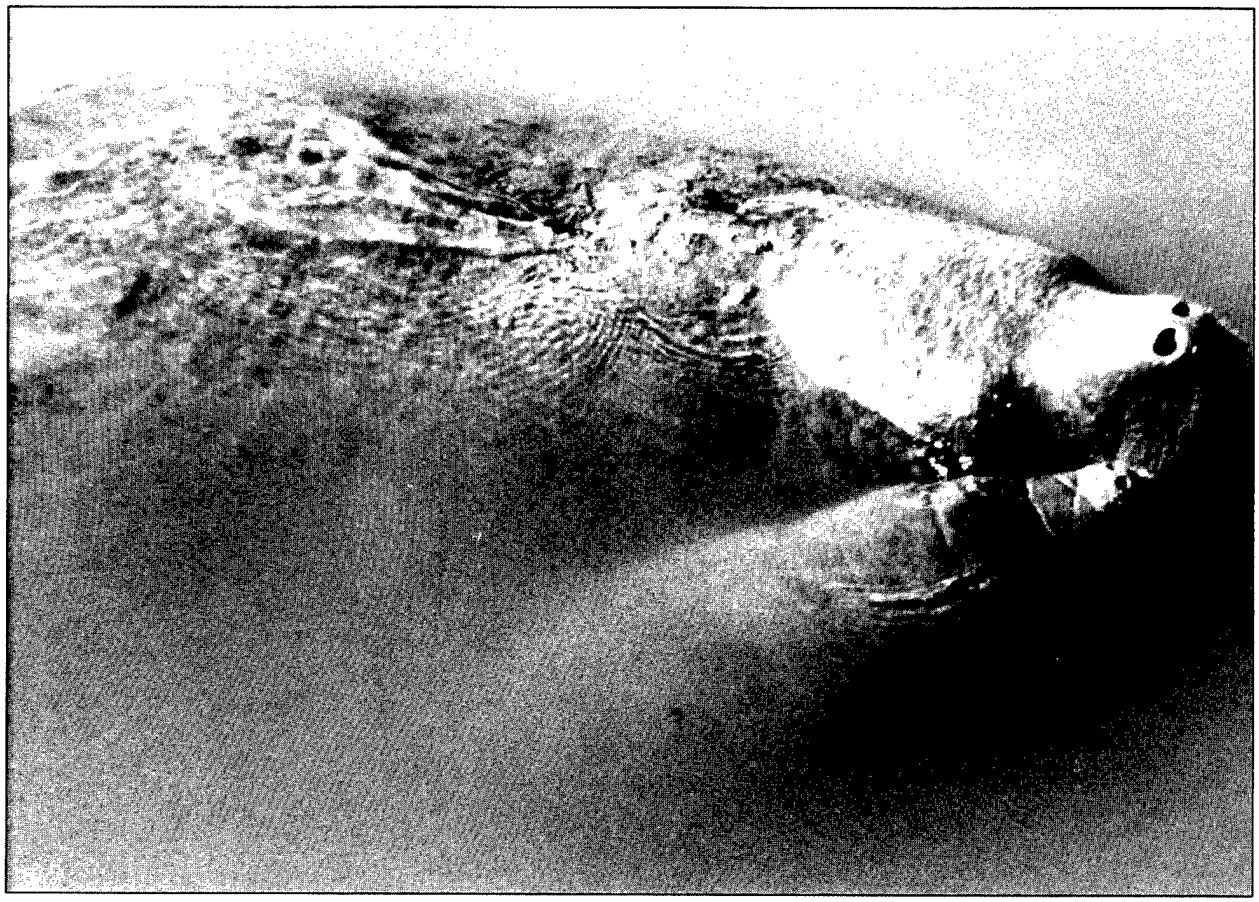


Fig. 9. Female Florida manatee (*Trichechus manatus latirostris*) with a 3-week-old male calf, Banana River, Brevard County, Florida, 1 September 1987. The female (TBC-09) weaned this calf in August 1989 after a period of dependency of 24 months. *Photo by R. Bonde.*

between 3 and 27 August 1989. During this latter period we believe the female was pursued by a herd of males. The tagged female and the tagged calf broke free of their transmitters, presumably as a result of jostling with males during mating, and we were unable to confirm the precise date of separation. The calf, however, was sighted alone on 27 August 1989.

Aspects of weaning were determined from seven calves. Five were weaned during July or August, one in March, and one between mid-November and mid-January. One accompanied his mother when she was first pursued by a herd of consorting males; no other cases of weaning were known to coincide with mating. One calf was weaned during the 200-km migration of her mother in late March 1991. We do not know the movements of the calf. Another female (TGA-01) was with her calf on 17 November 1989 at the Indian River power plants in Brevard County. She traveled south to the Sebastian River during late December. When she was seen near Melbourne on 20 January 1990, soon after her departure from the Sebastian River, she no longer was accompanied by her calf. This is the only case of weaning we observed during cold winter weather. Her calf was large, and we therefore assumed it was weaned at this time. However, the calf may have died during the extremely cold weather of late December 1989, when many manatees in this size and age class succumbed to stress from cold (Ackerman et al. 1995; Marmontel 1993).

The most detailed recorded weaning was of a female (TPE-04) and her radio-tagged male calf. They were in the Banana and Indian rivers for 7.5 months in fall 1990 and winter and spring 1991. During this time, they were always within a few m of one another and were in frequent physical contact. On 8 May 1991, the calf was seen with other manatees in a boat basin while his mother was simultaneously located approximately 1 km outside the basin, presumably feeding in seagrass beds. The female and the calf were seen together again on the next

Table 6. Tagged manatees (*Trichechus manatus latirostris*) recovered by the manatee carcass salvage program on the Atlantic Coast of Florida, 1986–1991. Ancillary information on these individuals is in Table 1.

ID	Sex	Tagging date	Tagging location	Date reported	Recovery location	Carcass number	Cause of death
TBC-08[1]	F	23 Apr 1987	Brevard County	4 Sep 1987	St. Johns River, Jacksonville	KDL-87-44	Undetermined
TBC-18[1]	M	30 Mar 1988	Brevard County	21 Dec 1989	Indian River, Brevard Co.[a]	UCF-89-05	Undetermined
TNC-08[1]	M	16 Mar 1989	Nassau County	2 Feb 1990	Fernandina Beach, Nassau Co.	MJAV-90-17	Undetermined
TGA-01[2]	F	26 Jul 1989	Georgia	7 May 1990	Kings Bay, Georgia	MJAV-90-26	Boat collision
TBC-20[2]	F	21 Apr 1988	Brevard County	21 Oct 1990	Port Canaveral, Brevard Co.	UCF-90-59	Undetermined
TBC-33[2]	M	6 Jun 1991	Brevard County	17 Aug 1991	Banana River, Brevard Co.	UCF-91-31	Human related-other

[1] Recovered wearing only the belt.
[2] Recovered wearing the belt and the tethered transmitter.
[a] Carcass identity verified but not recovered.

day and on several subsequent tracking dates, including 7 June. By 12 June, they had separated again. Although they were occasionally tracked to the same sites, they never again displayed close association or contact. On 20 June, 13 days after the young was last located with his mother, he was seen attempting to nurse from a different radio-tagged lactating female. His attempts were unsuccessful.

The known birth dates of the two sequential calves of one female (TBC-09) also provided the most precise estimate of an interval between births during radio-tracking. This interval was slightly longer than 37 months. A second female (TBC-03) provided a less precise estimate for an interval between births; 32.0–34.5 months elapsed between two births.

Mortality

Six tagged manatees died during the 6-year tagging period (Table 6). Two of the deaths were due to anthropogenic causes, and the causes of death of the remaining four were not determined. Three of the recovered carcasses were wearing the complete belt and transmitter assembly, and three wore only peduncle belts. None of the previously tagged manatees that had broken free of belts (or had belts removed) was verified as dead based on scar pattern identification. However, some tagged manatees have only minor scarring or are relatively indistinct, making verification of carcass identity difficult if recovered without tags or belts. The percentage of tracked or belted manatees whose carcasses were recovered was 0.0–10.7/year. A crude estimate of overall mortality can be expressed as six deaths in approximately 126 tagged manatee-years or 4.7% (Table 7).

We did not observe the death of any of the 22 calves associated with tagged females. Many calves remained alive for relatively long periods while their mothers were tracked (Table 8). The carcasses of two females, who were probably nursing calves at the time of death, were found. The fates of these calves were not determined. However, one of the young was only 76 days old when her mother died, and she probably did not survive on her own. A female who was accompanied by a large calf was tracked for almost 2 months until she broke free of her transmitter. Her carcass was recovered more than 80 days later and the cause of her death was not determined.

Reproduction Histories Based on Photo-identification

We made 641 sightings of females during the fall–winter seasons (Table 9). The average number of years each female was sighted was 4.1 (range = 1–12 years). Of all females (n = 185), 155 (84%) produced at least one calf, but this proportion may be biased because non-reproductive females whose sex was not identified during sightings because of the absence of calves were not included in the analyses and because the proportion was not corrected for the numbers of years. A total of 271 calves was produced. The sex of 17 calves was determined: 11 females and six males.

Based on photo-identification records of females in the censored data set, 29 calves were dependent for 1

Table 7. Number of tracked and tagged Florida manatees (*Trichechus manatus latirostris*) by years, Atlantic Coast of Florida, 1986–1991. Some individuals were tracked in consecutive years.

Category	1986	1987	1988	1989	1990	1991
Number of tracked manatees (with belt and transmitter)	5	18	20	20	24	24
Known number of manatees with only belts (no transmitter)	0	1	2	7	4[a]	1
Total with belt and transmitter or belt only	5	19	22	27	28	25
Number of missing manatees (possibly with belt)	0	0	2	6	12	17
Total (including missing manatees)	5	19	24	33	40	42
Recovered tagged manatee carcasses		1		1	3	1

[a] Includes one manatee that was not tracked during the year and whose carcass with belt was recovered.

Table 8. Lengths of observations of calves associated with tagged manatee (*Trichechus manatus latirostris*) females. No calves accompanying females died during this study. Short lengths of observation periods indicated termination of the study period or loss of ability to track the female. *Blanks* indicate no data are available.

Calf ID	Sex	Date of birth or first sighting	Date of last sighting of female with calf	Date of first sighting of female without calf	Total number of days the calf was known to be alive
TBC-01/C[1]		24 Jan 1987 (S)	29 Jun 1988		524
TBC-02/C[1]	M	19 Feb 1988 (S)	19 Feb 1988		1
TBC-03/C[1]	F	30 Sep 1986 (S)	5 Jul 1987	18 Aug 1987	279
TBC-03/C[2]	F	30 Jun 1988 (B)	15 Jan 1990	30 May 1990	564
TBC-03/C[3]	M	25 May 1991 (S)	31 Dec 1991		220[a]
TBC-05/C[1]	M	13 Nov 1986 (S)	14 Jul 1987	15 Jul 1987	245
TBC-08/C[1]		23 Apr 1987 (S)	15 Jun 1987	[b]	53
TBC-09/C[1]	M	12 Aug 1987 (B)	1 Aug 1989	27 Aug 1989	720
TBC-09/C[2]	F	15 Sep 1990 (B)	31 Dec 1991		472[a]
TBC-15/C[1]	M	13 Sep 1989 (S)	14 Jun 1990		275
TBC-20/C[1]	M	6 Aug 1990 (B)	21 Oct 1990[c]		76
TBC-24/C[1]	F	1 Jun 1990 (B)	31 Dec 1991		578[a]
TBC-32/C[1]		30 Dec 1991 (S)	31 Dec 1991		2[a]
TGA-01/C[1]	F	26 Jun 1989 (S)	17 Nov 1989	20 Jan 1990	144
TNC-01/C[1]	F	18 Dec 1989 (S)	3 Apr 1991	4 Apr 1991	472
TNC-03/C[1]	M	25 Feb 1988 (S)	12 May 1988		77
TNC-04/C[1]	F	25 Feb 1988 (S)	21 Apr 1988		56
TNC-05/C[1]	M	18 Jan 1989 (S)	31 May 1989		134
TPE-01/C[1]	M	27 Jan 1989 (S)	26 Mar 1989	19 Dec 1989	59
TPE-01/C[2]	M	24 Oct 1990 (S)	29 Apr 1991		188
TPE-03/C[1]		17 Jan 1991 (S)	5 Jun 1991	2 Jul 1991	140
TPE-04/C[1]	M	16 Mar 1990 (S)	5 Jun 1991	13 Jun 1991	447

(S) = First sighted with calf, date of birth unknown.
(B) = approximate birth date.
[a] Calf observed alive with mother at termination of study, 31 Dec 1991.
[b] Mother reported dead 4 September 1987, fate of large calf unknown.
[c] Mother reported dead 21 October 1990, fate of 76-day-old calf unknown.

Table 9. Number of identifiable adult female Florida manatees (*Trichechus manatus latirostris*) observed in the fall-winter season of each year and number of accompanying first- or second-year calves, Atlantic Coast of Florida, 1978–1979 through 1991–1992. Information excludes females tracked by telemetry (Table 3).

Year	Total females	Females without calves	Females with first-year calf	Females with second-year calf	Total females with calves	Proportion females with calves
1978–79	3	0	3	0	3	1.000
1979–80	4	2	2	0	2	0.500
1980–81	8	6	2	0	2	0.250
1981–82	20	4	16	0	16	0.800
1982–83	26	14	12	0	12	0.462
1983–84	17	12	5	0	5	0.294
1984–85	73	37	36	0	36	0.493
1985–86	66	35	25	6	31	0.470
1986–87	61	33	22	6	28	0.459
1987–88	75	45	28	2	30	0.400
1988–89	45	30	14	1	15	0.333
1989–90	66	48	18	0	18	0.273
1990–91	94	51	42	1	43	0.457
1991–92	83	53	24	6	30	0.361
Totals	641	370	249	22	271	0.423

year and eight calves were dependent for 2 years. Although records from only 3 consecutive years could introduce a bias of 1-year dependent calves, records were kept for 4 or more consecutive years of 21 of the 29 1-year-dependent calves. However, an additional 17 calves were dependent for at least two fall-winter seasons but were excluded from the data summary because they were not bracketed by sightings of the mother without a calf, suggesting that 2-year dependencies are more frequent than the censored data set reveals.

The censored data set included 10 females with consecutive annual records that included observations of successively born calves. This enabled us to determine 11 intervals between births. The average time between the first sighting of a female with a calf and the first sighting of the same female with a subsequent calf was 10.5 seasons (SD = 2.54) or 2.6 years. These intervals ranged from 8 to 16 seasons (2–4 years).

The proportion of adult females with calves each year was variable (Table 9); the pooled proportion was 0.423 during the entire period. The mean proportion of females with calves each year during winter 1981–82 through 1990–91 was not significantly different from similar data from manatees in the Crystal River study area ($P = 0.517$) reported by Rathbun et al. (1995; Table 1). The pooled proportion of females with calves in the photo-identification sample (0.387) during 1986–87 through 1991–92 (Table 9) was not significantly different from that derived from the smaller sample of radio-tagged females with calves (0.348) during the same period (Table 3).

Discussion

Studies of radio-tagged manatees are used primarily for determining migration and movement patterns and for identifying locations of high-use areas for habitat protection (*U.S. Fish and Wildlife Service 1989; O'Shea and Kochman 1990; Reynolds and Haddad 1990). The secondary use of radio-tagging to study aspects of reproduction and mortality in Florida manatees has advantages and disadvantages. The major advantage is that it allows direct, repeated observations of individuals on a year-round basis. The major disadvantage is that tag loss results in frequent and unpredictable interruptions in the continuity of these observations. These interruptions complicate the estimations of gestation duration, early calf mortality, length of calf dependency, timing of weaning, and lengths of intervals between births because most of these aspects of manatee life history are longer than the durations of uninterrupted tagging bouts. We do not foresee major advances in tagging apparatus that will correct this problem. Many causes of tag loss are beyond the control of researchers. The designed weak links and corrodible connectors that contribute to tag loss are necessary for the safety of the tagged manatees. Although no tags were recovered as a result of the designed corrosion of connectors at the belt,

some of the eight individuals whose signals were lost and were not resighted may have lost their tags for this reason.

The inherent drawbacks of studying manatees by radio-tagging resulted in only a small number of estimates of certain life-history traits. However, despite the small number of samples, some estimates based on tracking females on the Atlantic Coast are probably some of the most accurate reported of wild manatees and complement those obtained from long-term observations of scarred individuals in aggregations in winter (O'Shea and Hartley 1995; Rathbun et al. 1995), examinations of carcasses (Marmontel 1995), and records from captive husbandry (Odell et al. 1995).

The most comparable study of reproduction with telemetry is that of Bengtson (1981), who tracked manatees in a 2-year study in the freshwater habitats of the upper St. Johns River near Blue Spring. Three tagged females gave birth during that study in quiet waters away from the main channel of the river. The females gave birth in April, May, and August. Two females spent a relatively large percentage of their time moving prior to parturition, presumably attempting to locate suitable sites for giving birth (Bengtson 1981). These observations are similar to those on the Atlantic Coast where we observed five births. Each birth on the Atlantic Coast was in a warm month (May to September) and, if known, took place in quiet canals, basins, or adjacent waters away from the main channels. Two of the five births were preceded by major long-distance moves of about 100 km by the mothers. Bengtson (1981) did not report long distance moves by tagged females outside their normal summering areas but found instead that females in the upper St. Johns River spent a greater amount of time traveling prior to giving birth. The manatees in both study areas seemed to favor locations away from disturbance, such as heavy and fast boat traffic, and possibly away from male manatees in search of estrous females (O'Shea and Hartley 1995). Other aspects of the adaptive significance of the long prepartum moves, however, are not clear. Other seemingly suitable sites were closer to the normal ranges of the females on the Atlantic Coast, and the choice of widely separated locations by the same female in two consecutive births suggested that individuals do not repeatedly use specific locations.

No other researchers who used telemetry accurately measured the birth-to-weaning intervals or gestation periods in manatees. We determined a period of dependency of 24.0 months by one calf and one probable gestation period of 13.2–13.9 months (396–417 days). Births of two calves to one female were separated by an interval of slightly more than 37 months and to another female by 32.0–34.5 months. Weaning of seven calves was also recorded. Five of them were weaned in July and August, one in late March during northward migration, and presumably only one in December or January. These observations suggested that most females probably do not wean offspring in winter. An absence of weaning in winter has also been noted in manatees at Blue Spring (O'Shea and Hartley 1995). A greater susceptibility of subadult animals to cold-related mortality has been well documented (O'Shea et al. 1985b; Marmontel 1993; Ackerman et al. 1995) and may provide an explanation for the tendency toward weaning in seasons other than winter. Only one young was weaned while its mother was pursued by a herd of males. Bengtson (1981) noted that one of two females pursued by such herds in the St. Johns River was accompanied by a nursing calf, and Rathbun et al. (1995) reported six cases of large dependent calves that accompanied females in herds of pursuing males.

Rathbun et al. (1995) noted that lengths of time between the pursuits of females by herds of males and the first subsequent sightings of those females with young calves ranged from less than 9 to more than 15 months. Most of these rough estimates for gestation were from 13 to 15 months. These estimates based on sightings without telemetry are wide because dates of births were not recorded and females in these herds are not always impregnated (Hartman 1979; Bengtson 1981). Seasonal timing of births reported in other studies also indicated that most females give birth in warm months and few in winter (Marmontel 1995; O'Shea and Hartley 1995; Rathbun et al. 1995). Our observations of intervals between births of 37 and 32.0–34.5 months in two radio-tagged females are also within the range estimated with data from photo-identification studies on the Atlantic Coast. The latter are not significantly different from those obtained by long-term, photo-identification studies at Blue Spring and on the Crystal River (O'Shea and Hartley 1995; Rathbun et al. 1995). The small number of telemetry-based estimates of intervals between births in manatees on the Atlantic Coast are also comparable to indirect estimates based on examination of reproductive tracts of carcasses collected statewide (Marmontel 1995).

The number of each sex of calves, based on the combined samples from studies with telemetry and from photo-identification on the Atlantic Coast, was nearly even (13:12). Approximately equal sex ratios of calves were also reported in statewide samples of salvaged carcasses (O'Shea et al. 1985b; Marmontel 1993; Ackerman et al. 1995) and long-term observations at the Crystal River (Rathbun et al. 1995) and at Blue Spring (O'Shea and Hartley 1995). The proportion of females with calves in each winter in photo-identification studies

on the Atlantic Coast was also similar to proportions in the Crystal River and at Blue Spring. These similarities suggested that manatees on the Atlantic Coast are maintaining the same levels of reproduction as manatees in other regions.

Tag losses complicated calculations and interpretation of observed mortality of manatees on the Atlantic Coast. However, two of the six (33%) deaths of tagged or belted manatees were due to anthropogenic causes, and the carcasses were recovered in northeastern Florida or in Georgia. This proportion is similar to the 36.8% of non-perinatal deaths attributed to anthropogenic causes in northeastern Florida (Ackerman et al. 1995). We also report a crude estimate of mortality of six deaths in approximately 126 manatee-years (4.7%). However, this estimate has no confidence intervals and is probably less accurate than estimates made with other methods. O'Shea and Langtimm (1995) calculated survival based on the adults monitored during our study and rates based on resightings of distinctively scarred individuals and suggested that calculations of survival based on photo-identification records may provide a more accurate estimate of mortality in this population. Estimated survival from radio-tagged manatees otherwise requires tremendous sampling effort to obtain narrow confidence intervals. The use of data from radio-tagged manatees for calculating these estimates is also difficult because of the tag loss and retagging processes that are peculiar to studies of manatees with telemetry. (Calculation of survival rates from tagging data of most species requires the assumption that tags remain on individuals throughout study [Heisey and Fuller 1985; Pollock et al. 1989; Siniff and Ralls 1991.]) However, the use of radio-tracking can provide more detailed information that can be of significant value to manatee research and conservation. For example, the death from a boat collision during our study (Table 6) was associated with a specialized tug boat operation at the Kings Bay Naval Submarine Base in Georgia. Structural modifications were subsequently made to the propeller systems of these vessels to prevent the killing of manatees; a manatee-safety program was also implemented at the base (*Turner and Buckingham 1993).

Our research with telemetry also revealed that the survival of young calves may be reasonably high, but we are unable to provide firm estimates. Data from other studies suggested that survival of manatee calves may be as high as 0.60 to 0.82 during the first 18 months (Eberhardt and O'Shea 1995; O'Shea and Hartley 1995). Our general observations provided support for this suggestion, but as pointed out by Eberhardt and O'Shea (1995), additional, more detailed observations on calf survival on the Atlantic Coast are highly desirable for a better understanding of manatee population dynamics in this region.

The Atlantic Coast of Florida provides habitat for approximately half of the manatee population in the United States (Ackerman 1995). However, more than twice the number of anthropogenic deaths of manatees occurs in eastern Florida than on the Gulf Coast (O'Shea et al. 1985b; Ackerman et al. 1995). Our data suggested that reproduction traits of manatees on this coast are similar to those of manatees studied elsewhere. Survival of adults, however, may be lower on this coast than in the Crystal River or at Blue Spring (O'Shea and Langtimm 1995), and population modeling suggested that the potential population growth rate is also lower on the Atlantic Coast (Eberhardt and O'Shea 1995). The primary purpose of radio-tracking manatees has been the determination of locations that allow the creation of sanctuaries and boat-speed-regulation zones as a means to reduce mortality. This information and management actions are valuable and should continue. Radio-tagging will also continue to provide more detailed information about specific aspects of manatee reproduction and mortality. However, the larger sample sizes and long histories from photo-identification-based studies provide a solid basis for future long-term monitoring of manatee populations in eastern Florida. These studies should be maintained and enhanced over the long term, beyond the cessation of telemetry research when habitat protection goals have been achieved.

Acknowledgments

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Cited References[3]

Ackerman, B. B. 1995. Aerial surveys of manatees: a summary and progress report. Pages 13–33 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Ackerman, B. B., S. D. Wright, R. K. Bonde, D. K. Odell, and D. J. Banowetz. 1995. Trends and patterns in mortality of manatees in Florida, 1974–1992. Pages 223–258 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Beck, C. A., and J. P. Reid. 1995. An automated photo-identification catalog for studies of the life history of the Florida manatee. Pages 120–134 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Bengtson, J. L. 1981. Ecology of manatees (*Trichechus manatus*) in the St. Johns River, Florida. Ph.D. thesis, University of Minnesota, Minneapolis. 126 pp.

Bullock, T. H., T. J. O'Shea, and M. C. McClune. 1982. Auditory evoked potentials in the West Indian manatee (Sirenia: *Trichechus manatus*). Journal of Comparative Physiology 148:547–554.

Eberhardt, L. L., and T. J. O'Shea. 1995. Integration of manatee life-history data and population modeling. Pages 269–279 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Fancy, S. G., L. F. Pank, D. C. Douglas, C. H. Curby, G. W. Garner, S. C. Amstrup, and W. L. Regelin. 1988. Satellite telemetry: a new tool for wildlife research and management. U.S. Fish and Wildlife Service Resource Publication 172. 54 pp.

Hammond, P. S., S. A. Mizroch, and G. P. Donovan, editors. 1990. Individual recognition of cetaceans: use of photoidentification techniques to estimate population parameters. Report of the International Whaling Commission, Special Issue 12. International Whaling Commission, Cambridge, England. 440 pp.

Harris, R. B., S. G. Fancy, D. C. Douglas, G. W. Garner, S. C. Amstrup, T. R. McCabe, and L. F. Pank. 1990. Tracking wildlife by satellite: current systems and performance. U.S. Fish and Wildlife Service Fish and Wildlife Technical Report 30. 52 pp.

Hartman, D. S. 1979. Ecology and behavior of the manatee (*Trichechus manatus*) in Florida. American Society of Mammalogists, Special Publication 5. Lawrence, Kans. 153 pp.

Heisey, D. M., and T. K. Fuller. 1985. Evaluation of survival and cause specific mortality rates using telemetry data. Journal of Wildlife Management 49:668–674.

Marmontel, M. 1993. Age determination and population biology of the Florida manatee, *Trichechus manatus latirostris*. Ph.D. dissertation, University of Florida, Gainesville. 408 pp.

Marmontel, M. 1995. Age and reproduction in female Florida manatees. Pages 98–119 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

*Mate, B., G. B. Rathbun, and J. P. Reid. 1986. An ARGOS-monitored radio-tag for tracking manatees. Argos Newsletter 26:3–7.

*Mate, B., J. P. Reid, and M. Winsor. 1987. Long-term tracking of manatees through the Argos satellite system. Pages 211–220 *in* Proceedings of the 1987 North American Argos Users Conference. Service Argos, Inc., Landover, Md. 300 pp.

Moore, J. C. 1956. Observations of manatees in aggregations. American Museum of Natural History Novitiates 1,811:1–24.

Odell, D. K., G. D. Bossart, M. T. Lowe, and T. D. Hopkins. 1995. Reproduction of the West Indian manatee in captivity. Pages 192–193 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

O'Shea, T. J., and H. I. Kochman. 1990. Florida manatees: distribution, geographically referenced data sets, and ecological and behavioral aspects of habitat use. Pages 11–22 *in* J. E. Reynolds, III, and K. D. Haddad, editors. Report of the workshop on geographic information systems as an aid to managing habitat for West Indian manatees in Florida and Georgia. Florida Marine Research Publications 49:1–57.

O'Shea, T. J., and W. C. Hartley. 1995. Reproduction and early-age survival of manatees at Blue Spring, upper St. Johns River, Florida. Pages 157–170 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

O'Shea, T. J., and C. A. Langtimm. 1995. Estimation of survival of adult Florida manatees in the Crystal River, at Blue Spring, and on the Atlantic Coast. Pages 194–222 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

O'Shea, T. J., G. B. Rathbun, E. D. Asper, and S. W. Searles. 1985a. Tolerance of West Indian manatees to capture and handling. Biological Conservation 33:335–349.

O'Shea, T. J., C. A. Beck, R. K. Bonde, H. I. Kochman, and D. K. Odell. 1985b. An analysis of manatee mortality patterns in Florida, 1976–1981. Journal of Wildlife Management 49:1–11.

*Packard, J. M. 1981. Abundance, distribution, and feeding habits of manatees (*Trichechus manatus*) wintering between St. Lucie and Palm Beach Inlets, Florida. U.S. Fish and Wildlife Service Contract Report 14-16-004-80-105. 142 pp.

[3] An asterisk denotes unpublished material.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53:7–15.

Rathbun, G. B., J. P. Reid, and G. Carowan. 1990. Distribution and movement patterns of manatees (*Trichechus manatus*) in northwestern peninsular Florida. Florida Marine Research Publications 48:1–33.

*Rathbun, G. B., J. P. Reid, and J. B. Bourassa. 1987a. Design and construction of a tethered, floating radio-tag assembly for manatees. National Technical Information Service, Springfield, Va. Document PB 87-161345/AS. 49 pp.

*Rathbun, G. B., J. P. Reid, and Tas'an. 1987b. Design and construction of a tethered, floating radio-tag assembly for dugongs. National Technical Information Service, Springfield, Va. Document PB 87-161352/AS. 36 pp.

Rathbun, G. B., J. P. Reid, R. K. Bonde, and J. A. Powell. 1995. Reproduction in free-ranging Florida manatees. Pages 135–156 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida Manatee. National Biological Service Information and Technology Report 1.

*Reid, J. P., and T. J. O'Shea. 1989. Three years operational use of satellite telemetry on Florida manatees: tag improvements based on challenges from the field. Pages 217–232 *in* Proceedings of the 1989 North American Argos Users Conference. Service Argos, Inc., Landover, Md. 361 pp.

Reid, J. P., G. B. Rathbun, and J. R. Wilcox. 1991. Distribution patterns of individually identifiable West Indian manatees (*Trichechus manatus*) in Florida. Marine Mammal Science 7:180–190.

Reynolds, J. E., III, and K. D. Haddad, editors. 1990. Report of the workshop on geographic information systems as an aid to managing habitat for West Indian manatees in Florida and Georgia. Florida Marine Research Publications 49:1–57.

Shane, S. H. 1983. Abundance, distribution, and movements of manatees (*Trichechus manatus*) in Brevard County, Florida. Bulletin of Marine Science 33:1–9.

Shane, S. 1984. Manatee use of power plant effluents in Brevard County, Florida. Florida Scientist 47:180–187.

Siniff, D. B., and K. Ralls. 1991. Reproduction, survival and tag loss in California sea otters. Marine Mammal Science 7:211–229.

*Turner, R., and C. Buckingham. 1993. Navy is enlisted in plan to protect manatees. Endangered Species Technical Bulletin 18:1–11.

*U.S. Fish and Wildlife Service. 1989. Florida manatee (*Trichechus manatus latirostris*) recovery plan. U.S. Fish and Wildlife Service, Atlanta, Ga. 98 pp.

Reproduction of the West Indian Manatee in Captivity

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Abstract. Manatees (*Trichechus manatus*) have been held in captivity in the United States intermittently since the first quarter of the twentieth century and continuously since the birth of Snooty at the Miami Aquarium in 1984. The Miami Seaquarium has maintained a breeding pair since they were captured as juveniles in the late 1950's. Since that time (through February 1991), 28 Florida manatees (*T. m. latirostris*) were conceived and born in captivity. Captive Antillean manatees (*T. m. manatus*) have bred in Europe, China, and Japan.

The maintenance of breeding manatees in marine zoological parks and aquaria has provided unique opportunities to observe and quantify aspects of manatee biology that are difficult or impossible to observe in the field. Behavior of estrous females, mating, gestation, parturition, nursing, and calf growth and development can be observed in detail. In spite of many births in captivity, circumstances until recently have been less than ideal for data collection. This is because holding facilities are primarily designed for the rescue and rehabilitation of sick and injured manatees and not for the study of the biology of reproduction.

We gathered a large database on reproduction of manatees in captivity. Of 28 calves, 3 were stillborn and 2 were twins. Thirteen (including the stillbirths and twins) died. Thirteen were still alive in captivity in February 1992, and two were released in the wild but are presumed dead. One manatee at the Miami Seaquarium has had six calves, the first of which herself produced 3 calves. The youngest known-age female to reproduce was a rehabilitated orphan that conceived when she was about 5.5 years old. Despite these births, the duration of gestation has not been determined, and the best estimates are still in the 12–14 month range. Observations of mating behavior to predict reproductive status (pregnant

vs. non-pregnant) strongly suggest that pregnant females mate throughout pregnancy. Therefore, a female's reproductive status may not be predictable from field observations of mating. Births in captivity occurred from February through November but conspicuously not in December and January; only one birth occurred in February. These observations are in agreement with findings by others of low spermatogenic activity in manatees during December, January and February. Females that lost calves (stillborn or perinatal) cycled again and became pregnant within 2 months (minimum). Intervals between births in females who experienced two or more pregnancies ranged from 14 (stillbirth or perinatal death) to about 103 months (mature males were assumed to be present at all times).

Observations of reproduction in captive manatees confirmed and supplemented information from observations of wild manatees. However, well planned, detailed studies must be done to determine the duration of gestation and estrous cycling and of calf growth and development. These data are necessary for proper management of this endangered species.

Estimation of Survival of Adult Florida Manatees in the Crystal River, at Blue Spring, and on the Atlantic Coast

by

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Abstract. We applied Cormack-Jolly-Seber open population models to manatee (*Trichechus manatus latirostris*) photo-identification databases to estimate adult survival probabilities. The computer programs JOLLY and RECAPCO were used to estimate survival of 677 individuals in three study areas: Crystal River (winters 1977–78 to 1990–91), Blue Spring (winters 1977–78 to 1990–91), and the Atlantic Coast (winters 1984–85 to 1990–91). We also estimated annual survival from observations of 111 manatees tagged for studies with radiotelemetry. Survival estimated from observations with telemetry had broader confidence intervals than survival estimated with the Cormack-Jolly-Seber models. Annual probabilities of capture based on photo-identification records were generally high. The mean annual adult survival estimated from sighting-resighting records was 0.959–0.962 in the Crystal River and 0.936–0.948 at Blue Spring and may be high enough to permit population growth, given the values of other life-history parameters. On the Atlantic Coast, the estimated annual adult survival (range of means = 0.877–0.885) may signify a declining population. However, for several reasons, interpretation of data from the latter study group should be tempered with caution. Adult survivorship seems to be constant with age in all three study groups. No strong differences were apparent between adult survival of males and females in the Crystal River or at Blue Spring; the basis of significant differences between sexes on the Atlantic Coast is unclear. Future research into estimating survival with photo-identification and the Cormack-Jolly-Seber models should be vigorously pursued. Estimates of annual survival can provide an additional indication of Florida manatee population status with a stronger statistical basis than aerial counts and carcass totals.

Key words: Survival, photo-identification, telemetry, capture–recapture, Jolly-Seber, manatee, open population models.

Annual numbers of recovered carcasses of Florida manatees (*Trichechus manatus latirostris*) have increased since record keeping began in 1974 (Ackerman et al. 1995), but the causes of this increase are not known. The greater number of carcasses may be due to rising mortality rates, increases in the discovery and reporting of carcasses, increases in manatee population size, or to some combination of these factors. Knowledge of survival would improve the understanding of the relative magnitudes of the alternative causes with different implications for the conservation of manatees.

Estimation of adult survival is important because large mammals like manatees with relatively long life spans and low reproductive rates typically require high adult survival to maintain stable or growing population sizes (Eberhardt and Siniff 1977; Eberhardt 1985). Simulations with preliminary population models by Packard (*[3]1985) indicated that population growth rates in Florida manatees were more sensitive to changes in adult survival and secondarily to subadult survival than to any other single factor, including the proportion of breeding females, age structure, and survival of neonates and young.

High adult survival in Florida manatee populations should, therefore, be a primary objective of conservation.

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However, survival has not been estimated because in part traditional tagging poses daunting problems in terms of sampling effort, sample sizes, and waiting times required to obtain results with high statistical precision (*Packard and Nichols 1983). Precision is important because even small differences in adult survival of large mammals can cause changes in trends in population growth from increases to decreases (Eberhardt 1985).

The development of a substantial photo-identification database of manatees (Reid et al. 1991; Beck and Reid 1995) and recent statistical advances in estimation of survival from resightings of recognizable animals (Buckland 1990; Pollock et al. 1990; Lebreton et al. 1992; Nichols 1992) now allow these calculations. We investigated the utility of estimating adult survival with the resighting histories of living individuals with distinctive scar patterns and from information on death rates in a population of animals monitored by radiotelemetry. We applied these techniques to manatees in three study areas in Florida: the Crystal River in the Big Bend area of the northern Gulf Coast, Blue Spring on the upper St. Johns River, and the entire Atlantic Coast. We discuss the merits of each approach, provide a preliminary interpretation of the estimated survival, and make recommendations for future research and conservation.

Methods and Materials

Study Groups

In winter, manatees aggregate in warm water. They are more accessible for photo-identification in these aggregations, but individuals in groups do not necessarily comprise distinct populations. Although high site-fidelity from year to year is typical, interchange of individuals among certain aggregation sites in Florida is well documented (Reid et al. 1991). However, the interchange among the three study groups from which our data are drawn is limited (Rathbun et al. 1990; Reid et al. 1991). The study groups differ in several important characteristics related to habitat quality and protection, population attributes, and photo-identification efforts (Table 1). The three study sites comprise the range of the subspecies except southwestern Florida (from Tampa Bay south through the Florida Keys).

Crystal River Group

Manatee habitat in the Crystal River region is described in Hartman (1979), Powell and Rathbun (1984), and Rathbun et al. (1990). The sampling area includes the Crystal and Homosassa rivers (Table 1). Manatees move readily between the two during and between winter seasons (approximately November to March); the typical warm-season range is the Big Bend Coast of northwestern peninsular Florida (Rathbun et al. 1990; Table 1). Application of photo-identification to manatees in the Crystal River was described in these reports and in publications by Reid et al. (1991), Beck and Reid (1995), and Rathbun et al. (1995). The manatees in the Crystal River are entered into a scar-pattern catalog (Manatee Individual Identification System; Beck and Reid 1995), which is the database for the Cormack-Jolly-Seber models of our analysis. Unlike the other two study groups (Table 1), however, Rathbun et al. (1995) established a convention of cataloging only individuals that were seen in at least two winter seasons. Collection of sighting data on the Crystal River was done almost exclusively by the Sirenia Project of the U.S. Fish and Wildlife Service; personnel were not the same throughout the study but overlapped in time (Table 1). Person-day effort in collecting sighting data each winter ranged from 20 to 63 during 1980–81 to 1990–91 ($\bar{x}$ = 32.1 ± 10.9 days; Rathbun et al. 1995) and varied with weather patterns and other factors. Updated information on population characteristics of manatees in this study area were detailed by Rathbun et al. (1990, 1995), Ackerman (1995), and Ackerman et al. (1995). There are 251 adult manatees in this data set (Table 1; Appendix Table A-1).

Blue Spring Group

Descriptions of the manatee refugium at Blue Spring were presented by Hartman (1979), Bengtson (1981), and Powell and Waldron (*1981). Blue Spring is a clear artesian spring located 240 km upstream (south) from the mouth of the St. Johns River. It is the most confined of the sampling areas, measuring approximately 650 m in length, 20–30 m in width, and about 5 m in greatest depth. The annual range of the manatees in this study group primarily are the waters of the St. Johns River within about 100 km of the spring, although some individuals make excursions to the mouth of the river or beyond (Bengtson 1981). The summer range overlaps the range of manatees that typically do not spend the entire winter at Blue Spring but migrate from the river to the lower Atlantic Coast (Reid et al. 1991). The aggregation usually lasts from November to late March. Manatees use Blue Spring only as a thermal refuge and must leave to forage in the St. Johns River. The amount of time manatees spend at Blue Spring varies with temperature patterns. All overwintering animals are present on the coldest days and may stay at Blue Spring for as many as 7 days without leaving to feed during cold spells (Bengtson 1981). The clear water and lack of aquatic vegetation allows unobstructed views of manatees. The public has been prohibited from entering the water in the manatee aggregation area of Blue Spring since 1978, but many of the surrounding areas where manatees forage in winter and the annual range have only recently come under protection (Table 1).

Table 1. Comparison of habitat and population characteristics and photo-identification among three study groups of manatees (*Trichechus manatus latirostris*) in Florida, 1977–1991.

Characteristics	Crystal River	Blue Spring	Atlantic Coast
Habitat and population			
Maximum numbers of manatees (1990–1991)	280 (Ackerman 1995)	63 (Ackerman 1995)	462 (Garrott et al. 1995)
Trends in counts of manatees	Toward increase (Ackerman 1995; Rathbun et al. 1990)	Toward increase (Ackerman 1995; O'Shea 1988)	Seemingly toward increase but variable interpretations (Garrott et al. 1995)
Number of sites where manatees aggregate in winter	Two major, and scattered minor sites in same region	One	10 or more
Location and relative isolation in winter	Northwestern end of range in Florida; low interchange with other refugia in Tampa Bay and south, not connected by deep channels or Intracoastal Waterway Powell and Rathbun 1984; Rathbun et al. 1990)	Upstream (southern) end of range in St. Johns River, low interchange with other Atlantic Coast refugia through connecting channels (U.S. Fish and Wildlife Service, unpublished data; Reid et al. 1991)	Georgia to Miami area, including northern St. Johns River. High interchange among aggregation sites (Reid and O'Shea 1989; Reid et al. 1991, 1995)
Annual range	Primarily northwestern peninsular Florida	Primarily upstream St. Johns River	Georgia to Miami, including St. Johns River (Reid and O'Shea 1989; Reid et al. 1991, 1995)
General habitat quality	Much undeveloped habitat surrounding warm-season range, some protected; winter habitat includes wide area of thermal refuge also encompassing feeding areas; intensive enforcement of boating and diving regulations at winter aggregation since the late 1970's	Moderate amount of undeveloped habitat surrounding warm-season range, but included waterways unprotected until recently; winter habitat involves confined thermal refuge without forage; intensive enforcement at winter aggregation site since the late 1970's	Most warm-season and especially winter habitat occurs in highly developed regions, with exceptions in disjunct areas; winter aggregation sites generally are confined thermal refuges without significant forage; most warm-season habitat unprotected until recently; regulations less well enforced at aggregation sites in winter than at Blue Spring or on the Crystal River
Adult human-related mortality	Low relative to other two study groups (Ackerman 1995; O'Shea et al. 1985; Rathbun et al. 1990)	Moderate relative to Crystal River group (U.S. Fish and Wildlife Service and Florida Department of Natural Resources, unpublished data)	Moderate to high relative to Crystal River group (Ackerman et al. 1995; O'Shea et al. 1985)
Photo-identification efforts			
Number of adults cataloged (all years; see Appendix)	251 (Appendix Table A-1)	79 (Appendix Table A-2)	347 (Appendix-3)
Number sex undetermined	2 (Appendix Table A-1)	4 (Appendix Table A-2)	121 (Appendix-3)
Number known dead	5 (Appendix Table A-1)	10 (Appendix Table A-2)	14 (Appendix-3)
Study period	Winters 1977–1978 through 1990–1991	Winters 1977–1978 through 1990–1991	Winters 1977–1978 through 1990–1991, but 1977–1978 to 1983–1984 with higher heterogeneity excluded from estimates

Table 1. *Continued.*

Characteristics	Crystal River	Blue Spring	Atlantic Coast
Annual capture probabilities	High (Table 2)	High (Table 2)	Low 1977–1978 through 1983–1984; moderate 1984–1985 through 1990–1991 (Table 2)
Data censoring	Individuals included only if observed in more than one winter (Rathbun et al. 1995)	May include individuals seen only one winter	May include individuals seen only one winter
Mode and ease of sampling	Primarily underwater photography in clear water, targeting predictable periods of aggregation; lengthy field season with repetitive sampling	Surface and underwater photography in clear water augmented by detailed field notes; aggregation period lengthy with repetitive sampling	Surface photography in dark water at all but a few sites; aggregations more short-lived at southern sites, with limited sampling intensity
Observer continuity and consistency of effort	Relatively small number of observers, from one laboratory over entire study period; overlapping observer team membership	Relatively small number of observers, from one laboratory and one agency over entire study period; same two individuals led efforts the last 10 years	Larger number of observers than at Crystal River or Blue Spring, drawn from several organizations, including volunteers
Degree of additional editing of records likely to be required	Most revisions completed, small number of minor changes based on corrected identifications expected	Most revisions completed, small number of minor changes based on corrected identifications expected	Additional revisions pending and necessary; moderate number of changes to database likely

Unlike other study areas, characteristics of this aggregation site allow complete censuses of the manatees. Censuses are conducted several times weekly by people in canoes directly over the resting manatees (usually within 1 to 5 m) during morning hours when the greatest number of the animals are typically seen. The number of daily censuses has ranged from 59 to 89 each winter during 1981–82 to 1990–91. Observations were made during 1977–78 through 1990–91; one person was consistently responsible for identifications during 1981–82 to 1990–91. Scar patterns were committed to memory and verified by voucher photographs and field sketches. Photo-identification records are matched with photographs from salvaged carcass files. Biologists who are familiar with marking patterns of manatees from Blue Spring are usually notified when carcasses are collected in the upper St. Johns River and examine them before necropsy. Unlike manatees in the Crystal River study group, manatees at Blue Spring are cataloged in the first winter of identification. The number of manatees that come to Blue Spring has generally increased since the early 1970's (O'Shea 1988; Ackerman 1995). The increase has been due to internal recruitment and to a lesser extent to immigration (U.S. Fish and Wildlife Service and Florida Park Service, unpublished data) and not to changes in intensity of effort. Seventy-nine manatees are listed in this data set (Table 1; Appendix Table A-2).

Atlantic Coast Group

The Atlantic Coast study area spans much of the range of the subspecies between coastal Georgia and Biscayne Bay. The emphasis in the collection of photo-identification records on the Atlantic Coast is on manatees in several aggregation sites as described by Reid et al. (1991) and Beck and Reid (1995). Based on data from studies with telemetry, movement patterns of manatees on the Atlantic Coast are complex; long-distance travel and lengthy seasonal migrations are more common to these manatees than to manatees from the Crystal River or Blue Spring. Some manatees may remain inside a relatively circumscribed area throughout the annual cycle, whereas others typically make within-season (summer or winter) trips of 200–300 km in a few days, maintaining steady paces as high as 50 km/day (*Reid and O'Shea 1989). Seasonal movements can be short distance moves of 100 km or can be over distances of 600–800 km. Some manatees on the Atlantic Coast visited most major aggregation sites during one winter migration circuit. Whereas aggregations in the Crystal River and at Blue Spring can be more easily defined as study groups in circumscribed locations, manatee movement patterns on the Atlantic Coast precluded the inclusion of aggregations at various power-plant sites or other sighting locations as separate groups in our analyses. Furthermore, observations of aggregations on the Atlantic Coast have been less intensive than at Blue Spring or Crystal River because the areas are large, water clarity is generally poor, seasonal and daily periods of manatee attendance are shorter at some locations, and access and personnel are more limited. The data set from the Atlantic Coast includes the photo-identification records from aggregation sites at the Kennedy and Southside generating stations of the Jacksonville Electric Authority in Jacksonville, Duval County; at the Container Corporation pulp mill, Fernandina Beach, Nassau County, in northeastern Florida; and at the Fort Pierce power plant, Indian River County. The Florida Power and Light Company Canaveral power plant in Brevard County, Riviera power plant in Palm Beach County, and Port Everglades and Lauderdale power plants in Broward County in southeastern Florida were important aggregation sites for obtaining photo-identification records. Several other minor aggregation sites and high-use areas also were visited during winter to obtain photographic records. Descriptions of habitat use and distribution of the manatees in this region were presented by Beeler and O'Shea (*1988). Estimates of data-collection efforts in the Atlantic Coast study areas are not available; more people collected data there than in the Crystal River or Blue Spring study areas. This data set consists of 347 manatees (Table 1; Appendix Table A-3).

Estimation of Survival

Modified Cormack-Jolly-Seber Estimates

Assumptions. We estimated survival by two different statistical methods that model the capture–recapture (resighting) histories of live, marked manatees. Both methods are based on the Cormack-Jolly-Seber model for open populations (Cormack 1964; Jolly 1965; Seber 1965; Lebreton et al. 1992). Several assumptions are required to apply open-population models to manatee resighting data. The first is that every individual in the population has the same probability (p_i) of being identified in the ith time period (i.e., capture probabilities are not heterogeneous). Because we were interested in estimating survival, not population size, unmarked animals were irrelevant to the analysis, and this assumption applied only to the marked portion of the population (Cormack 1964; Lebreton et al. 1992). This assumption is frequently violated in field capture–recapture studies, and probably was violated by the manatee data sets. For example, some individuals may be more prone to disperse from the study areas (although rates are probably not high for the regions as defined), and some individuals may tend to be more accessible for photography. Effects of departures from this assumption, however, are not severe: survival estimators of the model have been robust when capture probabilities are heterogeneous, particularly when capture probabilities are high (Carothers 1973, 1979; Pollock et al. 1990). Capture probabilities are high in our study groups (usually greater than 0.50; Table 2) because sampling is

intensive during aggregations of manatees in warm-water sites, when probably most animals are present on the coldest days.

A second assumption is that every manatee has the same probability (ϕ_i) of surviving from sample I to sample $I + 1$. To improve the probability of meeting this assumption, we analyzed homogeneous subsets of individuals subject to similar mortality factors by restricting our analyses to only adults in the three geographic regions. In addition, we tested for evidence of differential survival by age and sex. The results generally supported the assumption of equal probability of survival with age and sex.

Also important for meeting the assumption of equal probability of survival is a restriction of the sampling interval (Lebreton et al. 1992). If sampling periods are long, the interval between samples over which survival is estimated differ among individuals, depending on when they were observed. Individuals that are identified at the end of the sampling period have a greater probability of surviving to the next sample than those identified at the beginning. However, instantaneous sampling of the marked population is not possible with manatees, and longer periods are needed for adequate photographic documentation. Longer sampling periods also increase the probability of observing a larger number of previously identified individuals. Thus, increasing the length of the sampling period improves the probability of meeting the assumption of equal probability of capture but at the same time compromises the assumption of equal probability of survival. Although photo-identification records are gathered during all times of the year (Beck and Reid 1995), for our analyses we chose to limit the sampling period each year to the period 1 November–31 March when sampling effort is most intense. Thus, the sample period was 5 months, and the interval between samples was 7 months. Multiple sightings of individuals were usually made during the sampling period, but the data were collapsed to represent simply the presence (1) or absence (0) of the individual during that sample year. This is the design recommended by Pollock (1982) for long-term studies and is robust to heterogeneity in capture probabilities.

A third assumption is that the manatees are correctly identified. Cataloging criteria for the Manatee Individual Identification System are generally conservative (Beck and Reid 1995) and the amount of information in scar patterns is large, which minimizes the probability of misidentifications. However, these probabilities have not been quantitatively estimated (Beck and Reid 1995) and may vary among study areas (Table 1).

A final assumption is that identifying one manatee in a sample does not affect the probability of identifying any other individual. Because manatees do not maintain stable social groups as adults (Hartman 1979; Bengtson 1981), this assumption is probably not violated.

The survival that is estimated by these models applies only to the marked portion of the population. To extrapolate the results to the remaining population, the marked subset must be assumed to be representative of the whole population (Cormack 1964). Most markings that identify individuals are scars from collisions with boats and boat propellers

Table 2. Estimated annual probabilities of capture ($\hat{p}_i$) of adult Florida manatees (*Trichechus manatus latirostris*) based on photo-identification records in three study areas in winter, 1 November–1 April 1978–1979 through 1989–1990. Probabilities of capture and standard errors calculated with Model A (ϕ_t, p_t) of program JOLLY (Pollock et al. 1990).

	Crystal River		Blue Spring		Atlantic Coast	
Year	$\hat{p}_i$	SE	$\hat{p}_i$	SE[a]	$\hat{p}_i$	SE[a]
1978–79	0.914	0.037	1.00		0.000	
1979–80	0.766	0.051	1.00		0.294	0.259
1980–81	0.844	0.043	1.00		0.333	0.193
1981–82	0.844	0.041	0.801	0.080	0.323	0.155
1982–83	0.879	0.036	0.811	0.076	0.292	0.090
1983–84	0.932	0.027	0.830	0.069	0.163	0.051
1984–85	0.867	0.034	0.551	0.086	0.634	0.061
1985–86	0.732	0.043	0.846	0.063	0.502	0.047
1986–87	0.863	0.031	0.895	0.050	0.389	0.043
1987–88	0.888	0.027	0.973	0.027	0.539	0.043
1988–89	0.893	0.026	0.948	0.036	0.386	0.039
1989–90	0.747	0.038	1.00		0.532	0.043
$\hat{p}$	0.847	0.012	0.888		0.366	
Number of individuals	251		79		347	

[a] No values are provided where standard errors of estimates could not be calculated because input statistics included denominators of zero (see Pollock et al. 1990:21).

(Beck and Reid 1995). No data suggest that boat-scarred manatees behave differently from unmarked animals in a manner that alters the expected survival, although this has not been tested. Because such a large number of Florida manatees are marked by scars (Beck and Reid 1995) and the total number of individuals in our photo-identification database is high (677), the samples represent a significant fraction of the population of concern and are extremely important for conservation.

Age and size criteria. We categorized individuals as adults according to several criteria, depending on data available for each animal. Individuals of known birth dates or years were categorized as subadults if they were 3, 4, or 5 years old, and as adults after their fifth year. This classification is conservative because it excludes from adult status the earliest known ages of sexual maturity (Hernandez et al. 1995; Marmontel 1995; O'Shea and Hartley 1995; Rathbun et al. 1995). If age was not known but total body length was determined, we classified manatees if they were longer than 275 cm as adult (O'Shea et al. 1985; O'Shea and Reep 1990; Marmontel 1995). Non-nursing animals that were shorter than 275 cm were classified as weaned subadults. Females without known histories and accompanied by calves were categorized as adults regardless of size. In all other instances, we relied on subjective estimation of body size (larger animals classified as adults), and did not classify subadult-sized animals as adults in any of our analyses until the third or fourth year after the first sighting record.

Period of study. The capture–recapture data were collected and analyzed by winter (1 November through 31 March) during 1977–78 through 1990–91. Because of potential future analyses, we documented the sighting histories of animals on which our analyses are based (Appendix).

Estimates from program JOLLY. Program JOLLY (Pollock et al. 1990) estimates capture probabilities ($\hat{p}_i$), survival probabilities ($\hat{\phi}_i$), their respective standard errors, and 95% confidence intervals by sampling period (years). Average survival and capture probabilities over all years are calculated as unweighted arithmetic means. The maximum likelihood estimators in this program exist in closed form as a simple algebraic formula (in contrast to an iterative numerical solution). Some annual survival estimates can exceed unity.

Five variations of the Cormack-Jolly-Seber model that require different assumptions are available in program JOLLY. Selection of the most appropriate model is facilitated for the researcher by goodness-of-fit tests and between-model tests developed by Brownie et al. (1985). We examined three of the five alternative models provided by Program JOLLY: Model A, which is the basic Jolly-Seber model in which capture and survival probabilities vary over sampling periods (ϕ_t, p_t model in notation of Lebreton et al. [1992]); Model B, for which constant survival over time must be assumed but capture probabilities vary (ϕ, p_t model in notation of Lebreton et al. [1992]); and Model D, for which constant survival and constant capture probabilities over time must be assumed (ϕ, p in notation of Lebreton et al. [1992]). The remaining two models were not investigated because of *a priori* assumptions about their lack of applicability to our study (Model A′ requires the assumption of variable capture and survival probabilities but effects of births and immigration are considered negligible; Model 2 allows a trap-response effect of initial capture on first period survival rate).

The survival estimates we provide for each study group are calculated with the model selected on the basis of the between-model tests. However, for all of these groups the goodness-of-fit tests (Table 3) of the data indicated that the model did not account for all the variation and more complex modeling may be required. Despite the lack of fit, we felt that the selected model was the least biased and most accurate available estimate. The variances of the estimates, however, were based on the theoretical model and did not reflect actual variability. To adjust the variances, we used quasi-likelihood theory and calculated a variance-inflation factor when goodness-of-fit tests did not meet the $P > 0.2$ criteria (Burnham et al. 1987; Lebreton et al. 1992).

Initially we calculated annual capture probabilities in each study area with Model A (ϕ_t, p_t) of program JOLLY. Early years in which sample sizes were lower and standard errors of estimates were higher than in later years were dropped for subsequent analyses.

Estimates from program RECAPCO. To our knowledge, this program (*Buckland 1991) provides the only method for estimating survival that has been used with photo-identification records of other marine mammal species (Buckland 1990; Slooten et al. 1992). Statistical procedures that form the basis for RECAPCO are described by Buckland (1980, 1982, 1990) and Buckland and Garthwaite (1991). Program RECAPCO uses a modified Cormack-Jolly-Seber model but differs from program JOLLY in several aspects. The RECAPCO analysis groups the capture histories into cohorts of individuals that were first captured during the same sampling period. Because no new manatees can enter a cohort after it was defined, the model is a special case of the Cormack-Jolly-Seber model without recruitment (deaths and emigration occur, but births and immigration do not occur). In contrast to program JOLLY, no other alternative models are considered. The cohort analysis allows an examination of changes in survival estimates with increasing age. Each cohort contains members that vary in age, negating age-specific estimates, but each member is known to age with passing years, and therefore, survival can be estimated from the number of years after first identification. A survivorship curve is calculated similarly to the l_x matrix of life-table analyses but is based on years from first identifi-

Table 3. Results of the model selection tests with program JOLLY and sighting-resighting data of adult Florida manatees (*Trichechus manatus latirostris*) from the Crystal River (winters 1977–1978 to 1990–1991), Blue Spring (winters 1977–1978 to 1990–1991), and the Atlantic Coast (winters 1984–1985 to 1990–1991).

	Crystal River			Blue Spring[a]			Atlantic Coast		
Test	χ^2	df	*P*	χ^2	df	*P*	χ^2	df	*P*
Goodness-of-fit to A (ϕ_t, p_t)	50.4	16	<0.001	12.2	3	0.007	15.8	13	0.258
Goodness-of-fit to B (ϕ, p_t)	62.3	24	<0.001				20.9	17	0.230
Goodness-of-fit to D (ϕ, p)	108.8	36	<0.001	71.1	15	<0.001	89.5	22	<0.001
Model B vs. Model A (ϕ, p_t) (ϕ_t, p_t)	11.9	8	0.157				5.1	4	0.278
Model D vs. Model A (ϕ, p) (ϕ_t, p_t)	58.4	20	<0.001	58.9	12	<0.001	73.7	9	<0.001
Model D vs. Model B (ϕ, p) (ϕ, p_t)	49.1	12	<0.001				67.8	5	<0.001

[a] Iteration attempts to estimate parameters for the Blue Spring data set with Model B (ϕ, p_t) failed, probably because of small sample size.

cation rather than age classes. Departures from linearity in the survivorship curve indicate a violation of the assumption of constant survival with age (Buckland 1982, 1990). We followed this approach in plotting these relations for each study group.

Survival ($\hat{\phi}$) of each cohort is estimated by RECAPCO. Estimates of capture probabilities ($\hat{p}$) are also calculated to estimate survival but are not available to the user in the output. The maximum likelihood estimators in this program exist in open form as an iterative numerical solution, and survival estimates—unlike the estimates calculated by JOLLY—are constrained to never exceed unity (Buckland 1980). Survival estimates are then combined by either date or years from first identification. A mean survival of the entire sample can be estimated as a geometric mean, which is preferred if survival is variable with age. Average survival is also estimated as an arithmetic mean weighted by the estimated number of individuals remaining alive in the cohort after the year of each estimate, which is preferred if survival is constant with age (Buckland 1990). RECAPCO calculates standard errors and confidence limits of survival estimates with the nonparametric bootstrap technique of Buckland and Garthwaite (1991). Tests to assess the goodness-of-fit of the data are not available in this program.

RECAPCO employs capture histories of live individuals and information based on the recovery of dead marked animals (Buckland 1980, 1990), whereas program JOLLY uses only resighting data of live animals. The statistics r_i, z_i, and χ_i, are defined differently from the Cormack-Jolly-Seber model to include known deaths, but the estimation process is only slightly modified by this inclusion (Buckland 1980). Including information on deaths requires an assumption that every marked animal that dies between the sample periods has the same probability of being recovered and identified (Buckland 1980). The degree to which this assumption may be violated has not been addressed for data from Florida manatees.

To reduce effects of heterogeneity in capture probabilities when estimating mean survival, Buckland (1982, 1990) recommended deleting estimates from each cohort (after combining by date) that subjectively seemed to be most affected by bias. It was not necessary to follow this procedure in our analysis because none of the estimates showed strong departure from others.

We used survival estimates generated by RECAPCO to compute mean life expectancy after the first sighting record following Cormack (1964) and Brownie et al. (1985). Mean life expectancy was calculated as $-1/\ln(\hat{\phi})$. This is not an estimate of true mean longevity because it does not consider pre-adult survival, and by definition all manatees in our databases are at least 5 years old before they are included in the analyses.

Hypothesis testing with program CONTRAST. Sauer and Williams (1989) developed a generalized χ^2 statistic to test null hypotheses on homogeneity among several survival estimates. Program CONTRAST (Hines and Sauer 1989) allows rapid computation of these statistics, which we used to test hypotheses about the homogeneity of survival among the three study groups and among sex categories within study groups. We used the two programs JOLLY and RECAPCO to estimate survival and their associated covariance or standard errors and used these data for input into program CONTRAST.

Summary of general approach. We performed a series of exploratory analyses to determine the feasibility of estimating survival with photo-identification databases from each

of three study groups with contrasting characteristics. Initially, we subjectively examined the annual capture probabilities within each study group with the generalized Model A (ϕ_t, p_t) of program JOLLY, considering the possibility of having to modify the temporal span of the databases because of small sample sizes and high standard errors. Two survival estimates of each study group were calculated, one based on the cohort model from RECAPCO and one based on the particular model selected by JOLLY. We used the model selection procedures of program JOLLY to determine which of several modifications to the basic Cormack-Jolly-Seber model best fit the data. We used program CONTRAST to conduct a preliminary test for potential differences of survival among sex categories in each study area as generated by JOLLY and RECAPCO and used a test for differential survival with age with output from RECAPCO. The primary purpose of searching for possible age or sex influences on survival was to evaluate the effects of such potential sources of heterogeneity on the validity of pooling all sighting records in comparisons among study areas. Subsequent to finding no age-related differences in survival, we also calculated life expectancy after the first sighting record based on the cohort analysis of RECAPCO.

Estimates Based on Radio-tracked Individuals

We based these estimates on manatees that were tracked in studies with radiotelemetry designed to determine movement patterns and behavioral ecology rather than survival (Bengtson 1981; Rathbun et al. 1990; Reid et al. 1995). Although this is a post hoc approach, it allows comparison with the results of the Cormack-Jolly-Seber estimates and allows assessment of the practicality of employing telemetry to estimate survival in future studies. Tagging methods varied among study areas and are described elsewhere (Bengtson 1981; Rathbun et al. *1987, 1990; *Reid and O'Shea 1989; Reid et al. 1995).

Annual survival (ASR) of radio-tracked individuals was calculated with the technique of DeMaster and Drevenak (1988), which followed the approaches of Trent and Rongstad (1974), Mayfield (1975), and Heisey and Fuller (1985). Unlike some studies of other animal species, studies of manatees with telemetry include complex histories of transmitter loss and reattachment and do not have well defined periods of initiation and termination of observations common to the entire sample. Transmitters, particularly the floating, tethered tags used in all study areas except at Blue Spring, frequently fail or become detached. The belt, however, usually remains attached to the animal, and new tags are regularly attached to existing belts (Reid et al. 1995). Furthermore, floating tags not uncommonly cease to transmit because they are damaged by boat strikes or are seized by humans or alligators or because of other factors that do not affect the survival of the tagged individual. The mean length of attachment of tethered transmitters in the study on the Atlantic Coast, for example, was 64 days (Reid et al. 1995). Siniff and Ralls (1991) recommended using projected length of battery life as a criterion for terminating observation periods in studies of sea otters (*Enhydra lutris*), but battery life in studies of manatees with telemetry is typically much longer than the period of transmitter attachment (Reid et al. 1995). For computation, we limited our analyses to dates when the manatees carried functioning transmitters and omitted time periods when transmitters were not operating. In the Crystal River and at Blue Spring, the period of survival estimation extended from the date of tagging of the first manatee to the date of the last observation with telemetry. The period of observation of all animals in the ongoing Atlantic Coast study was terminated on 31 December 1991. Our use of this technique also varied from previous studies for a second reason: although animals were typically observed several times weekly, they were not always observed daily.

For each tagged animal, we entered the date of tagging and the date of the last telemetry observation and whether the animal was dead or alive at the last observation. Manatees tagged for only 1 day or sightings of belts or other markings during periods of transmitter failure were excluded from the analysis. Telemetry data of manatees at Blue Spring are based on studies conducted during 1979–84 (Bengtson 1981; Sirenia Project, unpublished data). Research with telemetry on the Crystal River was conducted during 1980–85 (Powell and Rathbun 1984; Rathbun et al. 1990; Sirenia Project, unpublished data). Studies with telemetry on the Atlantic Coast were conducted from 1986 through 1991 (Reid et al. 1995; Sirenia Project, unpublished data). The study on the Atlantic Coast also included 13 individuals that had been rehabilitated in captivity and tagged at release. Because survival does not seem to differ between rehabilitated manatees and wild individuals (Sirenia Project, unpublished data), we included these cases to increase the sample size.

Annual survival was estimated by first calculating a daily survival (DSR):

$$\mathrm{DSR} = 1 - \sum_{(i=1)}^{K} (y_i) / \sum_{(i=1)}^{K} (x_i) \qquad (1)$$

where $y_i = 1$ if the ith individual died and $y_i = 0$ if it was alive at the end of the observation period; x_i is the total number of days the ith individual survived while under observation (animal-days); and K is the number of tagged manatees. The sum of y_i is the total number of

deaths that occurred; the sum of x_i is the total number of animal-days.

Annual survival (ASR) was extrapolated from DSR as:

$$ASR = DSR^{365.25} \quad (2)$$

The exponent is the average number of days in the year. Calculating the 95% confidence interval (CI) of the ASR is dependent on determining the number of deaths expected to occur during the observed number of animal-days with a probability of $P = 0.025$ (at the upper CI) and $P = 0.975$ (at the lower CI). Because each animal-day is a binomial event with a probable outcome of either death or survival, deaths over a year have a binomial distribution. The expected number of deaths can be estimated directly from this distribution with the binomial probability distribution function of SAS (SAS Institute 1985) and the binomial parameter of the function set equal to the daily mortality estimate (1-DSR) and n set equal to the total number of animal-days. The number of deaths at each of these probabilities was then estimated to the nearest 0.001 decimal by inverse interpolation (Sokal and Rohlf 1981), and we estimated the ASR confidence limits by substituting these mortality estimates in equation (1).

Two assumptions are made for estimating survival by this method (Trent and Rongstad 1974): (1) each animal-day is an independent trial (death of one animal does not affect the probability of survival of another, and all animals have the same underlying survival probabilities); (2) the probability of survival each day is constant. Available knowledge and long-term data suggested the first assumption was valid. Although our capture–recapture analyses of resighting data suggested a constant probability of survival of adults with age (see Figs. 1–3 and below), we were unable to evaluate the validity of either assumption or the magnitude of effects of possible violations.

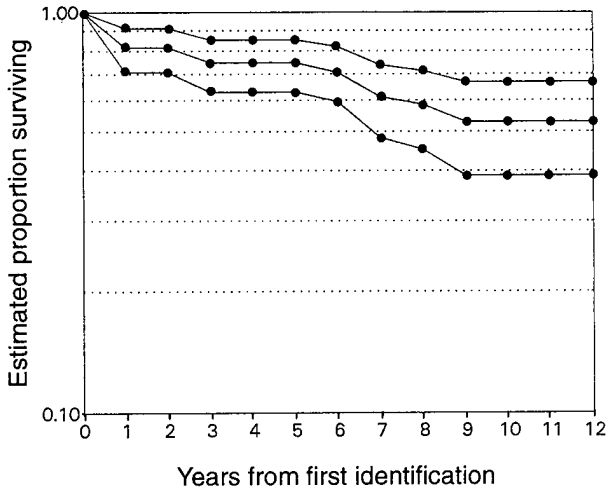


Fig. 2. Estimated proportion (and 95% confidence interval) of surviving adult Florida manatees (*Trichechus manatus latirostris*) based on years from first identification at Blue Spring (winter 1977–1978 through winter 1990–1991). The semi-ln plot shows a significant fit to a linear function (r^2 = 0.919; $P < 0.0001$; $y = -0.02112\,x + 0.644330$), indicating a constant probability of survival with age.

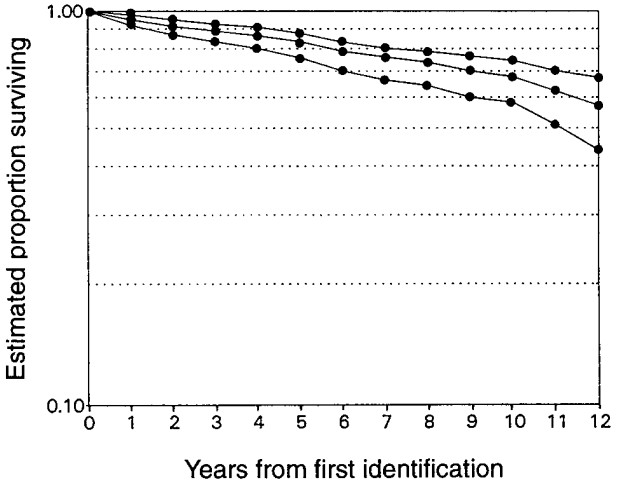


Fig. 1. Estimated proportion (and 95% confidence interval) of surviving adult Florida manatees (*Trichechus manatus latirostris*) based on years from first identification in the Crystal River (winter 1977–1978 through winter 1990–1991). The semi-ln plot shows a significant fit to a linear function (r^2 = 0.990; $P < 0.0001$; $y = -0.01866\,x + 0.693198$), indicating a constant probability of survival with age.

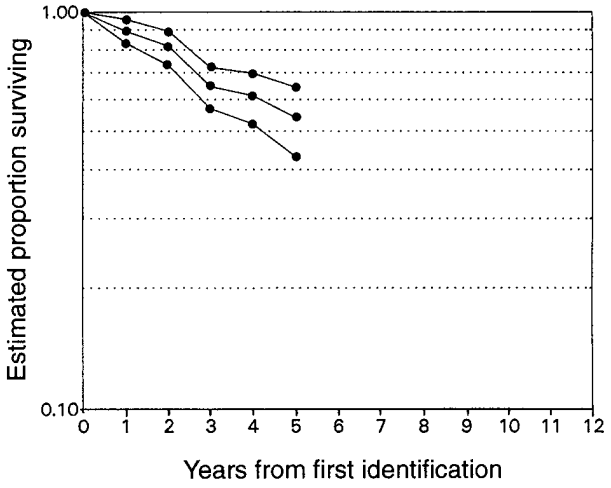


Fig. 3. Estimated proportion (and 95% confidence interval) of surviving adult Florida manatees (*Trichechus manatus latirostris*) based on years from first identification on the Atlantic Coast (winter 1984–1985 through winter 1990–1991). The semi-ln plot shows a significant fit to a linear function (r^2 = 0.976; $P < 0.0002$; $y = -0.05383\,x + 0.690815$), indicating a constant probability of survival with age.

Results

Cormack-Jolly-Seber Estimates

Probability of Capture

The mean probability of capture ($\hat{p}_i$) was high in the Crystal River (0.847) and at Blue Spring (0.888; Table 2) and lower (mean 0.366) on the Atlantic Coast. However, the annual mean capture probabilities on the Atlantic Coast were consistently higher during the last 6 years than during the previous 6 years (Table 2). We limited subsequent analyses to survival of the Atlantic Coast study group during winters 1984–85 through 1990–91.

Survival

Estimates with program JOLLY. Model B (ϕ, p_t, constant survival probability but time-dependent capture probabilities) was selected for estimating survival of the manatees in the Crystal River and on the Atlantic Coast, and Model A (time-dependent survival and capture probabilities, ϕ_t, p_t) for estimating survival at Blue Spring (Table 3). Goodness-of-fit tests of the data to the selected models (Table 3), however, indicated poor fit. A variance inflation factor was incorporated into our confidence interval estimates to reflect the excess variation.

In the Crystal River, the estimated constant annual survival during the period winter 1977–78 through winter 1990–91 was 0.962 (CI = 0.943–0.981; Table 4). At Blue Spring, the mean annual survival during the same period was 0.948 (CI = 0.908–0.988; Table 4). The constant annual survival on the Atlantic Coast from 1984–85 through 1990–91 was 0.877 (CI = 0.848–0.906; Table 4).

Estimates with program RECAPCO. Survival estimated with program RECAPCO was similar to survival obtained with program JOLLY (Table 4). The weighted arithmetic mean adult survival was 0.959 in the Crystal River (CI = 0.943–0.967), 0.936 at Blue Spring (CI = 0.909–0.958), and 0.885 along the Atlantic Coast (CI = 0.855–0.909; Table 4).

Based on output from program RECAPCO, plots of the ln of the estimated proportion of surviving manatees against years from first identification fit a linear function (Crystal River: $r^2 = 0.990$, Blue Spring: $r^2 = 0.919$, Atlantic Coast: $r^2 = 0.976$), indicating that the assumption of a constant rate of survival with age is true of adult Florida manatees in each study group (Figs. 1–3).

Homogeneity of estimates between females and males. Survival, computed by either RECAPCO or JOLLY, did not differ between males and females within the Crystal River and Blue Spring groups (Table 5). On the Atlantic Coast, where the sex of many manatees was not known, survival estimates significantly differed by sex category in either program. Survival was lowest of manatees in the unknown-sex category (Table 6). Sex categories of the Atlantic Coast group were pooled for all other analyses, however, because we judged that deleting animals in the unknown-sex category may add greater bias to survival estimates than pooling. The individuals in the unknown-sex category were assumed to have had shorter and less complete sighting histories, and the identification of their sexes was therefore less probable (see Discussion). Large differences in annual capture probabilities between females and males and consistent trends of differences among sex categories were not evident; the greatest difference was between males ($\hat{p} = 0.79$) and females ($\hat{p} = 0.90$) in the Crystal River (Table 7).

Homogeneity of estimates among study groups. Program CONTRAST revealed significant differences in survival

Table 4. Estimated annual adult survival ($\hat{\phi}$; standard errors SE and 95% confidence limits CI) of Florida manatees (*Trichechus manatus latirostris*) in three study areas. The modified Cormack-Jolly-Seber models and photo-identification records were used to estimate survival. Estimates are based on records of manatees during winter 1977–1978 through 1990–1991 at Crystal River and at Blue Spring, and during winter 1984–1985 through 1990–1991 on the Atlantic Coast. Estimated variances with program JOLLY were adjusted with a variance inflation factor because of poor fit of the data to the model.

Computer program	Blue Spring[a]	Crystal River[b]	Atlantic Coast[b]
JOLLY			
$\hat{\phi}$	0.948	0.962	0.877
SE	0.020	0.009	0.015
CI	0.908–0.988	0.943–0.981	0.848–0.906
RECAPCO			
$\hat{\phi}$	0.936	0.959	0.885
SE	0.013	0.007	0.014
CI	0.909–0.958	0.943–0.967	0.855–0.909

[a] Results from program JOLLY computed with Model A (ϕ_t, p_t).

[b] Results from program JOLLY computed with Model B (ϕ, p_t).

Table 5. Tests of hypotheses on homogeneity of estimated survival ($\hat{\phi}$) between sexes of Florida manatees (*Trichechus manatus latirostris*) in the Crystal River and at Blue Spring (winters 1977–1978 to 1990–1991). Program CONTRAST and survival estimates computed by programs JOLLY and RECAPCO were used.

Computer program and sex	Blue Spring $\hat{\phi}$	SE	n	χ^2	df	P	Crystal River $\hat{\phi}$	SE	n	χ^2	df	P
JOLLY												
Males	0.950[a]	0.013	54	0.005	1	0.95	0.963[c]	0.013	136	0.224	1	0.64
Females	0.949[b]	0.017	21				0.970[d]	0.008	113			
RECAPCO												
Males	0.939	0.018	54	0.014	1	0.91	0.950	0.009	136	0.834	1	0.36
Females	0.935	0.022	21				0.962	0.009	113			

[a] Results computed with JOLLY Model A (ϕ_t, p_t). No variance-inflation factor required ($P = 0.69$).

[b] Results computed with JOLLY Model A (ϕ_t, p_t). Insufficient data for goodness-of-fit test.

[c] Results computed with JOLLY Model B (ϕ, p_t). Includes variance-inflation factor of 2.6 based on goodness-of-fit $P = 0.0002$).

[d] Results computed with JOLLY Model A (ϕ_t, p_t). No variance-inflation factor required ($P = 0.94$).

estimates among the three study groups from 1984–85 through 1990–91 (Table 8). No differences were detected in the pair-wise contrasts of survival estimates of manatees at Blue Spring, on the Atlantic Coast, or in the Crystal River; however, survival in the Crystal River was significantly different from survival on the Atlantic Coast (Table 8). These contrasts were based on the overall survival during the entire study estimated with Model B (ϕ, p_t), constant probability of survival and time-dependent capture probabilities in the Crystal River (1977–78 through 1990–91) and on the Atlantic Coast (1984–85 through 1990–91). Because the assumption of constant survival was not true of the Blue Spring group, the survival was estimated as an arithmetic mean of yearly estimates during the same period of observation as on the Atlantic Coast (Table 8). A separate comparison of survival estimates at Blue Spring and in the Crystal River during the period 1977–78 through 1990–91 (Table 4) also revealed no significant differences ($\chi^2 = 0.39$, df = 1, $P = 0.533$).

Estimates of life expectancy after the first sighting record. The estimated mean life expectancy of manatees after the first sighting record was 23.59 years in the Crystal River group, 15.14 years in the Blue Spring group, and 8.17 years in the Atlantic Coast group.

Estimates Based on Radio-tracked Manatees

Thirty-two manatees (13 adult females, 16 adult males, and 3 subadult females) in the Crystal River were tracked from 1980 through 1985. The mean number of days of observation was 90 ± 86 days (range = 6–346)

Table 6. Tests of hypotheses on homogeneity of survival estimates ($\hat{\phi}$) between sexes of Florida manatees (*Trichechus manatus latirostris*) at Atlantic Coast study sites (winters 1984–1985 through 1990–1991). Program CONTRAST and mean survival estimates computed by programs JOLLY (Model B; ϕ, p_t) and RECAPCO were used. No adjustments of the variances were required based on goodness-of-fit tests to Model B (ϕ, p_t) of program JOLLY.

Computer program and sex	$\hat{\phi}$	SE	n	χ^2	df	P
JOLLY						
Males	0.952	0.021	54	13.4	2	0.001
Females	0.891	0.017	172			
Unknown	0.820	0.030	118			
RECAPCO						
Males	0.947	0.021	54	6.0	2	0.050
Females	0.889	0.019	172			
Unknown	0.862	0.036	118			

Table 7. Estimated annual capture probabilities ($\hat{p}$) of female, male, and undetermined-sex Florida manatees (*Trichechus manatus latirostris*) in the Crystal River (winters 1977–1978 to 1990–1991), at Blue Spring (winters 1977–1978 to 1990–1991), and on the Atlantic Coast (winters 1984–1985 to 1990–1991). Capture probabilities computed by program JOLLY. *Blanks* denote standard errors could not be calculated because input statistics included denominators of zero.

Study area	Sex	$\hat{p}$	SE	n
Crystal River	Females[a]	0.900		113
	Males[b]	0.794	0.003	136
Blue Spring	Females[a]	0.908		21
	Males[b]	0.879		54
Atlantic Coast	Females[a]	0.552	0.003	172
	Males[b]	0.598	0.011	54
	Undetermined[b]	0.500	0.007	118

[a] Estimates with Model A (ϕ_t, p_t).

[b] Estimates with Model B (ϕ, p_t).

per adult and 53 ± 28 days (range = 23–78) per subadult. No deaths occurred among radio-tagged animals in the Crystal River during the period of study; the estimated ASR was 1.0 (Table 9).

Twenty-five manatees (7 adult females, 8 adult males, 2 subadult females, and 8 subadult males, including 1 subadult male later classified as an adult as it matured during the study) were monitored by telemetry at Blue Spring during 1979 through 1984. The mean number of days of observation was 310 ± 222 days (range = 64–790) per adult and 251 ± 171 days (range = 90–650) per subadult. No adults died (ASR = 1.0). Two subadult males died (ASR = 0.748, CI = 0.500–0.991).

Fifty-four manatees were tagged on the Atlantic Coast from 1986 through 1991. The 54 included 33 adult females, 12 adult males, 3 subadult females, and 6 subadult males. The mean number of days of observation was 273 ± 300 days/adult (range = 4–1,152) and 303 ± 166 days/subadult (range = 138–563). Three monitored adults died (2 females, 1 male); the adult ASR was 0.915 (CI = 0.827–0.996). No subadults died (Table 9).

Discussion

Estimation of Survival in Manatees

The survival of Florida manatees had not been estimated prior to our study. In general, prior research on other species relied on three basic approaches to gathering data for esti-

Table 8. Tests of hypotheses on homogeneity of annual survival estimates ($\hat{\phi}$) of adult Florida manatees (*Trichechus manatus latirostris*) at Blue Spring, in the Crystal River, and on the Atlantic Coast (1984–1985 through 1990–1991), sexes combined. Survival estimates computed by program JOLLY based on the best-fit model. Hypothesis tests computed by program CONTRAST; input includes variance-inflation factor adjustments.

Study area comparisons	$\hat{\phi}$	χ^2	df	P
Blue Spring[a]	0.909	24.04	2	<0.0001
Crystal River[b]	0.962			
Atlantic Coast[b]	0.877			
Blue Spring[a]	0.909	1.76	1	0.1848
Crystal River[b]	0.962			
Blue Spring[a]	0.909	0.57	1	0.4487
Atlantic Coast[b]	0.877			
Crystal River[b]	0.962	23.50	1	<0.0001
Atlantic Coast[b]	0.877			

[a] Arithmetic mean of estimated variable annual survival rates 1984–1985 through 1990–1991 (Model A; ϕ_t, p_t). Yearly estimates are 0.937, 0.858, 0.952, 0.893, and 0.905.

[b] Estimated constant survival (Model B; ϕ, p_t).

Table 9. Annual survival of Florida manatees (*Trichechus manatus latirostris*) estimated with data from radio-tracked individuals.

	Crystal River 1980–85	Blue Spring 1979–84	Atlantic Coast 1986–91
Adults			
ASR[a]	1.00	1.00	0.915
CI[b]			0.827–0.996
Individuals	29	15	45
Animal-days	2,621	4,658	12,325
Subadults			
ASR	1.00	0.748	1.00
CI		0.500–0.991	
Individuals	3	10	9
Animal-days	159	2,511	2,726

[a] ASR = Annual survival rate.
[b] CI = 95% confidence interval.

mating survival from living populations that may be suitable for estimating survival in Florida manatees: (1) recording resighting histories of naturally marked individuals without trapping and handling; (2) intensively monitoring the fate of animals with radiotelemetry or with other means of direct observation; and (3) tagging or marking animals after capture or with other traumatic techniques (e.g., harpooning) and basing estimates on recaptures, resightings, or recoveries of tagged individuals. Our results indicated that the analysis of resighting histories based on photo-identification records of naturally marked individuals with the Cormack-Jolly-Seber models seems most suitable for the estimation of survival of Florida manatees. Confidence intervals computed with either JOLLY or RECAPCO from photo-identification data were acceptably narrow for data from manatees in the Crystal River group (0.038, 0.024) and somewhat broader for those on the Atlantic Coast (0.058, 0.054) and at Blue Spring (0.080, 0.049).

In contrast, estimation of survival from direct observation with telemetry had much wider confidence intervals, and other methods that require capture and tagging of animals require logistically infeasible sample sizes for estimating precise survival. Methods for computing survival with data from telemetry (Heisey and Fuller 1985; Pollock et al. 1989) are probably not sufficiently precise without large sample sizes and in manatees are complicated by the loss and reattachment of tags (Reid et al. 1995). Our analysis of telemetry data from manatees on the Atlantic Coast was based on the most intensive radio tracking ever conducted of Florida manatees (Reid et al. 1995), yet the tracking of 45 adults for 12,325 days provided a survival with a 95% confidence interval of 0.83 to 1.00 (Table 9). Such a range of adult survival in manatees would span populations that could be growing or declining at a high rate and would therefore have little use for management.

Accurate estimation of survival with other methods of mark–recapture, such as application of visual tags or passive integrated transponders (PIT tags; Thomas et al. 1987) requires handling or harassing many animals. Packard and Nichols (*1983) calculated that at survival of 0.90 (and 80% carcass recovery rates), 770 manatees/year must be handled and marked during each of 4 years to estimate annual survival with a coefficient of variation of 0.10. Carcass recovery rates of Florida manatees are unknown. In addition, the effort to mark such a large number of manatees is probably beyond the capabilities of research agencies without sacrificing other programs, is dangerous to manatees and researchers, and is probably unacceptable to major segments of the public.

The use of photo-identification techniques and Cormack-Jolly-Seber approaches for analysis of population dynamics were only recently successfully applied to other marine mammals (Buckland 1990; Hammond 1986; Hammond et al. 1990; Slooten et al. 1992). By comparison, results from our analyses are especially encouraging. Buckland (1990), who estimated survival from resighting data with photographs of fluke markings of North Atlantic humpback whales (*Megaptera novaeangliae*), suggested that useful results can be generated when data sets are long-term (≥10 years) and recapture probabilities are 0.2 or higher (Buckland 1990). The photo-identification databases of manatees clearly satisfy these criteria; standard errors of estimated survival are less than or equivalent to those of humpback whales or Hector's dolphins (*Cephalorhynchus hectori*; Buckland 1990; Slooten et al. 1992). In addition to encouragingly high capture probabilities with low variance and databases gathered during 14 consecutive winters on the Crystal River ($\hat{p} = 0.85$) and at Blue Spring ($\hat{p} = 0.89$), our estimates of survival in each study group from photo-identification were concordant with estimates obtained by direct observation with radiotelemetry (despite wide confidence intervals with radiotelemetry). Other aspects of life history, population growth, and mortality factors in these study groups also support the accuracy of these estimates.

RECAPCO and JOLLY provided equivalent estimates of mean survival; however, each program provided different additional categories of information and both provide different insights. JOLLY provided estimates of annual probabilities of capture and also allowed model-selection procedures and goodness-of-fit tests of data models. RECAPCO does not provide such information but includes data from dead animals (future efforts to improve gathering such information from the field will probably increase) and allows assessment of cohort-specific differences in survival over time. Our results suggested that photo-identification data provide a useful basis for the estimation of survival. However, analyses were conducted in a post hoc fashion. Results and inferences should be considered preliminary, particularly because the data from the study groups did not adequately fit the models, as indicated by the significant goodness-of-fit test computed by program JOLLY. The excess variation in the data may be due to problems in the database or to true biological variation that may be accounted for with more complex models. Both possibilities need further exploration. Several measures should be taken to reduce bias and increase the precision of survival estimates in subsequent analyses, including selection of narrower sampling periods within years; establishment of uniform criteria for inclusion of individuals into the Manatee Individual Identification System among study groups (e.g., first-year sightings are not entered in the database of manatees in the Crystal River but are included elsewhere); establishment of consistent criteria for defining dates of first capture of individuals; increasing field sampling intensity (primarily on Atlantic Coast aggregation sites) to improve recapture probabilities; and reexamining all databases for potential errors in individual identifications, including omissions and duplications of records.

The models we examined here and more complex and realistic models should be explored to further examine the nature of the variation in the sighting data. Since we undertook our study, Lebreton et al. (1992) summarized new procedures and computer programs (e.g., SURGE and RELEASE) that should facilitate building and selecting the most appropriate and biologically realistic capture–recapture models for the manatee data set. These programs allow more rigorous hypothesis testing than we conducted in our preliminary analyses, particularly for an analysis-of-variance approach to partition differences in survival among biologically important categories such as time period, location, and sex.

Future investigators should determine the confounding influence of immigration and emigration on survival and use the manatee photo-identification database in conjunction with new applications of Cormack-Jolly-Seber models to refine estimates of rates of movement, site fidelity, and reproduction characteristics (Hestbeck et al. 1991; Nichols 1992; Brownie et al. 1993). Applicability of these models for investigating subadult survival should also be determined, and the potential for developing a combined likelihood approach for estimation of survival from telemetry and photo-identification data should also be evaluated.

Comparisons of Study Groups

Despite the preliminary nature of our analyses, some estimates from the Cormack-Jolly-Seber approach illuminate important aspects of manatee population biology and point toward further research. This is particularly evident in comparisons of data by study area. Lack of apparent deviations from linearity in proportions that survive with time were apparent in all three study areas (Figs. 1–3), indicating that survival is not dependent on age when adulthood is attained; such patterns are similar to those of other long-lived mammals (Eberhardt 1985). However, the estimated survival during winter 1984–85 through 1990–91 differed between the manatees in the Crystal River group and those in the Atlantic Coast group but not between those in the Crystal River group and the Blue Spring group or between manatees in the Blue Spring group and those in the Atlantic Coast group. We suspect that the long-term estimates from the Blue Spring and Crystal River study groups are accurate and approach estimates that would probably be observed in growing, relatively undisturbed populations of manatees (Table 1). Habitat and population-related factors and sampling conditions support this interpretation. At Blue Spring and in the Crystal River but not on the Atlantic Coast, manatee population sizes are growing; aggregation sites are fewer and sampling is logistically easier; histories of protection are longer; anthropogenic mortality (primarily in the Crystal River) is less; habitat quality is better; urbanization is less; migration and movement patterns of manatees are less complex; periods of seasonal use (and availability for sampling) by manatees in winter are longer; the water is clearer; the emphasis on underwater photography is greater; and the continuity of effort is greater (Table 1). Restricted movement patterns in winter, limited numbers of warm-water aggregation sites, superior sampling conditions, and intensity and continuity of effort at Blue Spring and the Crystal River probably have contributed to the high annual capture probabilities of these two groups and the accuracy and precision of the estimates. The higher survival is also reflected in the apparent increases of population size in the Crystal River and at Blue Spring during the study (Ackerman 1995). These differences notwithstanding, the lower survival of the Blue Spring group during the shorter, more recent period of study may signal a decline of survival with time. Additional analyses to determine the validity of such temporal trends are needed.

Interpretation of the survival of manatees on the Atlantic Coast is more problematic. Less favorable habitat

conditions and degree of anthropogenic mortality (Table 1) seem to depress manatee survival on the Atlantic Coast, supporting the accuracy of the low estimates. The telemetry-based estimates also suggested lower adult survival on the Atlantic Coast (Table 9), and survival of the Atlantic Coast group that was estimated with the Cormack-Jolly-Seber models was calculated over a shorter, more recent time span, when mortality factors (particularly numbers of boats) were more intense (Ackerman et al. 1995; Wright et al. 1995). However, efforts to improve sampling and further edit the Atlantic Coast database (Table 1) must be strengthened for more firm conclusions about the accuracy of the survival estimates presented in this paper.

Differences in survival by sex were found only in the Atlantic Coast study group in which survival of male manatees was highest and survival of manatees of unknown sex, the lowest (Table 6). The sex of more than one-third of the manatees in the Atlantic Coast database was unknown (Table 1). The opportunity for an observer to assign a sex category should not affect the manatee's probability of survival. Rather, the probability of determining or verifying the sex of animals that are not observed on multiple occasions is less. At this stage of our understanding, we do not know whether characteristics that reduce the probability of observation somehow bias survival downward or correlate with greater risks to survival. Alternatively, the determination of sex of reproductive females is easier because of the presence of calves. This could advance the speculation that a larger proportion of manatees in the sex-unknown category were males or non-reproductive females and that survival of manatees in these categories is lower. However, this speculation is not supported by the overall higher survival of known males than of known females in the Atlantic Coast group or by the lack of male-female differences in survival in the Crystal River and Blue Spring groups. Rathbun et al. (1990) suggested that males show less year-to-year fidelity in the Crystal River and that females with calves arrived earlier in the winter. This generalization may somehow relate to possible biases in survival estimates in the sex-unknown category on the Atlantic Coast if the latter also consisted largely of males and non-reproductive females. However, the generalization is consistent with capture probabilities of males and females in the Crystal River group but not in the Atlantic Coast group (Table 7). The analysis of mortality data from the hundreds of recovered manatee carcasses in Florida also indicated no substantial differential mortality between the sexes (O'Shea et al. 1985; Marmontel 1993; Ackerman et al. 1995). At this stage, we believe that conclusions about differential survival by sex on the Atlantic Coast are premature and require further analysis.

Implications of Preliminary Survival Estimates for Manatee Population Dynamics

The implied effects of the survival estimates on the long-term growth of Florida manatee populations must be considered in the context of other life-history parameters. We interpret the significance of these estimates to manatee population dynamics within three previously published frameworks: (1) a general population model for marine mammals (Eberhardt and Siniff 1977); (2) the dugong (*Dugong dugon*, Sirenia: Dugongidae) population model (Marsh et al. 1984); and (3) the preliminary population model developed for Florida manatees by Packard (*1985). Further discussion of survival estimates and other aspects of manatee life history in relation to a more updated manatee population model appear in Eberhardt and O'Shea (1995).

Each of the early models defined key variables and assumptions, some of which deviate from more recent knowledge of manatee life-history traits. However, an assumption for each of the early models was a constant probability of survival with age among adults, which our analyses revealed as a realistic assumption for the Florida manatee. Mean life expectancies after the first sighting record are also compatible with the estimated longevity of Florida manatees obtained with skeletochronology (*Marmontel et al. 1990; Marmontel 1995) and from longevity of manatees in captivity (Odell et al. 1995). Our estimates of survival of males and females did not reveal differential mortality between the sexes, except in manatees on the Atlantic Coast, and we remain unsure of the biological foundation for this result.

Eberhardt and Siniff (1977) provided a general model of the relation between adult survival, age at first reproduction, and reproduction rate in marine mammal populations at equilibrium. Adult survival of about 0.93–0.94 is necessary in their model to maintain equilibrium in marine mammal species with an age at first reproduction of 4 or 5 years and a reproduction rate (female births per adult female per year) of 0.18. Manatee data are comparable. Rathbun et al. (1995) calculated a reproduction rate of 0.18 female births/female in manatees in the Crystal River in live-animal studies. However, the relation between these three factors elucidated by Eberhardt and Siniff's (1977) model required a constant survival of immature manatees that was half the adult rate. Survival of immature manatees is poorly known but has been estimated from the minimum number that returned to Blue Spring each winter (O'Shea and Hartley 1995). Survival was at least 0.82 between the first and second winter and essentially reached the adult rate in each year thereafter, making the assumed survival of immature manatees in Eberhardt and Siniff's (1977) calculations seem conservative. Rathbun et al. (1995) also gave a minimum early-calf (neonatal) survival of 0.67 in the Crystal River, based on observations of 82 assumed pregnancies in 51 females during an 8-year period. O'Shea and Hartley (1995) estimated

a similar value of 0.600 based on a smaller sample at Blue Spring. Survival of subadult manatees (approximately aged 2 to 5 years) that we estimated with the telemetry data set lacks precision but is also consistently higher than half the estimated adult rates in these areas (Table 9). Even without taking into account the conservative nature of this model about survival of immature marine mammals, the mean and 95% confidence limits of adult survival in the Crystal River (Table 4) exceeded levels that are necessary for equilibrium growth rates (Eberhardt and Siniff 1977). Adult survival at Blue Spring during the entire study were probably high enough for growth or at least equilibrium. Preliminary estimates of rates of the Atlantic Coast study group are subject to revision (probably upward) but currently indicate a declining population size (Table 4).

Marsh et al. (1984) developed a simple population model for the dugong that suggested a necessary adult survival of about 0.90 to maintain a stable population if intervals between births were 2.5 years, and the mortality of immature dugongs (to age 4 years) was 20%/year. The interval between births and mortality of immature dugongs used in the dugong model are reasonably close to those obtained in studies of the Florida manatee. However, Marsh et al. (1984) assumed an age at first reproduction of 10 years, whereas Florida manatees first reproduce when they are as young as 4 years (Marmontel 1995; O'Shea and Hartley 1995; Rathbun et al. 1995). Nonetheless, at juvenile survival similar to Marsh's et al. (1984) estimate, the adult survival of stable manatee populations according to the dugong model is slightly lower than 0.90 because the manatee population-growth models may be less sensitive to changes in age at first reproduction than to changes in certain other life-history attributes (Eberhardt and Siniff 1977; *Packard 1985). Based on the dugong model, the estimated adult survival of the Blue Spring and Crystal River groups is sufficient to promote population growth, but the preliminary estimates of the Atlantic Coast group are probably less than those required for equilibrium (Table 4).

Packard (*1985) did not provide a specific level of adult survival at which manatee populations maintain equilibrium in her 10-age class model, but growth rates were positive with annual increases of 4.2%/year at $\phi = 0.98$ and barely positive (0.1%) at $\phi = 0.93$. These rates were based on a 2-year interval between births, a 0.61 proportion of breeding females, an annual 0.85 survival of all pre-adult stages, and an initial age structure characteristic of a growing population. In light of recent information (Marmontel 1993, 1995; O'Shea and Hartley 1995; Rathbun et al. 1995; Reid et al. 1995), some of these estimates of life-history traits may also be inaccurate. Ignoring potential discrepancies in lieu of an updated manatee population model (Eberhardt and O'Shea 1995), according to Packard's (*1985) 10-age class model our estimated adult survival (Table 4) also indicated population-size increases in the Crystal River and at Blue Spring but a decline in the Atlantic Coast study group.

The population status of the three study groups supports our interpretations of survival with these models. Although the influences of immigration and internal recruitment have not yet been quantified, manatee populations in the Crystal River and at Blue Spring have clearly grown steadily from the early 1970's to the early 1990's (O'Shea 1988; Rathbun et al. 1990; Ackerman 1995). Analyses of aerial counts of manatees in the Atlantic Coast aggregation sites revealed a statistically significant increase, but the influence of numerous confounding factors and unexplained variation (e.g., improved counting ability, changes in conditions, or true population growth) obscure the true basis for this apparent increase (Ackerman 1995; Garrott et al. 1995). High survival and population growth in the Crystal River are probably due, at least in part, to lower pressures from anthropogenic mortality than in other parts of Florida, significant amounts of less developed habitat and abundant forage throughout the annual range, and a longer history of protection (Powell and Rathbun 1984; O'Shea et al. 1985; O'Shea 1988; Rathbun et al. 1990; Ackerman 1995; Ackerman et al. 1995). Manatees at Blue Spring have also experienced greater protection since the mid-1970's, although much of the annual range encompasses habitat that has probably been subjected to greater development pressure and increased human activities than the annual range of habitat of manatees in the Crystal River group. For several years, manatees in the Atlantic Coast study area (including the entire St. Johns River) experienced a significantly higher proportion and total number of anthropogenic deaths than the group in the Crystal River area (O'Shea et al. 1985; Ackerman et al. 1995). These anthropogenic sources of mortality may be additive to natural causes and may contribute to the lower estimated survival of the Atlantic Coast group in our analyses. Conservation may be particularly troublesome if the lower survival of adult females on the Atlantic Coast is verified in future analyses. Two major caveats to these interpretations are that our results do not provide information that reflects changes in survival trends during the last 2 years of study and that we have not further subdivided survival to determine whether significant changes occurred in study groups over time.

Conclusions and Recommendations

Unlike other methods of estimating survival, the application of the Cormack-Jolly-Seber models to the manatee photo-identification database has great potential. The survival we estimated is concordant with other manatee population data and independent of some of the problems associated with interpretation of mortality from data from

carcasses and from aerial counts (Ackerman 1995; Ackerman et al. 1995; Garrott et al. 1995; Lefebvre et al. 1995). The survival data have a more robust statistical basis, are complementary to the survey and carcass counts, and, when considered with other aspects of manatee population dynamics, allow a better definition of long-term management objectives. We therefore encourage future detailed investigations of survival estimation that include greater emphasis on model selection and hypothesis testing. In addition to adult survival, estimation of subadult survival should also be investigated. We also recommend that the photo-identification data collection and data processing activities be continued and enhanced wherever possible. In particular, standardizing cataloging criteria among study groups and determining whether new sampling procedures in Atlantic Coast sites result in higher probabilities of capture values should be priorities. Our findings imply that maintenance of habitat quality and protective measures such as those long instituted on the Crystal River are accompanied by the high adult survival that is critical to population growth. Similar efforts must be continued or strengthened elsewhere to achieve or maintain high adult survival and greater progress toward recovery of the Florida manatee.

Acknowledgments

The data in this project were gathered by numerous individuals. Emphasis on long-term observations of manatees to meet other objectives was recommended in a 1978 workshop (*Brownell and Ralls 1981), and initial field efforts of developing photo-identification techniques for individual recognition of manatees over broad areas were made by G. Rathbun and J. Powell with support from J. Wilcox and the Florida Power and Light Company. W. Hartley, Florida Park Service, conducted identification surveys at Blue Spring with dedication and a meticulous eye for detail since assuming this responsibility in 1981. Numerous other individuals conducted research involving manatee identification and radio-tracking at Blue Spring during our study including L. Barnes, J. Bengtson, D. Blomstrom, K. Brugger, S. Fitzgerald, J. Kenner, S. Shane, J. Powell, and R. Summers. Radio-tracking data from Blue Spring in 1978 and 1979 were collected as part of the study with telemetry by J. Bengtson and his colleagues of the University of Minnesota. Manatee capture and tagging at Blue Spring and Crystal River from 1978 to 1985 were supervised by the Sirenia Project under G. Rathbun and included capture teams of numerous individuals and organizations. Most photo-identification and tagging data from studies on the Crystal River were gathered by G. Rathbun, J. Reid, R. Bonde, and J. Powell. On the Atlantic Coast, numerous individuals have provided assistance and collected data during tracking and photo-identification, which were coordinated by J. Reid. Those involved in studies on the Atlantic Coast were K. Abbott, C. Beck, R. Bonde, K. Curtin, D. Easton, M. Eifler, D. Perrine, J. Powell, J. Provancha, S. Shane, M. Suarez, S. Tyson, J. Valade, and B. Zoodsma. C. Beck and C. Campbell provided extra efforts to organize the Manatee Individual Identification System database and photographic files for these and other analyses. Identifications of dead manatees from recovered carcasses involved numerous personnel coordinated by the Florida Department of Environmental Protection, U.S. Fish and Wildlife Service, and University of Miami. The Florida Power and Light Company, Florida Audubon Society, and Save The Manatee Club provided critical support for various aspects of this research. Program RECAPCO was provided by S. Buckland and K. Catanach, Scottish Agricultural Statistics Service, Macaulay Land Use Research Institute, Craigiebuckler, Aberdeen AB9 2QJ, Scotland. Programs JOLLY and CONTRAST were provided by J. Hines, J. Nichols, and J. Sauer of the Population Estimation and Modeling Group at the Patuxent Wildlife Research Center, U.S. Fish and Wildlife Service, Laurel, Maryland. D. DeMaster, L. Eberhardt, J. Nichols, and K. Pollock provided many useful suggestions at the 1992 workshop that improved preliminary analyses. H. Kochman and J. Nichols provided additional guidance to Langtimm, who conducted and interpreted the computer analyses. The manuscript was improved by comments of C. Deutsch, J. Nichols, and two anonymous referees.

Cited References[4]

Ackerman, B. B. 1995. Aerial surveys of manatees: a summary and progress report. Pages 13–33 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Ackerman, B. B., S. D. Wright, R. K. Bonde, D. K. Odell, and D. J. Banowetz. 1995. Trends and patterns in mortality of manatees in Florida, 1974–1992. Pages 223–258 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Beck, C. A., and J. P. Reid. 1995. An automated photo-identification catalog for studies of the life history of the Florida manatee. Pages 120–134 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

*Beeler, I. E., and T. J. O'Shea. 1988. Distribution and mortality of the West Indian manatee (*Trichechus manatus*) in the southeastern United States: a compilation and review of recent information. National Technical Information Service, Springfield, Va. Document PB 88-207980/AS. 613 pp.

[4] An asterisk denotes unpublished material.

Bengtson, J. L. 1981. Ecology of manatees (*Trichechus manatus*) in the St. Johns River, Florida. Ph.D. dissertation, University of Minnesota, Minneapolis. 126 pp.

Brownie, C., D. R. Anderson, K. P. Burnham, and D. S. Robson. 1985. Statistical inference from band recovery data: a handbook. Second edition. U.S. Fish and Wildlife Service Resource Publication 156. 305 pp.

Brownie, C., J. E. Hines, J. D. Nichols, K. H. Pollock, and J. B. Hestbeck. 1993. Capture–recapture studies for multiple strata including non-Markovian transitions. Biometrics 49:1173–1187.

Buckland, S. T. 1980. A modified analysis of the Jolly-Seber capture–recapture model. Biometrics 36:419–435.

Buckland, S. T. 1982. A mark–recapture survival analysis. Journal of Animal Ecology 51:833–847.

Buckland, S. T. 1990. Estimation of survival rates from sightings of individually identifiable whales. Pages 149–153 *in* P. S. Hammond, S. A. Mizroch, and G. P. Donovan, editors. Individual recognition of cetaceans: use of photo-identification techniques to estimate population parameters. Report of the International Whaling Commission Special Issue 12. International Whaling Commission, Cambridge, England.

*Buckland, S. T. 1991. RECAPCO. Program for a mark–recapture survival analysis using the modified Jolly-Seber model. Scottish Agricultural Statistics Service, Aberdeen Unit, Macaulay Land Use Research Institute, Craigiebuckler, Aberdeen, Scotland. 5 pp.

Buckland, S. T., and P. H. Garthwaite. 1991. Quantifying precision of mark–recapture estimates using the bootstrap and related methods. Biometrics 47:255–268.

Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release–recapture. American Fisheries Society Monograph 5:1–437.

Carothers, A. D. 1973. The effects of unequal catchability on Jolly-Seber estimates. Biometrics 29:79–100.

Carothers, A. D. 1979. Quantifying unequal catchability and its effect on survival estimates in an actual population. Journal of Animal Ecology 48:863–869.

Cormack, R. M. 1964. Estimates of survival from the sighting of marked animals. Biometrika 51:429–438.

DeMaster, D. P., and J. K. Drevenak. 1988. Survivorship patterns in three species of captive cetaceans. Marine Mammal Science 4:297–311.

Eberhardt, L. L. 1985. Assessing the dynamics of wild populations. Journal of Wildlife Management 49:997–1012.

Eberhardt, L. L., and D. B. Siniff. 1977. Population dynamics and marine mammal management policies. Journal of the Fisheries Research Board of Canada 34:183–190.

Eberhardt, L. L., and T. J. O'Shea. 1995. Integration of manatee life-history data and population modeling. Pages 269–279 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Garrott, R. A., B. B. Ackerman, J. R. Cary, D. M. Heisey, J. E. Reynolds, III, and J. R. Wilcox. 1995. Assessment of trends in sizes of populations at several Florida manatee aggregation sites. Pages 34–55 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Hammond, P. S. 1986. Estimating the size of naturally marked whale populations using capture–recapture techniques. Pages 253–282 *in* G. P. Donovan, editor. Behaviour of whales in relation to management. Report of the International Whaling Commission Special Issue 8. International Whaling Commission, Cambridge, England.

Hammond, P. S., S. A. Mizroch, and G. P. Donovan, editors. 1990. Individual recognition of cetaceans: use of photo-identification techniques to estimate population parameters. Report of the International Whaling Commission Special Issue 12. International Whaling Commission, Cambridge, England. 440 pp.

Hartman, D. S. 1979. Ecology and behavior of the manatee (*Trichechus manatus*) in Florida. American Society of Mammalogists Special Publications 5. Lawrence, Kans. 153 pp.

Heisey, D. M., and T. K. Fuller. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. Journal of Wildlife Management 49:668–674.

Hernandez, P., J. E. Reynolds, III, H. Marsh, and M. Marmontel. 1995. Age and seasonality in spermatogenesis of Florida manatees. Pages 84–97 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Hestbeck, J. B., J. D. Nichols, and R. A. Malecki. 1991. Estimates of movement and site fidelity using mark-resight data of wintering Canada Geese. Ecology 72:523–533.

Hines, J. E., and J. R. Sauer. 1989. Program CONTRAST: a general program for the analysis of several survival or recovery rate estimates. U.S. Fish and Wildlife Service Fish and Wildlife Technical Report 24. 7 pp.

Jolly, G. M. 1965. Explicit estimates from capture–recapture data with both death and immigration—stochastic model. Biometrika 52:225–247.

Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67–118.

Lefebvre, L. W., B. B. Ackerman, K. M. Portier, and K. H. Pollock. 1995. Aerial survey as a technique for estimating trends in manatee population size—problems and prospects. Pages 63–74 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Marmontel, M. 1993. Age determination and population biology of the Florida manatee, *Trichechus manatus latirostris*. Ph.D. dissertation, University of Florida, Gainesville. 408 pp.

Marmontel, M. 1995. Age and reproduction in female Florida manatees. Pages 98–119 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

*Marmontel, M., T. J. O'Shea, and S. R. Humphrey. 1990. An evaluation of bone growth-layer counts as an age-determination technique in Florida manatees. National Technical Information Service, Springfield, Va. Document PB 91–103564. 94 pp.

Marsh, H., G. E. Heinsohn, and L. M. Marsh. 1984. Breeding cycle, life history, and population dynamics of the dugong, *Dugong dugon* (Sirenia: Dugongidae). Australian Journal of Zoology 32:767–788.

Mayfield, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456–466.

Nichols, J. D. 1992. Capture–recapture models: using marked animals to study population dynamics. BioScience 42:94–102.

Odell, D. K., G. D. Bossart, M. T. Lowe, and T. D. Hopkins. 1995. Reproduction of the West Indian manatee in captivity. Pages 192–193 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

O'Shea, T. J. 1988. The past, present, and future of manatees in the southeastern United States: realities, misunderstandings and enigmas. Pages 184–204 *in* R. R. Odom, K. A. Riddleberger, and J. C. Ozier, editors. Proceedings of the Third Southeastern Nongame and Endangered Wildlife Symposium. Georgia Department of Natural Resources, Game and Fish Division, Social Circle.

O'Shea, T. J., C. A. Beck, R. K. Bonde, H. I. Kochman, and D. K. Odell. 1985. An analysis of manatee mortality patterns in Florida, 1976–1981. Journal of Wildlife Management 49:1–11.

O'Shea, T. J., and W. C. Hartley. 1995. Reproduction and early-age survival of manatees at Blue Spring, upper St. Johns River, Florida. Pages 157–170 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

O'Shea, T. J., and R. L. Reep. 1990. Encephalization quotients and life-history traits in the Sirenia. Journal of Mammalogy 71:534–543.

*Packard, J. M. 1985. Preliminary assessment of uncertainty involved in modeling manatee populations. Manatee Population Research Report 9. Technical Report 8–9. Florida Cooperative Fish and Wildlife Research Unit, University of Florida, Gainesville. 19 pp.

*Packard, J. M., and J. D. Nichols. 1983. Sample size estimates: a preliminary analysis of sample sizes required for mark-recovery and mark-resighting studies of manatees (*Trichechus manatus*) in Florida. Manatee Population Research Report 4. Technical Report 8. Florida Cooperative Fish and Wildlife Research Unit, University of Florida, Gainesville. 14 pp.

Pollock, K. H. 1982. A capture–recapture design robust to unequal probability of capture. Journal of Wildlife Management 46:752–757.

Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture–recapture experiments. Wildlife Monographs 107:1–97.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53:7–15.

Powell, J. A., and G. B. Rathbun. 1984. Distribution and abundance of manatees along the northern coast of the Gulf of Mexico. Northeast Gulf Science 7:1–28.

*Powell, J. A., and J. C. Waldron. 1981. The manatee population in Blue Spring, Volusia County, Florida. Pages 33–40 *in* *R. L. Brownell, Jr., and K. Ralls, editors. 1981. The West Indian manatee in Florida. Proceedings of a workshop held in Orlando, Fla., 27–29 March 1978. Florida Department of Natural Resources, Tallahassee. 154 pp.

Rathbun, G. B., J. P. Reid, R. K. Bonde, and J. A. Powell. 1995. Reproduction in free-ranging Florida manatees. Pages 135–156 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

*Rathbun, G. B., J. P. Reid, and J. B. Bourassa. 1987. Design and construction of a tethered, floating radio-tag assembly for manatees. National Technical Information Service, Springfield, Va. Document PB 87-161345/AS. 49 pp.

Rathbun, G. B., J. P. Reid, and G. Carowan. 1990. Distribution and movement patterns of manatees (*Trichechus manatus*) in northwestern peninsular Florida. Florida Marine Research Publications 48:1–33.

Reid, J. P., R. K. Bonde, and T. J. O'Shea. 1995. Reproduction and mortality of radio-tagged and recognizable manatees on the Atlantic Coast of Florida. Pages 171–191 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

*Reid, J. P., and T. J. O'Shea. 1989. Three years operational use of satellite telemetry on Florida manatees: tag improvements based on challenges from the field. Pages 217–232 *in* Proceedings of the 1989 North American Argos Users Conference. Service Argos, Inc., Landover, Md.

Reid, J. P., G. B. Rathbun, and J. R. Wilcox. 1991. Distribution patterns of individually identifiable West Indian manatees (*Trichechus manatus*) in Florida. Marine Mammal Science 7:180–190.

Rohlf, R. R., and Sokal, F. J. 1981. Statistical tables. Second edition. W. H. Freeman and Company, San Francisco. 219 pp.

SAS Institute, Inc. 1985. SAS language guide for personal computers. Version 6 edition. SAS Institute, Cary, N.C. 429 pp.

Sauer, J. R., and B. K. Williams. 1989. Generalized procedures for testing hypotheses about survival or recovery rates. Journal of Wildlife Management 53:137–142.

Seber, G. A. F. 1965. A note on the multiple-recapture census. Biometrika 52:249–259.

Siniff, D. B., and K. Ralls. 1991. Reproduction, survival and tag loss in California sea otters. Marine Mammal Science 7:211–229.

Slooten, E., S. M. Dawson, and F. Lad. 1992. Survival rates of photographically identified Hector's dolphins from 1984 to 1988. Marine Mammal Science 8:327–343.

Thomas, J. A., L. H. Cornell, B. E. Joseph, T. D. Williams, and S. Dreischman. 1987. An implanted transponder chip used as a tag for sea otters (*Enhydra lutris*). Marine Mammal Science 3:271–274.

Trent, T. T., and O. J. Rongstad. 1974. Home range and survival of cottontail rabbits in southwestern Wisconsin. Journal of Wildlife Management 38:459–472.

Wright, S. D., B. B. Ackerman, R. K. Bonde, C. A. Beck, and D. J. Banowetz. 1995. Analysis of watercraft-related mortality of manatees in Florida, 1979–1991. Pages 259–268 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Appendix. Sighting histories of adult Florida manatees (*Trichechus manatus latirostris*) used in the analyses with the Cormack-Jolly-Seber model.

The estimated survival of the manatees in each study area will change in future analyses as the photo-identification database is revised and new sightings and classifications are made every year. Refinements in cataloging criteria and other improvements in methodological approaches may cause revisions of estimates. We therefore recorded the database that we used for our calculations in this appendix. In each table, the manatees are identified by their catalog numbers, consisting of a two-letter code that represents the initial sighting area (for an explanation in abbreviations for place names see Beck and Reid 1995) and a three-digit number. The sex of each manatee is then given (M = male, F = female, ? = unknown) and is followed by the sighting history that consists of a series of 14 single-digit numbers in columns that represent each consecutive winter beginning 1977–78 and ending 1990–91. The single-digit numbers are coded as follows: 0 = individual not observed that winter; 1 = individual observed alive that winter; 3 = known to die that winter; 4 = known to die before the following winter.

Table A-1. Sighting histories of Florida manatees (*Trichechus manatus latirostris*) in the Crystal River area in winter.

ID	SEX	Sighting record 1977–78 to 1990–91	ID	SEX	Sighting record 1977–78 to 1990–91
CR002	M	10011111001000	CR090	F	01100000000000
CR003	M	11010000001000	CR091	M	00001111111111
CR004	M	11010000000000	CR093	F	11011111111111
CR005	M	11111111111101	CR094	M	11111111111111
CR006	M	11011111110100	CR097	F	01111111111111
CR009	F	11111113000000	CR099	F	01101111111100
CR010	M	11011111111111	CR100	M	01111111111111
CR014	F	11111111100000	CR101	M	01010000111101
CR016	M	11010111011101	CR104	F	00000111111111
CR017	M	10011011011100	CR105	F	11111111101010
CR018	M	00011111111111	CR106	F	00111111011111
CR019	F	11111111111111	CR107	F	00000011011000
CR020	M	11111111101111	CR108	M	11111100000000
CR021	M	11101111111111	CR110	F	01111111011101
CR022	F	11111111011111	CR111	F	00000010111111
CR023	M	10111110111111	CR113	M	00000011111111
CR025	M	11111111111110	CR114	M	01000111111100
CR026	F	11111111111111	CR117	M	10100000000000
CR027	F	11110111111111	CR119	M	00000011011001
CR028	F	11111111111111	CR120	M	00010000000000
CR029	F	11100000000000	CR121	F	00000010010101
CR030	M	11111111111111	CR123	F	00111111111111
CR031	M	11111111110101	CR125	F	00011111111110
CR032	F	11111111111111	CR126	F	00000001111101
CR033	F	11111111011101	CR128	M	00011111011110
CR034	M	11111111111111	CR130	F	00000001111111
CR035	F	10000000000000	CR131	F	00111110000000
CR036	M	11111111000000	CR132	M	00001040000000
CR037	M	11111111011110	CR133	F	00001111111111
CR038	M	11110000000000	CR134	F	01101111111111
CR039	F	11111130000000	CR137	M	00011111400000
CR040	F	11111111100000	CR138	M	10111111000100
CR041	F	11011111111111	CR139	F	01001111101110
CR042	M	11000111111111	CR140	M	01111111111111
CR043	F	11111111011000	CR141	M	00010111111001
CR045	F	11111011111100	CR142	M	01011111110000
CR046	F	11111111111110	CR144	M	00011111011011
CR047	?	11100010000000	CR145	M	00111111111011
CR049	F	11111111111111	CR146	M	00001111111111
CR051	F	11111100000000	CR147	M	00000001111101
CR052	M	11011011000000	CR150	F	00000000011111
CR054	F	11101111011111	CR151	F	00000000010111
CR058	M	11100100000000	CR152	M	00000000010101
CR059	M	11110000010000	CR157	F	00000000011111
CR060	F	11111111100101	CR158	F	00000100000000
CR061	F	11111111111111	CR159	M	00000011111111
CR063	M	11111111111111	CR160	F	00111110111111
CR069	M	11110000000000	CR161	M	00000010101110
CR070	F	11111111111111	CR162	M	00000001111111
CR071	F	11111111111111	CR163	M	00000001011100
CR075	F	11111111011110	CR165	M	00000011101100
CR078	M	01110111110101	CR166	F	00000100000000
CR083	F	11111111110000	CR167	M	00000000111110
CR085	M	11000111111111	CR168	F	00000111011101
CR087	F	11111111111111	CR169	F	00001111001000
CR089	M	01111111111101	CR170	M	00000000001111

Table A-1. *Continued.*

ID	SEX	Sighting record 1977–78 to 1990–91	ID	SEX	Sighting record 1977–78 to 1990–91
CR171	F	00000001110111	CR241	F	00000000000111
CR172	M	00001111111101	CR242	M	00000000000001
CR175	M	00000001111111	CR243	M	00000100011010
CR176	M	00000000111111	CR244	M	00000010111111
CR177	F	00001110011111	CR245	M	00000000111111
CR179	F	00101111111111	CR246	M	00000000111100
CR180	F	00000000001010	CR247	M	00000000000111
CR181	M	00000000001111	CR248	M	00000000000111
CR183	M	00000000001111	CR249	M	00000000000011
CR184	M	00001111111101	CR250	F	00000000011000
CR185	M	00000010000011	CR251	F	00000000001111
CR186	F	00000000111110	CR252	M	00000000000111
CR188	M	00000000101110	CR253	M	00000000011111
CR189	M	00000000111110	CR254	F	00000000000111
CR191	F	00000011111110	CR255	F	00000000111111
CR193	F	00000000001110	CR256	F	00000000011101
CR194	M	00000001111001	CR257	F	00000000000010
CR195	M	00000000101101	CR258	M	00000000000001
CR197	F	00000000111110	CR259	M	00000000000110
CR198	F	00000000000110	CR260	M	00000000001110
CR200	M	00000001110100	CR261	M	00000000000111
CR201	M	00000011111111	CR262	F	00000000010010
CR202	F	00000000011111	CR263	F	00000000000111
CR203	F	00000111013000	CR264	M	00000000001111
CR205	F	00000001111110	CR265	M	00000000000110
CR207	F	00000111111110	CR266	F	00000000000110
CR208	M	00000000001110	CR267	M	00000000000011
CR209	M	00000111111100	CR270	F	00000000010101
CR210	M	00000000111101	CR271	F	00000000000110
CR211	F	00000111111111	CR273	M	00000000000100
CR212	M	00000000111111	CR274	M	00000000001100
CR214	F	00000000111101	CR275	F	00000001111010
CR215	M	00000010111111	CR276	M	00000000001101
CR216	M	00000000011111	CR277	F	00000000000011
CR217	M	00001001000000	CR278	F	00000000000010
CR218	M	00000000010101	CR279	M	00000000001000
CR219	M	00000000011111	CR280	F	00000000111111
CR220	F	00000000001000	CR281	M	00000000000110
CR221	M	00000011001000	CR282	F	00000000011100
CR222	F	00000011000000	CR283	F	00000000000111
CR223	M	00000000011101	CR284	M	00000000011101
CR224	M	00000000111111	CR285	M	00000000000111
CR225	F	00000000000100	CR287	M	00000000001111
CR226	F	00000000011111	CR288	M	00000000000101
CR227	F	00000011111111	CR289	M	00000000111000
CR228	F	00001001100000	CR290	M	00000000111011
CR229	M	00000000100000	CR292	M	00000000011010
CR230	M	00000000000010	CR293	M	00000000001111
CR231	M	00000001011100	CR294	F	00000000001110
CR232	M	00000001000000	CR295	F	00000001011010
CR235	F	00000000001111	CR296	M	00000000000100
CR236	F	00000000011011	CR298	M	00000000101111
CR237	F	00000001101110	CR299	F	00000000001110
CR238	F	00000000000111	CR301	M	00000000000111
CR239	?	00000001100000	CR302	F	00000000000101
CR240	F	00000000000101	CR303	F	00000000000111

Table A-1. *Continued.*

ID	SEX	Sighting record 1977–78 to 1990–91	ID	SEX	Sighting record 1977–78 to 1990–91
CR304	F	00000000010110	CR319	M	00000000000111
CR305	F	00000000000101	CR322	M	00000000001110
CR307	M	00000000001100	CR323	F	00000000000111
CR308	M	00000000000110	CR324	F	00000000000001
CR309	M	00000000000010	CR325	M	00000000011111
CR310	M	00000000011000	CR326	M	00000000001111
CR311	F	00000000001100	CR327	M	00000000001111
CR312	M	00000000000111	CR328	M	00000000000100
CR313	F	00000000000111	CR329	F	00000000001000
CR314	M	00000000000100	CR331	M	00000000011000
CR315	M	00000000000111	CR332	M	00000000000111
CR316	F	00000000101000	CR333	F	00000000000001
CR317	F	00000000000110	CR336	M	00000000001101
CR318	M	00000000000001			

Table A-2. Sighting histories of Florida manatees (*Trichechus manatus latirostris*) in the Blue Spring area in winter.

ID	Sex	Sighting record 1977–78 to 1990–91	ID	Sex	Sighting record 1977–78 to 1990–91
BS001	M	00011111111111	BS054	F	00000000001111
BS002	M	11111111111111	BS055	F	00000000001111
BS003	M	00111111111111	BS056	F	00000100000100
BS004	F	11111111111111	BS057	M	00000111111111
BS005	F	11111111111111	BS058	M	00000110111111
BS006	M	11111300000000	BS059	M	00000110011113
BS008	F	11111111100000	BS060	M	00000110111111
BS009	F	11111111300000	BS063	M	00000000000111
BS010	M	11111111111111	BS064	M	00000010111111
BS011	M	11111111111111	BS065	M	00000010111111
BS013	M	11111111111111	BS066	M	00000010100000
BS014	M	11111111111111	BS067	M	00000000000011
BS017	F	11111111111113	BS068	M	00000001111011
BS019	M	11111111111111	BS069	M	00000001000000
BS020	M	01110110000000	BS071	M	00000000000011
BS022	M	11111111111110	BS072	M	00000000000001
BS023	M	03000000000000	BS073	F	00000000000001
BS024	F	01111111111111	BS079	M	00000000100000
BS025	M	00000011111111	BS080	M	00000000101000
BS026	M	01111110111111	BS081	M	00000000100000
BS028	M	00000011111111	BS082	M	00000000111111
BS029	M	00000001111111	BS083	M	00000000111111
BS030	M	00000001000000	BS086	M	00000000100000
BS032	M	00111110111111	BS088	M	00000000011110
BS033	M	00111110111111	BS089	M	00000000000011
BS034	M	00011010111111	BS090	?	00000000010000
BS035	M	00000000111111	BS093	M	00000000001000
BS036	F	00000000113000	BS094	M	00000000001010
BS037	F	00000000111111	BS104	M	00000000000100
BS039	F	00010000111000	BS105	M	00000000000100
BS040	F	00011111011111	BS106	F	00000000000011
BS041	M	00010000010000	BS107	F	00000000000011
BS042	M	00010000101111	BS109	F	00000000000001
BS043	M	00010100000000	BS112	M	00000000000001
BS045	M	00000000011111	BS114	M	00000000000001
BS047	M	00000030000000	BS116	?	00000000000001
BS049	F	00001111111400	BS117	?	00000000000010
BS050	F	00001000000000	BS123	?	00000000000001
BS051	M	00001000004000	BS124	F	00000000000003
BS053	M	00000000001111			

Table A-3. Sighting histories of Florida manatees (*Trichechus manatus latirostris*) in the Atlantic Coast area in winter.

ID	Sex	Sighting record 1977–78 to 1990–91	ID	Sex	Sighting record 1977–78 to 1990–91
BC004	?	00000010000111	BC295	M	00000000000101
BC009	M	00011101001011	BC296	?	00000000010110
BC012	F	00001111101101	BC297	?	00000000000111
BC013	?	00001000001011	BC298	?	00000000010011
BC031	F	00111111011101	BC299	?	00000000000001
BC057	F	00001001001001	BC300	F	00000000000111
BC058	F	10000001010011	BC301	F	00000000011111
BC068	M	00011011110001	BC302	F	00000000000011
BC085	F	01110101000000	BC303	F	00000000000011
BC092	?	00000000010000	BC304	?	00000000000011
BC103	F	00000000000001	BC305	M	00000000000001
BC110	?	00001000011011	BC306	F	00000000001001
BC145	?	00000000000030	BC309	M	00000000000111
BC146	?	00000101000400	BC310	?	00000000000001
BC155	M	00000000011101	BC311	?	00000000010011
BC156	M	00000100101010	BC313	M	00000000000011
BC179	F	00100011110111	BC314	F	00000000000011
BC180	F	00001001110111	BC315	F	00000000000010
BC187	M	00000000001011	BC316	?	00000000001001
BC191	?	00000101110000	BC317	M	00000000001001
BC200	F	00000101111111	BC319	?	00000000000101
BC202	M	00000011101111	BC320	?	00000000000011
BC209	?	00100000000100	BC322	?	00000000000001
BC216	M	00000001111001	BC323	?	00000000001101
BC218	M	00000000011104	BC324	?	00000000001111
BC229	F	00000011111000	BC325	?	00000000000101
BC237	F	00000000010000	FP001	?	00000000000011
BC240	?	00000011000000	FP002	?	00000000000001
BC246	M	00000100011011	FP003	M	00000000000011
BC248	F	00000010001110	FP004	?	00000000000001
BC249	?	00000100010000	JX001	?	00000100000004
BC253	M	00000000111111	JX004	M	00000011001101
BC256	?	00000011101100	JX014	?	00000000000100
BC257	M	00000000001011	JX015	F	00000101000000
BC258	F	00000011000110	JX019	?	00000101001000
BC260	F	00000010001000	JX020	?	00000001001101
BC261	?	00000000010000	JX029	?	00000000000001
BC263	F	00000010000000	JX032	?	00000000001000
BC264	?	00000000011010	MI003	?	00000011110000
BC265	F	00000010101000	MI006	?	00000011113000
BC266	F	00000011100000	MI007	?	00000000000001
BC267	F	00000011101100	MI009	?	00000001000010
BC268	M	00000000010001	MI012	?	00000001010000
BC269	F	00000000000101	MI017	M	00000000011111
BC271	F	00000001000001	MI019	?	00000000010000
BC272	?	00000000001100	MI020	F	00000000011000
BC274	M	00000000000011	MI021	?	00000000001111
BC278	?	00000100100111	MI022	?	00000000000111
BC280	F	00000000001101	MI023	?	00000000001111
BC281	F	00000000001104	MI024	M	00000000000011
BC285	F	00000000111000	MI025	?	00000000000001
BC287	?	00000000001001	MI026	F	00000000000001
BC290	F	00000000001100	MI027	M	00000000000011
BC291	F	00000000000110	MI028	F	00000000000001
BC292	?	00000000000100	MI030	F	00000000001111
BC293	?	00000000000011	PE009	F	00000001110011

Table A-3. *Continued.*

ID	Sex	Sighting record 1977–78 to 1990–91	ID	Sex	Sighting record 1977–78 to 1990–91
PE011	F	00001011101111	PE147	F	00000001001000
PE015	F	00001001101100	PE148	?	00000000000110
PE016	F	00001000000011	PE149	F	00000000010001
PE021	F	00001000000110	PE150	?	00000001100000
PE026	?	00000000100000	PE151	F	00000001100000
PE032	F	00001100101111	PE152	F	00000000101000
PE038	F	00001001100001	PE154	F	00000000111111
PE041	F	00000000100011	PE155	?	00000000001101
PE043	F	00001000000010	PE156	?	00000000101000
PE045	F	00000001000010	PE157	F	00000000111011
PE046	F	00000111111100	PE158	M	00000000100003
PE047	F	00000101010000	PE159	F	00000000100011
PE049	F	00000101000000	PE160	?	00000001100000
PE051	?	00000000001010	PE161	F	00000001100000
PE052	F	00000101001101	PE162	?	00000000000101
PE056	F	10000111101111	PE163	F	00000001100010
PE064	?	00000000100000	PE164	M	00000000011001
PE065	F	00000001111111	PE165	F	00000000110111
PE069	F	00000101111101	PE166	F	00000000000011
PE073	?	00000001100001	PE167	F	00000001110000
PE076	M	00000000100111	PE168	F	00000000010000
PE077	F	00000100000000	PE171	?	00000000110000
PE082	?	00000110000000	PE172	F	00000000011111
PE094	?	00000000111000	PE173	F	00000000010000
PE095	?	00000001100000	PE174	F	00000000010100
PE096	?	00000000100000	PE175	F	00000000000011
PE098	?	00000011000000	PE176	M	00000000000111
PE099	F	00000000110111	PE178	?	00000000000011
PE102	F	00000011000001	PE179	?	00000000000011
PE103	?	00000000101110	PE180	M	00000000001111
PE105	F	00000001110111	RB006	F	00000000001000
PE106	F	00000001110001	RB007	F	00000001100000
PE107	M	00000000110110	RB027	F	00000001000111
PE112	F	00000001001101	RB031	F	00000001001000
PE114	F	00000001010000	RB045	M	00000001011011
PE117	?	00000000000111	RB046	F	00000000101000
PE119	F	00000011111101	RB048	F	00000001011010
PE120	F	00000001111101	RB050	F	00000100011001
PE121	F	00000101010000	RB059	M	00000000000001
PE123	F	00000001000000	RB068	F	00000101010111
PE125	?	00000000010001	RB069	?	00000000100000
PE127	?	00000001100000	RB071	F	00000001101001
PE128	?	00000001111011	RB101	F	00000000010000
PE130	?	00000000011111	RB116	F	00000001100000
PE131	F	00000001100000	RB131	F	00000101101011
PE132	M	00000000010001	RB132	?	00000001100000
PE133	?	00000001100001	RB137	?	00000100000000
PE134	?	00000001110001	RB156	?	00000001001000
PE135	F	00000001000001	RB160	F	00000100000101
PE136	F	00000000000101	RB165	F	00000001111011
PE138	F	00000001100000	RB229	F	00010000110000
PE139	?	00000000100000	RB257	F	00000001011011
PE143	?	00000001010010	RB260	F	00001101011011
PE144	?	00000001101000	RB264	F	00000000100000
PE145	F	00000001111111	RB265	F	00000000001011
PE146	F	00000000001000	RB268	?	00000001000000

Table A-3. *Continued.*

ID	Sex	Sighting record 1977–78 to 1990–91	ID	Sex	Sighting record 1977–78 to 1990–91
RB274	F	00000101111000	RB413	F	00000000001000
RB279	F	00000100000001	RB415	F	00000001000000
RB280	M	00000001101011	RB416	?	00000001000000
RB281	M	00000001100000	RB417	?	00000001000000
RB283	?	00000000001010	RB418	?	00000001000001
RB284	?	00000001000000	RB419	F	00000001101100
RB289	F	00000000010001	RB420	M	00000000001010
RB294	?	00000000100000	RB421	?	00000000001010
RB295	M	00000001011010	RB422	F	00000001101100
RB297	F	00000000101010	RB424	F	00000001100000
RB301	F	00001101100010	RB425	?	00000001300000
RB302	F	00000001000000	RB426	?	00000000001000
RB304	F	00000100000000	RB428	?	00000000001000
RB306	F	00000000011000	RB429	M	00000000001000
RB308	F	00000100000001	RB430	F	00000001101000
RB311	?	00000100000000	RB431	F	00000000110000
RB312	M	00000000011111	RB433	?	00000000010000
RB315	?	00000000001000	RB434	F	00000000100000
RB320	F	00000000010000	RB435	F	00000000100010
RB321	F	00000000101000	RB436	F	00000001110000
RB322	?	00000000010000	RB437	F	00000000100000
RB323	?	00000000111011	RB439	F	00000000100001
RB324	?	00000101101001	RB442	M	00000001101011
RB327	M	00000000001001	RB443	F	00000000111010
RB329	F	00000001000000	RB444	M	00000000010011
RB330	?	00000000000010	RB445	M	00000000010000
RB334	F	00000000010000	RB447	F	00000000110000
RB337	M	00000001110000	RB449	F	00000000110001
RB349	?	00000011001010	RB450	M	00000000110000
RB350	?	00000001000000	RB451	F	00000000101001
RB353	F	00001001111011	RB452	F	00000000110010
RB368	?	00000001111110	RB453	?	00000000111000
RB377	F	00001000011000	RB454	F	00000000001010
RB378	F	00001000000000	RB455	?	00000000011000
RB379	?	00000001000000	RB456	F	00000000011010
RB383	F	00000001000000	RB457	F	00000000010010
RB385	?	00000001101000	RB458	F	00000000010000
RB387	F	00000000000001	RB459	F	00000000011011
RB388	?	00000001010000	RB460	?	00000000010100
RB389	?	00000001101400	RB461	F	00000000001010
RB390	F	00000000000111	RB462	M	00000000000001
RB391	F	00000000001111	RB463	F	00000000000011
RB392	?	00000001000000	RB464	?	00000000000001
RB395	?	00000000001010	RB465	F	00000000001110
RB396	M	00000000001004	RB466	M	00000000001100
RB397	F	00000001010001	RB467	F	00000000000011
RB398	F	00000001000000	RB468	F	00000000010010
RB401	F	00000001000000	RB469	F	00000000000011
RB403	M	00000000001001	RB471	F	00000000001000
RB404	F	00000001000000	RB472	?	00000000000011
RB405	F	00000001000000	RB473	F	00000000001001
RB407	?	00000001000000	RB474	M	00000000001011
RB409	?	00000000010000	RB475	?	00000000000001
RB410	?	00000000100000	RB476	F	00000000000101
RB411	F	00000001001101	RB477	?	00000000001001
RB412	M	00000000001000	RB478	F	00000000001001

Table A-3. *Continued.*

ID	Sex	Sighting record 1977–78 to 1990–91	ID	Sex	Sighting record 1977–78 to 1990–91
RB479	F	00000000000001	BC069	F	00000114000000
RB480	F	00000001001000	JX012	F	00000300000000
RB481	M	00000000000011	RB441	F	00000000140000
RB482	M	00000000001011	RB310	M	00000103000000
RB483	M	00000000001111	BC176	F	00300000000000
			BS085	F	00000000001130

Trends and Patterns in Mortality of Manatees in Florida, 1974–1992

by

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Abstract. During 1974–92, we recorded 2,074 carcasses of the endangered Florida manatee (*Trichechus manatus latirostris*) in Florida and an additional 69 carcasses in seven other southeastern states and Puerto Rico. The number of recovered carcasses increased steadily at 5.9%/year (exponential regression; 1976–92) while the size of the human population (2.7%/year) and the number of registered watercraft (3.4%/year) in Florida increased less rapidly. Deaths from collisions with watercraft increased at 9.3%/year. Deaths of perinatal calves from any cause increased at 11.9%/year. Two less common categories of cause of death—crushing or drowning in flood-control gates and canal locks and other human-related causes—did not change significantly. However, deaths in these categories decreased more than deaths from other causes. The causes of the remaining deaths were natural or

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were undetermined because of the decomposition of the carcasses. Deaths of 30 or more manatees in four winters were attributed to severe cold. Deaths in a fifth winter were attributed to red-tide toxicity. Analysis of contingency tables with log-linear models was used to assess patterns in number of deaths by cause of death, carcass length, sex, season, region, degree of decomposition, and three time periods (1976–81, 1981–86, 1986–92). Watercraft-related mortality was highest in eastern Florida but had increased most rapidly in southwestern Florida. In the most recent time period, anthropogenic mortality was greater in warm months, and natural mortality was greater in winter. Anthropogenic mortality was greater on the eastern coast and disproportionately affected adult manatees. The mortality data presented here are widely used for the protection of manatees. Threats to manatees and their habitat are expected to increase, and conservation must be continued.

Key words: Catastrophe, mortality, perinatal, trends, *Trichechus manatus latirostris*, watercraft collision, Florida manatee.

A long-term study of manatee (*Trichechus manatus latirostris*) mortality, which included intensive recovery of carcasses, has been conducted in Florida since 1974. The purposes are the recovery of all dead manatees from Florida and other states, the determination of the causes of death, and the maintenance of a detailed database of information for agencies and other parties concerned with the management and conservation of manatees. Odell and Reynolds (1979), Beck et al. (*[2]1981), and *Irvine et al. (1981) recorded data from the early years and O'Shea et al. (1985) provided the first detailed statistical analysis of data on mortality. We evaluated long-term trends and patterns of manatee mortality in Florida through 1992 by cause of death, geographic location, sex, carcass size, season, time period, and degree of carcass decomposition.

Methods

Data on deaths of manatees were collected through December 1992. Carcass recovery was conducted by the U.S. Fish and Wildlife Service and the University of Miami from 1974 to 1985 and by the Florida Department of Environmental Protection from July 1985 to the present. We analyzed the number of deaths by *cause of death*, *region*, *time period*, *season*, *sex*, *size class*, and *carcass condition*.

Necropsies in the field and in the laboratory were conducted to determine probable cause of death. Standardized techniques for necropsies were followed (*Bonde et al. 1983; O'Shea et al. 1985). Basic procedures were as consistent as possible but were improved throughout the study. Carcasses were measured and tissue samples were taken for histological examination. Some carcasses were weighed. The date a carcass was first reported to authorities and its first reported location were used in our analyses. More precise dates and locations of deaths usually could not be determined. When the date of reporting was not known or recorded, the date of the carcass recovery was used. Locations where carcasses were first reported were digitized and entered into the Marine Resources Geographic Information System of the Florida Department of Environmental Protection (Weigle and Haddad 1990) with ARC/INFO Version 6.1 software (Environmental Systems Research Institute, Inc., Redlands, California).

Causes of Death

Each case was assigned to one of six long-standing categories of cause of death: watercraft, gate or lock, other human-related, other natural, and undetermined (O'Shea et al. 1985). Various causes of death of perinatal manatees were grouped in a category called *deaths of perinatal manatees*. The causes of death of perinatal manatees were often not determined but were listed in a separate category to distinguish them from the undetermined-cause-of-death category of adult manatees. Dead perinatal manatees were largely stillbirths and neonates (often characterized by the presence of meconium in the digestive tracts and by unhealed umbilici) or diseased or orphaned young. Cause of death from watercraft propellers, flood gates, nets, and similar structures and objects usually could be determined by gross examinations of external wounds; cause of death from broken ribs, internal injuries, hemorrhage, depletion of fat stores, and other lesions was determined by internal examination (Odell and Reynolds 1979; Beck et al. 1982; *Bonde et al. 1983; O'Shea et al. 1985). Samples from some fresh carcasses were tested for the presence of heavy metals, organic compounds, pesticides, and other contaminants (O'Shea et al. 1984). When the carcass condition allowed them, samples of microbiological cultures were collected to further substantiate diagnoses. The advanced state of decomposition of nearly half the carcasses often precluded detailed examination. Some cause-of-death categories were revised over time, and some past records were revised to be consistent with current practices.

[2] An asterisk denotes unpublished material.

Human-related Causes of Death

Collisions with watercraft. Deaths of manatees from collisions of watercraft included deaths from collisions with large and small boats, barges, and other vessels, and the carcasses were characterized by deep propeller wounds, massive internal injuries, or infections from lesser wounds (Beck et al. 1982; *Bonde et al. 1983; O'Shea et al. 1985). Deaths from watercraft were separated into those caused principally by propeller wounds, by only the impact of the collision, or by both (Beck et al. 1982; Wright et al. 1995).

Flood gates and canal locks. This category included manatees that were accidentally killed when they were crushed or asphyxiated in flood-control gates and navigation-canal locks (Odell and Reynolds 1979; *Bonde et al. 1983; O'Shea et al. 1985).

Other human-related causes. This category included deaths from a wide variety of other anthropogenic causes including poaching, vandalism, entanglement of manatees in nets and lines, entrapment of manatees in other structures such as pipes and culverts, and ingestion of fishing gear or debris (*Bonde et al. 1983; Buergelt et al. 1984; Laist 1987; Beck and Barros 1991). Some deaths were included here based on unidentifiable massive trauma that was not attributable specifically to either watercraft collisions or to water-control structures.

Natural Causes of Death

Deaths of perinatal manatees. Perinatal manatees that died of natural causes near birth or within a few months of birth were placed in this category. These included presumed natural deaths of manatees of 150 cm total length (TL) or shorter (*Bonde et al. 1983; O'Shea et al. 1985), including almost all recorded neonates. Stillbirths and aborted fetuses were also included in this category. Seven carcasses of neonates that were unusually long (151–160 cm) but showed evidence of having been born recently were also listed in this category. No methods currently exist to estimate the ages of fetuses and calves under the age of 1 year. Perinatal manatees can die from poor neonatal nutrition, infection of the umbilicus, diarrhea, or bacterial infection (*Bonde et al. 1983). Some may die from separation from the mother (abandonment, orphaning). Cause of death was often undetermined because of advanced autolysis. Decomposition of small carcasses can be rapid.

In utero fetuses were measured but not included in analyses. However, small carcasses that were found separated from an adult female's body were judged to be premature, spontaneously aborted fetuses, or full-term natural births and were included in the analyses. Nine 42–86-cm-long carcasses believed to be aborted fetuses were formerly categorized in the other natural category (1976–89) as described by Bonde et al. (*1983). In later years, aborted fetuses were placed in the category of deaths of perinatal manatees. These nine carcasses were therefore re-categorized in accordance with current practice.

Other natural causes of death. Deaths from natural causes (e.g., disease, low temperatures, red tide, starvation, complications during parturition, and non-anthropogenic injuries; *Bonde et al. 1983) of animals that were longer than 150 cm were placed in this category. Mortality from low temperatures can result from either long- or short-term exposure. Long-term exposure to moderately cold temperatures can cause manatees to cease feeding, expend fat reserves, starve, and slowly die (Buergelt et al. 1984; O'Shea et al. 1985.) Carcasses exhibit reduced fat reserves, cachexia, and little food in digestive tracts. Buergelt et al. (1984) and O'Shea et al. (1985) suggested that subadults (see definition under *Death by Sex and Size Class*) and injured or nutritionally stressed animals are most vulnerable because of their lowered capacity for heat production, insufficient fat reserves, minimal insulation, and inadequate experience in finding warm-water refuges. In contrast, death from hypothermia can result from short-term exposure to cold temperatures and leaves no diagnostic features (O'Shea et al. 1985). Hypothermia may affect manatees of all ages.

During 1974–80, the cause of death from low temperatures was categorized as *undetermined*; during 1981–85, it was categorized as *other natural* (O'Shea et al. 1985); and since 1986, it has been placed in a separate subcategory of the *other natural* causes. This change in coding was made because of improved information about cold-related mortality (Buergelt et al. 1984; O'Shea et al. 1985) but confounded the other natural and undetermined categories. This caused major shifts in the relative proportions of deaths in these three categories.

Undetermined Causes of Death

Deaths for which a cause could not be determined (often because of advanced decomposition of the carcass) were classified as *undetermined* (*Bonde et al. 1983). A small number of carcasses was seen and verified by biologists but could not be recovered for necropsy (*verified, not-recovered*). These were included in the category of undetermined causes.

Deaths by Region

Florida was divided into four regions (O'Shea et al. 1985). The northern region was separated from the southern regions at latitude 27° 39′ N. At longitude 82° 00′ W, the northwestern region was separated from the northeastern regions. The northeastern region included the St. Johns River. The southeastern region was separated from the southwestern region at longitude 80° 53′ W, which divides the state from western Monroe County east of Flamingo through Lake Okeechobee. For some analyses, data were pooled into eastern and western Florida.

Deaths by Time Period

O'Shea et al. (1985) analyzed 5 separate years of data and began each year in April to avoid dividing mortality in winter across 2 calendar years. Much of their variability resulted from large mortality events in 2 particular years (1976–77, 1980–81), therefore, we examined mortalities on a longer timescale. We examined three time periods: April 1976–March 1981 (5 years; data analyzed by O'Shea et al. 1985); April 1981–March 1986 (5 years); April 1986–March 1992 (6 years).

Deaths by Season

Deaths were also analyzed by four seasons following O'Shea et al. (1985): spring (April–June), summer (July–September), fall (October–December), and winter (January–March). One case was omitted here because the month in which the carcass was reported was not known.

Deaths by Sex and Size Class

Mortality was analyzed by sex and three size classes defined by O'Shea et al. (1985): aborted fetuses and dependent calves (42–175 cm TL), subadults (176–275 cm), and adults (276–411 cm). These life-stage designations were based on observations of lengths at weaning and on first-known breeding in identifiable wild animals. They were also supported by length measurements made through time on free-swimming, identifiable, known-age animals (O'Shea and Reep 1990). Cases were omitted from analyses by sex and size if sex or lengths of the carcasses were unknown.

Deaths by Carcass Condition

Stage of decomposition was based on carcass condition at necropsy (*Bonde et al. 1983). Carcass condition was rated by six codes during current necropsy protocols. These codes were pooled into three for analysis with log-linear models: fresh (codes 1, 2), moderately decomposed (code 3), and badly decomposed (codes 4, 5, and 6, only dried skin and bones).

Watercraft Data

Data on Florida watercraft were obtained to investigate relations between trends in watercraft-related deaths and boating. Annual summaries (July to June) of the number of pleasure and commercial watercraft registered in Florida by county and watercraft size-class were obtained from the Bureau of Vessel Titling and Registration of the Florida Department of Environmental Protection. Watercraft must be registered if they have an engine or are 4.8 m long or longer. Trends in watercraft data from 1976–77 to 1992–93 (July to June, ending June 1993) were analyzed.

Statistical Analyses

Mortality data were entered in dBase III Plus (Ashton-Tate Corp., Torrance, California) and then transferred to the mainframe computer system of the Department of Environmental Protection or to personal computers. Analyses were conducted with the PC SAS Version 6.03 (SAS Institute 1988). The SAS Procedure GLM was used for linear and exponential regressions (SAS Institute 1988).

Trend Analysis

Exponential regression. Because yearly trends in the number of deaths in each category were often nonlinear, they were determined with exponential regression analysis (which fit most data sets better than linear regression). Exponential regressions of annual counts by category were:

$$\text{count} = a \times e^{bt}, \quad (1)$$

which is equivalent to the linear regression form,

$$\ln(\text{count}) = \ln(a) + bt, \quad (2)$$

where t is the year and $\ln(a)$ and b are the respective linear regression coefficients of intercept and slope (Eberhardt and Simmons 1992). The annual percentage change in numbers each year is

$$(e^{b}-1) \times 100\%. \quad (3)$$

Zero counts are not permissible in exponential regression because ln(0) is undefined (Zar 1974). When zero counts occurred in a regression, the standard $\ln(x + 1)$ transformation was used. Data were back-transformed for plotting. As recommended by Irvine et al. (*1981), trends were analyzed only from 1976 to 1992 to eliminate bias seemingly caused by low recovery rates during the 2 initial years of carcass recovery (1974–75).

Trend analysis excluding catastrophic deaths. Catastrophic deaths are defined here as relatively large numbers of deaths at one time as the result of unpredictable events. More than 30 such deaths occurred in each of 5 years during 1974–92. These large and variable numbers of deaths in some years weaken analyses of trends in deaths from other causes. To reduce this source of variability, we omitted all deaths that were related to cold and deaths from red tides and recalculated trends in the remaining noncatastrophic deaths with exponential regression. This provided a smoother baseline from which to assess the relative proportions of other causes of death (Draper and Smith 1981). However, there were two complications. First, deaths from low temperatures in a severe winter often extended from December of one calendar year to February of the next. Therefore, deaths were tabulated over annual periods extending from April

of one year through March of the next (O'Shea et al. 1985). Second, deaths from low temperatures have only been specifically categorized in the mortality database since January 1986.

Log-linear Models and Associations Among Categorical Variables

Analyses for determining associations among various categorical variables characterizing manatee deaths were performed with multidimensional contingency tables (Bishop et al. 1975) following the procedures of O'Shea et al. (1985). The objective was to determine whether patterns of mortality in each cause-of-death category varied by geographic region, season, sex, size class, carcass condition, or time period. O'Shea et al. (1985) analyzed a multidimensional contingency table with data on manatee deaths in Florida from April 1976 to March 1981. They used 2–5-way log-linear model tests of interactions (with BMDP software). We determined whether the patterns of mortality revealed by that analysis changed during 1982–92.

Analysis closely followed that of O'Shea et al. (1985). Two-way tables were made of all combinations of cause of death and the five other factors. Multi-way models with three time periods were used to determine whether the patterns within each pairwise table had remained similar during the subsequent 11 years. Three- and four-way tables were analyzed by fitting log-linear models to the observed cell frequencies (Bishop et al. 1975). All variables were considered to be independent factors; none was considered to be a dependent response variable. Multi-way models were simplified when possible by sequentially deleting nonsignificant interaction terms (backwards stepwise regression). Models were hierarchical; any model that included factors in a higher-order interaction term was required to also include all possible lower-order terms involving those factors. The most parsimonious model was obtained from each three-way model. The selected model in each case was the simplest model that adequately fit the data ($\alpha = 0.05$). Significant interactions (associations) were assessed as appropriate to the remaining interaction terms. Significant interactions in three-way models were interpreted from standardized parameter estimates [$S(\hat{\lambda})$] of log-linear models (Everitt 1977:97–99). Significant relations in two-way tables were identified by standardized residuals (Everitt 1977:46–48). Cells with higher-than-expected mortality were determined based on magnitude of standardized log-linear model parameter estimates (Everitt 1977; Upton 1978). Computations were done with SAS procedures FREQ (2-way) and CATMOD (3- and 4-way; SAS Institute 1988).

Results and Discussion

We recorded 2,074 manatee carcasses in Florida from 1974 through 1992 (Table 1). Reports on 69 deaths in seven other states and Puerto Rico were also obtained (Table 2) but were not included in the analyses.

Trends by Cause of Death

Total annual deaths increased an average of 5.9%/year from 1976 to 1992 ($r^2 = 0.69$, $P = 0.0001$; Table 3; Fig. 1). Record numbers of deaths occurred in 1988, 1989, and 1990, but the number of deaths declined in 1991 and 1992. Deaths from collisions with watercraft and deaths of perinatal manatees increased most and were also the two most common causes of death.

Human-related Causes of Death

The three categories of human-related causes of death of manatees (collisions with watercraft, deaths in floodgates and canal locks, and other human-related) were the largest percentage of all deaths from identifiable causes (45% of determined causes, 34% of total deaths; 1986–92; Table 4).

Collisions with watercraft. Death from collisions with watercraft was the largest category of identified causes. Deaths in this category increased at 9.3%/year ($r^2 = 0.79$, $P = 0.0001$; Table 3; Fig. 2) and increased as a percentage of all deaths from 21% in 1976–80 to 28% in 1986–92 (Table 4). The number of manatees killed in watercraft collisions began to drastically increase in 1984; however, the cause for this sudden increase remains unknown. Watercraft collisions caused 83% of deaths from all human-related causes (1986–92) and 37% of all deaths from identified causes.

The number of manatees killed in collisions with watercraft each year correlated with the total number of pleasure and commercial watercraft registered in Florida from July 1976 to June 1993 ($r^2 = 0.87$, $n = 17$ years, $P = 0.0001$, linear regression; Table 3; Fig. 3). The number of watercraft registered in Florida increased at 3.4%/year from 447,000 in 1976–77 to a peak of 718,500 in 1989–90 (exponential regression, $r^2 = 0.97$, $n = 17$ years, $P = 0.0001$; Table 3; Fig. 4). Watercraft registrations declined to 715,500 during 1992–93. The number of registered and unregistered watercraft in Florida increased to nearly one million in recent years because some watercraft do not require registration if they are shorter than 4.8 m and not powered or if they are owned by seasonal visitors from out-of-state (Florida Department of Environmental Protection Marine Patrol, unpublished data).

Flood gates and canal locks. Manatee deaths in gates and locks decreased slightly (1.3% year; Table 3; Fig. 2). The number of deaths was small in most years (0–9/year), and

Table 1. Number of manatee (*Trichechus manatus latirostris*) deaths in Florida by seven categories, 1974–1992. The categories of death of nine aborted fetuses were recoded from other natural causes to deaths of perinatal manatees.

Cause of death	Year																			
	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	Total
Watercraft collision	3	6	10	13	21	24	16	24	20	15	34	33	33	39	43	50	47	53	38	522
Flood gate/ canal lock		1	4	6	9	8	8	2	3	7	3	3	3	5	7	3	3	9	5	89
Other human-related	2	1		5	1	9	2	4	1	5	1	3	1	2	4	5	4	6	6	62
Various perinatal		8[b]	15[b]	9	10	9	14[b]	13	15[b]	18	26[b]	23	27	31[b]	32[c]	39[b]	44	53	49	435
Cold-related[a]													12	6	9	14	46	1	0	88
Other natural			1	1	3	4	4	9	40	6	23	19	1	9	14	17	21	13	19	203
Undetermined	2	13	32	80	40	23	19	64	35	30	41	38	45	22	25	40	41	39	46	675
Total	7	29	62	114	84	77	63	116	114	81	128	119	122	114	133	168	206	174	163	2,074

[a] The cold-related designation was not used until 1986. Deaths from low temperatures were placed in the category of deaths from undetermined causes during 1974–80 and in the category of deaths from other natural causes during 1981–85.

[b] Indicates that for our analyses, one aborted fetus was categorized as a perinatal manatee that died from an undetermined cause rather than from other natural causes in that year.

[c] Indicates that two aborted fetuses were categorized as deaths of perinatal manatees rather than deaths from other natural causes.

Table 2. Number of manatee (*Trichechus manatus latirostris*) deaths in the southeastern United States, excluding Florida, by seven categories and state 1979–1992.Deaths in Texas ($n = 2$) and Puerto Rico ($n = 26$) were excluded.

	Year																			
	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	Total
Cause of death																				
Watercraft collision												2				1	2			5
Flood gate/canal lock																				
Other human-related				1					1					2						4
Various perinatal											1					1	1			3
Cold-related[a]																1	4	1	1	7
Other natural							2				1	1								4
Undetermined	1					1		1	2			1	2	1	1	5	1		2	18
State																				
Alabama																			1	1
Georgia	1					1		1	3		1	3	1	3	1	8	7		2	32
Mississippi							1													1
North Carolina											1		1				1			3
South Carolina				1								1						1		3
Virginia							1													1
Total	1			1		1	2	1	3		2	4	2	3	1	8	8	1	3	41

[a] The cold-related designation was not used until 1986. Deaths from low temperatures were placed in the category of deaths from undetermined causes during 1974–80 and in the category of deaths from other natural causes during 1981–85.

Table 3. Trends in manatee (*Trichechus manatus latirostris*) deaths in Florida by cause of death, 1976–1992. Exponential regression values are given (sample size n, regression coefficient b, SE(b), annual change [%/year], r^2, P). r^2 is given for linear regression for comparison. Catastrophic deaths (low temperature, red tide) were adjusted with the best available information.

Years	Cause of death	Exponential						Linear
		n	b	SE(b)	%/year	r^2	P	r^2
1976–92	All causes	17	0.057	0.010	5.9	0.69	0.0001*	0.71
(calendar)	Watercraft	17	0.089	0.012	9.3	0.79	0.0001*	0.82
(1/76–12/92)	Flood gate/canal lock	17	−0.013	0.025	−1.3	0.02	0.59	0.03
	Other human, ln(x+1)	17	0.048	0.029	4.9	0.16	0.12	0.07
	Various perinatal	17	0.111	0.009	11.7	0.91	0.0001*	0.89
	Other natural[a] (including cold related 1986–92)	17	0.193	0.037	21.2	0.65	0.0001*	0.35
	Undetermined[a]	17	−0.001	0.019	−0.1	0.00	0.94	0.02
	Verified, not recovered	17	−0.170	0.035	−15.7	0.61	0.0002*	0.53
1976–92	All causes	16	0.050	0.011	5.3	0.58	0.0006*	0.60
(April to March)	All causes (excluding catastrophic deaths)	16	0.059	0.009	6.1	0.79	0.0001*	0.78
(4/76–3/92)	Watercraft	16	0.090	0.007	9.4	0.92	0.0001*	0.90
	Catastrophic (cold related, red tide)	16	0.016	0.100	1.6	0.00	0.88	0.01
	Other natural[a] (excluding catastrophic deaths)	16	0.142	0.033	15.3	0.58	0.0006*	0.60
	Undetermined[a] (excluding catastrophic) and verified, not recovered deaths	16	0.009	0.016	0.9	0.02	0.60	0.01
1976–93 (July to June) (7/76–6/93)	Watercraft registrations	17	0.034	0.002	3.4	0.97	0.0001*	0.96

[a] Trends of other natural and undetermined deaths are confounded because of improvements in diagnostic procedures through time.
* Indicates statistical significance of regression at $P < 0.05$.

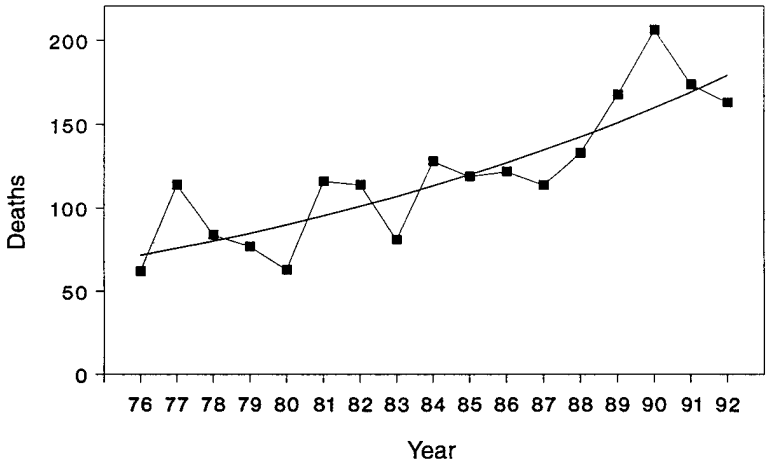


Fig. 1. Trends in the number of deaths of Florida manatees (*Trichechus manatus latirostris*) from all causes, Florida, calendar years 1976–1992 (exponential regression).

Table 4. Number of manatee (*Trichechus manatus latirostris*) deaths by four time periods (calendar years) and six categories, Florida, 1974–1992.

Time period	Cause of death: Watercraft collision	Flood gate/ canal lock	Other human	Various perinatal	Other natural	Undetermined	Total
Number of deaths in time period							
(1974–75)	9	1	3	8	0	15	36
(1976–80)	84	35	17	57	13	194	400
(1981–85)	126	18	14	95	97	208	558
(1986–92)	303	35	28	274	182	258	1,080
Total	522	89	62	434	292	675	2,074
Mean number of deaths per year							
(1974–75)	4.5	0.5	1.5	4.0	0.0	7.5	18.0
(1976–80)	16.8	7.0	3.4	11.4	2.6	38.8	80.0
(1981–85)	25.2	3.6	2.8	19.0	19.4	41.6	111.6
(1986–92)	43.3	5.0	4.0	39.1	26.0	36.9	154.3
Total	27.5	4.7	3.3	22.8	15.4	35.5	109.2
Percentage of deaths by category							
(1974–75)	25.0	2.8	8.3	22.2	0.0	41.7	100.0
(1976–80)	21.0	8.8	4.3	14.3	3.3	48.5	100.0
(1981–85)	22.6	3.2	2.5	17.0	17.4	37.3	100.0
(1986–92)	28.1	3.2	2.6	25.4	16.9	23.9	100.0
Total	25.2	4.3	3.0	20.9	14.1	32.5	100.0

Comparison of deaths by combined categories (%)

Time period	Watercraft ÷ all human	Watercraft ÷ total	Watercraft ÷ all determined	All human ÷ total	All human ÷ all determined	All natural[a] ÷ total
(1974–75)	69.2	25.0	42.9	36.1	61.9	63.9
(1976–80)	61.8	21.0	40.8	34.0	66.0	66.0
(1981–85)	79.7	22.6	36.0	28.3	45.1	71.7
(1986–92)	82.8	28.1	36.9	33.9	44.5	66.1
Total	77.6	25.2	37.3	32.4	48.1	67.6

[a] All natural causes of death include various perinatal, other natural, and undetermined causes.

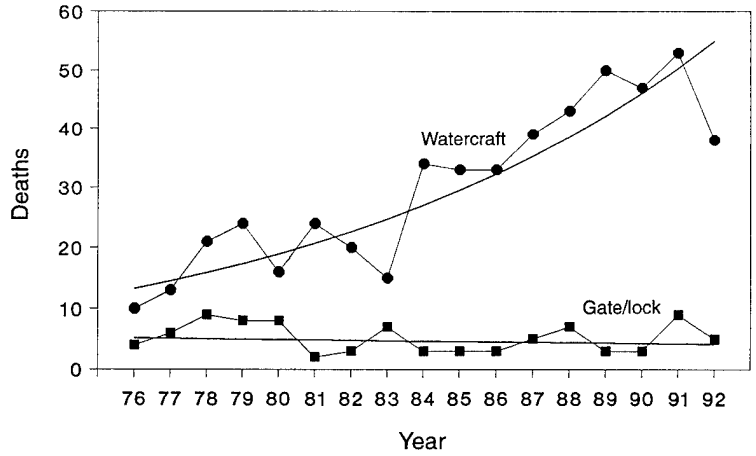


Fig. 2. Trends in the number of deaths of Florida manatees (*Trichechus manatus latirostris*) from collisions with watercraft (*circles*) and from flood gates and canal locks (combined; *squares*), Florida, calendar years 1976–1992 (exponential regression).

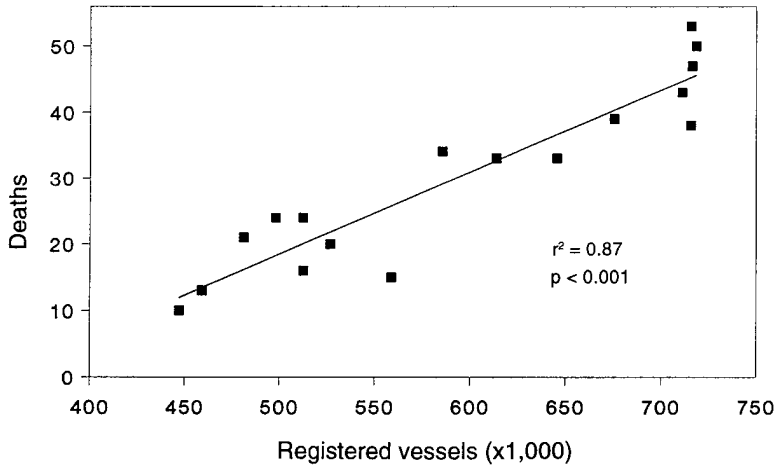


Fig. 3. Regression of Florida manatee (*Trichechus manatus latirostris*) deaths from collisions with watercraft (calendar years) and number of registered watercraft (×1,000, July–June), Florida, 1976–1992 (linear regression).

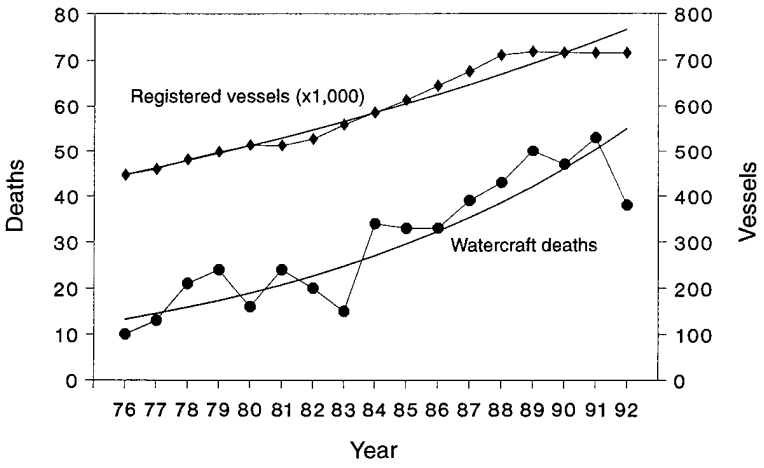


Fig. 4. Trends in Florida manatee (*Trichechus manatus latirostris*) deaths from collisions with watercraft (*circles*, calendar years) and the number of registered watercraft (*diamonds*, ×10,000, July–June), Florida, 1976–1992 (exponential regression).

deaths as a percentage declined from 9% in 1976–80 to 3% in 1986–92 (Table 4).

Other human-related causes. The number of other human-related deaths was small (0–9/year, maximum of 6 since 1980). The number of deaths in this category did not change (+4.9%/year, $r^2 = 0.16$, $P = 0.12$; Table 3; Fig. 5). Other human-related causes of deaths were 3% of all deaths during 1986–92 (Table 4).

Natural Causes of Death

Deaths of perinatal manatees. Deaths of perinatal manatees were 25% of all deaths in 1986–92, increasing at 11.7%/year ($r^2 = 0.91$, $P = 0.0001$; Table 3; Fig. 5). Deaths of perinatal manatees increased as a percentage from 14% in 1976–80 to 25% in 1986–92 (Table 4).

Other natural causes of death. Deaths from all other natural causes were 17% of all deaths in 1986–92 (Fig. 6), increasing from 3% in 1976–80 (Table 4). A rapid and significant increase of 21.2%/year ($r^2 = 0.65$, $P = 0.0001$; Table 3; Fig. 6) was deemed invalid because of changes in categorization of certain natural causes over time.

Undetermined Causes of Death

Deaths from undetermined causes were 24% of all deaths during 1986–92. The number of undetermined deaths did not change significantly (Table 3; Fig. 6). However the percentage of all deaths classified as undetermined dropped substantially from 49% in 1976–80 to 24% in 1986–92 (Table 4). Numbers in the other-natural and undetermined categories showed an inverse relation through time (Fig. 6). As diagnostic procedures improved, more deaths were assigned to specific natural causes and deaths from undetermined causes decreased (Table 4; Fig. 6). Deaths that were classified as verified-not recovered declined at −15.7%/year ($r^2 = 0.61$, $P = 0.0002$) as the efficiency of the recovery network improved. Deaths in this category were most frequent in 1976 and 1977 and were rare in recent years (0–2/year since 1987).

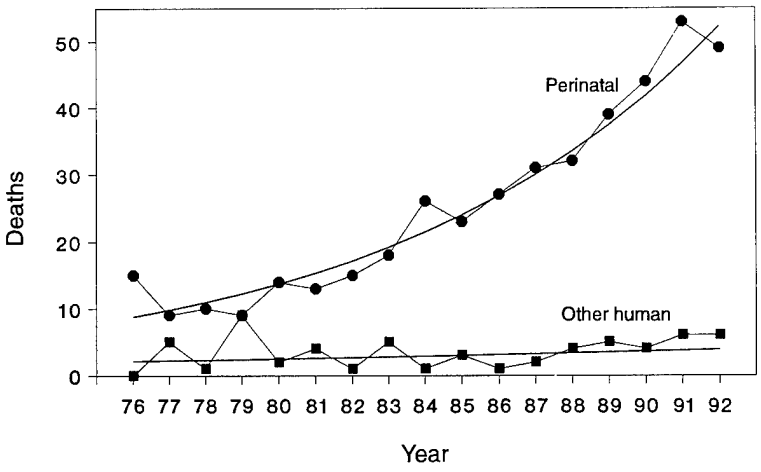


Fig. 5. Trends in the number of deaths of perinatal calves (*circles*) and in the number of deaths from other human-related causes (*squares*) in Florida manatees (*Trichechus manatus latirostris*), Florida, calendar years 1976–1992 (exponential regression).

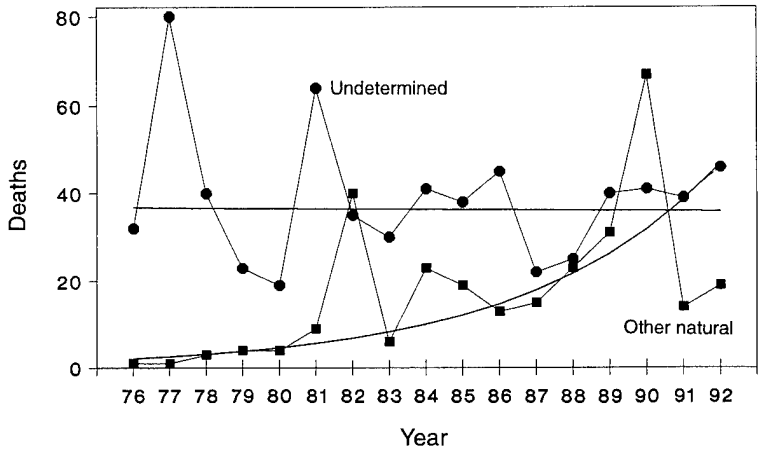


Fig. 6. Trends in the number of deaths of Florida manatees (*Trichechus manatus latirostris*) from undetermined causes (*circles*) and from other natural causes (*squares*), Florida, calendar years 1976–1992 (exponential regression).

Trends in Non-catastrophic Deaths

Total deaths increased at 5.3%/year from 1976–77 to 1991–92 when tabulated from April to March each year ($r^2 = 0.58$, $n = 16$ years, $P = 0.0006$; Table 3). The regression was more variable than when trend in total deaths was calculated on a calendar-year basis (+5.9%/year, $r^2 = 0.69$, $n = 17$, $P = 0.0001$) because calendar years divided deaths in cold winters among 2 adjacent years. After the catastrophic deaths (from low temperatures and red tide; Table 5) were removed, the remaining deaths increased at +6.1%/year and the regression was improved substantially (April to March, $r^2 = 0.79$, $P = 0.0001$; Fig. 7). Catastrophic deaths were variable between years and without trends (+1.6%/year, $r^2 < 0.01$, $P = 0.88$; Fig. 7). When deaths from low temperatures and red tide were removed, deaths from other natural causes still substantially increased at 15.3%/year ($r^2 = 0.58$, $P = 0.0006$; Table 3), whereas deaths from undetermined causes did not increase.

The percentage of deaths from watercraft increased through time when catastrophic deaths were excluded (linear regression, $r^2 = 0.54$, $n = 16$ years, $P = 0.001$, April–March annual periods). The adjusted percentage increased from 22% in 1976–77 to 34% in 1991–92, and the regression was more significant than when catastrophic deaths were included ($r^2 = 0.42$, $P = 0.006$). The high numbers of catastrophic deaths in some years caused watercraft percentages to be low in those years.

The percentage of undetermined deaths decreased significantly over time when catastrophic deaths were excluded ($r^2 = 0.58$, $n = 16$, $P = 0.0006$), and the regression was more significant than when catastrophic deaths were included ($r^2 = 0.45$, $P = 0.005$). The adjusted percentage of undetermined deaths decreased from 48% in 1976–77 to 21% in 1991–92.

Log-linear Models and Associations Among Categorical Variables

Mortality frequency distributions were characterized by significant interactions among cause of death, geographic region, season, time period, sex, carcass size, and carcass condition. The numbers of deaths and their relative distribu-

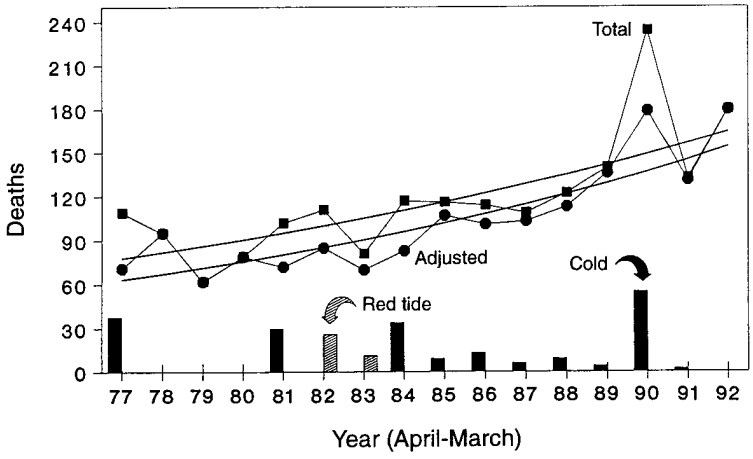


Fig. 7. Trends in the number of deaths of Florida manatees (*Trichechus manatus latirostris*) from all causes, unadjusted (*squares*) and adjusted (*circles*) for catastrophic deaths (low temperatures, red tide), Florida, 1976–1992 (exponential regression). Mortalities are tabulated by years from April to March. *Bars* indicate catastrophic deaths.

Table 5. Listing of catastrophic deaths of manatees (*Trichechus manatus latirostris*) in Florida, 1976–1992, documented from various sources and used to calculate adjusted trends in manatee deaths. Lowest air temperature at Titusville each winter is given.

Years	Cause of death	*n*	Comments	Minimum Titusville temperature (° C), date	Source
1976–77	Low temperature	38	January–March 1977 (38 undetermined)	–6.7, 1/20/1977	Campbell and Irvine (1981)
1977–78		0		–1.7, 1/10/1978	
1978–79		0		–2.2, 1/3/1979[b]	
1979–80		0		–3.3, 3/3/1980	
1980–81[a]	Low temperature	30	January–February 1981 (4 other natural, 26 undetermined)	–5.0, 1/14/1981	Buergelt et al. (1984)
1981–82	Low temperature	0		–5.0, 1/12/1982	
	Red tide	37	February–April 1982 (37 other natural)		O'Shea et al. (1991)
1982–83		0		–1.7, 12/19/1982	
1983–84	Low temperature	34	January–February 1984 (19 other natural, 15 undetermined)	–5.6, 12/26/1983	Buergelt et al. (1984)
1984–85	Low temperature	9	December 1984–February 1985 (9 other natural)	–7.2, 1/22/1985	FDEP mortality database
1985–86	Low temperature	1	December 1985 (1 other natural)	–4.4, 1/28/1986	FDEP mortality database
Categorized as cold-related after January 1986					
1985–86	Low temperature	12	January–March 1986	–4.4, 1/28/1986	FDEP mortality database
1986–87	Low temperature	6	December 1986–February 1987	0.6, 1/28/1987	FDEP mortality database
1987–88	Low temperature	9	January–March 1988	0.6, 1/26/1988	FDEP mortality database
1988–89	Low temperature	4	January–March 1989	–2.2, 2/24/1989	FDEP mortality database
1989–90	Low temperature	56	November 1989–March 1990	–7.2, 12/24/1989	FDEP mortality database
1990–91	Low temperature	1	February 1991	1.1, 1/21/1991	FDEP mortality database
1991–92	Low temperature	0		0.0, 1/16/1992	FDEP mortality database

[a] Some deaths from low temperatures were specifically diagnosed during 1981–85 and classified as deaths from other natural causes. From 1974 to 1980, deaths were not attributed to low temperatures and were classified as deaths from undetermined causes.

[b] Temperature in Daytona Beach; temperature in Titusville was not available.

tion by cause-of-death category varied among combinations of factors. Of these factors, only sex was not significantly related to all of the others.

Time Period

Changes in cause of death during three time periods were similar to the trends described above ($\chi^2 = 249.5$, $P < 0.001$; Table 6). The proportions of watercraft collision and deaths of perinatal manatees increased significantly through time, whereas flood gate-canal lock and other human-related causes of deaths decreased (although annual numbers increased, they were a lower percentage of the total number of deaths). Deaths from low temperatures, other natural, and undetermined causes were confounded because of changes in classification. Decreases in numbers in the undetermined category were mirrored by increases in the other natural (1981–86) and cold-related (1986–92) causes of deaths. Peaks in these three categories exactly corresponded to whichever category the catastrophic mortality was assigned to during a given time period (undetermined 1976–81; other natural, including red tide, 1981–86; cold-related 1986–92). Combined deaths in these categories increased slowly in number but were a lower percentage of total deaths in 1986–92 (40%) than in previous years (55%, 1976–81; 53%, 1981–86), probably because of the steady increase in watercraft-related deaths and deaths of perinatal manatees. Verified carcasses which were not recovered decreased significantly from 9% in 1976–81 to 1% in 1986–92 (Table 6).

Regions

The number of deaths differed between regions (Table 7). The highest number of deaths occurred in the northeastern (40%, including Brevard County) and southwestern (33%) regions. The numbers of deaths were lower in the southeastern (18%) and northwestern (9%) regions. The distribution of deaths among regions changed through time ($\chi^2 = 32.7$, $P < 0.001$; Table 8). In 1976–81, signifi-

Table 6. Frequency distribution of manatee (*Trichechus manatus latirostris*) deaths in Florida by eight cause-of-death categories and three time periods (April 1976 to March 1992; $n = 1{,}903$).

	Time period			
Cause of death	April 1976 to March 1981	April 1981 to March 1986	April 1986 to March 1992	Total
Watercraft collision	87	129	266	482
	(19.5)	(23.9)	(29.0)	(25.3)
	–		+	
Flood gate/canal lock	35	18	31	84
	(7.9)	(3.3)	(3.4)	(4.4)
	+++			
Other human-related	20	12	21	53
	(4.5)	(2.2)	(2.3)	(2.8)
	+			
Various perinatal	59	96	229	384
	(13.2)	(17.8)	(25.0)	(20.2)
	––		++	
Natural/cold-related (1986–92 only)	0	12	76	88
	(0.0)	(2.2)	(8.3)	(4.6)
	–––	––	+++	
Other natural	18	92	82	192
	(4.0)	(17.1)	(8.9)	(10.1)
	–––	+++		
Verified, not recovered	40	16	9	65
	(9.0)	(3.0)	(1.0)	(3.4)
	+++		–––	
Undetermined	187	164	204	555
	(41.9)	(30.4)	(22.2)	(29.2)
	+++		–––	
Total	446	539	918	1,903
	[23.4]	[28.3]	[48.2]	

+ and – indicate level of cell significance (standardized residuals, see Methods). One *symbol* indicates $P < 0.05$, two indicate $P < 0.01$, and three indicate $P < 0.001$; $\chi^2 = 249.5$, $P < 0.001$.

Brackets [] indicate percentages across a row; *parentheses* () indicate percentages down a column.

Table 7. Frequency distribution of manatee (*Trichechus manatus latirostris*) deaths in Florida by eight cause-of-death categories and four geographic regions (April 1976 to March 1992; $n = 1{,}903$).

	Region				
	West		East		
Cause of death	Northwest	Southwest	Northeast	Southeast	Total
Watercraft collision	27	144	203	108	482
	(16.0)	(22.7)	(27.0)	(31.1)	(25.3)
	–			+	
Flood gate/canal lock	4	8	13	59	84
	(2.4)	(1.3)	(1.7)	(17.0)	(4.4)
		---	---	+++	
Other human-related	5	9	20	19	53
	(3.0)	(1.4)	(2.7)	(5.5)	(2.8)
		–		++	
Various perinatal	73	113	158	40	384
	(43.2)	(17.8)	(21.0)	(11.5)	(20.2)
	+++			---	
Natural/cold	6	9	68	5	88
related	(3.6)	(1.4)	(9.0)	(1.4)	(4.6)
(1986–92 only)		---	+++	--	
Other natural	14	90	68	20	192
	(8.3)	(14.2)	(9.0)	(5.8)	(10.1)
		++		–	
Verified, not	5	31	14	15	65
recovered	(3.0)	(4.9)	(1.9)	(4.3)	(3.4)
		+	–		
Undetermined	35	230	209	81	555
	(20.7)	(36.3)	(27.8)	(23.3)	(29.2)
	–	+++		–	
Total	169	634	753	347	1,903
	[8.9]	[33.3]	[39.6]	[18.2]	
	803		1,100		
	[42.2]		[57.8]		

+ and – indicate level of cell significance (standardized residuals, see Methods). One symbol indicates $P < 0.05$, two indicate $P < 0.01$, and three indicate $P < 0.001$; cause by region $\chi^2 = 340.4$, $P < 0.001$; cause by coast $\chi^2 = 57.5$, $P = 0.001$.
Brackets [] indicate percentages across a row; *parentheses* () indicate percentages down a column.

cantly more deaths than expected (standardized residual = 2.85, $P < 0.004$) occurred in the southeastern region (24%), and in 1981–86, more deaths than expected (standardized residual = 3.01, $P < 0.003$) occurred in the southwestern region (41%). The highest overall mortality, although not significantly larger than expected, was in the northeastern region in 1976–81 (standardized residual = 0.27, 40% of the statewide total, $n = 180$, $P = 0.80$) and again in 1986–92 (standardized residual = 1.25, 42%, $n = 387$, $P = 0.21$). Mortality in the southwestern region was highest in 1981–86 (standardized residual = 3.02, 41%, $n = 220$, $P < 0.003$). Deaths declined proportionately through time in the southeastern region from 24% to 16% (Table 8). This reflected an overall decline in causes of death that occurred most frequently in the southeastern region (gate/lock, other-human), increases in watercraft-related and natural deaths (including cold-related, 1982 red tide) in the southwestern region 1981–86, and increases in watercraft-related and cold-related causes (1989–90 event) and in deaths of perinatal manatees in the northeastern region (1986–92). Similarly, the number of deaths was greater in eastern Florida (1976–81, 64% of statewide total; 1986–92, 58% of statewide total) than in western Florida, except in 1981–86 (51% east; 1982 red tide in southwestern region; $\chi^2 = 32.7$, $P < 0.001$; Table 8).

Seasons

The pattern of mortality among seasons changed through time (Table 9). More manatees died in winter (39% of total) than in other seasons (spring 23%, summer 20%, fall 18%). The proportion of deaths in winter declined significantly from 46% in 1976–81 to 33% in 1986–92, and the proportion in summer increased significantly from 17% to 23% (Table 9). This reflects a relative decrease in deaths from

Table 8. Frequency distribution of manatee (*Trichechus manatus latirostris*) deaths in Florida by four geographic geographic regions and three time periods (April 1976 to March 1992; $n = 1,903$).

Region	Time period: April 1976 to March 1981	Time period: April 1981 to March 1986	Time period: April 1986 to March 1992	Total: Region	Total: Coast
West					
Northwest	34 (7.6)	42 (7.8)	93 (10.1)	169 (8.9)	
Southwest	125 (28.0)	220 (40.8) ++	289 (31.5)	634 (33.3)	
Subtotal Coast	159 (35.7)	262 (48.6)	382 (41.6)		803 (42.2)
East					
Northeast	180 (40.4)	186 (34.5)	387 (42.2)	753 (39.6)	
Southeast	107 (24.0) ++	91 (16.9)	149 (16.2)	347 (18.2)	
Subtotal Coast	287 (64.3)	277 (51.4)	536 (58.4)		1,100 (57.8)
Total	446 [23.4]	539 [28.3]	918 [48.2]	1,903	1,903

+ indicates level of cell significance (standardized residuals, see Methods). Two *symbols* indicate $P < 0.01$; region by time $\chi^2 = 32.7$, $P < 0.001$; coast by time $\chi^2 = 17.1$, $P < 0.001$.
Brackets [] indicate percentages across a row; *parentheses* () indicate percentages down a column.

Table 9. Frequency distribution of manatee (*Trichechus manatus latirostris*) deaths in Florida by four seasons and three time periods (April 1976 to March 1992; $n = 1,903$).

Season	Time period: April 1976 to March 1981	Time period: April 1981 to March 1986	Time period: April 1986 to March 1992	Total
April to June	89 (20.0)	132 (24.5)	226 (24.6)	447 (23.5)
July to September	74 (16.6)	96 (17.8)	212 (23.1) +	382 (20.1)
October to December	77 (17.3)	84 (15.6)	180 (19.6)	341 (17.9)
January to March	206 (46.2) ++	227 (42.1)	300 (32.7) −−	733 (38.5)
Total	446 [23.4]	539 [28.3]	918 [48.2]	1,903

+ and – indicate level of cell significance (standardized residuals, see Methods). One *symbol* indicates $P < 0.05$ and two indicate $P < 0.01$; $\chi^2 = 31.3$, $P < 0.001$.
Brackets [] indicate percentages across a row; *parentheses* () indicate percentages down a column.

causes that were most common in winter (undetermined, other natural) and an increase in deaths in categories that were most common in summer (watercraft-related, perinatal).

The distribution of deaths between regions and seasons changed (Table 10). Significantly more manatees died in the northeastern region in summer and in the southeastern region in fall. These differences match high numbers of deaths from watercraft and deaths of perinatal manatees in summer and deaths from gates and locks in fall and also reflect the large southward migration of manatees along the eastern coast at that time. However, no difference existed between eastern and western Florida by season (Table 10).

Associations Among Cause-of-death Categories and Other Variables

Collisions with Watercraft

Collisions with watercraft caused the largest number of deaths in northeastern Florida (n = 203, 27% of deaths in northeastern Florida) and were the largest percentage in southeastern Florida (31%; Table 7). The lowest number and percentage of deaths from watercraft occurred in northwestern Florida (n = 27, 16%). The number of deaths from watercraft increased rapidly in the southwestern region where the annual number of deaths is now only slightly lower than in the northeastern region. The mean number of watercraft-related deaths in southwestern Florida was 14.8/year in 1986–92, which was 5.7 times higher than in 1976–81; in northeastern Florida the mean of 17.3/year in 1986–92 was 1.8 times higher than in 1976–81. Deaths from watercraft increased from 11% to 31% of the total in southwestern Florida, but the percentage remained the same in northeastern Florida (27%). Deaths from watercraft were a larger percentage of deaths in eastern Florida (29% of deaths) than in western Florida (21%), but the percentage in western Florida increased significantly from 11% (1976–81) to 27% (1981–92). Deaths from watercraft in eastern Florida were most common in northeastern Florida in warm seasons and in the southeastern region in winter.

Watercraft collisions caused the highest number of deaths in spring (n = 147; 33% of deaths in spring, significantly greater than expected; Table 11); the next highest number of deaths occurred in winter (n = 126, 17% of deaths in winter, significantly less than expected, low percentage because of high mortality from other causes). Deaths from collisions with watercraft were 27–30% of the number of

Table 10. Frequency distribution of manatee (*Trichechus manatus latirostris*) deaths in Florida by four geographic regions and four seasons (April 1976 to March 1992; n = 1,903).

Region	Season: April to June	July to September	October to December	January to March	Total: Region	Total: Coast
West						
Northwest	40 (9.0)	28 (7.3)	31 (9.1)	70 (9.6)	169 (8.9)	
Southwest	151 (33.8)	119 (31.2)	112 (32.8)	252 (34.4)	634 (33.3)	
Subtotal Coast	191 (42.7)	147 (38.5)	143 (41.9)	322 (43.9)		803 (42.2)
East						
Northeast	186 (41.6)	179 (46.9) +	112 (32.8) −	276 (37.7)	753 (39.6)	
Southeast	70 (15.7)	56 (14.7)	86 (25.2) ++	135 (18.4)	347 (18.2)	
Subtotal Coast	256 (57.3)	235 (61.5)	198 (58.1)	411 (56.1)		1,100 (57.8)
Total	447 [23.5]	382 [20.1]	341 [17.9]	733 [38.5]	1,903	1,903

+ and − indicate level of cell significance (standardized residuals, see Methods). One *symbol* indicates $P < 0.05$ and two indicate $P < 0.01$; region by season $\chi^2 = 25.9$, $P = 0.002$; coast by season $\chi^2 = 3.13$, $P = 0.373$.
Brackets [] indicate percentages across a row; *parentheses* () indicate percentages down a column.

Table 11. Frequency distribution of manatee (*Trichechus manatus latirostris*) deaths in Florida by eight cause-of-death categories and four seasons (April 1976 to March 1992; $n = 1{,}903$).

Cause of death	Season				Total
	April–June	July–September	October–December	January–March	
Watercraft collision	147	116	93	126	482
	(32.9)	(30.4)	(27.3)	(17.2)	(25.3)
	++			−−−	
Flood gate/canal lock	27	19	25	13	84
	(6.0)	(5.0)	(7.3)	(1.8)	(4.4)
			+	−−−	
Other human-related	15	12	15	11	53
	(3.4)	(3.1)	(4.4)	(1.5)	(2.8)
				−	
Various perinatal	121	116	59	88	384
	(27.1)	(30.4)	(17.3)	(12.0)	(20.2)
	++	+++		−−−	
Natural/cold	1	0	10	77	88
related	(0.2)	(0.0)	(2.9)	(10.5)	(4.6)
(1986–92 only)	−−−	−−−		+++	
Other natural	34	9	34	115	192
	(7.6)	(2.4)	(10.0)	(15.7)	(10.1)
		−−−		+++	
Verified, not recovered	16	14	14	21	65
	(3.6)	(3.7)	(4.1)	(2.9)	(3.4)
Undetermined	86	96	91	282	555
	(19.2)	(25.1)	(26.7)	(38.5)	(29.2)
	−−−			+++	
Total	447	382	341	733	1,903
	[23.5]	[20.1]	[17.9]	[38.5]	

+ and − indicate level of cell significance (standardized residuals, see Methods). One *symbol* indicates $P < 0.05$, two indicate $P < 0.01$, and three indicate $P < 0.001$.
Brackets [] indicate percentages across a row; *parentheses* () indicate percentages down a column.

deaths in other seasons. No significant changes in the proportion of deaths from watercraft among seasons occurred through time.

Flood Gates and Canal Locks

Deaths from flood gates and canal locks occurred almost exclusively in eastern Florida (86%; Table 7) but significantly decreased as a percentage of all deaths there since 1976–81 (from 12% to 5%). They were a higher percentage of all deaths in southeastern Florida (17%) than in any other region (1–2%). In southeastern Florida, these deaths decreased significantly more than deaths from the other causes (from 30% to 14%). The number of deaths from flood gates and canal locks was greatest in spring and fall (7% of all deaths in fall; 5–6% in spring and summer; 2% in winter; Table 11).

Other Human-related Causes of Death

Deaths in the other human-related causes category were more frequent in eastern Florida (74% of other human-related) and were a higher proportion (5%) of all deaths in southeastern Florida than in other regions (1–3%; Table 7). The number of deaths from other human-related causes was not large anywhere in the state; however, in 1986–92, it was proportionately lower in southeastern and higher in northeastern Florida. Other human-related causes of death were 2–4% of the deaths in all seasons (Table 11).

Deaths of Perinatal Manatees

The number of deaths of perinatal manatees steadily increased statewide (Table 6). The number of deaths of perinatal manatees was highest in northeastern Florida ($n = 158$, 21%) and in southwestern Florida ($n = 113$, 18%; Table 7). Deaths of perinatal manatees were a much higher percentage of deaths in northwestern Florida ($n = 73$, 43%) than in any other region, partly because overall mortality in northwestern Florida was low. The pattern by region did not change through time. The number of deaths of perinatal manatees was similar between coasts (eastern coast 52%), but the number of deaths of perinatal manatees increased at a greater rate than the number of deaths of

older manatees on the eastern coast (especially in the northeastern region).

Deaths of perinatal manatees were most common from March to July but occurred in every month (Table 12). The lowest monthly number (3%) occurred in February. Deaths of perinatal manatees were a significantly higher percentage of all deaths in spring (27%) and summer (30%; Table 11). Fewer deaths of perinatal manatees occurred in fall ($n = 59$, 17%), although they were the lowest percentage in winter ($n = 88$, 12%, January–March), in part because of the large number of deaths from other causes in winter. The number of deaths of perinatal manatees was highest in eastern Florida in spring (25%) and summer (33%) and highest in western Florida in winter (19%) and spring (35%). The pattern by season did not change through time. Deaths of perinatal manatees occurred earlier (some in March) in northwestern Florida than in any other region.

Cold-related Deaths

The number of cold-related deaths were 10% of all deaths in northeastern Florida during 1986–92 and only 2–4% in other regions. However, this category has been used only since 1986; in that time, the only major mortality event was in winter 1989–90 when most manatees that died from low temperatures were in northeastern Florida. The number of deaths from low temperatures was 22% of the number of deaths in winter during 1986–92 and was smaller in other months (88% of deaths from low temperatures occurred during January–March; Table 11). However, some deaths from low temperatures occurred from late November until mid-April.

Fifty-six deaths were attributed to low temperatures in Florida and five in other southeastern states (4 in Georgia, 1 in North Carolina) in winter 1989–90 (Table 5). This was the largest known mortality event from low temperatures and was not previously described. These deaths occurred from 26 November 1989 to 12 April 1990, and almost all occurred in December (9) and January (44). Most followed a severe cold front that passed through the state on 24 December 1989 (minimum air temperature was −7.2° C in Titusville). Water temperatures were below 10° C for 7 days (minimum of 4.4° C on 25 December 1989) in various areas in the Indian and Banana rivers and in the Mosquito Lagoon (Schroeder et al. 1990). Almost all of the carcasses were reported between 24 December 1989 and 19 January 1990; most were found during 6–8 January. However, these manatees probably died several days before their carcasses were discovered. The five deaths in other states occurred between 29 December and 22 January. No manatees died from low temperatures in February, which was warmer, but one each was recovered in March and in April 1990. Most manatees that died from low temperatures in Florida were in counties in northeastern Florida ($n = 44$, November 1989 to April 1990; Nassau 1, Duval 5, Clay 3, St. Johns 1, Flagler 1, Volusia 2, Brevard 31); 35 died in northeastern Florida in January (27 in Brevard County). Only 7 manatees died from low temperatures in the southwestern region (November 1989 to April 1990), 4 in northwestern Florida, and 1 in southeastern

Table 12. The number of manatee (*Trichechus manatus latirostris*) deaths in Florida by category and by month, 1974 to 1992 ($n = 2,073$). The percent of the count is given in parentheses in each category.

	Month reported												
Cause of death	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Watercraft collision	40 (7.7)	44 (8.4)	48 (9.2)	47 (9.0)	70 (13.4)	43 (8.2)	46 (8.8)	53 (10.2)	27 (5.2)	40 (7.7)	23 (4.4)	41 (7.9)	522
Flood gate/ canal lock	4 (4.5)	2 (2.3)	7 (7.9)	2 (2.3)	10 (11.2)	18 (20.2)	7 (7.9)	4 (4.5)	9 (10.1)	8 (9.0)	12 (13.5)	6 (6.7)	89
Other human-related	5 (8.1)	3 (4.8)	4 (6.5)	5 (8.1)	5 (8.1)	6 (9.7)	6 (9.7)	4 (6.5)	5 (8.1)	7 (11.3)	6 (9.7)	6 (9.7)	62
Various perinatal	21 (4.9)	14 (3.3)	52 (12.2)	57 (13.4)	55 (12.9)	37 (8.7)	51 (12.0)	41 (9.7)	29 (6.8)	26 (6.1)	23 (5.4)	19 (4.5)	425
Cold-related[a]	61 (69.3)	10 (11.4)	6 (6.8)	1 (1.1)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	1 (1.1)	9 (10.2)	88
Other natural	44 (20.7)	48 (22.5)	29 (13.6)	27 (12.7)	10 (4.7)	6 (2.8)	4 (1.9)	3 (1.4)	4 (1.9)	8 (3.8)	6 (2.8)	24 (11.3)	213
Undetermined	91 (13.5)	132 (19.6)	94 (14.0)	45 (6.7)	32 (4.8)	37 (5.5)	43 (6.4)	40 (5.9)	40 (5.9)	31 (4.6)	33 (4.9)	56 (8.3)	674
Total	266 (12.8)	253 (12.2)	240 (11.6)	184 (8.9)	182 (8.8)	147 (7.1)	157 (7.6)	145 (7.0)	114 (5.5)	120 (5.8)	104 (5.0)	161 (7.8)	2,073

[a] The cold-related category was not used until 1986. These deaths were included in the category of deaths from undetermined causes during 1974–80 and in the category of deaths from other natural causes during 1981–85.

Florida. Deaths from low temperatures were 60% of the 73 deaths in January 1990 and 35% of 130 deaths during December 1989–March 1990. The numbers of deaths from other natural (9) and undetermined (18) causes were also unusually high in January and February 1990; some of them may have been from low temperatures. This was similar to previous low-temperature events. As in previous years and analyses, most carcasses that were associated with this event were in the subadult size range (73%, November–April; 77%, January). A high percentage of the carcasses was decomposed (January 1990, $n = 44$, 54% moderately decomposed, 39% badly decomposed), despite the cold temperatures.

Other Natural Causes of Death

Deaths from other natural causes occurred most frequently in the southwestern region (14% of all deaths in southwestern Florida, 6–9% in other regions; Table 7), including 37 deaths ascribed to red tide in Lee County in spring 1982 (results previously described in detail by O'Shea et al. 1991). The number of deaths from other natural causes was second highest in the northeastern region (9% of deaths); 58% of all other natural deaths occurred in eastern Florida. Catastrophic mortality caused most of the significant relations in this category. When the deaths from low temperatures were included, mortality was higher than expected in southwestern Florida in 1981–86 (several cold events; red tide during March–April 1982) and in northeastern Florida in 1986–92 (1989–90 cold event). This strong interaction (southwestern Florida 1981–86; northwestern Florida 1986–92) complicated the interpretation of many other results. Other natural deaths were much less common in the northwestern and southeastern regions, probably because of warmer or more consistent sources of warm water in winter.

Deaths from other natural causes (including deaths from low temperatures) were 26% of the deaths in winter over all years (33% in winter 1986–92) and 2–13% in other seasons (Table 11).

Undetermined Causes of Death

The number of undetermined deaths remained constant through time, but the percentage decreased markedly, mostly because deaths from low temperatures were removed from this category in 1981 (Table 6). Most deaths from undetermined causes (51% of total) occurred in winter (Table 11). This was especially evident in earlier years when deaths from low temperatures were included in this category (1974–85) but remained true in recent years. Deaths from undetermined causes decreased more in winter than in other seasons (62% in winter 1976–81, 37% 1986–92), suggesting that a higher proportion of deaths in winter is now being assigned to specific categories (e.g., cold-related deaths or from other natural causes). Sixty-nine percent of the other natural deaths (including cold-related deaths) also occurred in winter (Table 6). These four combined causes of death (low temperature, other natural, undetermined, and verified without recovery of the carcass) were higher in winter (68% of deaths in winter) than in other seasons (31–44%). The number of verified deaths without recovery of the carcasses was 3–4% of deaths in each season.

Undetermined causes of death (including verified without recovery of the carcass) were 24–41% of deaths in all regions; the highest percentages were in southwestern ($n = 261$, 41% by region) and northeastern ($n = 223$, 30%) Florida (Table 7). The proportion of deaths from undetermined causes by region did not change through time. The number of deaths from undetermined causes was similar on both coasts but significantly higher than other causes of death on the western coast (Table 7). In 1986–92, the highest numbers of deaths from undetermined causes occurred in winter, mostly in the northeastern and southwestern regions.

Combined Human-related Causes of Death

The combined human-related causes of death (watercraft, flood gate–canal lock, and other human-related) were responsible for more deaths in eastern Florida (422 deaths, 39% of deaths) than in western Florida (197, 26%; Table 7). In contrast, the number of deaths from natural causes (cold-related, other natural, perinatal) and undetermined causes were similar on the two coasts (649 in eastern Florida and 570 in western Florida). The proportion of human-related deaths was significantly higher in southeastern (56%) and lower in northwestern (22%) and southwestern Florida (27%) than in northeastern Florida (32%; Table 7). The statewide proportion of human-related deaths (33%) did not change through time or in eastern Florida (39%) but increased through time in western Florida from 18% in 1976–81 to 31% in 1986–92.

The number of human-related deaths was similar between seasons (150 deaths in winter, 133–189 deaths in warm seasons), but human-related deaths were a significantly higher proportion of deaths in warm seasons (40–44%) than in winter (21%).

Sizes of Carcasses

Of the carcasses for which total length was available (1976–92, $n = 1{,}809$), 27% were calves, 41% were subadults, and 33% were adults. The percentage of carcasses that was calves increased through time (Table 13).

Cause of death by size class. Size classes were differentially associated with various causes of death (Table 14; Figs. 8–9). The number of deaths from watercraft, gates

Table 13. Frequency distribution of manatee (*Trichechus manatus latirostris*) deaths in Florida by three size classes and three time periods (April 1976 to March 1992; n = 1,809). The percent of the count is given in parentheses in each category.

	Time period			
Size class (cm)	April 1976 to March 1981	April 1981 to March 1986	April 1986 to March 1992	Total
42–175	85 (21.9)	117 (22.8)	278 (30.6) +	480 (26.5)
176–275	162 (41.8)	225 (43.9)	346 (38.1)	733 (40.5)
276–411	141 (36.3)	171 (33.3)	284 (31.3)	596 (33.0)
Total	388 [21.4]	513 [28.4]	908 [50.2]	1,809

+ indicates level of cell significance (standardized residuals, see Methods). One *symbol* indicates $P < 0.05$; $\chi^2 = 16.5$, $P = 0.002$.
Brackets [] indicate percentages across a row; *parentheses* () indicate percentages down a column.

Table 14. Frequency distribution of manatee (*Trichechus manatus latirostris*) deaths in Florida by seven cause-of-death categories and three size classes (April 1976 to March 1992; n = 1,809). The percent of the count is given in parentheses in each category.

	Size class (cm)			
Cause of death	42–175	176–275	276–411	Total
Watercraft collision	22 (4.6) −−−	213 (29.1)	245 (41.1) +++	480 (26.5)
Flood gate/ canal lock	2 (0.4) −−−	26 (3.6)	56 (9.4) +++	84 (4.6)
Other human-related	8 (1.7)	16 (2.2)	26 (4.4) +	50 (2.8)
Various perinatal	379 (79.0) +++	0 (0.0) −−−	0 (0.0) −−−	379 (21.0)
Natural/cold-related (1986–92 only)	9 (1.9) −−	68 (9.3) +++	11 (1.9) −−−	88 (4.9)
Other natural	10 (2.1) −−−	117 (16.0) +++	65 (10.9)	192 (10.6)
Undetermined	50 (10.4) −−−	293 (40.0) +++	193 (32.4)	536 (29.6)
Total	480 [26.5]	733 [40.5]	596 [33.0]	1,809

+ and − indicate level of cell significance (standardized residuals, see Methods). One *symbol* indicates $P < 0.05$, two indicate $P < 0.01$, and three indicate $P < 0.001$; $\chi^2 = 1433.6$, $P < 0.001$.
Brackets [] indicate percentages across a row; *parentheses* () indicate percentages down a column.

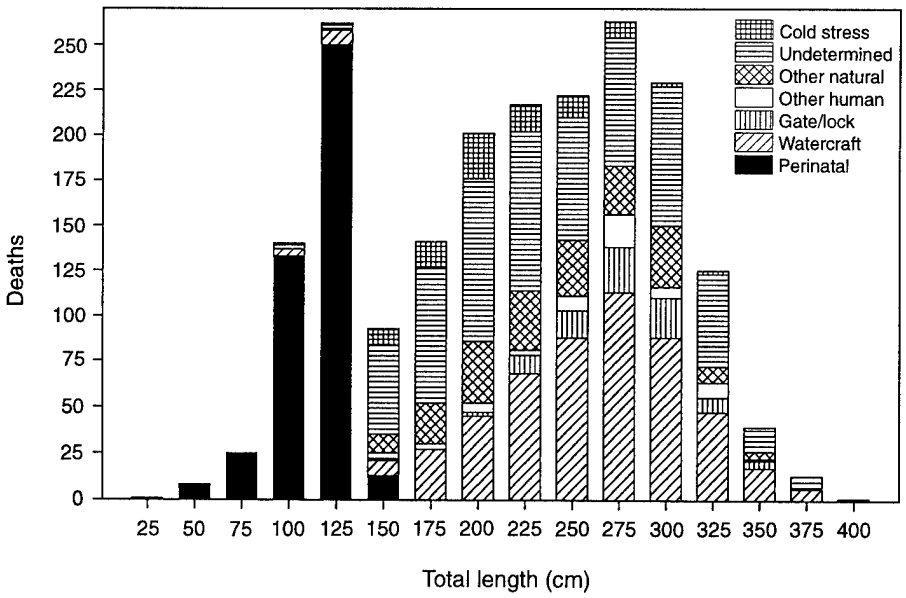


Fig. 8. Frequency of deaths of Florida manatees (*Trichechus manatus latirostris*) by seven causes of death and by total length of carcass (cm), Florida, 1974–1992 (n = 1,903).

and locks, and other human-related causes included significantly more adults than did other causes. Deaths from low temperatures (1986–92) and from other natural and undetermined causes included more subadults than adults. The calf size-class (≤175 cm) included all deaths of perinatal manatees, but it also included some larger calves that died from other causes, which produced the significant interaction between calf size category and the category of deaths of perinatal manatees. Omitting the 379 perinatal carcasses, the size distribution of the remaining 1,430 carcasses changed substantially (7% calves, 51% subadults, and 42% adults). The small number of large calves in the other human-related and undetermined cause-of-death categories became larger than expected. The large number of subadults in the undetermined cause-of-death category was no longer larger than expected.

Carcass size was related to region (χ^2 = 73.2, P < 0.001; Table 15); the proportion of calf carcasses was higher in the northwestern region, and the proportion of adult carcasses was higher in southeastern Florida. This agrees with findings from the analyses of cause-of-death frequencies by size and by region (proportionately more deaths of perinatal manatees in northwestern Florida; proportionately more deaths from flood gates and canal locks and other human-related causes in southeastern Florida). Carcass size distributions did not differ between the eastern and western coasts of Florida. Carcass size was also related to season (χ^2 = 125.6, P < 0.001; Table 16); the proportions of calf carcasses were higher in spring and summer, of subadults in winter, and of adults in summer. This agrees with findings from the analyses of cause-of-death frequencies by size and by season.

Most carcasses ≤150 cm were categorized as perinatal (Fig. 8). The number of carcasses that were 150–199 cm long was low because of the rapid growth of manatees at this age (*Odell 1981). The most frequent length of the larger carcasses was 275–299 cm; many carcasses were in the 200–324-cm range. The rapid decline in numbers of carcasses that were 325 cm long or longer indicated the smaller number of adults that achieved long lengths. The shift in causes of death from those most prevalent in subadults to those most prevalent in adults was at about 275 cm (Fig. 8).

Cause of death by size and sex. More carcasses of male (53%) than of female manatees were recovered (Table 17), which differs from a 50:50 ratio. The proportion by sex did not vary with time, cause of death, region, or season. Males were more numerous among the carcasses of calves and subadults (45% female; <276 cm), and females were more numerous among the carcasses of adults (51% female; ≥276 cm; χ^2 = 7.1, P = 0.03; Table 17; Fig. 9). The carcasses of adult females prevailed in the 351–411-cm size category (90% female). The proportion of large animals (≥351 cm; 7%) among adults did not change through time. More carcasses of males than of females that died from low temperatures and in gates and locks were recovered.

Cause of death by carcass condition. Information about the condition of 1,860 carcasses was available: 21% were fresh, 26% were moderately decomposed, and 53% were badly decomposed (Table 18). More carcasses (25%) were fresh in 1986–92 and fewer (47%) were badly decomposed (Table 19) than in earlier time periods. The proportion of fresh carcasses was lowest (15%) in 1981–86. Carcass condition did not differ among the four regions (Table 20).

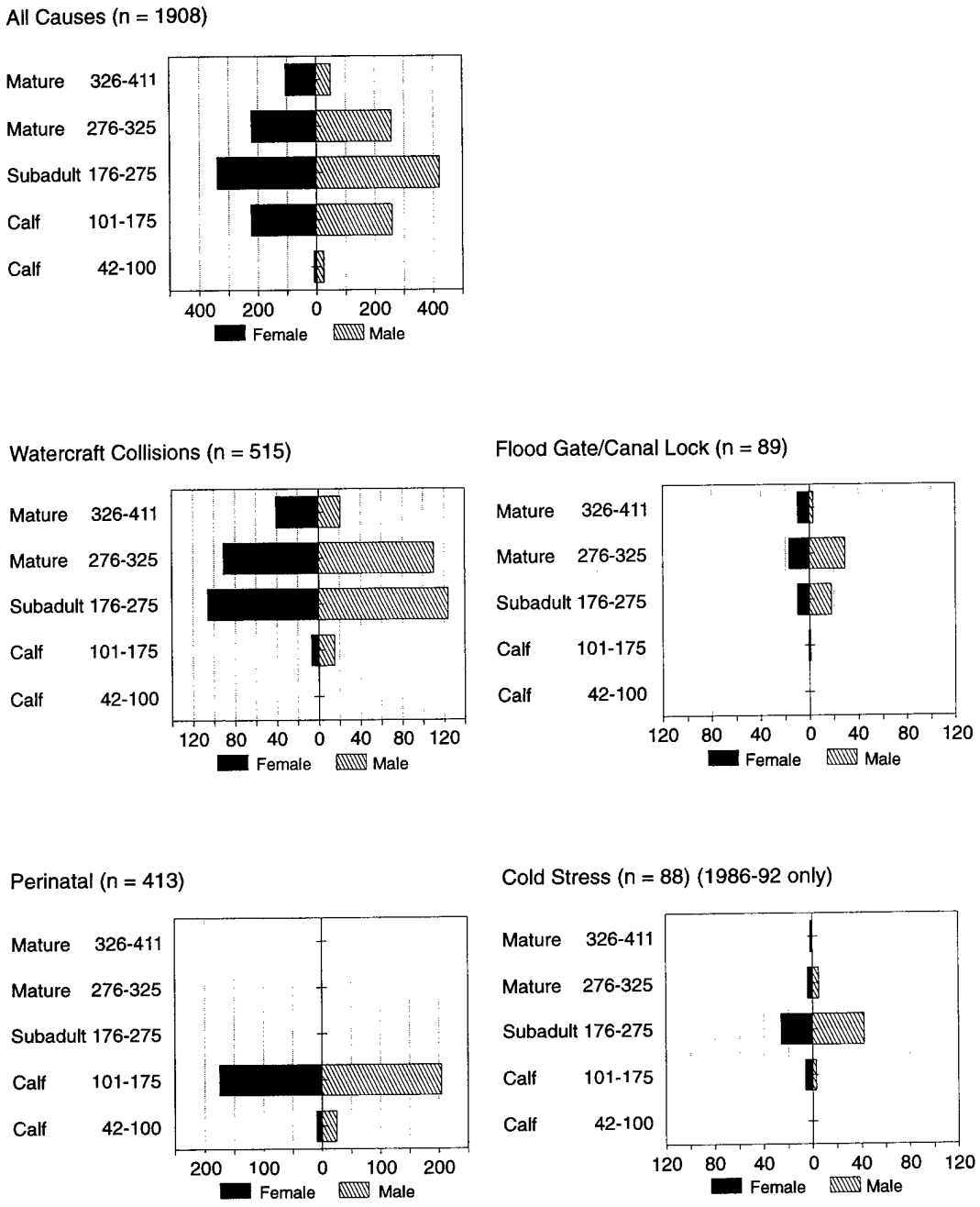


Fig. 9. Frequency of deaths of Florida manatees (*Trichechus manatus latirostris*) by size classes of males and females (n = 1,903) and by four causes of death and the total number of all causes, Florida, 1974–1992. Note that the horizontal scale varies between charts.

Table 15. Frequency distribution of manatee (*Trichechus manatus latirostris*) deaths in Florida by three size classes and four geographic regions (April 1976 to March 1992; $n = 1{,}809$).

		Region				
		West		East		
Size class (cm)		Northwest	Southwest	Northeast	Southeast	Total
42–175		80	138	203	59	480
		(49.1)	(23.4)	(27.8)	(18.1)	(26.5)
		+++			−−	
176–275		38	263	308	124	733
		(23.3)	(44.6)	(42.2)	(38.0)	(40.5)
		−−−				
276–411		45	189	219	143	596
		(27.6)	(32.0)	(30.0)	(43.9)	(33.0)
					+++	
Total	Region	163	590	730	326	1,809
		[9.0]	[32.6]	[40.4]	[18.0]	
	Coast	753		1,056		
		[41.6]		[58.4]		

+ and − indicate level of cell significance (standardized residuals, see Methods). Two *symbols* indicate $P < 0.01$ and three indicate $P < 0.001$; size by region $\chi^2 = 73.2$, $P = 0.001$; size by coast $\chi^2 = 4.31$, $P = 0.116$.
Brackets [] indicate percentages across a row; *parentheses* () indicate percentages down a column.

Table 16. Frequency distribution of manatee (*Trichechus manatus latirostris*) deaths in Florida by three size classes and four seasons (April 1976 to March 1992; $n = 1{,}809$).

	Season				
Size class (cm)	April to June	July to September	October to December	January to March	Total
42–175	133	130	84	133	480
	(31.4)	(36.0)	(25.9)	(19.0)	(26.5)
		+++		−−−	
176–275	132	88	122	391	733
	(31.2)	(24.4)	(37.7)	(55.8)	(40.5)
	−−	−−−		+++	
276–411	158	143	118	177	596
	(37.4)	(39.6)	(36.4)	(25.3)	(33.0)
		+		−−−	
Total	423	361	324	701	1,809
	[23.4]	[20.0]	[17.9]	[38.7]	

+ and − indicate level of cell significance (standardized residuals, see Methods). One *symbol* indicates $P < 0.05$, two indicate $P < 0.01$, and three indicate $P < 0.001$; $\chi^2 = 125.6$, $P < 0.001$.
Brackets [] indicate percentages across a row; *parentheses* () indicate percentages down a column.

Table 17. Frequency distribution of manatee (*Trichechus manatus latirostris*) deaths in Florida by three size classes and by sex (April 1976 to March 1992; $n = 1{,}752$).

Size class (cm)	Sex		Total
	Female	Male	
42–175	214	250	464
	(25.9)	(27.0)	(26.5)
176–275	312	395	707
	(37.8)	(42.6)	(40.3)
276–411	299	282	581
	(36.2)	(30.4)	(33.2)
Total	825	927	1,752
	[47.1]	[52.9]	

Brackets [] indicate percentages across a row; *parentheses* () indicate percentages down a column. No cells were significant at $P < 0.05$; $\chi^2 = 7.12$, $P = 0.028$.

Table 18. Frequency distribution of manatee (*Trichechus manatus latirostris*) deaths in Florida by three carcass condition categories and four seasons (April 1976 to March 1992; $n = 1{,}860$). The percent of the count is given in parentheses in each category.

Carcass condition	Season				Total
	April to June	July to September	October to December	January to March	
Fresh	87	62	88	153	390
	(20.0)	(16.5)	(26.7)	(21.3)	(21.0)
			+		
Moderately decomposed	103	74	100	211	488
	(23.6)	(19.7)	(30.3)	(29.4)	(26.2)
		–			
Badly decomposed	246	240	142	354	982
	(56.4)	(63.8)	(43.0)	(49.3)	(52.8)
		++	–		
Total	436	376	330	718	1,860
	[23.5]	[20.2]	[17.7]	[38.6]	

+ and – indicate level of cell significance (standardized residuals, see Methods). One *symbol* indicates $P < 0.05$ and two indicate $P < 0.01$; $\chi^2 = 38.4$, $P < 0.001$.

Brackets [] indicate percentages across a row; *parentheses* () indicate percentages down a column.

Table 19. Frequency distribution of manatee (*Trichechus manatus latirostris*) deaths in Florida by three carcass condition categories and three time periods (April 1976 to March 1992; $n = 1,860$).

Carcass condition	Time period: April 1976 to March 1981	April 1981 to March 1986	April 1986 to March 1992	Total
Fresh	80	82	228	390
	(19.2)	(15.3)	(25.1)	(21.0)
		−−	++	
Moderately decomposed	94	141	253	488
	(22.6)	(26.4)	(27.8)	(26.2)
Badly decomposed	242	312	428	982
	(58.2)	(58.3)	(47.1)	(52.8)
			−	
Total	416	535	909	1,860
	[22.3]	[28.8]	[48.9]	

+ and − indicate level of cell significance (standardized residuals, see Methods). One *symbol* indicates $P < 0.05$ and two indicate $P < 0.01$; $\chi^2 = 30.0$, $P < 0.001$.
Brackets [] indicate percentages across a row; *parentheses* () indicate percentages down a column.

The proportion of badly decomposed carcasses (56%) was higher in the southwestern region than in the other regions (48–53%). More carcasses were badly decomposed in summer (64% vs 43–56% in other seasons) and fresh in fall (27% vs 16–21% other seasons; Table 18). The carcasses of calves were more decomposed (64%) than the carcasses of larger animals (46–49%; Table 21). The condition of carcasses did not vary by sex.

The condition of carcasses differed among causes of death (Table 22). If deaths were from watercraft, gates and locks, and other natural causes (including low temperatures), the carcasses were less frequently badly decomposed (28–34%). Carcasses of perinatal manatees (68%) and manatees that died from undetermined causes (74%) were more often badly decomposed than carcasses of manatees that died of other causes. This pattern was caused by the reduced ability to categorize badly decomposed carcasses. The number of badly decomposed carcasses was greater of manatees that died from low temperatures (1986–92) than of manatees that died of other natural causes.

Management and Conservation

Most management of the Florida manatee has been aimed at reducing human-related deaths (*U.S. Fish and Wildlife Service 1989), which should be more easily addressed than natural causes of death. Human-related causes of death (watercraft, gates and locks, and other anthropogenic causes) were responsible for more deaths in eastern than in

Table 20. Frequency distribution of manatee (*Trichechus manatus latirostris*) deaths in Florida by three carcass condition categories and four geographic regions (April 1976 to March 1992; $n = 1,860$).

Carcass condition		Region: West — Northwest	West — Southwest	East — Northeast	East — Southeast	Total
Fresh		41	120	153	76	390
		(24.9)	(19.5)	(20.5)	(22.7)	(21.0)
Moderately decomposed		43	149	199	97	488
		(26.1)	(24.2)	(26.7)	(29.0)	(26.2)
Badly decomposed		81	346	393	162	982
		(49.1)	(56.3)	(52.8)	(48.4)	(52.8)
Total	Region	165	615	745	355	1,860
		[8.9]	[33.1]	[40.0]	[18.0]	
	Coast	780		1,080		
		[42.0]		[58.0]		

Brackets [] indicate percentages across a row; *parentheses* () indicate percentages down a column. No cells were significant at $P < 0.05$; $\chi^2 = 7.38$, $P = 0.29$.

Table 21. Frequency distribution of manatee (*Trichechus manatus latirostris*) deaths in Florida by three carcass condition categories and three size classes (April 1976 to March 1992; $n = 1{,}810$).

Carcass condition	Size class (cm) 42–175	176–275	276–411	Total
Fresh	73	170	142	385
	(15.2)	(23.2)	(23.8)	(21.3)
	−−			
Moderately decomposed	99	223	163	485
	(20.6)	(30.4)	(27.4)	(26.8)
	−−			
Badly decomposed	308	341	291	940
	(64.2)	(46.5)	(48.8)	(51.9)
	+++	−		
Total	480	734	596	1,810
	[26.5]	[40.6]	[32.9]	

+ and − indicate level of cell significance (standardized residuals, see Methods). One *symbol* indicates $P < 0.05$, two indicate $P < 0.01$, and three indicate $P < 0.001$; $\chi^2 = 40.9$, $P < 0.001$.
Brackets [] indicate percentages across a row; *parentheses* () indicate percentages down a column.

Table 22. Frequency distribution of manatee (*Trichechus manatus latirostris*) deaths in Florida by seven cause-of-death categories and three carcass condition categories (April 1976 to March 1992; $n = 1{,}837$).

Cause of death	Carcass condition Fresh	Moderately decomposed	Badly decomposed	Total
Watercraft collision	144	172	166	482
	(37.3)	(35.5)	(17.2)	(26.2)
	+++	+++	−−−	
Flood gate/canal lock	26	30	28	84
	(6.7)	(6.2)	(2.9)	(4.6)
	+		−	
Other human-related	15	14	24	53
	(3.9)	(2.9)	(2.5)	(2.9)
Various perinatal	60	64	259	383
	(15.5)	(13.2)	(26.8)	(20.8)
	−	−−−	+++	
Natural/cold-related (1986–92 only)	16	45	27	88
	(4.2)	(9.3)	(2.8)	(4.8)
		+++	−−	
Other natural	78	62	52	192
	(20.2)	(12.8)	(5.4)	(10.5)
	+++		−−−	
Undetermined	47	98	410	555
	(12.2)	(20.2)	(42.4)	(30.2)
	−−−	−−−	+++	
Total	386	485	966	1,837
	[21.0]	[26.4]	[52.6]	

+ and − indicate level of cell significance (standardized residuals, see Methods). One *symbol* indicates $P < 0.05$, two indicate $P < 0.01$, and three indicate $P < 0.001$; $\chi^2 = 286.7$, $P < 0.001$.
Brackets [] indicate percentages across a row; *parentheses* () indicate percentages down a column.

western Florida. The numbers of deaths from natural causes (deaths of perinatal manatees, deaths from low temperatures and from other natural causes) and from undetermined causes on both coasts were similar. Human-related deaths were higher in the southwestern region than in northwestern Florida. Most manatees that died from anthropogenic causes were adults. Population modeling indicated that reductions in adult mortality will have a greater effect on increasing manatee population growth rates than any other life- history attributes (Marmontel 1993; Eberhardt and O'Shea 1995). Therefore, the focus of conservation on decreasing human-related deaths is highly justifiable, particularly in eastern and southwestern Florida. Counties where the most carcasses were recovered (Table 23; Figs. 10 a–d) should receive assistance with the reduction of mortality in manatees.

Mortality From Watercraft

The number of deaths from watercraft (Fig. 10a) in Florida increased more than the number of deaths from other causes. This is probably not the result of improved diagnosis because injuries from collisions were often distinctive even on decomposed carcasses. The number of deaths from watercraft increased most rapidly in the southwestern region. However, among counties, deaths from watercraft were highest in Brevard County (20% of all deaths from watercraft), which has the most shoreline and inland water area, the highest year-round manatee population, and a large number of registered watercraft (n = 27,479 in 1992–93, the county with the ninth highest number of registered watercraft in the state). The number of deaths from watercraft was also higher in Duval (12%), Collier (11%), Lee (10%), and Dade (6%) counties than in other counties. In each of these counties, the number of watercraft and the seasonal abundance of manatees was high, and the congestion of waterways was intense. O'Shea et al. (1985) reported that deaths from watercraft in 1976–81 were most frequent in northeastern Florida, especially in Brevard County and on the St. Johns River. However, in recent years, the number of deaths from watercraft increased to similar levels in southwestern Florida. Deaths from watercraft in southwestern Florida occurred mostly in Lee and Collier counties, indicating the need for continued management there.

The correlation between the number of watercraft-related manatee deaths and the number of registered watercraft was statistically highly significant (Figs. 3 and 4). However, the increasing number of watercraft alone may not be the direct cause of the increasing number of manatees that are killed in collisions. The rate of increase of deaths from watercraft was faster than the increase in registered watercraft, indicating a probable interaction that includes other factors. Wright et al. (1995) described several factors that may interact to increase mortality from watercraft, including the development of more powerful engines and new devices that provide access to previously less accessible habitats.

The number of watercraft registrations declined during an economic recession in 1980–83 from 512,600 in 1980–81 to 512,300 in 1981–82 (Fig. 4); and registered watercraft may also have been used less often. The number of manatee deaths from watercraft collisions was also low during this period, especially in 1980 (16), 1982 (20), and 1983 (15). The small reduction of watercraft registrations from 1990–91 to 1992–93 and the low number of deaths from watercraft in 1992 (38) and 1993 (35; Florida Department of Environmental Protection, unpublished data) may similarly be related to the economic conditions during 1992–93, during which recreational boating may have been low. There is currently no method to demonstrate a relation between the large decrease in manatee deaths and the small decrease in watercraft registrations in those years. However, data from the 2 years after the end of the recent economic recession may provide information about a relation between the present decline of the number of deaths from watercraft, the economic recession, and improved protection of the manatees. A more direct index of watercraft usage (e.g., total hours on the water, distance travelled per year, amount of sold fuel) would be desirable.

Most living adult manatees have healed wounds that are indicative of past collisions with watercraft; many adults are identifiable by patterns of scars and disfigurements (Reid et al. 1991; Beck and Reid 1995). Most carcasses of large adults, regardless of cause of death, have scars from previous watercraft collisions, and some have hidden internal injuries such as healed fractured ribs. These serious but sublethal injuries may increase mortality from other causes and may decrease rates of reproduction of injured individuals.

Mortality in Flood Gates and Canal Locks

The preponderance of deaths in flood gates and canal locks in southeastern Florida was understandable because of the larger number of canals and structures for water control and navigation in southeastern Florida than in other regions. The large number of deaths in these structures in spring and fall may be due to several factors. For example, migrating manatees may be killed while they move through areas with these structures. Because of frequent rain, the repositioning of flood gates is also most frequent in fall when manatees migrate (Odell and Reynolds 1979). Although relative proportions decreased with time, the absence of a trend toward annually declining numbers of deaths in these structures, despite their known locations and long recognition as a cause of death (Odell

Table 23. Florida manatee (*Trichechus manatus latirostris*) deaths in Florida from all causes by county and year, 1974 to 1992.

County	Year																			Total	
	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	*n*	%
Bay													1		1		1			3	0.2
Brevard	1	14	15	29	8	21	13	20	9	11	11	32	15	23	20	37	62	38	31	410	19.8
Broward	1	1	1	4	2	2	7	2	4	2	5	4	6	6	5	4	1	3	9	69	3.3
Charlotte		1	1	4		1		1	6	1	4	1	3	2	2	11	4	4	3	49	2.4
Citrus	1		1	4	2	2	2	1	4	1	5	3	4	6	7	5	5	5	9	67	3.2
Clay		1		1	2					1	1			2	1		3	2	4	18	0.9
Collier			1	3	3	4	5	13	5	9	9	13	12	11	14	19	13	14	20	168	8.1
Dade	2	4	15	12	12	9	2	5	4	7	1	4	2	8	9	3	4	7	10	120	5.8
DeSoto												2					1		2	5	0.2
Dixie			1				2											2		5	0.2
Duval			6	11	11	11	3	7	3	8	16	9	13	13	9	20	13	19	8	180	8.7
Flagler			2				1							2		2	4	2	2	15	0.7
Franklin																1	1			2	0.1
Glades			1	1	3	2	4	2		4	5	2	1	1	3	1	1		4	35	1.7
Hendry											2					1	1			4	0.2
Hernando												1								1	<0.1
Hillsborough				3	4	1	1	1	3	3	2	6	6	2	3	5	7	8	4	59	2.8
Indian River	1		2	2				2	3		6	2	1	1	2	5	3	4	1	35	1.7
Lake					1			1	1		1		1					1		6	0.3
Lee		1	4	11	9	4	7	18	48	15	19	16	15	10	19	16	27	18	19	276	13.3
Levy		3	1	1	1	1	4	1	2	1	4		3		2		2			26	1.3
Manatee			1		1	2		3	1		2		1	2	3	1	4	4	4	29	1.4
Martin		2	1	2	2	5	2	5	2	2	9	3	4	4	6	8	6	9	8	80	3.9
Monroe				4	10		2	20	4	1	3	4	7	1	3	4	8	1	5	77	3.7
Nassau								2		1	2	1	1		2	3	3	2	1	18	0.9
Okaloosa																	1			1	<0.1
Okeechobee					1		1					1	1					2	1	7	0.3
Palm Beach			1	7	3	3		3	2	3	5	3	6	3	4	1	6	6	3	59	2.8
Pasco											1							1	1	3	0.1
Pinellas			1		2		1			1		2	2	1	1	3	3	2	1	20	1.0
Putnam			3	4	1	4	2	1	2	5		2	2	2		2	1	2	3	36	1.7
Sarasota			1	2		1			2	1	3	2	3	4	7	5	7	5	1	44	2.1
Seminole															2			2		4	0.2
St. Johns			1	3	1			2	3	1	1	1			3	1	1			18	0.9
St. Lucie				3	1		1	4	2		3	2	4	1	2	3	5	1	4	36	1.7
Volusia	1	2	2	3	4	4	3	2	4	3	8	3	8	9	3	7	8	10	5	89	4.3
Total	7	29	62	114	84	77	63	116	114	81	128	119	122	114	133	168	206	174	163	2,074	100

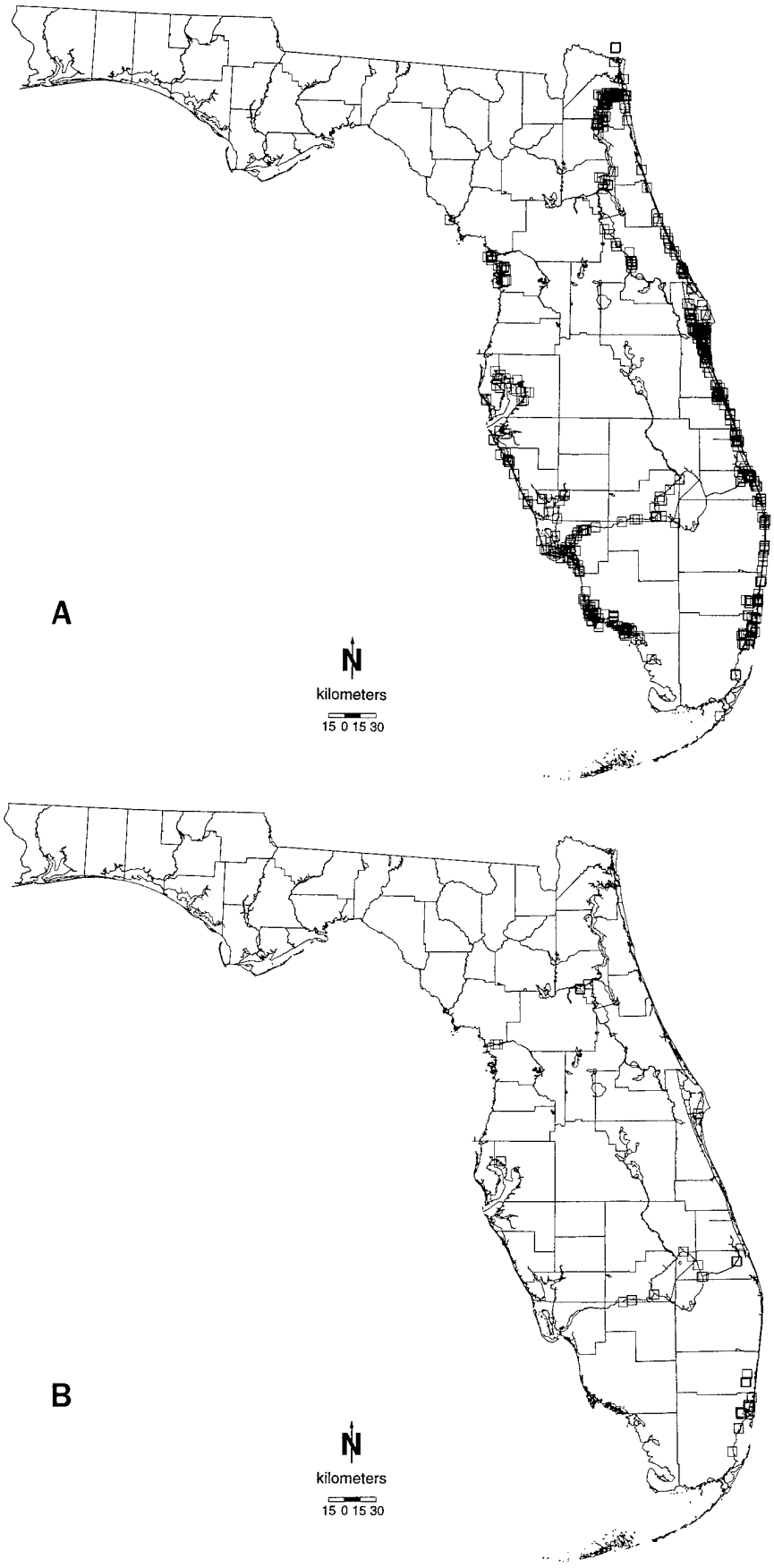
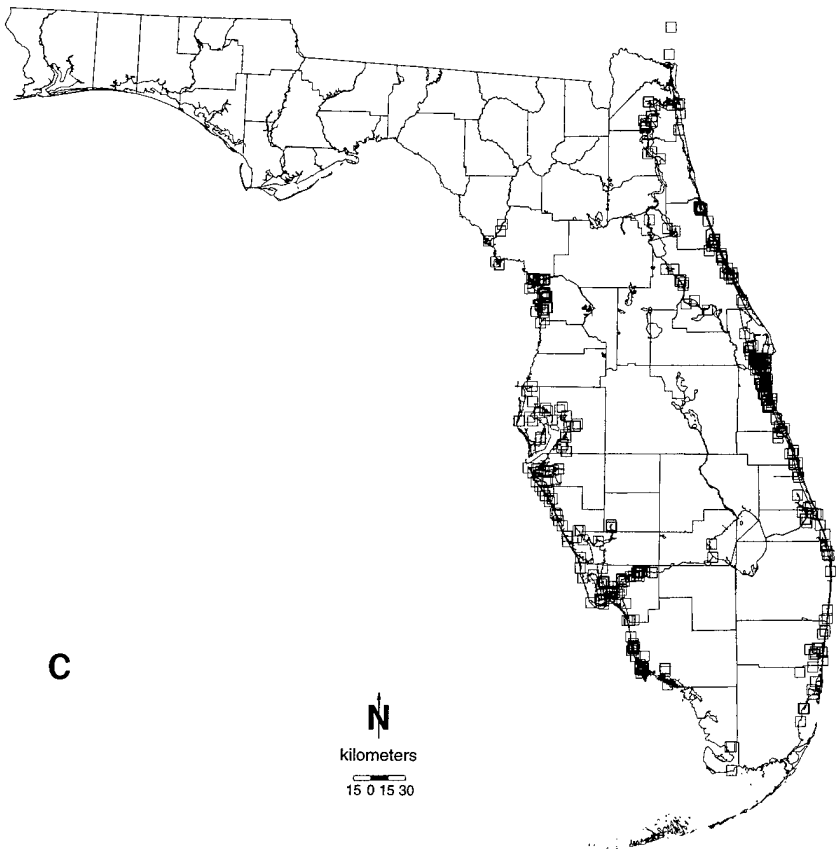
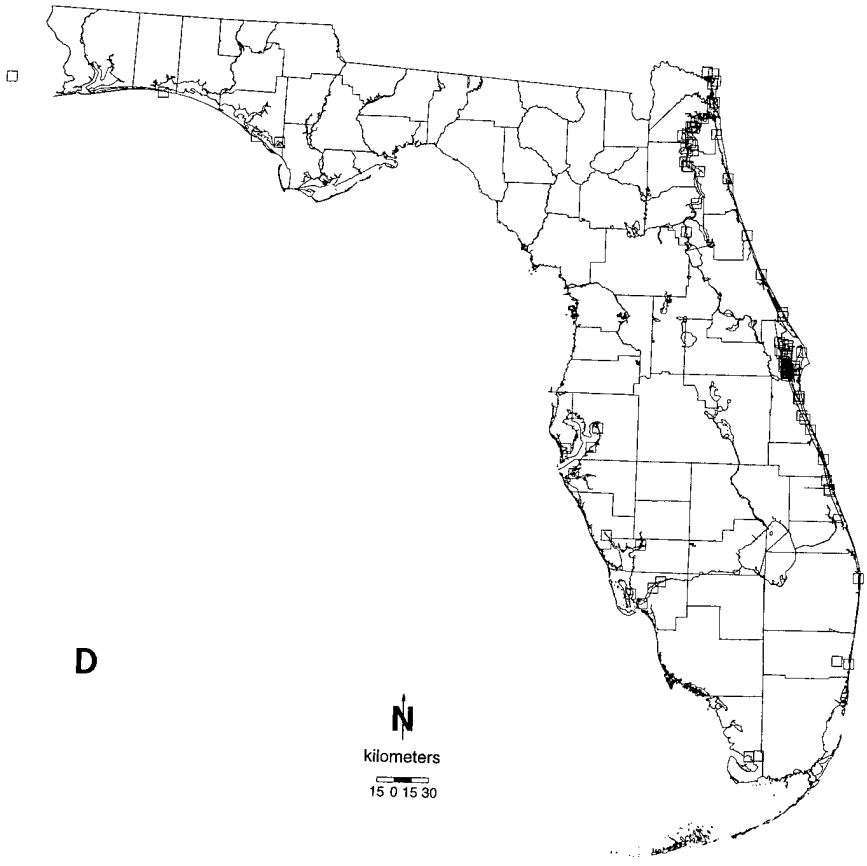


Fig. 10. Locations where Florida manatees (*Trichechus manatus latirostris*) were found dead from any of four causes of death in Florida and in adjacent states, 1974–1992. A. Collisions with watercraft (n = 522 in Florida and n = 5 in Georgia, 1974–1992). B. Flood-gate and canal lock (n = 89 in Florida and n = 0 in other states, 1974–1992). C. Various of perinatal manatee (n = 426 in Florida and n = 3 in Georgia, 1974–1992). D. Cold-related (n = 88 in Florida, n = 4 in Georgia, and n = 1 in Alabama. Single deaths in North Carolina and South Carolina are not shown. Note: The cold-related category was used only during 1986–1992).


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and Reynolds 1979), points out the need for more intensive management to stop the problem.

Recent Management

Management and conservation by the Florida Department of Environmental Protection accelerated in 1989 at the direction of the governor and the cabinet (*Florida Department of Natural Resources 1989) and are commensurate with the Florida Manatee Recovery Plan (*U.S. Fish and Wildlife Service 1989). The increasing number of deaths from watercraft collisions prompted the establishment of more protection zones and legislation to reduce watercraft speeds in areas that are frequented by manatees. The establishment of watercraft speed zones was based in large part on the number and location of manatee deaths from watercraft collisions but also on data from aerial surveys and from studies with telemetry and on other types of data. Many seasonal zones where watercraft must use slow or reduced speeds were created to protect manatees. A few closed refuges were created where no watercraft or only non-powered watercraft are permitted. Most are small, winter-only refuges at warm-water aggregation sites.

Staff of county governments and the Florida Department of Environmental Protection are developing manatee protection plans for 13 key counties—those with many manatees or many deaths of manatees. These plans are one part of the Comprehensive Growth Management Plans under Florida's Local Government Comprehensive Planning and Land Development Regulation Act of 1985 that are required from all counties for reducing the many effects of rapid development (O'Shea 1995; Reynolds 1995). Protection includes watercraft speed zones, limitations on expansion of marinas and shoreline developments, and determination of appropriate locations for boating facilities. Other recommended protection includes the establishment of maximum speed limits in congested areas, compulsory boating safety education, boater licensing, and additional Florida Marine Patrol officers to enforce these new statutes. Many of these measures would benefit manatees and increase boating safety for humans.

Geographic Information System (GIS) maps were created by the Florida Department of Environmental Protection that display locations of manatee deaths (Figs. 10 A–D), shorelines, aquatic habitats, manatee locations identified during aerial surveys and with radiotelemetry, boating facilities, boating speed zones, and more. O'Shea and Kochman (1990) described various manatee data sets available for use in GIS systems. The GIS mapping system has been used extensively by the Florida Department of Environmental Protection and other agencies to develop manatee protection plans in areas of manatee concentrations, important habitats, boating, and shoreline developments (Weigle and Haddad 1990).

The number of manatee deaths was lower in 1992 and 1993 (Florida Department of Environmental Protection, unpublished data) than in recent years, but whether this was random chance, a reflection of decreasing population size, or the result of recent protection must yet be determined. The assessment of the success of recent increased protection is difficult because the number of deaths per year in each protected area is small and usually highly variable.

Catastrophic Deaths

Uncommon, catastrophic mortality from various causes has occurred every few years. Most of these deaths were apparently from low temperatures (*Campbell and Irvine 1981; Buergelt et al. 1984; O'Shea et al. 1985) but seemingly once from red tide (O'Shea et al. 1991). Because specific lesions or pathogens were not found on manatees that died from low temperatures or from red tide, causes of deaths were based on associated environmental conditions.

Red-tide

Presumed red-tide toxicity was described by O'Shea et al. (1991). Exposure to red-tide toxins near the Ft. Myers aggregation area seemingly caused 37 deaths in Lee County in spring 1982 (O'Shea et al. 1991). Deaths were linked to an unusual combination of high salinities in the estuary (because of drought), which allowed high levels of red-tide organisms and ascidians to flourish inshore and early dispersal of manatees from the nearby aggregation sites into the estuary in spring. Manatees ingested the ascidians or came into direct contact with the red-tide brevetoxin (*Gymnodinium breve*), which caused neurologic symptoms. These deaths were placed in the category of other natural causes of death.

Hurricanes

Whether hurricanes have killed manatees is not known. However, Marsh (1989) described the stranding of at least 27 dugongs (*Dugong dugon*) by a tropical cyclone in northern Australia in 1984. Hurricane Andrew stranded at least one live Florida manatee in August 1992. Preen (*1993) reported extensive seagrass mortality in Hervey Bay, Australia, after a cyclone and flood. Hurricane Elena forced salt water into the Crystal River system in September 1985 and caused a reduction of freshwater aquatic plants (especially *Hydrilla*), which is the primary food in winter of the growing population of manatees there (J. Reid, National Biological Service, Sirenia Project, unpublished data). A similar decline occurred after an unnamed storm in March 1993.

Low Temperatures

Extremely low temperatures caused many deaths in some winters (*Campbell and Irvine 1981; Buergelt et al. 1984; O'Shea et al. 1985). Cold stress was described as a syn-

drome by Buergelt et al. (1984) and O'Shea et al. (1985). Hartman (1979) and O'Shea et al. (1985) reviewed historical accounts of deaths after cold fronts. Manatees cannot survive indefinitely in water that is colder than about 16° C. However, lethal temperatures and lethal exposure times are not well documented. Florida manatees travel to natural warm springs, to far southern Florida, or to warm-water effluents (e.g., power plants) in winter when water temperatures fall below 20° C and daily low air temperatures fall below 10° C (Hartman 1979; Bengtson 1981; *Powell and Waldron 1981; O'Shea 1988). Manatees only occasionally move voluntarily into water that is colder than 15° C; 13.5° C is the lowest published temperature (Hartman 1979), but documentation is not extensive. Buergelt et al. (1984) reported the death of a rehabilitating animal in a tank at 14° C. Campbell and Irvine (*1981) observed that feeding by captive manatees became irregular at 18–19° C, and feeding and other activity ceased below 16° C. Bengtson (1981) reported that some individuals remained in warm-water refuges without feeding for as many as 7 days when water temperatures were coldest. Irvine (1983) found that below 20° C, manatees had to increase their metabolic rates. Deaths from low temperatures occurred most frequently in subadults (O'Shea et al. 1985).

The number of deaths in winter (December to March) from the combined natural (cold-related, other natural) and undetermined causes were highest (21%) in Brevard County. The largest number of manatees that is at risk from cold is at two power plants in Brevard County where the surrounding water may be cold. High numbers of deaths in winter also occur in Lee (18%, including red tide 1982), Duval (12%), Monroe (9%), and Collier (7%) counties. In these counties, a relatively large number of manatees spend the winter in cold water (Brevard, Duval) or away from any source of warm water (Lee, Collier, Monroe). The number of deaths was much lower near the Crystal River and Blue Spring (*Campbell and Irvine 1981) and at Tampa Bay (S. Wright, Florida Department of Environmental Protection, St. Petersburg, unpublished data).

In northeastern Florida, the air and water temperatures are the coldest in the state, and sources of warm water are not reliable. Coastal areas north of Cape Canaveral are cooled by south-flowing, cold ocean currents. Large, shallow estuaries such as the northern Indian River Lagoon cool quickly when air temperatures drop after the passage of winter cold fronts (Witherington and Ehrhart 1989). Southeastern Florida is kept warmer by its proximity to the north-flowing, warm Florida Current.

Water temperatures of the natural, warm springs are consistently near 22° C (Rosenau et al. 1977). In contrast, temperatures of warm-water effluents of power plants vary with the intake water temperature and are usually no warmer than 7–10° C above the intake temperature. During severely cold weather, water temperatures can fall so low (4–8° C; Witherington and Ehrhart 1989) that even the warmed effluent is too cold for the survival of some manatees. In addition, power plant effluents are occasionally interrupted because of mechanical failure or for scheduled maintenance (Packard et al. 1989).

Evaluation of Data From Previous Cold-weather Events

Campbell and Irvine (*1981) reported that 38 carcasses were recovered after low temperatures on 20 January 1977 (Table 5). The carcasses were recovered from January to March 1977 (deaths from undetermined causes: 22 in Brevard, 8 in Duval, 3 in St. Johns, 2 in Lee, 3 in Monroe counties). Campbell and Irvine (*1981) documented water temperatures at the Florida Power and Light Company plant near Titusville. Intake temperature reached a low of 8° C on 20 January. Outlet temperatures were below 21° C during most of the winter and dipped to 11° C and 13° C during two partial shutdowns of the plant. The carcasses were recovered in the area several days after the partial shutdowns. O'Shea et al. (1985) noted that at least one generating unit remained in operation during the shutdowns and concluded that the plant shutdown was not responsible for the deaths. However, the deaths may have been caused by the combination of the shutdown and the already low ambient temperatures.

Buergelt et al. (1984) described 30 carcasses that were recovered during January–February 1981, mostly in southwestern Florida (O'Shea et al. 1985). We identified cases that matched these observations (4 deaths from other natural causes, 26 deaths from undetermined causes; Table 5). O'Shea et al. (1985) described the winters of 1976–77 and 1980–81 as two of the coldest recorded in Florida (Table 5). Witherington and Ehrhart (1989) recorded water temperatures of 4–8° C during these cold fronts. Buergelt et al. (1984) described 34 carcasses that were recovered during January–February 1984 (19 deaths from other natural causes, 15 deaths from undetermined causes; Table 5). Nine additional carcasses in 1984–85 and one in December 1985 were of manatees that died from low temperatures but were recorded in the database as manatees that died from other natural causes. The deaths were re-categorized for this analysis as catastrophic deaths and were combined with deaths from low temperatures since January 1986 and with the 37 deaths from a red tide in 1982.

Potential Catastrophes at Aggregation Sites

Catastrophic mortality is possible at warm-water sites where many manatees aggregate in winter. As much as 10–15% (200–300 manatees) of the known state population (Ackerman 1995) is sometimes at each of several sites. In

the past, many animals died from low temperatures (severely low temperatures or power plant shutdowns) near these aggregation sites and from red-tide toxicity (O'Shea et al. 1991). The animals in these concentrations are also vulnerable to rapid disease transmission because of frequent touching and social behavior (Hartman 1979). Concentrated animal waste products and warmer water temperatures promote the flourishing of disease organisms. Large numbers of manatees could also be exposed to oil or chemical spills near these sites. All industrial warm-water sites in Florida where manatees aggregate are near industrial ports or where fuel is unloaded to power plants.

The described deaths have not been catastrophic. Less than 5% of the population seemingly died in any one event, and no changes in population size were detected during aerial surveys. But these events demonstrated the vulnerability of manatees to stochastic mortality that may be catastrophic in the future. Plans are needed for responding to such events and must include provisions for the rescue and treatment of affected animals (Buergelt et al. 1984; O'Shea 1988).

Program and Database Changes

Contingency Table Analysis

O'Shea et al. (1985) made many analyses that either substantially pooled or omitted some cause-of-death categories (e.g., pooled human-related causes of death or used only determined causes of death). This was often necessitated by small sample sizes. We retained as many categories as possible because we were more interested in documenting the many possible significant associations rather than in obtaining pooled models with fewer, stronger significant interactions. Improved diagnostic procedures increased the number of deaths categorized as from natural causes (especially from low temperatures) and decreased the number of deaths categorized as from undetermined causes over time. This greatly complicated the analyses of trends and patterns.

Because the sample size (number of carcasses) is now more than five times larger than that reported by O'Shea et al. (1985), more interactions were significant and the power of tests to determine significance was higher. This also complicated the analysis and interpretation. O'Shea et al. (1985) found no significant three-way interactions; however, we found many.

Changes in the Recovery, Examination, and Categorization of Carcasses

The assessment of trends through time and space is critical to understanding changes in the number and causes of deaths. It provides valuable information about specific places or human activities that require action and may reveal areas where protection is effective. However, despite the large, long-term database of mortality records collected in a seemingly similar fashion, numerous pitfalls exist. These can cause several forms of bias that complicate the data for trend assessment.

- The carcasses were necropsied by individuals of unequal skills. The freshest carcasses—but not all carcasses of advanced decomposition—were usually necropsied by one of several veterinarians or pathologists.
- Decomposition can be rapid and therefore limit the possibility of detecting some causes of death, especially from cryptic, subtle natural causes.

The prompt recovery of carcasses increased. Recovery of carcasses is the primary duty of seven full-time employees of the Florida Department of Environmental Protection who are strategically stationed throughout the state. Formerly, only a few centrally located people who also had other duties recovered carcasses. A wildlife disease specialist-pathologist was added to the Florida Department of Environmental Protection staff in May 1989. In November 1992, a centralized facility for performing necropsies was completed where tissue, serum, and voucher specimens are stored. In 1993, refrigerated trailers for transporting manatee carcasses were developed to slow the decomposition of carcasses (J. M. Sweat and S. D. Wright, Florida Department of Environmental Protection, St. Petersburg, Florida, personal communication).

The intensity of recoveries was not always equal among regions of the state and was probably low in areas that were far from the few research stations. This remoteness probably lowered the carcass detection rate and lengthened the recovery times, as a result of which a higher proportion of causes of death were not determined (O'Shea et al. 1985).

The ability to detect subtle causes of death improved through time. Improvements in necropsy procedures and the recovery network were made over the years. Little was known about some natural causes of death when the recovery of carcasses began. Biomedical testing procedures and tissue and serum banks improved. Signs of some subtle causes of death became better understood (e.g., mortality from low temperatures; *Campbell and Irvine 1981; O'Shea et al. 1985). As a result, the proportion of cases for which cause of death remains undetermined decreased, although the number of deaths from undetermined causes did not decline.

As understanding of subtle causes of death became clearer, certain causes of death were categorized differently. For example, the cause of death of animals that died from low temperatures was categorized as undetermined from 1974 to 1981, as natural in 1981–85, and as cold-related since 1985. No concerted effort was made to reclassify cases

from the early years for which a more definitive diagnosis could perhaps now be made.

The awareness by the public and by local law enforcement agencies of the need for manatee protection also increased and may increase the reporting of carcasses to authorities. In addition, enforcement agencies such as the Florida Department of Environmental Protection Marine Patrol became more aware of the need to quickly respond to reports of carcasses before decomposition destroys valuable indicators of cause of death.

Many carcasses are reported by boaters, but the density of boaters is not equal throughout the state. Although some areas are heavily travelled, others are less populated or unpopulated. The number of boaters increased faster in some counties, such as Collier County, than in other areas and corresponded to the rapid increase in human populations there.

Presumably many manatees are killed by watercraft in the waterways with the largest number of boaters. This may result in a proportionately higher detection rate of deaths from watercraft.

Several of these changes through time have probably caused a series of biases, which to some degree may limit the usefulness of these data for determining trends in mortality. Retrospective testing of this hypothesis does not seem possible at present. Other changes through time such as faster recovery times and differing necropsy skills may have affected the proportion of undetermined causes of deaths.

Changes through time, such as increasing citizen awareness, increasing boating, and more Florida Marine Patrol officers and carcass recovery staff may have increased the detection rate of carcasses, causing an apparent increase in the number of deaths. Assessment of the percentage of detected carcasses (detection rate) has not been possible. The detection of almost all carcasses of large manatees and the detection of a smaller proportion of small calf carcasses was assumed. However, for accurate population assessment, an accurate estimate of the true number of deaths would be better.

Differences between regions in the number of manatees, citizens, boaters, and researchers may have caused an apparent difference in the number of deaths between regions of the state. Regions differ in the degree of environmental awareness and interest in manatees by citizens and law enforcement agencies and in the proximity to manatee research stations. The number of deaths must be assessed in relation to the size of the living manatee population in each region. As yet, the size and the sex and age compositions of the populations in most areas of Florida have not been determined (Ackerman 1995). Manatee population size and density differ between regions. The sizes of some subpopulations may be increasing, but those of others may be decreasing (Ackerman 1995).

Changes through time such as differing necropsy skills, increasing number of researchers and boaters in some areas, and changes in ability to detect subtle causes may have caused an apparent change in the proportions of deaths by causes and by region. Faster recovery and better understanding of subtle causes decreased the relative proportion of deaths from undetermined causes and therefore caused a corresponding increase in the proportion in several other categories. Causes of death such as watercraft collision and flood-gate and canal-lock crushings were more easily determined even on moderately decomposed carcasses and thus would not necessarily increase proportionally as much as the deaths from the more subtle undetermined causes that could be better detected with improved procedures.

The most remote waters are in southwestern Florida, which for many years was farthest from a research station. The higher proportion of deaths from undetermined causes in this region may have been related to the high proportion of badly decomposed carcasses there. This pattern probably surfaced because of the inability of researchers to categorize decomposed carcasses rather than from differences in decomposition rate from specific causes of death. Many small carcasses were categorized as perinatal calves based on size when specific causes of death could not be determined; many of these carcasses also were of manatees that died from undetermined causes.

Mortality in Relation to Population Status and Trends

The number of manatee deaths in Florida and the number of deaths in nearby states increased (O'Shea 1988). In the absence of detailed analysis, the reported number of deaths has seemed to be higher than the population can support without declining in size (*Brownell et al. 1981; *Eberhardt 1982; *Packard 1985; Eberhardt and O'Shea 1995). This increase in reported deaths was used to support increased protection and resulted in the impression by some that the manatee population has been decreasing for many years. This, however, may not be true.

Considerable evidence, such as increasing counts (Ackerman 1995; Garrott et al. 1995) and increasing extralimital sightings (O'Shea 1988), seems to indicate that the populations in many areas may have been increasing since the 1970's. Population trends and dynamics are poorly known, but 1,856 animals—more than were previously known—were counted in statewide aerial surveys in January 1992 (Ackerman 1995). The increasing number of deaths could conceivably be in part the result of constant mortality applied to an increasing population. However, no conclusive evidence exists to determine whether the population increased or decreased in the last few years; factors that can contribute to a true increase in mortality, however, were also increasing.

Research, management, and public awareness (e.g., watercraft speed zones, reduction of harm from shoreline developments) reduced some threats to manatees. Yet, the human population of Florida increased at 2.9%/year during 1980–90 (U.S. Census data, Florida Department of Environmental Protection, Office of Planning and Research, unpublished report). Many threats to manatees are still worsening; for example, the increasing number of registered watercraft, increasing speed and horsepower of watercraft (Wright et al. 1995), decreasing pristine habitat, increasing stormwater and upland runoff from development and agriculture, decreasing amounts of seagrasses, increasing turbidity in many areas, and increasing harassment by humans at warm-water refuges. The few favorable changes for manatees include increases in introduced freshwater aquatic plants (O'Shea 1988) and reductions of point-source pollution (sewage and industrial discharges).

Although evidence suggests that the manatee population may be able to increase in some areas, the number of deaths in the 1990's may exceed the capacity of the population to increase, and the population size may recently have begun to decline. Gerrodette (1987) discussed the difficulty of detecting slow changes in population size. Population modeling (*Packard 1985; Marmontel 1993; Eberhardt and O'Shea 1995) will assist researchers with understanding current population dynamics. Given the uncertainty in current trends in population size, continued protection and conservation of the manatees to the fullest extent possible seem prudent. Further information on causes of mortality and their contributing factors will improve manatee protection.

Recommendations for Further Research

The recovery of carcasses, which permits the monitoring of the number of deaths and provides biological specimens for research, should be continued. The development and improvement of diagnostic tools should continue. Despite recent improvements, the causes of death of many dead manatees remain unknown. These may be deaths from subtle natural causes. Natural mortality from epizootics and infectious diseases may have catastrophic effects because the populations in many areas are highly aggregated in winter. Improved microbiological, serological, and immunological techniques are necessary to establish the kinds and prevalence of disease agents such as viruses. Continued recovery and necropsy of carcasses are necessary to increase the understanding of manatee diseases and other causes of death.

Population models (*Packard 1985; Marmontel 1993; Eberhardt and O'Shea 1995) should be used to assist with assessing trends in manatee population dynamics. The number of deaths, age data, aerial-survey counts, and percentage of calves should be incorporated in population models. Comparisons should be made by region or at least between the eastern and western coasts. The number of deaths of calves and larger animals should be compared with estimates of the population size from aerial surveys. Deaths in nearby states should also be included.

The mortality database should be expanded to include a supplemental variable that allows the separate analyses of deaths from low temperatures and from red tides. Data from before 1986 should be re-evaluated to identify deaths that were probably caused by low temperatures.

The causes of death of calves in different developmental stages must be more specifically analyzed. A method is being developed to age calves that are younger than 1 year from layers in teeth (D. K. Odell, Sea World of Florida, Orlando, Florida, personal communication). The number of deaths of perinatal calves from specific identifiable causes should be assessed by age, length, weight, season, water temperature, and region.

Efforts to match photographs of carcasses to photographs in the living-animal scar catalog (Beck and Reid 1995) should be increased. This will help relate mortality data to information on recognizable living animals and improve survival estimates (O'Shea and Langtimm 1995).

The annual number of deaths from watercraft should be modeled by county in relation to human and seasonal manatee populations, number of registered watercraft, water area, shoreline, degree of waterway congestion, and other appropriate variables. The carcass recovery rates should be estimated by region so that total mortality can be estimated.

A possible relation between winter temperatures and the number of deaths from low temperatures should be examined with a temperature index that is sensitive to prolonged cold water temperatures, such as that used by Garrott et al. (1995). Winter temperatures may correlate with increases in mortality of perinatal manatees later in the same year and with lowered reproduction in the next few years.

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Cited References[3]

Ackerman, B. B. 1995. Aerial surveys of manatees: a summary and progress report. Pages 13–33 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Beck, C. A., and N. B. Barros. 1991. The impact of debris on the Florida manatee. Marine Pollution Bulletin 22:508–510.

*Beck, C. A., R. K. Bonde, and D. K. Odell. 1981. Manatee mortality in Florida during 1978. Pages 76–85 *in* *R. L. Brownell, Jr., and K. Ralls, editors. 1981. The West Indian manatee in Florida. Proceedings of a workshop held in Orlando, Fla., 27–29 March 1978. Florida Department of Natural Resources, Tallahassee. 154 pp.

Beck, C. A., R. K. Bonde, and G. B. Rathbun. 1982. Analyses of propeller wounds on manatees in Florida. Journal of Wildlife Management 46:531–535.

Beck, C. A., and J. P. Reid. 1995. An automated photo-identification catalog for studies of the life history of the Florida manatee. Pages 120–134 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Bengtson, J. L. 1981. Ecology of manatees (*Trichechus manatus*) in the St. Johns River, Florida. Ph.D. thesis, University of Minnesota, Minneapolis. 126 pp.

Bishop, Y. M. M., S. E. Fienberg, and P. W. Holland. 1975. Discrete multivariate analysis: theory and practice. MIT Press, Cambridge, Mass. 557 pp.

*Bonde, R. K., T. J. O'Shea, and C. A. Beck. 1983. A manual of procedures for the salvage and necropsy of carcasses of the West Indian manatee (*Trichechus manatus latirostris*). , National Technical Information Service, Springfield, Va. Document PB 83-255273. 175 pp.

*Brownell, R. L., Jr., K. Ralls, and R. R. Reeves. 1981. Report of the West Indian manatee workshop. Pages 3–16 *in* *R. L. Brownell, Jr., and K. Ralls, editors. 1981. The West Indian manatee in Florida. Proceedings of a workshop held in Orlando, Fla., 27–29 March 1978. Florida Department of Natural Resources, Tallahassee. 154 pp.

Buergelt, C. D., R. K. Bonde, C. A. Beck, and T. J. O'Shea. 1984. Pathologic findings in manatees in Florida. Journal of the American Veterinary Medical Association 185:1331–1334.

*Campbell, H. W., and A. B. Irvine. 1981. Manatee mortality during the unusually cold winter of 1976–1977. Pages 86–91 *in* *R. L. Brownell, Jr., and K. Ralls, editors. 1981. The West Indian manatee in Florida. Proceedings of a workshop held in Orlando, Fla., 27–29 March 1978. Florida Department of Natural Resources, Tallahassee. 154 pp.

Draper, N. R., and H. Smith. 1981. Applied regression analysis. Second Edition. John Wiley and Sons, Inc., New York. 709 pp.

*Eberhardt, L. L. 1982. Censusing manatees. Manatee Population Research Report 1. Florida Cooperative Fish and Wildlife Research Unit, University of Florida, Gainesville. 18 pp.

Eberhardt, L. L., and M. A. Simmons. 1992. Assessing rates of increase from trend data. Journal of Wildlife Management 56:603–610.

Eberhardt, L. L., and T. J. O'Shea. 1995. Integration of manatee life-history data and population modeling. Pages 269–279 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Everitt, B. S. 1977. The analysis of contingency tables. John Wiley and Sons, New York. 128 pp.

*Florida Department of Natural Resources. 1989. Recommendations to improve boating safety and manatee protection for Florida waterways. Report to the Governor and Cabinet. Final report. 24 October 1989. Florida Department of Natural Resources, Tallahassee. 20 pp.

Garrott, R. A., B. B. Ackerman, J. R. Cary, D. M. Heisey, J. E. Reynolds, III, and J. R. Wilcox. 1995. Assessment of trends in sizes of manatee populations at several Florida aggregation sites. Pages 34–55 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Gerrodette, T. 1987. A power analysis for detecting trends. Ecology 68:1364–1372.

Hartman, D. S. 1979. Ecology and behavior of the manatee (*Trichechus manatus*) in Florida. American Society of Mammalogy Special Publications 5. 153 pp.

Irvine, A. B. 1983. Manatee metabolism and its influence on distribution in Florida. Biological Conservation 25:315–334.

*Irvine, A. B., D. K. Odell, and H. W. Campbell. 1981. Manatee mortality in the southeastern United States from 1974 through 1977. Pages 67–75 *in* *R. L. Brownell, Jr., and K. Ralls, editors. 1981. The West Indian manatee in Florida. Proceedings of a workshop held in Orlando, Fla., 27–29 March 1978. Florida Department of Natural Resources, Tallahassee. 154 pp.

Laist, D. W. 1987. Overview of the biological effects of lost and discarded plastic debris in the marine environment. Marine Pollution Bulletin 18(6B):319–326.

Marmontel, M. 1993. Age determination and population biology of the Florida manatee, *Trichechus manatus latirostris*. Ph.D. dissertation, University of Florida, Gainesville. 408 pp.

Marsh, M. 1989. Mass stranding of dugongs by a tropical cyclone in northern Australia. Marine Mammal Science 5:78–84.

[3] An asterisk denotes unpublished material.

*Odell, D. K. 1981. Growth of a West Indian manatee, (*Trichechus manatus*) born in captivity. Pages 131–140 *in* *R. L. Brownell, Jr., and K. Ralls, editors. 1981. The West Indian manatee in Florida. Proceedings of a workshop held in Orlando, Fla., 27–29 March 1978. Florida Department of Natural Resources, Tallahassee. 154 pp.

Odell, D. K., and J. E. Reynolds. 1979. Observations on manatee mortality in south Florida. Journal of Wildlife Management 43:572–577.

O'Shea, T. J. 1988. The past, present, and future of manatees in the southeastern United States: realities, misunderstandings, and enigmas. Pages 184–204 *in* R. R. Odom, K. A. Riddleberger, and J. C. Ozier, editors. Proceedings of the Third Southeastern Nongame and Endangered Wildlife Symposium, Georgia Department of Natural Resources, Game and Fish Division, Social Circle.

O'Shea, T. J. 1995. Waterborne recreation and the Florida manatee. Pages 297–311 *in* R. L. Knight and K. J. Gutzwiller, editors. Wildlife and recreationists: coexistence through management and research. Island Press, Washington, D.C.

O'Shea, T. J., C. A. Beck, R. K. Bonde, H. I. Kochman, and D. K. Odell. 1985. An analysis of manatee mortality patterns in Florida. Journal of Wildlife Management 49:1–11.

O'Shea, T. J., and H. I. Kochman. 1990. Florida manatees: distribution, geographically referenced data sets, and ecological and behavioral aspects of habitat use. Pages 11–22 *in* J. E. Reynolds, III, and K. D. Haddad, editors. Report of the workshop on geographic information systems as an aid to managing habitat for West Indian manatees in Florida and Georgia. Florida Marine Research Publication 49:1–57.

O'Shea, T. J., and C. A. Langtimm. 1995. Estimation of survival of adult Florida manatees in the Crystal River, at Blue Spring, and on the Atlantic Coast. Pages 194–222 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

O'Shea, T. J., J. F. Moore, and H. I. Kochman. 1984. Contaminant concentrations in manatees in Florida. Journal of Wildlife Management 48:741–748.

O'Shea, T. J., G. B. Rathbun, R. K. Bonde, C. D. Buergelt, and D. K. Odell. 1991. An epizootic of Florida manatees associated with a dinoflagellate bloom. Marine Mammal Science 7:165–179.

O'Shea, T. J., and R. L. Reep. 1990. Encephalization quotients and life-history traits in the Sirenia. Journal of Mammalogy 71:534–543.

*Packard, J. M. 1985. Preliminary assessment of uncertainty involved in modeling manatee populations. Manatee Population Research Report 9. Technical Report 8-9. Florida Cooperative Fish and Wildlife Research Unit, University of Florida, Gainesville. 19 pp.

Packard, J. M., R. K. Frohlich, J. E. Reynolds, III, and J. Ross Wilcox. 1989. Manatee response to interruption of a thermal effluent. Journal of Wildlife Management 53:692–700.

*Powell, J. A., and J. C. Waldron. 1981. The manatee population in Blue Spring, Volusia County, Florida. Pages 41–51 *in* *R. L. Brownell, Jr., and K. Ralls, editors. 1981. The West Indian manatee in Florida. Proceedings of a workshop held in Orlando, Fla., 27–29 March 1978. Florida Department of Natural Resources, Tallahassee. 154 pp.

*Preen, A. 1993. Dramatic impact of seagrass loss on a large dugong population. Sixth International Theriological Congress, 4–10 July 1993, Sydney, Australia. Abstract only.

Rathbun, G. B., J. P. Reid, R. K. Bonde, and J. A. Powell. 1995. Reproduction in free-ranging Florida manatees. Pages 135–156 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Reid, J. P., G. B. Rathbun, and J. R. Wilcox. 1991. Distribution patterns of individually identifiable West Indian manatees (*Trichechus manatus*) in Florida. Marine Mammal Science 7:180–190.

Reynolds, J. E., III. 1995. Florida manatee population biology: research progress, infrastructure, and applications for conservation and management. Pages 6–12 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Rosenau, J. C., G. L. Paulkner, C. W. Handry, Jr., and R. W. Hull. 1977. Springs of Florida. Florida Department of Natural Resources, Division of Resource Management, Bureau of Geology, Tallahassee. Bulletin 31. 461 pp.

SAS Institute. 1988. SAS procedures guide, release 6.03 edition. SAS Institute, Inc., Cary, N.C. 441 pp.

Schroeder, B. A., L. M. Ehrhart, J. L. Guseman, R. D. Owen, and W. E. Redfoot. 1990. Cold stunning of marine turtles in the Indian River Lagoon system, Florida, December 1989. Pages 67–69 *in* T. H. Richardson, J. I. Richardson, and M. Donnelly, editors. Proceedings of the Tenth Annual Workshop on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFC-278. 286 pp.

Upton, G. J. G. 1978. The analysis of cross-tabulated data. John Wiley and Sons, New York. 148 pp.

*U.S. Fish and Wildlife Service. 1989. Florida manatee (*Trichechus manatus latirostris*) recovery plan. U.S. Fish and Wildlife Service, Atlanta, Ga. 98 pp.

Weigle, B. L., and K. D. Haddad. 1990. Applications of the Florida Department of Natural Resources' Marine Resources Geographic Information System to manatee biology and management. Pages 23–27 *in* J. E. Reynolds, III, and K. D. Haddad, editors. Report of the workshop on geographic information systems as an aid to managing habitat for West Indian manatees in Florida and Georgia. Florida Marine Research Publications 49:1–57.

Witherington, B. E., and L. M. Ehrhart. 1989. Hypothermic stunning and mortality of marine turtles in the Indian River Lagoon System, Florida. Copeia 1989:696–703.

Wright, S. D., B. B. Ackerman, R. K. Bonde, C. A. Beck, and D. J. Banowetz. 1995. Analysis of watercraft-related mortality of manatees in Florida, 1979–1991. Pages 259–268 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Zar, J. H. 1974. Biostatistical analysis. Second Edition. Prentice Hall, Inc., Englewood Cliffs, N.J. 718 pp.

Analysis of Watercraft-related Mortality of Manatees in Florida, 1979–1991

by

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Abstract. From 1974 to 1991, the annual number of manatee (*Trichechus manatus latirostris*) deaths in Florida increased. The most frequent cause of death from human activity is collision with watercraft. Scars and wounds from propellers are common. A total of 1,376 sets of fatal or healed wounds was measured on 628 dead manatees recovered from 1979 through 1991. Collisions with watercraft caused 406 of these deaths. Of the 406 deaths, propeller cuts caused 158 (39%); impact injuries (no propeller cuts) caused 224 (55%); propeller cuts and impact injuries, either of which would have been fatal, caused 16 (4%); and unidentified specifics of the collisions caused 8 (2%). Fatal cuts were usually larger (longer) than healed wounds. Many animals survived several boat collisions; one manatee had 22 separate patterns of propeller cuts. The mean length ($\bar{x}$ = 38.3 cm) of the longest fatal cut from a propeller indicated that death was most often caused by a direct-drive watercraft. In contrast, fatal-impact injuries may have resulted from fast-moving watercraft of many sizes and types. Impact injuries killed more manatees than propeller cuts and increased in proportion with time. Impact often resulted in massive internal injuries with only minor surface abrasions. Only 2% of the propeller strikes were to the head, but 98% were to the dorsum. In addition, nearly 90% of scar patterns were along the head-to-tail axis, indicating manatees were moving in response to an oncoming boat when struck.

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Changes in watercraft design may increase the frequency of operation of boats in shallow water. This increases the probability of collisions with manatees.

Key words: Manatee, *Trichechus manatus latirostris*, watercraft-related mortality, propeller scars, boats, Florida, United States.

Since 1974, the circumstances and causes of Florida manatee (*Trichechus manatus latirostris*) mortality have been carefully documented. Watercraft-related mortality of manatees (fatal collisions with watercraft of various sizes) is the leading cause of mortality from human activity (78% of anthropogenic deaths, 1974–91). It is also one of the leading overall causes of mortality (25% of all deaths, 38% of deaths with identified causes, 1974–91; Ackerman et al. 1995). Moreover, the annual number of these deaths has increased steadily, and at least 40% of all watercraft-related deaths during 1974–91 occurred during 1987–91. The highest annual mortality from watercraft was 53 deaths in 1991. By comparison, some categories of mortality have not increased (Fig. 1; Ackerman et al. 1995).

Witnessed collisions between manatees and watercraft are rarely reported to authorities. Details such as boat size, speed, or engine horsepower are only known of approximately 20 of nearly 600 documented watercraft-related deaths of manatees. As a result, no direct assessment is possible of the fatal interactions between boats and manatees. For that reason, Beck et al. (1982) initiated an indirect assessment of the types of boats that collided with manatees from 1974 through December 1979. They measured fatal wounds from propellers and nonfatal scars from propellers on manatee carcasses. They then examined the relations between propeller dimensions and engine horsepower of various hull lengths of boats and compared these with measurements of carcasses. We examined similar data by the same criteria described in Beck et al. (1982) during 12 years from January 1979 through December 1991. In addition, we describe changes in boating technology that may affect manatees.

Recoveries of Manatee Carcasses and Necropsies

Recoveries and necropsies of manatee carcasses were initiated in 1974 by the Sirenia Project of the U.S. Fish and Wildlife Service in Gainesville, Florida, and by the University of Miami. These two institutions began to cooperate and share data, resulting in the beginnings of a statewide perspective on mortality (*[2]Bonde et al. 1983). Over time, several other institutions and oceanaria became involved under the authority of the U.S. Fish and Wildlife Service. In 1985, the Florida Department of Natural Resources (currently reorganized under the Florida Department of Environmental Protection) assumed responsibility for conducting necropsies under the authority of the U.S. Fish and Wildlife Service. Almost all necropsies of manatees are presently conducted by Florida Department of Environmental Protection personnel; other institutions occasionally participate. Efforts in data collection have been variable, and the collection of data types has changed.

The purpose of the recovery of carcasses is the determination of the causes of deaths and the collection of the maximum amount of biomedical and anatomical data. The degree of carcass decomposition limits data collection. Carcasses from watercraft-related deaths are in two major groups (impact and propeller) that are determined by the type of damage and physical appearance at necropsy. Because few collisions are witnessed, the only available source of information on the size and type of the boats is the appearances of carcasses at necropsies. Beck et al. (1982) were the first to infer boat size from scar or wound dimensions on carcasses.

A major emphasis of this study and of that of Beck et al. (1982) was the appearance and dimensions of the fresh propeller cuts and healed wounds from propellers on manatees. Manatees struck by the propeller of a passing boat have distinctive measurable cuts. Fresh cuts, either fatal or nonfatal, have clean, well delineated edges, and healing has not begun. The knife-like edges of boat propellers cut through

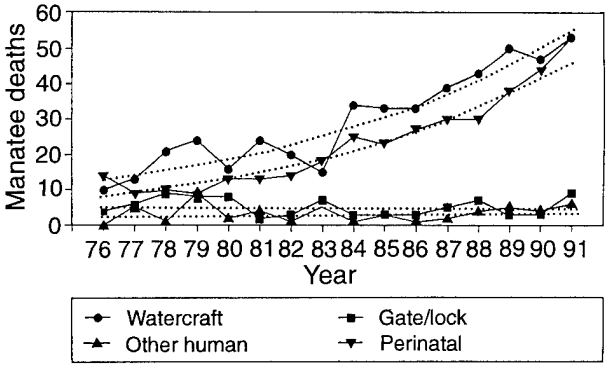


Fig. 1. Annual mortality of the Florida manatee (*Trichechus manatus latirostris*) from 1976 through 1991. The total number of deaths from three anthropogenic causes are compared with the total number of deaths of perinatal manatees. Exponential regression was used to fit the curves to number of deaths.

[2] An asterisk denotes unpublished material.

the thick manatee skin, rather than tearing it, leaving clearly defined wounds. Healing wounds often have less distinct edges of the cut. Deep wounds may become contaminated and necrotic. Necrosis slows healing and can change the shape of a wound and in some cases disfigure the animal (Jones and Hunt 1983). Contaminated wounds from propellers can cause prolonged illness and death. As a result, they are a potential delayed threat to an animal that initially survives a collision. Healed wounds initially appear white and are in the shape of the cuts. Over several years, most scar tissue re-pigments, becoming dark and visible only upon close examination (Beck and Reid 1995). The change in scar color from a more obvious white color to a less obvious dark gray color may give the false impression of shrinkage when actually the original size and shape of the cut remain the same.

Measurements of wound components were compared between scars and fatal wounds from propellers (fresh) during 1979–91. In nearly all cases, propeller cuts were in patterns (Fig. 2). The long axis of the propeller pattern paralleled the path of the boat, but a determination from the scar pattern as to which of the two possible directions the boat was traveling was impossible. The propeller pattern was measured (cm), including the total length of the pattern, the total length of each cut in the pattern, and the distance between each cut of the pattern (Fig. 2). The depth of the deepest cut was measured on fresh carcasses, but the value of this measurement was somewhat limited. Large propellers often cut completely through the body wall into the body cavity, and the actual depth of the cut could therefore not be measured. The length of the longest cut, combined with the greatest depth of the cut, was used for the best minimum estimate of the propeller diameter. Individual wounds were excluded from analyses when their sources could not be stated with certainty (propeller, impact, skeg, other). Not all measurements were or could be made on every set of wounds. The spatial pattern of scars (i.e., the position of the scar pattern relative to the head-to-tail axis of the carcass) was documented by sketches and by photographs. Data were entered into Dbase 3+, and statistical analyses were made with PC SAS 6.03 (SAS 1988).

Deaths from impact were from fatal strikes by the hull, by the lower unit of an outboard or stern-drive engine, or by some other blunt structure on the boat hull (rudder, keel, anti-pitch planes, and anti-crabbing planes). Impacts typically did not leave distinctive or measurable marks. Impact injuries sometimes disfigured the animal and occasionally were marked by hull paint or a skeg mark, but external indications of traumatic death usually were absent. Animals often had many dislocated or broken ribs or both. Often, organs were damaged from the sharp edges of the broken ribs, or organs were torn by the force of the impacts. Exsanguination into the abdomen or pleural spaces was common. Impact occurred in more than half of the deaths from watercraft. However, there were no measurable features and therefore almost no indication of the size of the boat that caused the mortality.

Skeg marks were another type of cut on carcasses. The skeg is the sharp portion of an outboard or stern-drive engine that extends below the propeller. It protects the propeller from striking objects and from bending. Skeg marks most often appeared as a single, relatively straight, narrow cut on the carcass. When present, skeg marks were aligned along the long axis of a pattern of propeller cuts (Fig. 2). Other sources of these long, single, shallow cuts

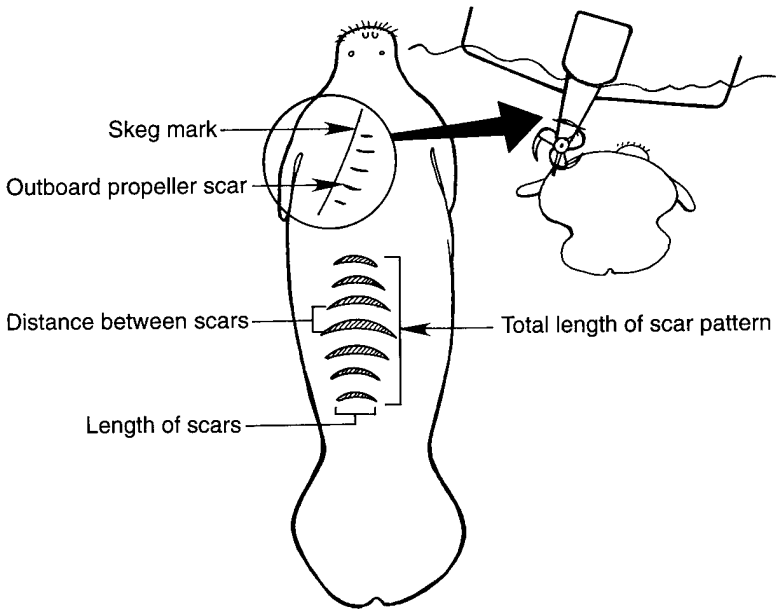


Fig. 2. The measurements taken on a typical pattern of propeller cuts. An example of a typical propeller pattern with a skeg mark is also shown. Inset shows how a manatee (*Trichechus manatus latirostris*) can sustain this wound during a collision with a boat with an outboard engine.

may have included rudders, keels, anti-pitch planes, and anti-crabbing planes below the hull. Manatees also may have injured themselves on other sharp objects (bottom debris, nails, or cables attached to pilings) in their environment that could have inflicted long, straight, shallow cuts. Therefore, we only included a skeg mark unaccompanied by propeller cuts in our analysis if there was internal injury associated with the mark. If not, these cuts were rejected from analyses because we were unsure of their origin.

Other kinds of marks on carcasses included those caused by the manatee being scraped or rolled along the bottom while trapped under a hull or squeezed between a hull and the wall of a canal lock chamber. These marks were occasionally accompanied by paint from hulls or impressions from tires used as docking fenders or bumpers. Marks from nets and ropes, impressions from canal locks and flood gates, and others were found also on manatee carcasses. However, these were distinguished easily from scars from propellers and not included in this analysis.

The location of sets of scars from propellers were plotted diagrammatically with sketches and photographs taken at necropsy. The carcass was divided into separate regions consisting of the head, dorsal thorax, dorsal mid-body, dorsal abdomen, and tail (Fig. 3). Because patterns overlapped regions, the pattern was scored in the region where the majority of the pattern occurred. A total of 381 scar sets was plotted from 227 carcasses. These carcasses were selected because all propeller patterns were measured and clearly illustrated on the necropsy reports. Carcasses with only a single propeller wound or scar were not included in this analysis. In addition, we recorded the number of patterns that clearly were perpendicular to the head-to-tail axis of the body.

Watercraft Registrations

Summaries of numbers of watercraft registered in Florida were obtained from the Florida Department of Environmental Protection Bureau of Vessels and Titling (unpublished data). All powered watercraft or those longer than 4.8 m are required to register. Watercraft are categorized as recreational or commercial and grouped by a range of hull lengths and by county (Florida Department of Environmental Protection Bureau of Vessels and Titling, unpublished data).

Trends in Watercraft-related Mortality and Boat Registrations

The number of watercraft-related manatee deaths has increased in Florida since the beginning of record keeping in 1974 (Ackerman et al. 1995; Fig. 4). This increase may have resulted in part from increased reporting of carcasses because of greater awareness and interest by the public. Also, coordination and cooperation improved with law-enforcement agencies, likewise increasing their participation in carcass recovery. During 1981–91, extended education of the general public and law enforcement probably maximized reporting efficiency, decreasing the influence of reporting efficiency as a factor in mortality increases. However, other factors, including an increase in recreational use and development along waterways have placed more people in previously remote areas, increasing the chances of carcass discovery.

At the same time, the number of boats registered in Florida has steadily increased (+3.6%/year; Fig. 4). In

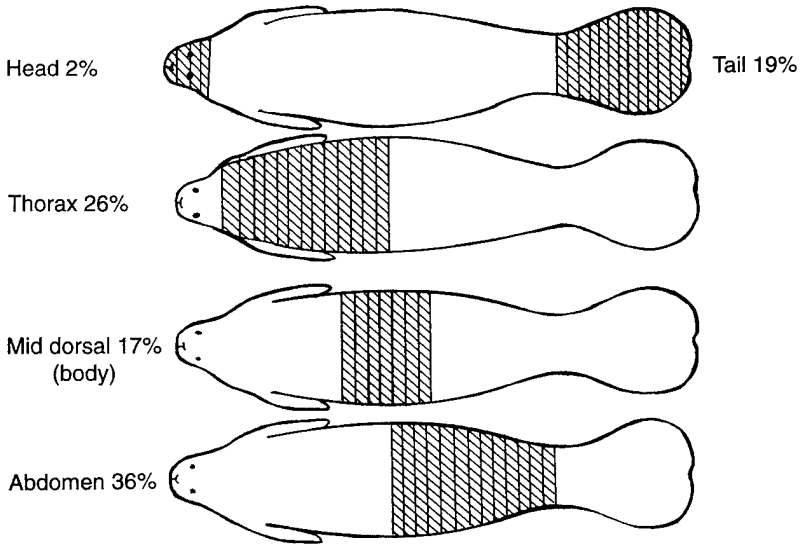


Fig. 3. Percentage of scars and wounds from propellers (381 patterns on 227 animals) in five regions of the body of a Florida manatee (*Trichechus manatus latirostris*; see text for definition of body regions).

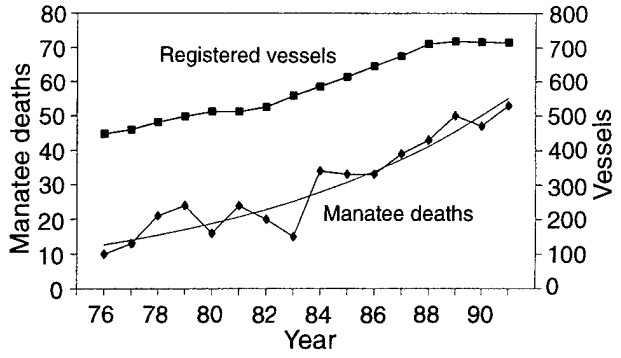


Fig. 4. Trends in Florida manatee (*Trichechus manatus latirostris*) deaths from collisions with watercraft and in numbers of registered watercraft (×10,000), Florida, 1976–1991. Exponential regression was used to fit the curve to Florida manatee deaths.

addition to the more than 716,000 boats currently registered in the state (fiscal year 1990–91, Florida Department of Environmental Protection, unpublished data), an estimated 300,000 more boats were brought into Florida during the winter tourist season (Jenna Venero, Major, Florida Marine Patrol, personal communication). Boat registration does not necessarily reflect boating use because some registered boats are only occasionally used throughout the year, whereas other boats are registered in other states. Variations in the economy may have affected sales and registration of boats in some years. Furthermore, scarcity of fuel during shortages and increased fuel costs may have also reduced boating and new boat sales. Nevertheless, increased boat registration and increased watercraft-related mortality during 1976–91 correlated ($r^2 = 0.89$, $P < 0.001$; Fig. 5). Watercraft-related deaths in 1974 and 1975 were omitted in trend analyses because the carcass recovery program was not fully operational until late 1975 (O'Shea et al. 1985).

Counties with the highest numbers of boat registrations did not necessarily correspond with counties with the highest watercraft-related mortality of manatees. For example, a large number of boats were registered in the Tampa Bay area (Hillsborough, Manatee, and Pinellas counties) on the west-central coast of Florida (96,000 registrations in three counties combined, fiscal year 1990–91; Florida Department of Environmental Protection, unpublished data). Yet only 18 watercraft-related mortalities were recorded from this area during 1974–91. In contrast, fewer boats were registered in Brevard County on the east-central coast of Florida (26,800 total registrations, fiscal year 1990–91; Florida Department of Environmental Protection, unpublished data), but 94 watercraft mortalities occurred in this area during 1974–91. The differences in numbers of deaths in the two areas may have several explanations. Historically, Brevard County waters supported a large manatee population (*Beeler and O'Shea 1988). However, some of the key manatee habitats (power-plant outfalls) are close to the Intracoastal Waterway. The Intracoastal Waterway is a heavily traveled corridor, used by seasonal out-of-state boaters and resident boaters who travel along the East Coast. The Tampa Bay area has a smaller manatee population that becomes widely dispersed during most of the year (*Weigle et al. 1988). Unlike in Brevard County, the aggregation sites of manatees in Tampa Bay are not adjacent to the Intracoastal Waterway, although manatees encounter ships coming to the power plants to deliver fuel. A larger number of watercraft-related manatee deaths may be related to larger manatee populations in areas of concentrated boat activity.

During fiscal year 1990–91, many more recreational boats than commercial boats were registered in Florida (Florida Department of Environmental Protection Vessel Registration, unpublished data; Fig. 6). Although the use of a watercraft has little to do with its size, in general, most commercial watercraft are larger (>7.9 m) and slower than recreational watercraft. At the same time, most ships (commercial watercraft) that visit Florida ports are not registered in Florida. Two classes of hull lengths, (3.7–4.9 and 4.9–7.9 m) composed a total of 554,100 registered recreational boats or 81% of all registered recreational boats and 77% of all registered boats. By comparison, recreational boats longer than 7.9-m were much less common but still numbered more than 47,300. These data do not provide more specific information on the most common hull length in each class. A new form of watercraft, the personal watercraft, is included in the hull-length category of 3.7 m or shorter. During 1990–91, 26,000 personal watercraft were registered in Florida (Florida Department of Environmental Protection, unpublished data).

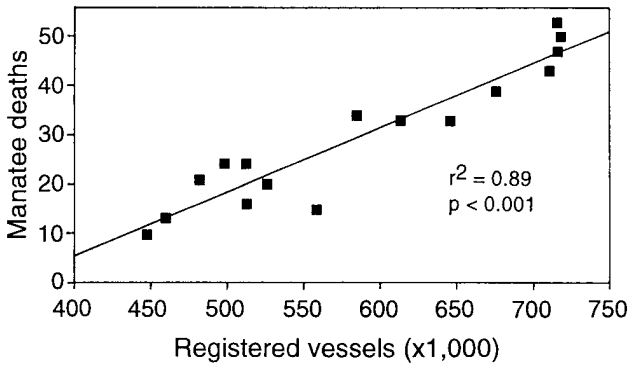


Fig. 5. Regression of Florida manatee (*Trichechus manatus latirostris*) deaths from watercraft collisions against number of registered watercraft (×1,000), Florida, 1976–1991. Data were provided by the Florida Department of Environmental Protection Bureau of Vessels and Titling.

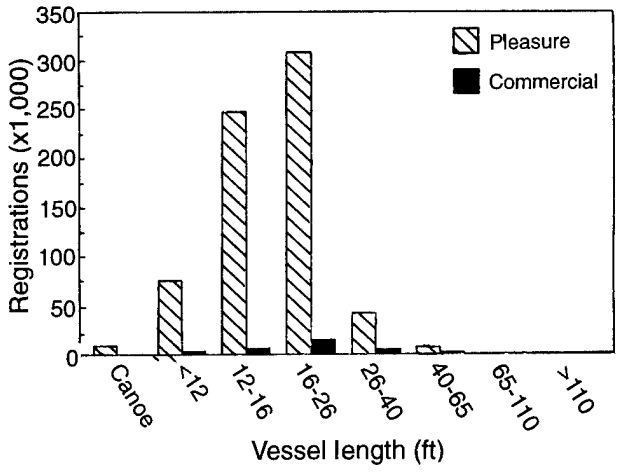


Fig. 6. Frequency distribution of registered watercraft ($n = 716,201$) by length class, Florida, 1990–1991. Data were provided by the Florida Department of Environmental Protection Bureau of Vessels and Titling.

Wounds From Propellers and Scar Patterns

A total of 1,376 sets of wounds or scars from various sources was recorded on 628 manatee carcasses recovered from 1979 through 1991. Not all manatees recovered during this period are included in this study. Carcasses without scars (rare), carcasses of perinatal manatees, and some badly decomposed carcasses were not included in this study. There were 703 sets of either wounds from propellers or scars from propellers (patterns). Collisions with watercraft caused 406 of the 628 manatee deaths. Most remaining animals that died of other causes had scars from propellers, and most animals that died from watercraft collisions had scars from previous propeller strikes. Of the 406 watercraft-related deaths, 158 (39%) were caused by propeller strikes, whereas 223 (55%) resulted from impact injuries. Another 16 (4%) deaths were attributed to a combination of impact injuries and propeller cuts, either of which would have been fatal. The exact categorization of the remaining 9 (2%) deaths was not determinable.

Beck et al. (1982) reported that 42 (58%) of the 72 watercraft-related deaths they investigated resulted from propeller cuts and 30 (40%) from impact. The frequency of death from impact seems to have increased in recent years from 40% to 55% (Table 1). Some of this increase may have resulted from a difference in classification that started in 1985 after the Florida Department of Environmental Protection took over the salvage and necropsies. If a carcass had superficial propeller cuts but extensive internal damage that is typical of death from impact, after 1985, the death was classified as impact-related, but Beck et al. (1982) may have classified the same death as propeller-related (defined by the presence of fresh propeller cuts).

Many animals survived propeller strikes, providing the basis for the scar catalog described by Beck and Reid (1995). In addition to healed wounds from propellers, occasionally healed skeletal fractures—probably caused by boat strikes—were encountered at necropsies but were not common. How many animals survived collisions could not be determined, but nonfatal bumps may have frequently occurred.

Sets of fatal wounds from propellers were significantly larger than scars from propellers in all respects (Table 2). The longest cuts were longer (38.3 vs. 17.8-cm mean length), cuts in the pattern were more numerous (5.4 vs. 3.0), cuts were spaced farther apart (14.3 vs. 10.4 cm,), and wound patterns were longer in total length (79.7 vs. 39.2 cm) in fresh fatal wounds from propellers than in healed scars from propellers. These differences in dimensions were the result of the actual size of the propeller and not of the shrinkage of a wound as it healed. Beck et al. (1982) observed similar differences with a smaller data set. Results were not significantly different between the 1974–79 and 1979–91 data sets (Table 2). Length of the longest cut was the only measurement for which data were available for comparison with data by Beck et al. (1982).

Most deaths from fatal impact injuries during 1979–91 included broken ribs (124 carcasses, mean 4.7 ribs, maximum 15) or luxated (dislocated) ribs (98 carcasses, mean 4.2 ribs, maximum 22). Combining broken and luxated ribs of these animals, the mean number of affected ribs was 6.3 (159 carcasses). One of these animals had a total of 34 affected ribs.

As found by Beck et al. (1982), our study revealed that most manatees that were directly killed by propellers had 25-cm and longer cuts (Fig. 7). (However, nearly as many

Table 1. Number of watercraft-related deaths of Florida manatees (*Trichechus manatus latirostris*) by category. Data from 1974–1979 are from Beck et al. (1982). Numbers in parentheses indicate percent of total sample size.

Category	1974–79	1979–91
Propeller	42 (57)	158 (39)
Impact	30 (41)	224 (55)
Both	not used[a]	16(4)
Unknown	2 (3)	8 (2)
Total	74	406

[a] This category of fatal wounds from impact and from propeller was not used by Beck et al. (1982).

Table 2. Measurements (cm) and other characteristics of scar patterns of wounds from propellers and fatal wounds from propellers and impact injuries on Florida manatees (*Trichechus manatus latirostris*). Data from 1974–1979 are from Beck et al. (1982).

Measurement	Period	Number of patterns	Number of animals	$\bar{x}$	Standard deviation	Maximum
Longest cut (cm)						
Scar	1974–79	40	32	16.4	10.4	58.0
	1979–91	521	257	17.8	9.7	58.0
Fatal wound[a]	1974–79	11	11	43.1	16.0	78.0
	1979–91	136	132	38.3	18.9	134.0
	t-test, scar vs. fatal wound, 1974–79, $t = 6.67$, df = 49, $P < 0.001$					
	t-test, scar vs. fatal wound, 1979–91, $t = 12.24$, df = 655, $P < 0.001$					
	t-test, scar 1974–79 vs. 1979–91, $t = 0.94$, df = 559, $P < 0.35$					
	t-test, fatal wound 1974–79 vs. 1979–91, $t = 0.86$, df = 145, $P < 0.39$					
Total length of pattern (cm)						
Scar	1979–91	439	230	39.2	29.8	196.0
Fatal wound[a]	1979–91	123	120	79.7	49.9	325.3
	t-test, scar vs. fatal wound, $t = 8.58$, df = 560, $P < 0.001$					
Mean distance between cuts (cm)						
Scar	1979–91	441	230	10.4	6.3	45.5
Fatal wound[a]	1979–91	122	119	14.3	6.2	45.5
	t-test, scar vs. fatal wound, $t = 5.97$, df = 563, $P < 0.001$					
Number of cuts						
Scar	1979–91	906	359	3.0	2.5	22
Fatal wound[a]	1979–91	159	156	5.4	3.5	23
	t-test, scar vs. fatal wound, $t = 8.36$, df = 1,063, $P < 0.001$					
Number of broken ribs						
Fatal wound from impact[b]	1979–91	124	124	4.7	3.3	15
Number of luxated ribs						
Fatal wound from impact[b]	1979–91	98	98	4.2	3.6	22
Number of combined broken and luxated ribs						
Fatal wound from impact[b]	1979–91	159	159	6.3	4.9	34

[a] Includes fatal wounds that were from propellers and from both propellers and impact.

[b] Includes fatal wounds that were from impact and from both propellers and impacts. Sample sizes included only animals with affected ribs; therefore, means do not represent animals without affected ribs.

animals had scars of comparable lengths, and some fatal cuts were smaller.) In addition, most healed scars were shorter than 25 cm. Although the propeller diameter was probably not smaller than the longest cut in a pattern, the diameter could have been greater. This is an identifiable limitation of these data. A glancing strike with a larger propeller could have left cuts that may suggest a smaller propeller (and thereby a smaller boat) was involved. This is further compounded by our observation that strikes from outboard and stern-drive engines do not always have skeg cuts and propeller cuts.

Locations of Scars From Propellers

Of the 381 examined scar patterns on 227 carcasses, only eight (2%) occurred to the head. Forty-three percent of the propeller patterns were located between the head and the center of the back, whereas 55% of the patterns were behind the center of the back (over the kidneys) to the end of the tail (Fig. 3). Because so few strikes occurred to the head and most strikes occurred over the kidneys and tail, the animals may have been diving when struck. We cannot determine the direction into which the

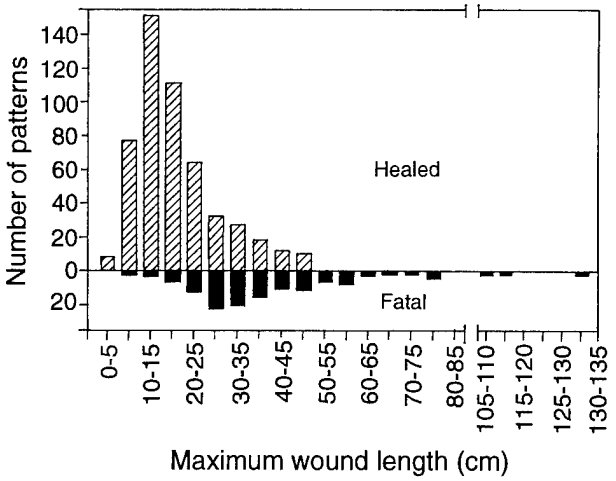


Fig. 7. Frequency distribution of length of longest cut (cm) in patterns of wounds from propellers between scars ($n = 524$) and fatal wounds ($n = 136$) on manatees (*Trichechus manatus latirostris*) in Florida, 1979–1991.

boat was traveling from the scar pattern. Eleven percent of the scar patterns were perpendicular to the head-to-tail axis of the animals. Therefore, in 89% of the strikes we documented, the animal was either facing or moving directly away from the oncoming boat when struck.

In addition to the scars from propellers on the dorsal portion of the body, only nine patterns were on the ventral portion. Seemingly, these few animals were either rolling when struck or the force of the hull strike rolled the animal before contact with the propeller.

Wounds From Propellers and Watercraft Characteristics

An important point by Beck et al. (1982) was that differences in propeller diameters were distinct between boats powered by inboard engines and boats powered by outboard or stern-drive engines. Therefore, they suggested that scar patterns measured on manatees could be used to determine the size of the watercraft. The propellers of smaller boats (shorter than 7.3 m) with outboard and stern-drive engines were too small (average 16.4 cm) to inflict fatal wounds, although they probably caused most of the nonfatal wounds from propellers. Only larger boats (>7.3 m) with large enough inboard engines had propellers (average 48 cm) that inflicted most of the fatal wounds from propellers.

More recent propeller specifications were collected from manufacturer's guidelines, which suggested propeller sizes for various combinations of hull length and engine horsepower. Recommended propeller sizes from 19 manufacturers of outboard and stern-drive engines and 12 types of inboard-engine propellers were reviewed (Michigan Wheel 1989). The most commonly recommended propeller for outboard or stern-drive engines of various horsepower had three blades and was 32.0–37.5 cm in diameter. By increasing the pitch (angle) of the propeller blades, the same diameter propellers can deliver greater speed. Outboard engines ranging from 50 to 335 hp use a 34-cm propeller. The largest-diameter propeller now available for smaller recreational boats is 51 cm for some high-horsepower stern-drive boats. During the past 10 years, the horsepower for outboard engines drastically increased, but this is not reflected by changes in propeller diameter.

Most large watercraft (>7.9 m) are powered by inboard engines and have exposed propellers driven by a straight shaft that protrudes from the bottom of the boat. Some exceptions to this, namely the long cigarette boats, are powered by multiple large horsepower outboard engines. In many inboard-powered boats, the propeller is protected by a rudder housing attached to a keel that extends below the propeller (Michigan Wheel 1989). This design offers only as much protection to manatees as the skeg on an outboard engine. Some small inboard-engine boats (<7 m), for example ski boats, have fully exposed propellers.

According to manufacturers, the diameters of propellers of several sizes for inboard engines and on outboard and stern-drive boats are comparable (Fig. 8). Some as small as 22 cm are recommended for inboard-engine cruisers and runabouts of average power (Michigan Wheel 1989). These are relatively slow cruising watercraft. Another size propeller is designed especially for inboard-engine boats that travel faster than 70 mph. These double- or triple-bladed propellers range in diameter from 22 cm to 35 cm. Another propeller design is exclusively for inboard-engine ski boats and has four blades and a 33-cm diameter. However, recommendations for propellers on inboard engines must be based on the horsepower and gear ratio from the engine to the transfer box and the intended use of the watercraft (Gerr 1989). These factors can be variable for inboard engines but are relatively uniform for outboard and stern-drive engines.

The small propeller diameters mentioned above are greater than the mean lengths of healed scars from propellers and smaller than the mean lengths of fatal propeller cuts measured in both studies (Table 2). Because of the overlap in sizes of propellers on outboard and stern-drive engines and on inboard-powered boats, the correlation of the wounds from propellers or scar dimensions with a particular size boat seems no longer useful. A reasonable guess can be made in obvious examples (as in a mortality caused by a large ship), but overall, there seems to be too much redundancy. Moreover, at least half of the watercraft-related manatee mortality resulted from impact for which neither propeller nor watercraft size was indicated in the records.

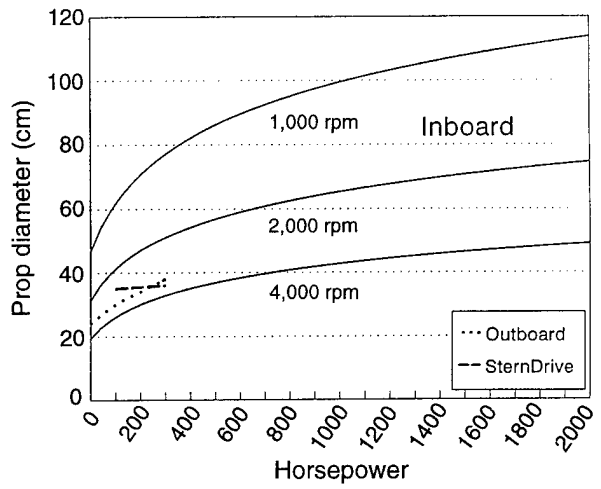


Fig. 8. Manufacturer's-recommended propeller diameter (cm) based on maximum rated revolutions per minute (rpm) and engine horsepower for outboard, stern-drive, and inboard engines. Data on outboard and stern-drive engines are from Michigan Wheel (1989). Data on inboard engines are from Gerr (1989).

Trends in Watercraft Propulsion and Implications for Manatee Conservation

A comparison of watercraft for sale at dealerships, boat shows, and marinas revealed some recent changes in hull designs and power configurations. During the past 10 years, boat manufacturing and boat dealerships in Florida increased (Florida Department of Environmental Protection Bureau of Vessels and Titling, unpublished data). In addition, the number of outboard-engine manufacturers increased. More boats are now designed to accommodate larger engines or twin outboard-engine configurations. More powerful outboard engines, such as 200 and 300 hp, 6-cylinder engines are readily available (Jenna Venero, Major, Florida Marine Patrol, personal communication). The current choices of hull styles and the sizes of boats and engines were not available to boaters when Beck et al. (1982) collected their data (1974–79). Outboard engines are now constructed with alloy metals that are much lighter than those used in the past. Electronic ignition systems and changes in carburation efficiency (electronic fuel injection) increased horsepower. Greater horsepower is available in smaller engines because of their decreased weight, increased efficiency, and more compact design. To some extent, the U.S. Coast Guard determines appropriate limits of engine size based largely on hull design and water-displacement characteristics. The regulations affect only new boats. Subsequent modifications by owners are not regulated.

We observed several new adaptations available to boaters that allow modifications of boats to facilitate travel in shallow water at high speed. However, little information is available on how frequently these modifications are used. Electric or hydraulic engine mounts can lift an outboard engine vertically to avoid striking the bottom in shallow water. Modifications of water intake ports for cooling outboard engines can prevent clogging with grass. The transom of a hull designed for one outboard engine can be more easily modified to accommodate two engines.

Several new types of watercraft either did not exist 20 years ago or were just appearing on the market (Florida Department of Environmental Protection, Bureau of Vessels and Titling, unpublished data). The outboard-driven flats boat is designed for fishing in shallow water. Most of these have wide hulls for stability and flat open decks for easy angling. Many have engine lifts to vertically raise the engine in shallow water. Anglers usually drift over grass flats or push along the bottom with fiberglass poles. Personal watercraft have become increasingly popular over time. They are small (<2 m), usually single-person craft that are powered by a 50–60 hp, 2-cylinder inboard engine. They use an impeller-driven system and do not have a propeller. A further recent modification of the personal watercraft is the jet boat. Jet boats are offered by several manufacturers and are powered by larger engines attached to jet-drive propulsion systems similar to personal watercraft. These new boats are an average length of 4–5 m and can travel 48–56 km/h. Because personal watercraft and jet boats have no propellers, are light weight, and have a shallow draft, they represent a new class of watercraft that can travel at high speed in shallow water (<1 m).

Since the study by Beck et al. (1982), much has changed in Florida. The human population greatly increased, resulting in more development along the coastline and a greater demand on natural resources to support recreation and commerce. The total number of registered boats in Florida during 1980–81 was 502,143 and increased to 716,201 by 1990–91. During 1980–81, 480,864 boats (96% of the total registration) were recreational. A total of 685,075 boats (97% of total registration) were listed as recreational during 1990–91 (Florida Department of Environmental Protection Bureau of Vessels and Titling, unpublished data). These numbers indicate a potential increase in threats to manatees but do not necessarily prove cause-and-effect relations in increased numbers of deaths. Additionally, one can only speculate about the effect of the increase in boating traffic on manatee movement, communication, and other key factors in manatee biology.

An inevitable result of more boats in the same area is crowding for space and increased traveling in shallower water. New modifications to hulls and engines and the advent of personal watercraft facilitate shallow-water

boating at higher speeds with less risk of engine or propeller damage. These changes may have as much of an effect on manatees as the overall increase in boat numbers. Increased boat traffic in shallow water may pose an indirect threat to manatees from the destruction of seagrass beds that serve as food.

Boating education, safety courses, and proposed operators licenses would seem to be effective means of reducing boating accidents and of better assuring safe boating. Such educational programs should include information on the need to prevent collisions with manatees and to avoid harm to their habitat. In addition, plans for county-specific manatee protection that address critical habitat, marina expansion, and boating speed zones show promise for the protection of manatees and for other components of the marine ecosystem (Ackerman et al. 1995; Reynolds 1995). In some cases, acquisition of habitat and designation of refuges that are complete sanctuaries from boat entry may ultimately be necessary for enhancing the protection of manatees.

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Cited References[3]

Ackerman, B. B., S. D. Wright, R. K. Bonde, D. K. Odell, and D. J. Banowetz. 1995. Trends and patterns in mortality of manatees in Florida, 1974–1992. Pages 223–258 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Beck, C. A., R. K. Bonde, and G. B. Rathbun. 1982. Analyses of propeller wounds on manatees in Florida. Journal of Wildlife Management 46:531–535.

Beck, C. A., and J. P. Reid. 1995. An automated photo-identification catalog for studies of the life history of the Florida manatee. Pages 120–134 *in* T J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

*Beeler, I. E., and T. J. O'Shea. 1988. Distribution and mortality of the West Indian manatee (*Trichechus manatus*) in the southeastern United States: a compilation and review of recent information. National Technical Information Service, Springfield, Va. Document PB 88-207980/AS. 613 pp.

*Bonde, R. K., T. J. O'Shea, and C. A. Beck. 1983. A manual of procedures for the salvage and necropsy of carcasses of the West Indian manatee (*Trichechus manatus*). National Technical Information Service, Springfield, Va. Document PB 83-255273. 175 pp.

Gerr, D. 1989. Propeller handbook: the complete reference for choosing, installing, and understanding boat propellers. International Marine Publishing Company, Camden, Maine. 225 pp.

Jones, T. C., and R. D. Hunt. 1983. Veterinary pathology (5th edition). Lea and Febiger, Philadelphia, Pa. 1,792 pp.

Michigan Wheel. 1989. Propeller catalog. Michigan Wheel Co., Grand Rapids, Mich. 38 pp.

O'Shea, T. J., C. A. Beck, R. K. Bonde, H. I. Kochman, and D. K. Odell. 1985. An analysis of manatee mortality patterns in Florida, 1976–1981. Journal of Wildlife Management 49:1–11.

Reynolds, J. E., III. 1995. Florida manatee population biology: research progress, infrastructure, and applications for conservation and management. Pages 6–12 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

SAS. 1988. SAS procedures guide, release 6.03 edition. SAS Institute, Inc., Cary, N.C. 441 pp.

*Weigle, B. L., J. E. Reynolds, III, G. W. Patton, and J. R. Wilcox. 1988. Manatee (*Trichechus manatus*) winter use of warm water discharges in Tampa Bay. Pages 153–164 *in* K. Mahadevan, R. K. Evans, P. Behrens, T. Biffar, and L. Olsen, editors. Proceedings of the Southeastern Workshop on Aquatic Ecological Effects of Power Generation, 3–5 December 1986, Sarasota, Fla. Mote Marine Laboratory Report 124.

[3] An asterisk denotes unpublished material.

Integration of Manatee Life-history Data and Population Modeling

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Abstract. Aerial counts and the number of deaths have been a major focus of attention in attempts to understand the population status of the Florida manatee (*Trichechus manatus latirostris*). Uncertainties associated with these data have made interpretation difficult. However, knowledge of manatee life-history attributes increased and now permits the development of a population model. We describe a provisional model based on the classical approach of Lotka. Parameters in the model are based on data from other papers in this volume and draw primarily on observations from the Crystal River, Blue Spring, and Atlantic Coast areas. The model estimates λ (the finite rate of increase) at each study area, and application of the delta method provides estimates of variance components and partial derivatives of λ with respect to key input parameters (reproduction, adult survival, and early survival). In some study areas, only approximations of some parameters are available. Estimates of λ and coefficients of variation (in parentheses) of manatees were 1.07 (0.009) in the Crystal River, 1.06 (0.012) at Blue Spring, and 1.01 (0.012) on the Atlantic Coast. Changing adult survival has a major effect on λ. Early-age survival has the smallest effect. Bootstrap comparisons of population growth estimates from trend counts in the Crystal River and at Blue Spring and the reproduction and survival data suggest that the higher, observed rates from counts are probably not due to chance. Bootstrapping for variance estimates based on reproduction and survival data from manatees at Blue Spring and in the Crystal River provided estimates of λ, adult survival, and rates of reproduction that were similar to those obtained by other methods. Our estimates are preliminary and suggest improvements for future data collection and analysis. However, results support efforts to reduce mortality as the most effective means to promote the increased growth necessary for the eventual recovery of the Florida manatee population.

Key words: Florida manatee, *Trichechus manatus latirostris*, population model, population dynamics, life history.

A population model with life-history data may provide a useful tool for the evaluation of information on trends in counts and annual numbers of recorded deaths of Florida manatees (*Trichechus manatus latirostris*). Thus far, the interpretation of information about population dynamics from the latter two data sets has been difficult. The history of manatee studies in Florida has been dominated by concern about the effect of watercraft-caused mortality on a small population of unknown size. The recovery of carcasses revealed a steady increase in total recorded mortality since

1974 (Ackerman et al. 1995). An increase in public awareness of the problem possibly improved the efficiency of locating carcasses that probably stabilized in many areas because the program has now been of long duration. However, efficiency may continue to increase in other areas as more people continue to settle along the coast and use waterways and where public education and media attention continue to increase. Although the increase in deaths in many areas is clearly not an artifact of data collection, the effect of changing and uneven reporting and recovery rates and the proportion of recovered carcasses remain unknown.

Lack of certainty about the size of the Florida manatee population is similar. Initial efforts to census manatees from the air resulted in an estimated minimum population size of about 1,000 individuals in the 1970's and early 1980's (*[1]Brownell et al. 1981; O'Shea 1988). Counts from subsequent surveys were higher, and 1,200 was given as the minimum population size after 1985 (O'Shea 1988). A large number of aircraft were used in the most recent (beginning 1991) surveys that were conducted after cold fronts, when manatees concentrate in sites where they can be more readily counted. Counts from these surveys were 1,465 in February 1991 and 1,856 in January 1992 (Ackerman 1995). The higher tally was probably due to better conditions, timing, and more intensive coverage rather than a 26% growth in population between 1991 and 1992.

Because manatees reproduce slowly (Hartman 1979; Rathbun et al. 1995), data on manatee numbers from carcass recovery and aerial surveys seem to be inconsistent. Clearly, the mortality during any protracted period was too high for the relatively low tallies from aerial counts (particularly those prior to 1991). In addition to numerous manatees that were killed in collisions with boats and major increases in numbers of registered boats, the high number of individuals that are scarred by propellers (Beck and Reid 1995) made it nonetheless evident that the manatee population was suffering much pressure. The subspecies has been and is currently properly classified as endangered (*U.S. Fish and Wildlife Service 1989), and public education and regulatory efforts to reduce mortality are essential if manatees are to be maintained as a conspicuous and functional component of Florida's fauna.

Because of increased knowledge from research and a longer period of record-keeping, a portion of the increased recorded mortalities may have been due to an increase in the actual numbers of manatees (O'Shea 1988). Such a prospect is encouraging for the conservation of the manatee but increases the complexity and difficulties of planning. This workshop thus served as the initiation of a review of the data and the identification of means to improve an understanding and clarification of the interpretation of the data. Population modeling is one approach for accomplishing such improvements.

For the development of a population model, we apply demographic information from longitudinal field studies that entail direct observations of known individuals through time. Manatee population dynamics have been studied intensively with these methods in two relatively small study areas (Blue Spring and Crystal River) for more than 15 years (O'Shea and Hartley 1995; Rathbun et al. 1995). These are naturally warm waters that attract manatees during winter and to which manatees return at high annual rates (O'Shea and Langtimm 1995). However, these aggregations of manatees are not considered geographic stocks that are separate from manatees in other areas of Florida. Trend data collected at these aggregation sites indicated that the number of manatees increased over the years; 260 manatees were in the Crystal River and 67 were at Blue Spring in January 1992 (Ackerman 1995). Modeling (below) also revealed increases in these two study areas; the joint counts in these areas are about 18% of the total manatee count in Florida in winter. Information from remaining areas in the state is less complete, and trends in counts elsewhere are more ambiguous (Ackerman 1995; Garrott et al. 1995). Consequently, an effort was made to test the model that we describe here in these two study areas. To evaluate the situation in other parts of Florida, we also applied modeling to manatees in the Atlantic Coast study area, where some estimated survival and reproduction data are also now available (O'Shea and Langtimm 1995; Reid et al. 1995). Detailed background information and population data on manatees in these three study areas were provided in Ackerman (1995), Garrott et al. (1995), O'Shea and Hartley (1995), O'Shea and Langtimm (1995), Rathbun et al. (1995), and Reid et al. (1995).

A Provisional Model

The revised manatee recovery plan (*U.S. Fish and Wildlife Service 1989) calls for the construction of a population model, and one purpose of the workshop was to assemble data for subsequent analysis and modeling. Some initial elements of a new model are included here. Several uncertainties about the best use of the data may ultimately require separate, specialized modeling, and several iterations and versions of a population model will no doubt be useful. We do not anticipate one final and conclusive model for the Florida manatee population. Instead, we believe that the simple model presented here should be regarded only as another tool in population analysis to be used repeatedly as better data become available. This work will serve as the next step beyond Packard's (*1985) initial manatee population model, which was useful but was based on data with greater uncertainty than the data that are now available.

[1] An asterisk denotes unpublished material.

Background for Modeling

The basic model was developed by A. J. Lotka in the early 1900's (Lotka 1907) and was extensively used in demographic studies. Ecological applications of Lotka's model often followed the matrix formulation detailed by Leslie (1945, 1948) that was also independently developed by Bernadelli (1941) and Lewis (1942). In a later paper, Leslie (1966) gave a simplification of the matrix model based on the assumption of constant rates of reproduction and survival rather than on the age-specific rates used in the full matrix model. Various applications of this simplification have since been made. One early use for marine mammals was that of Eberhardt and Siniff (1977).

As better information on survival of adult marine mammals began to accumulate, Leslie's (1966) use of constant adult survival to accommodate the sharp decline in survival accompanying senescence had to be modified. This can most conveniently be accomplished by adopting a truncation point, as done by Eberhardt (1985). Thus far, data on manatee ages (Marmontel 1993, 1995) suggested that manatees may live as long as 50 years. Marsh (1995) reported dugongs that were older than 70 years. For initial purposes, we use a maximum age of 50 to provide a truncation point in lieu of data on senescence. Two other modifications to the basic approach may ultimately be useful for various purposes. First, initial reproduction is spread over several age classes, so that full reproduction is probably not achieved at a single age, as demonstrated by observations in the field (O'Shea and Hartley 1995; Rathbun et al. 1995) and by anatomical studies (Marmontel 1995). Thus, the choice of an appropriate age of first reproduction for use in the simplified model may require more data than are now available. Second, three rates may eventually be useful. One is the survival from birth to weaning, a second is the annual survival of subadults, and the third is the survival of adults.

Thus, several degrees of approximation may be considered. Given a very large sample of reproduction data one may construct a reproduction (m_x) curve like that used by Eberhardt (1985) for the Pribilof fur seals (*Callorhinus ursinus*). With less extensive data, that curve may be replaced by a simple rectangle. With better data, a curve could be fitted for the early ages, but the truncation for the right side of the curve should be retained to accommodate senescence. Here, m_x denotes the number of female births per female, so that the usual rate of births per female must be divided by two if sex ratio at birth is approximately even, as seems to be the case in manatees (O'Shea et al. 1985; O'Shea and Hartley 1995; Rathbun et al. 1995).

Similar considerations apply to the survivorship (l_x) curve. With a large sample, one can use age-specific rates throughout. With minimal data, one may use only two rates, survival to the age of first parturition (l_a) followed by a constant rate of adult survival (s) to the truncation age (w). Furthermore, the Lotka-Leslie model can be variously formulated, depending on the timing of reproduction. In the original (Lotka) equation, reproduction is considered continuous at a constant rate throughout the year. Consequently, the basic equation is expressed as an integral equation. However, many large mammal populations exhibit what Caughley (1977) termed *birth-pulse reproduction*, in which births are concentrated in a short time period each year. Under these circumstances, the equation may be approximated by a summation:

$$1 = \sum_{a}^{w} \lambda^{-x} l_x m_x \qquad (1)$$

Cole (1954) showed that equation (1) provides nearly an exact replacement for the integral equation of Lotka for birth-pulse populations. Reproduction in manatees, however, takes an intermediate form, being distributed over most months of the year with a peak in spring and summer and a marked reduction in winter. Such a seasonal pattern is evident in the reports by Hernandez et al. (1995), Marmontel (1995), O'Shea and Hartley (1995), and Rathbun et al. (1995).

When we replace age-specific reproduction (m_x) and survivorship (l_x) terms in equation (1) by constant rates, the equation can be simplified. When the reproduction curve (m_x) is replaced by a rectangular function, we approximate m_x by a constant (m) from age a to age w. However, this is further complicated because manatees do not reproduce annually but give birth at 2-year or longer intervals (Hartman 1979; Marmontel 1995; O'Shea and Hartley 1995; Rathbun et al. 1995; Reid et al. 1995).

If we use two rates for survivorship, the l_x values can be written as $l_x = l_a s^{x-a}$ when $x \geq a$, where l_a denotes survival to age a, and s denotes the constant adult rate. With these approximations, equation 1 becomes:

$$1 = \lambda^{-a} l_a m \left[1 - (s/\lambda)^{w-a+1} \Big/ 1 - (s/\lambda) \right] \qquad (2)$$

This equation can be rearranged as a polynomial:

$$\lambda^a - s\lambda^{a-1} - m\, l_a\, [1-(s/\lambda)^{\,w-a+1}] = 0 \qquad (3)$$

In this form, it can be equated to the *characteristic polynomial* of the Leslie matrix (elements of the matrix are replaced by constants, as described above) with one proviso. The Leslie matrix formulation often is written so that the youngest age class is that of 1-year-olds. We then must write the reproduction term as $m = s_o F$ where s_o is survival from birth to age 1, and F is the number of female births per female as normally used in the Leslie matrix (but expressed as F_x for age-specific rates).

For the data on manatees, equation 3 must be modified to use $l_a = l_k s^{a-k}$ (i.e., we can expect that much of survivor-

ship to age of first parturition will be at the adult rate (s) as suggested by observations at Blue Spring [O'Shea and Hartley 1995] and by limited evidence from telemetry in several study areas [O'Shea and Langtimm 1995], rather than at the subadult rate incorporated in l_k). We then write equation (3) as:

$$\lambda^a - s\lambda^{a-1} - l_k s^{a-k} m [1 - (s/\lambda)^{w-a+1}] = 0 \qquad (4)$$

Inasmuch as a direct expression of λ (the finite rate of increase) is not available, the above equations must be solved by iteration.

A necessary assumption for use of the Lotka-Leslie model is that of the stable age distribution. The development of a stable age distribution requires that the population is changing at a constant rate for some period of time. The consequences of a deviation from a stable age distribution are usually not substantial, unless there is a major change in age structure. Such changes may be more probable in small populations, but age-distribution data from manatee-carcass studies seem not to have changed during 1976–91 (Marmontel 1993).

Applying the Delta Method to the Model

An approximation to a variance of λ may be obtained by the delta method (Seber 1982:8):

$$V(\hat{\lambda}) \doteq \sum V(x_i) [\partial\lambda(x_i)/\partial x_i]^2 \qquad (5)$$

where x_i denotes the three constant values (s, l_k, m) used in equation 4, and $V(x_i)$ the variance of the estimates of these parameters. Seber (1982) includes covariance terms, but these were not included in the present example because separate data sources were used for various components.

Implicit differentiation of equation 4 was used to obtain the several partial derivatives:

$$\partial\lambda/\partial s = -s\lambda^{a+1} - (a-k) l_k m \lambda s^{a-k} [1 - {}^{w-a+1}\!/_{a-k} (s/\lambda)^{w-a+1} - (s/\lambda)^{w-a+1}] / sB$$

$$\partial\lambda/\partial m = -s^{a-k}\lambda^2 l_k [1 - (s/\lambda)^{w-a+1}]/B \qquad (6)$$

$$\partial\lambda/\delta l_k = -s^{a-k}\lambda^2 m [1 - (s/\lambda)^{w-a+1}]/B$$

where

$$B = s\lambda^a (a-1) - a\lambda^{a+1} - (w-a+1) l_k m \lambda s^{a-k} (s/\lambda)^{w-a+1}.$$

With the delta method approximation, one can estimate how to best allocate field efforts for estimating λ (i.e., how much sampling should be devoted to each component).

A second aspect for consideration is the relative importance of the three components in management. Changes in adult survival have a large influence on λ in marine mammals (as noted of dugongs by Marsh [1995]). This aspect is concisely expressed by the partial derivative,

$$\partial\lambda(x_i)/\partial x_i.$$

These partial derivatives were then used in equation 5 to estimate a variance of λ and to examine the relative importance of the three main variance components and the relative effect of changes in survival and rates of reproduction on λ. Another statistical technique, bootstrapping, provides an alternative estimate of overall variances, as described in a later section of the paper.

Parameters in the Model

Calculation of λ from equation 4 requires a choice of the maximum age (w), which, as noted above, was set at 50. Use of older ages (e.g., 60) has only a trivial effect on estimates of λ. Field observations provided 14 records of age at first parturition, seven from Blue Spring (O'Shea and Hartley 1995) and seven from the Crystal River (Rathbun et al. 1995). Age 4 was used for the value of a because in the field studies, four females reproduced at the age of 4 years, four at the age of 5 years, four at the age of 6 years, and two at the age of 7 years. These data are compatible with observations on carcasses; the seven youngest females with anatomical evidence of maturity were between 3 and 4 years old (Marmontel 1995). As noted above, because initial reproduction is spread over several age classes, more data may suggest other options for estimating this parameter.

Rates of reproduction of manatees in the Crystal River were taken from Table 3 of Rathbun et al. (1995) from which records of 147 calves (very young, less-than-1-year-old manatees observed with their mothers; see Rathbun et al. 1995) born in 389 manatee-years (adults only) were used. At Blue Spring (O'Shea and Hartley 1995:Table 2), records of 43 calves in 144 manatee-years were used in our calculations. In both instances, the records are based on long-term observations of individual manatees. Data from the Atlantic Coast population (Reid et al. 1995) are based on similar observations but on lower resighting frequencies. Reid et al. (1995) recorded 254 first-year calves in 664 manatee-years. Because most calves are not born in aggregation sites in winter and are thus not observed until in the winter of their first year, the rate of reproduction (m) in equation 4 is calculated at that time and is considerably lower than the actual birth rate. Calf survival from neonatal to about 6 months has been calculated at 0.60 in manatees at Blue Spring and at 0.67 in manatees in the Crystal River (O'Shea and Hartley 1995; Rathbun et al. 1995). Equation 4 thus applies to about 6-months old manatees rather than to true neonates, and the first-year survival (l_1) used in the equation is survival

from about 6 months to 1.5 years (first to second winter of life). Survival after age 1.5 has been assumed to be at the adult rate.

Adult survival (s) was obtained by the methods of O'Shea and Langtimm (1995). Further assessment of the records resulted in an improved database (C. A. Langtimm, National Biological Service, San Simeon, California, personal communication), which was used for analyses reported here. O'Shea and Hartley (1995:Table 1) reported the survival of 37 of 45 calves to the next winter or an early survival (l_k) of 0.82. Rathbun et al. (1995) reported a minimal survival to age 3 of 22 tail-nicked calves but indicated that these data underestimate early survival because observations of calves are less comprehensive in the Crystal River than at Blue Spring. This information is therefore not incorporated in our calculations. Similarly, no satisfactory estimated early survival is available from the Atlantic Coast population. Marmontel (1993:Table 4.8) reported the ages of a large sample of dead manatees and used these data to estimate first-year survival as 0.685. However, this survival was estimated with the classical life-table approach for which a constant population size ($\lambda = 1$) must be assumed. Also, it presumably applies from birth to age 1, whereas here we use a rate from winter to winter or roughly 6–18 months of age. The rate used here would be appreciably higher because it excludes perinatal deaths, which peak in warm months (Marmontel 1995; O'Shea and Hartley 1995; Rathbun et al. 1995).

A crude first-year survival of 0.78 in the Atlantic Coast population can be estimated by applying the ratio of first-year to adult survival at Blue Spring (0.82/0.96) to the estimated adult survival on the Atlantic Coast (0.91). For this calculation, one assumes the ratio of first-year to adult survival is the same on the Atlantic Coast as at Blue Spring, which may not be the case. We believe that this estimate may nonetheless be the best available at present and have used it for illustrative calculations to show the effect of sample sizes on variances. Observations by Reid et al. (1995) do not suggest that survival of young is radically lower on the Atlantic Coast than at Blue Spring.

Estimated parameters in the model included rates of reproduction, adult survival, and early survival of manatees in each of the three areas (Table 1). The age of first reproduction ($a = 4$) and the maximum age ($w = 50$) were assumed to be the same in the different areas. Estimated variances are included for use in equation 6. Variances of rates of reproduction were calculated from the average rates in adult females in the Crystal River and at Blue Spring (where sampled individuals represented a large proportion of the total population of adult females). Because few replicate observations of individual females from the Atlantic Coast were available, an estimated binomial variance was used for those data. Adult survival variances were derived in the same manner as those reported in O'Shea and Langtimm (1995:Table 4), and binomial variances of early survival were calculated. Rates of reproduction were divided by 2 for equation 1, in which the number of daughters per female is used.

Inasmuch as each of the partial derivatives incorporates all three survival and reproduction terms, the results must be evaluated in terms of specific values of these rates. Because the only satisfactory estimate of early survival was from manatees at Blue Spring, that value was also used for manatees in the Crystal River, where other parameters and conditions in general seemed comparable. Because the early survival value of the Atlantic Coast population is estimated under the assumption that the ratio of early survival to adult survival is the same as at Blue Spring, the calculation of λ is uncertain, but the results were included to illustrate probable results from calculations of variance components and the relative importance of the parameters.

Results From the Model

Estimates of λ, components of variance, and partial derivatives were obtained (Table 2). Considering the partial derivatives first, changing adult survival clearly has the major effect on λ because a change of one percentage point in adult survival results in about the same degree of change in λ. Reproduction has the next largest partial, and

Table 1. Estimated parameters used in the model of population dynamics of Florida manatees (*Trichechus manatus latirostris*) in the Crystal River, at Blue Spring, and on the Atlantic Coast of Florida. Standard errors are in parentheses.

Area	Rate of reproduction (m)	Adult survival (s)	Early survival (l_k)
Crystal River	0.189(0.049)	0.965(0.0060)	[a]
Blue Spring	0.15(0.060)	0.961(0.0180)	0.822(0.057)
Atlantic Coast	0.19(0.009)	0.907(0.0098)	0.78[b]

[a] Early survival estimates from Blue Spring used in calculations.
[b] Calculated from ratio of adult and early survival at Blue Spring.

Table 2. Values of λ, variance components, and partial derivatives calculated from life-history data of Florida manatees (*Trichechus manatus latirostris*) in the Crystal River, at Blue Spring, and on the Atlantic Coast. Coefficients of variation for λ (standard error/estimate) are in parentheses.

Study area/ parameter	Estimate of λ	Variance component	Partial derivatives
Crystal River[a]	1.074(0.009)		
Adult survival		0.41	1.02
Reproduction		0.19	0.46
Early survival		0.40	0.11
		1.00	
Blue Spring	1.057(0.012)		
Adult survival		0.82	1.02
Reproduction		0.11	0.51
Early survival		0.07	0.09
		1.00	
Atlantic Coast[b]	1.01(0.012)		
Adult survival		0.63	1.03
Reproduction		0.10	0.43
Early survival		0.27	0.11
		1.00	

[a] Using the early survival data from Blue Spring.
[b] Assuming the ratio of early survival to adult survival is the same as that at Blue Spring.

early survival is the smallest. In comparisons of these values with the variance components, the partials indicate the approximate effect of changing a parameter value on the magnitude of λ,whereas the variance components indicate how increasing sample size may reduce the variance of an estimated λ.

In the case of the variance components, the relatively small standard error of adult survival in the Crystal River (Table 1) results in dominance of the variance of early survival. A higher standard error of adult survival results in the dominance of that variance component at Blue Spring. Because trustworthy estimates of early survival in the Crystal River and on the Atlantic Coast are not available, such estimates must be obtained. The same sample size (45) for early survival was used to calculate variances of survival in all sites because the only useful early survival was that of manatees at Blue Spring. If an early survival of manatees on the Atlantic Coast can be estimated, it will probably be done with a larger sample size because of the larger number of observed manatees there.

Because the adult survival at Blue Spring represents most or all of the manatees that use the study area, the sample size cannot be substantially increased by more intensive effort and only increases over time. A large ($n = 414$) sample of adults was observed for the estimation of survival along the Atlantic Coast, but further improvements in data collection may help improve results from this region by producing an estimate with smaller variance (O'Shea and Langtimm 1995).

The estimates of λ of manatees in the Crystal River (1.07) and at Blue Spring (1.06) are appreciably smaller than rates of increase in counts obtained by Ackerman (1995) from trend data (about $\lambda = 1.10$ from the Crystal River and $\lambda = 1.08$ from Blue Spring). The coefficients of variation of λ (Table 2) are small enough to suggest that the differences may not be due to sampling errors. The only complete set of reproduction and survival data is that from Blue Spring. As a further check on this seeming disparity, bootstrapping (Efron and Tibishirani 1993) was independently applied to the trend data (bootstrapping deviations from regression) and to the reproduction and survival data (described below in the section on bootstrapping), and the frequency distribution of the differences of the two estimates of λ (one from trend, one from reproduction and survival data) was used to examine the prospect that the observed difference arises from chance alone (Fig. 1). Because few (about 2%) of the differences are less than zero, some real differences in the two data sets are possible.

Some of the differences between demographic estimates of population growth rates and trend counts in the Crystal River and at Blue Spring may be due to an influence of immigration on trend counts. Rathbun et al. (1995) suggested possible immigration into the Crystal River study area, and immigrant manatees from southeastern Florida have overwintered at Blue Spring (National Biological Service and Florida Park Service, unpublished data). Protection of these areas as manatee refuges may play a role in attracting immigrants. Furthermore, because the estimated rate of reproduction from Blue Spring is

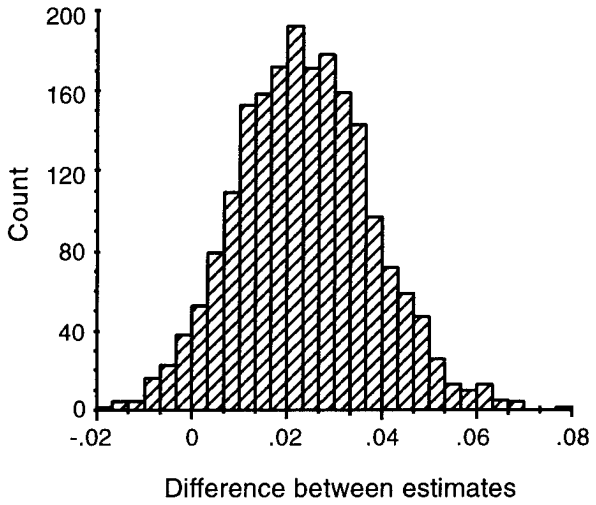


Fig. 1. Frequency distribution of differences between values of λ of Florida manatees (*Trichechus manatus latirostris*) obtained from bootstrap samples. Bootstrap samples were separately derived from trend data from aerial counts and from reproduction and survival data obtained by direct observation.

lower than the nearly equal rates from the other two sites (Table 1), this estimate may also be assumed responsible for part of the lower estimate of λ. A calculation with m set equal to the value from the other two sites ($m = 0.38$) gives $\lambda = 1.07$, which is appreciably closer to the value from trend data (1.08). Another prospect for underestimation comes from the early survival data, which depend on reidentification of surviving individuals in some future year. Pollock et al. (1990) pointed out that such estimates can be biased because an individual may survive to the next year but may subsequently not be seen and die and thus may never be seen again and is assumed to have died in the year subsequent to marking. Pollock et al. (1990) recommended the Jolly-Seber method in such cases because that method corrects for the probability of resighting. However, at Blue Spring, many surveys are conducted in each year, and the probability of sighting an individual, if it is present, approaches unity (only one individual of 37 was not seen in the year after recruitment as a calf but was then seen in subsequent years and is believed to have wintered elsewhere during the interim; O'Shea and Hartley 1995).

As previously pointed out here, the estimate of λ from the Atlantic Coast is uncertain because of the need to assume an early survival value with the same ratio to adult survival as observed at Blue Spring. An indirect estimate may be obtained from the state-wide age data of Marmontel (1993:Table 4.8). Applying the method of Chapman and Robson (1960) to data from 4-year-old and older manatees gives an estimated survival of 0.896. Because the Chapman-Robson methods also require the assumption that $\lambda = 1$, this estimate is biased, but the bias is of the form $s^* = s/\lambda$ (c.f., Eberhardt 1988), where s^* is the Chapman-Robson estimate and s is the true survival. Because the estimated survival (Table 2) is relatively precise and presumably unbiased, we can calculate

$$\lambda = s/s^* = 0.907/0.896 = 1.01.$$

This is the same rate as obtained by the delta method. Lambda from the Atlantic Coast data indicates a slow rate of increase. The only trend data from that region (Garrott et al. 1995) also suggested an increase in the manatee population size.

Bootstrapping for Estimating Variances

As noted previously, the only complete set of reproduction and survival data is from Blue Spring. Using the delta method (equation 5) with equation 4 provides an estimate of the coefficient of variation for the estimate of λ (1.06) from these data. This estimate is 0.012 with 95% confidence limits of about 1.02–1.10. Because calculations of this kind in the study of large-mammal population dynamics are relatively new, a cross-check of the results with the bootstrapping technique seemed desirable (Efron and Tibishirani 1993). Three estimated parameters were examined. Rate of reproduction (m) was evaluated by using data from Blue Spring of O'Shea and Hartley (1995; Table 3). Records of number of years of observation and number of young born to each of 20 individual adult female manatees were entered into a file, samples of 20 were drawn with replacement, and a rate of reproduction was calculated.

Table 3. Bootstrapping estimates of λ, rates of reproduction, and adult survival in Florida manatees (*Trichechus manatus latirostris*) in the Crystal River and at Blue Spring in comparison with direct estimates. Standard errors are in parentheses.

	Blue Spring		Crystal River	
Parameter	Bootstrap	Direct	Bootstrap	Direct
λ	1.057(0.012)	1.051(0.019)	1.074(0.009)	1.074(0.010)
Reproduction	0.15(0.010)	0.15(0.060)	0.19(0.008)	0.189(0.049)
Adult survival	0.967(0.009)	0.961(0.018)	0.963(0.006)	0.965(0.006)

Bootstrapping the adult survival (s) was more complicated. The file of capture records of manatees at Blue Spring (similar to that in Appendix A-2 of O'Shea and Langtimm [1995]) contains 68 survival records (from more than 15 years). This file was also sampled by drawing 68 samples with replacement, and the resulting sample was used to estimate survival with the Jolly-Seber method (and the formulation by Pollock et al. 1990). Results of an execution of 2,000 bootstraps provided a mean survival of 0.967 with a standard error of 0.009 (Table 3). With the methods of O'Shea and Langtimm (1995), the rate was 0.961 with a standard error of 0.018.

The remaining parameter in the bootstrapping was that of early survival (l_k). O'Shea and Hartley (1995) observed 45 calves and noted that 37 survived from one winter to the next. Bootstrapping these data was simple and was based on a file containing 8 zeros and 37 ones, which was sampled with a sample size of 45 with replacement. Results from such sampling essentially follow the binomial distribution, which was assumed in the delta method.

The final bootstrapping contained the described four subprograms; each was set up to return an estimate of the appropriate parameter in each bootstrapping execution of the main program. An execution of 2,000 bootstraps gave a mean of 1.057 for λ with a standard error of 0.012, whereas the delta method gave $\lambda = 1.051$ with a standard error of 0.019. Bootstrapping results can be used to obtain approximate 95% confidence limits by tabulating such limits from a frequency distribution of outcomes. Such a frequency distribution (Fig. 2) gave approximate limits of 1.03–1.08, appreciably narrower than those from the delta method.

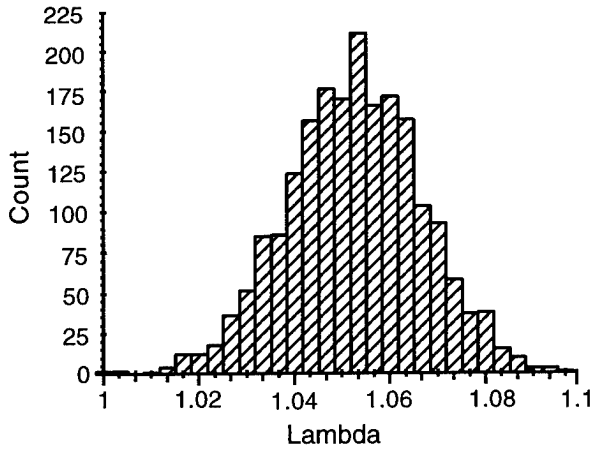


Fig. 2. Frequency distribution of 2,000 bootstrap estimates of λ of Florida manatees (*Trichechus manatus latirostris*) at Blue Spring on the upper St. Johns River, Florida.

Bootstrapping the data on manatees from the Crystal River was based on using early survival data on manatees at Blue Spring. A larger sample of survival data of manatees in the Crystal River was available (234 records). The calculated survival of O'Shea and Langtimm (1995) was obtained with Model B of Jolly (1982), who used a rather complex method to obtain a weighted estimate of s from the estimates from each year. A simple average was used for the bootstrapping, rather than attempting to program this complex procedure. Various estimates from bootstrapping and the delta method generally agreed (Table 3).

Integrating Life-history Data and Population Models

The major question about Florida manatee populations is simply how well they will persist into the future. The evidence thus far is ambiguous. Carcass-recovery data show a trend of increasing boat-related deaths, and this trend significantly correlated with increasing boat registrations (Ackerman et al. 1995). Regarded as a crude catch-effort relation, this suggested that manatee numbers may have been keeping up with losses, but the manatee population cannot indefinitely sustain such losses. Manatee counts from two study areas (Blue Spring and Crystal River) show annual rates of increase of about 8% and 10% (Ackerman 1995), and the analysis of manatee counts at power plants on the Atlantic Coast (Garrott et al. 1995) also suggested an increasing population. However, the analyses of survival data from the Atlantic Coast population indicated appreciably lower adult survival there than in the Blue Spring and Crystal River study sites.

The recovery plan (*U.S. Fish and Wildlife Service 1989:21) indicates that "Downlisting should be considered when population modeling indicates that the population is growing or is stable, when mortality factors are controlled at acceptable levels or are decreasing, and when habitats are secure and threats are controlled or are decreasing".

Quite clearly, modeling cannot indicate the status of the population, but it is a means to integrate the several sources of population data in a way that supplies an approximation to a test of a null hypothesis that the population is decreasing. Given a valid estimate of the total population size, the population-dynamics analyses may also serve to indicate the level of mortality that the population can sustain. However, the difficulties of accurately and precisely estimating total population size (Lefebvre et al. 1995) are such that perhaps the best prospect is the testing of the null hypothesis that λ is less than unity because it does not need to involve absolute population size. Doing this for the Atlantic Coast

population requires early-survival data, which are not currently available.

Implications for Future Research and Management

For about the last 15 years, the annual number of manatee deaths raised concerns about the future of the population. Many observers pointed to the relative size of the kill and maximum aerial counts as evidence of a catastrophic state of affairs. Others noted that a relatively small population could not support such a large loss, suggesting that the actual population must be much larger. In addition, all dead manatees are probably not found, so that the recorded mortality and the aerial counts are below their true magnitudes. Thus, Eberhardt (*1982) speculated that the population at that time may actually have contained 3,000 manatees. O'Shea (1988), however, advanced reasons to believe that the increasing number of deaths could have been due, in part, to increases in population size.

An understanding of the situation would be considerably improved if reliable estimates of losses and population size were available. Such estimates may in fact be possible with further advances in the use of scar-pattern recognition of individuals. Careful scrutiny of dead manatees should make the identification of previously sighted individuals possible. Because estimates of survival are now available (O'Shea and Langtimm 1995), the total mortality may be estimated by a simple proportionality. Similarly, recording the number of live manatees scrutinized for identity may make possible the use of the data from which survival is now estimated to also estimate population size.

In the absence of useful estimates of total mortality or total population size, estimates of needed reductions in mortality to achieve management goals are not definitive. In a previous section, λ was estimated as being about unity in the Atlantic Coast population. This suggests that the population may have been holding its own or slightly increasing in the past. However, the future course of the population cannot be forecast without key improvements in data collection. Important segments of the Florida manatee population have been omitted from our analyses simply because corresponding life-history data do not exist. Unlike manatees in the three study areas for which reproduction and survival data are available, the number of manatees in southwestern Florida has not increased (Garrott et al. 1995) despite extensive suitable habitat that may be able to support large numbers of manatees. At the same time, manatees in southwestern Florida seem to be suffering from increased mortality (Ackerman et al. 1995; Wright et al. 1995). In addition, the largest number of manatees in our three study areas is on the Atlantic Coast, but manatee population attributes from this area include the lowest estimate of λ and are based on weaker reproduction and survival data than those of manatees in the Crystal River and at Blue Spring. Current management aimed at mortality reduction should continue as the most effective means of promoting population growth, as indicated by the sensitivity of our model to adult survival. Future researchers should focus on obtaining improved estimates of life-history and survival parameters of larger segments of the statewide population and of manatees in the existing study areas.

Although we compared trend data with our calculations of population growth rates based on demography and found concurrence in the positive growth in three study areas, we did not carry out extensive formal hypothesis testing about manatee population growth rates. We had several reasons for not doing so. First, although substantial improvements in knowledge of manatee life-history traits have been made since previous modeling attempts, we identified significant gaps that must be filled by additional research. Some key input parameters in our models from some areas were not based on direct measurements in those areas but were substitute values or estimates derived from data from other study areas; some are based on small data sets. Despite 15 or more years of sampling in some areas, the sampling interval remains shorter than the manatee lifespan and possible year-to-year changes in the environment that could affect birth and death rates. For example, the extent of variability in reproduction or survival based on stochasticity in weather patterns or disease episodes may not be adequately reflected in sampling efforts. Finally, we recommend that future researchers who attempt to test hypotheses about population growth rates based on either demography or trend data also consider statistical power, the probability of rejecting a null hypothesis when it is false.

An eventual decrease in population size should be accompanied by a decrease in total observed mortality. However, extensive experience with over-fishing in fishery management revealed that this is often not true. Ackerman et al. (1995) showed a steady increase in recorded manatee mortality with increasing boat registrations. Additionally, Wright et al. (1995) indicated that changes in propulsion arrangements made operating boats at high speeds in shallow water with heavy vegetation growth possible. One can thus argue that such information reflects a catch-effort relation and that more efficient effort may well keep the catch (accidental kill) at high levels until the affected population ultimately collapses, as it has in many commercial fisheries where declines in catch are accompanied by increasing fishing efficiency and continued high yields, to the point where the fish population virtually disappears.

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Cited References[2]

Ackerman, B. B. 1995. Aerial surveys of manatees: a summary and progress report. Pages 13–33 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Ackerman, B. B., S. D. Wright, R. K. Bonde, D. K. Odell, and D. J. Banowetz. 1995. Trends and patterns in mortality of manatees in Florida, 1974–1992. Pages 223–258 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Beck, C. A., and J. P. Reid. 1995. An automated photo-identification catalog for studies of the life history of the Florida manatee. Pages 120–134 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Bernadelli, H. 1941. Population waves. Journal of the Burma Research Society 31:1–18.

*Brownell, R. L., Jr., K. Ralls, and R. R. Reeves. 1981. Report of the West Indian manatee workshop. Pages 3–16 *in* *R. L. Brownell, Jr. and K. Ralls, editors. 1981. The West Indian manatee in Florida. Proceedings of a workshop held in Orlando, Fla., 27–29 March 1978. Florida Department of Natural Resources, Tallahassee. 154 pp.

Caughley, G. 1977. Analysis of vertebrate populations. John Wiley & Sons, London, U.K. 234 pp.

Chapman, D. G., and D. S. Robson. 1960. The analysis of a catch curve. Biometrics 16:354–368.

Cole, L. C. 1954. The population consequences of life history phenomena. Quarterly Review of Biology 29:103–137.

*Eberhardt, L. L. 1982. Censusing manatees. Manatee Population Research Report 1, Technical Report 8-1, Florida Cooperative Fish and Wildlife Research Unit, University of Florida, Gainesville. 18 pp.

Eberhardt, L. L. 1985. Assessing the dynamics of wild populations. Journal of Wildlife Management 49(4):997–1012.

Eberhardt, L. L. 1988. Using age structure data from changing populations. Journal of Applied Ecology 25:373–378.

Eberhardt, L. L., and D. B. Siniff. 1977. Population dynamics and marine mammal management policies. Journal of the Fisheries Research Board of Canada. 34:183–190.

Efron, B., and R. J. Tibishirani. 1993. An introduction to the bootstrap. Chapman and Hall, New York.

Garrott, R. A., B. B. Ackerman, J. R. Cary, D. M. Heisey, J. E. Reynolds, III, and J. R. Wilcox. 1995. Assessment of trends in sizes of manatee populations at several Florida aggregation sites. Pages 34–55 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Hartman, D. S. 1979. Ecology and behavior of the manatee (*Trichechus manatus*) in Florida. American Society of Mammalogists, Special Publication 5. Lawrence, Kans. 153 pp.

Hernandez, P., J. E. Reynolds, III, H. Marsh, and M. Marmontel. 1995. Age and seasonality in spermatogenesis of Florida manatees. Pages 84–97 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Jolly, G. M. 1982. Mark–recapture models with parameters constant in time. Biometrics 38:301–321.

Lefebvre, L. W., B. B. Ackerman, K. M. Portier, and K. H. Pollock. 1995. Aerial survey as a technique for estimating trends in manatee population size—problems and prospects. Pages 63–74 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Leslie, P. H. 1945. On the use of matrices in certain population mathematics. Biometrika 33:183–212.

Leslie, P. H. 1948. Some further notes on the use of matrices in population mathematics. Biometrika 35:213–245.

Leslie, P. H. 1966. The intrinsic rate of increase and the overlap of successive generations in a population of guillemots (*Uria aalge* Pont.). Journal of Animal Ecology 35:291–301.

Lewis, E. G. 1942. On the generation and growth of a population. Sankya 6:93–96.

Lotka, A. J. 1907. Relation between birth rates and death rates. Science 26:21–22.

Marmontel, M. 1993. Age determination and population biology of the Florida manatee, *Trichechus manatus latirostris*. Ph.D. dissertation, University of Florida, Gainesville. 408 pp.

Marmontel, M. 1995. Age and reproduction in female Florida manatees. Pages 98–119 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Marsh, H. 1995. The life history, pattern of breeding, and population dynamics of the dugong. Pages 75–83 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

O'Shea, T. J. 1988. The past, present, and future of manatees in the southeastern United States: realities, misunderstandings and enigmas. Pages 184–204 *in* R. R. Odom, K. A. Riddleberger, and J. C. Ozier, editors. Proceedings of the Third Southeastern Nongame and Endangered Wildlife Sympo-

[2] An asterisk denotes unpublished material.

sium. Georgia Department of Natural Resources, Game and Fish Division, Social Circle. 253 pp.

O'Shea, T. J., C. A. Beck, R. K. Bonde, H. I. Kochman, and D. K. Odell. 1985. An analysis of manatee mortality patterns in Florida, 1976–1981. Journal of Wildlife Management 49:1–11.

O'Shea, T. J., and W. C. Hartley. 1995. Reproduction and early-age survival of manatees at Blue Spring, upper St. Johns River, Florida. Pages 157–170 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

O'Shea, T. J., and C. A. Langtimm. 1995. Estimation of survival of adult Florida manatees in the Crystal River, at Blue Spring, and on the Atlantic Coast. Pages 194–222 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

*Packard, J. M. 1985. Preliminary assessment of uncertainty involved in modeling manatee populations. Manatee Population Research Report 9. Technical Report 8-9. Florida Cooperative Fish and Wildlife Research Unit, University of Florida, Gainesville. 19 pp.

Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture–recapture experiments. Wildlife Monographs 107:1–97.

Rathbun, G. B., J. P. Reid, R. K. Bonde, and J. A. Powell. 1995. Reproduction in free-ranging Florida manatees. Pages 135–156 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Reid, J. P., R. K. Bonde, and T. J. O'Shea. 1995. Reproduction and mortality of radio-tagged and recognizable manatees on the Atlantic Coast of Florida. Pages 171–191 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Seber, G. A. F. 1982. The estimation of animal abundance. Second edition. Oxford University Press, New York. 654 pp.

*U.S. Fish and Wildlife Service. 1989. Florida manatee (*Trichechus manatus latirostris*) Recovery Plan. Prepared by the Florida Manatee Recovery Team for the U.S. Fish and Wildlife Service, Atlanta, Ga. 98 pp.

Wright, S. D., B. B. Ackerman, R. K. Bonde, C. A. Beck, and D. J. Banowetz. 1995. Analysis of watercraft-related mortality of manatees in Florida, 1979–1991. Pages 259–268 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Population Biology of the Florida Manatee: An Overview

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Overview and Recommendations

In the following overview we discuss progress toward meeting the three objectives of the 1992 workshop: to provide a synthesis of existing information about manatee population biology; to evaluate the strengths and weaknesses of current data sets and approaches to research on manatee population biology; and to provide recommendations for research. We discuss progress in six topics that were assigned to working groups at the workshop: aerial survey and estimation of population size, reproduction, age structure, mortality, photoidentification and estimation of survival, and integration and modeling of population data. The overview includes recommendations by working group participants (*[2]O'Shea et al. 1992). This workshop on manatee population biology was the most recent conference on the topic since 1978 (*Brownell and Ralls 1981). Partly as a result of recommendations made at the 1978 workshop, several long-term population-related research projects were established. Therefore, we also measure progress in relation to knowledge available at the time of the earlier workshop. Finally, we provide a brief synopsis of pertinent new information on manatee population biology that became available between the 1992 workshop and publication of the proceedings and our conclusions about the status of the Florida manatee.

Aerial Survey Techniques and Estimation of Population Size and Trend

At the time of the 1978 workshop, one uncorrected total count of 738 manatees was tallied based on surveys at aggregation sites in 1976 (Irvine and Campbell 1978); routine replicated surveys of manatees at power plant outfalls had just begun (*Rose 1981). Since then, numerous surveys of manatee distribution have been conducted in most suitable habitats in Florida, and many counts were made at sites where manatees aggregate each winter (Ackerman 1995). Attempts to develop new aerial survey techniques also were made, including field experiments (*Packard 1985a; Packard et al. 1985, 1986; Ackerman 1995; Lefebvre et al. 1995). Currently, the need for improvement in survey technique is acknowledged (Lefebvre et al. 1995). Uncorrected synoptic counts in winter were of 1,856 animals in winter 1992 (Ackerman 1995), and long-term data from counts at power plant outfalls were analyzed for trends with complex statistical models (Garrott et al. 1995). Trends in

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[2] An asterisk denotes unpublished material.

numbers of manatees counted at most major aggregation sites during the past 8–15 years increased or remained stable (Ackerman 1995; Garrott et al. 1995). Data from aerial counts of manatees in additional study areas such as Tampa Bay, sites in southwestern Florida, and the Banana River are accumulating. These data should be evaluated to supplement information reported in these proceedings.

Techniques for estimating size and trends of manatee populations were a central theme of discussion, but many problems were not easily resolved. Results from aerial surveys include counts from synoptic surveys that are much higher than previous composite counts. Synoptic survey counts, however, have no measure of precision, and are not corrected for individuals that were not seen. Many variables, including availability, absence, and observer perception, affect biases in counts of manatees (Ackerman 1995; Lefebvre et al. 1995). Aerial surveys are used also to determine distribution, and sightings from the numerous distribution studies are useful for management because they revealed high-use areas for further protection. Data from most of the distribution surveys since 1984 were added to geographic information systems and are used to support managers' decisions.

Despite advances, the ability to estimate manatee population size and trend in size remains poor. Additional research is needed before aerial-survey results may be applied to statewide population assessment. The possibility must also be recognized that such estimates may not be achievable with existing technology. Improvements may allow detection of trends in population size in specific areas rather than statewide. Even if feasible, results may be difficult to interpret because of the mobility of manatees and their ability to shift habitat-use patterns. In addition, because of small population sizes of manatees and limitations in statistical power (Gerrodette 1987), detection of even major trends with acceptable levels of statistical confidence may take many years, as discussed by Marsh (1995a) in relation to the more quantitative surveys of dugongs.

Reproduction

Previous information on reproduction of Florida manatees consisted of reports in the proceedings of the 1978 workshop (*Brownell and Ralls 1981) and Hartman's (1979) study based on field work in the Crystal River area during the late 1960's and early 1970's. In Hartman's (1979) study, no females had been followed to age of sexual maturity; reproduction was assumed to be year-round; an estimate of gestation was based on observation of one female in a herd of pursuing males and subsequent sighting with a calf; data about intervals between births were limited to one interval by one individual; and the duration of dependency of calves on their mothers was based on observations of six calves. The 1978 workshop provided data on intervals between births from one female in the Crystal River observed during a 10-year period, incomplete data on age at first reproduction of a second female in the Crystal River, and an incomplete record of intervals between births by one female at Blue Spring (*Powell 1981; *Powell and Waldron 1981). Anatomical studies of reproduction were limited to body size-gonad weight relations from 10 females and 12 males and smears of sperm from only three males (*Odell et al. 1981). One calf had been conceived and born in captivity in Florida by the time of the 1978 workshop (*Zeiller 1981).

Information on reproduction from carcasses reported in these proceedings includes the reproductive status and estimated ages of 275 females (Marmontel 1995), and results of histological examination for 72 males with estimated ages (Hernandez et al. 1995). Twenty-eight births occurred in captivity through 1991 (Odell et al. 1995). Rathbun et al. (1995) provided information on reproduction traits from a 15-year study at Crystal River, based on photo-identification records of 117 recognizable adult females and 243 calves. The ages at sexual maturity of seven females observed since their year of birth and the duration of 99 intervals between births were determined. O'Shea and Hartley (1995) also provided data on age at sexual maturity for seven wild females and information on other reproduction traits based on observations at Blue Spring. Additional information also emerged from observations during aerial surveys and during studies with telemetry, and study areas expanded to include the Atlantic Coast (Rathbun et al. 1995; Reid et al. 1995).

New information on manatee reproduction includes more convincing evidence of seasonality in spermatogenesis, mating, birthing, and weaning; minimum ages of sexual maturity as young as 3 years and at smaller sizes than previously assumed; more frequent observations of shorter (2-year and 3-year) intervals between births; a higher proportion of reproducing adult females; and an indication of relatively long reproduction life spans. Details of mating and pre-birthing behavior and birthing areas have been revealed. Much of the current data confirm or extend the optimistic end of the range of reproduction traits in relation to potential for population growth. Use of dugong reproduction data (Marsh 1995b) as a proxy to model manatee population dynamics is no longer appropriate.

Despite advances in knowledge about manatee reproduction, gaps remain. Larger sample sizes and age-specific estimates of reproduction characteristics of manatees in additional study areas are desirable. Some databases, such as that of manatees at Blue Spring, can only be increased through time. Information about manatee reproduction at the Atlantic Coast can be increased

with stronger efforts in the field. Important segments of the Florida manatee population are not well represented by live animal studies. These include critical areas in southwestern Florida from Tampa Bay to the Everglades. Reproduction traits of manatees seem similar among study areas (O'Shea and Hartley 1995), but differences with information based on carcass examination (which results in less optimistic characterization of some reproduction traits) must be reconciled (Marmontel 1995). If regional differences in reproduction traits emerge, they should be assessed for underlying causes, including density-dependent effects, which are improbable at existing population levels. The necessary level of effort in collecting data on manatee reproduction to improve information for population models should be determined.

The phenomenon of herds of males that pursue females (mating herds; Rathbun et al. 1995) requires additional study, particularly in relation to estrus, mating strategies, and social dynamics. The gestation period is poorly known, in part because of possible sterile cycles of females attended by herds of pursuing males. Studies at oceanaria have the greatest potential for increasing knowledge on gestation and estrus and should be encouraged. Future research should establish whether senescence in reproduction occurs, although its effects on manatee population dynamics may be trivial (Eberhardt and O'Shea 1995).

Age Structure

Techniques for age determination of manatees had not been developed in 1978. Techniques applied to dugongs were counts of growth layers in tusks (Marsh 1995b). Age determination by teeth could not be applied to manatees because of the absence of tusks and lack of permanent dentition. A breakthrough was the verification that carcasses could be assigned to age classes by histological examination of growth-layer-groups in the periotic bone (*Marmontel et al. 1990). The first applications of this technique were in relation to manatee reproduction (Hernandez et al. 1995; Marmontel 1995).

The merits of the technique and its potential applications were discussed at the workshop. The participants recommended the testing of assumptions about the age-structure of the carcass sample relative to the living population, the investigation of consequences of error in age determination, the improvement of age determination in manatees less than 1 year old (particularly for understanding the deaths of perinatal manatees), and the establishment of a routine protocol and permanent facility for age determination. The ability to determine the age of manatees will probably fill gaps of knowledge and provide corroborative data (in the form of a life table approach) for the interpretation of other data sets in manatee population biology.

Mortality

Information in the proceedings is from more than 2,000 carcasses recovered during a 19-year period (Ackerman et al. 1995; Wright et al. 1995); at the 1978 workshop, reports were based on fewer than 275 carcasses recovered during 4 years (*Beck et al. 1981; *Irvine et al. 1981). Analyses of mortality data presented in this volume show trends through time, regional differences in patterns, changes in proportions in cause-of-death categories, and correlations with human-related changes in the environment (Ackerman et al. 1995; Wright et al. 1995). Interpretation of the carcass-based mortality data in relation to population-size trends is difficult. Continued accrual of survival data (O'Shea and Langtimm 1995), based primarily on a large and expanding photo-identification catalog (Beck and Reid 1995), will improve interpretation of the mortality information.

The number of recovered carcasses increased annually, particularly those of manatees that collided with watercraft and of perinatal manatees. What proportion of the rise in numbers of carcasses is due to increases in mortality factors, possible increases in manatee numbers, or increases in rates of carcass detection and recovery is unknown. However, the number and the power of boats and the ability of recreational craft to maintain high speeds in shallow areas increased drastically during the last 18 years (Wright et al. 1995). The number of manatee deaths from collisions with boats positively correlates with the number of registered boats. Without better data on population size, trend, or rates of carcass recovery, an increase in the number of deaths cannot be taken as evidence for a declining population. However, there is a limit beyond which mortality cannot be sustained. Without additional protection of the manatee, the anticipated growth of human effects will continue until such a point is surpassed, if it has not been already. The most prudent management strategy is the continuation of efforts aimed at reduction of manatee mortality.

Workshop participants and Ackerman et al. (1995) recommended that further research include improvements in the use of diagnostic microbiological, serological, and immunological techniques to diagnose and classify causes of natural mortality, to use models to aid in interpretation of trends in population size in relation to regional numbers and ages of carcasses recovered, and to improve matching of carcasses to the photo-identification database. Particular focus should be placed on determining the causes of death of perinatal manatees, including further evaluation of the suggestion that disturbance of females by breeding males could result in

mortality of neonates (O'Shea and Hartley 1995). In addition to providing useful information for management, recovered carcasses are a major source of material for anatomical, biochemical, genetic, and other basic biological research. The carcass recovery program should be maintained.

Photo-identification and Estimation of Survival

Photo-identification for the study of manatee life-history traits was first established at the time of the 1978 workshop, when it was aimed at developing information on the reproduction of females during long-term studies (*Powell 1981; *Powell and Waldron 1981). The technique is also suitable for studies of manatee social behavior and for the determination of gross movement patterns (Shane 1983; Rathbun et al. 1990; Reid et al. 1991). The maintenance of a large, automated photo-identification database and retrieval system (Beck and Reid 1995) allowed the development of information on manatee reproduction in several study areas (O'Shea and Hartley 1995; Rathbun et al. 1995; Reid et al. 1995). The newest use of the database is the estimation of survival in a detailed but preliminary comparative study by O'Shea and Langtimm (1995). Estimated survival is important for modeling manatee population dynamics (Eberhardt and O'Shea 1995), and for the interpretation of mortality data from the recovered carcasses. The estimation of survival from photo-identification was done with larger samples and had much narrower confidence intervals than estimates with data from studies with telemetry.

Future efforts should focus on experimental design, selection of appropriate capture-recapture models, testing of assumptions, improvements in cataloging efficiency, standardization of field protocols, and consistent application to carcasses (Beck and Reid 1995; O'Shea and Langtimm 1995). The suitability of the photo-identification database for estimating abundance must be further researched. New protocols should be attempted for the estimation of the proportion of marked manatees in a population, considering large areas as well as small areas during short periods (for example, during one cold spell at a single aggregation site in winter), perhaps parallel with aerial surveys. Management of the photo-identification database will require significant increases in effort during the coming years and additional resources for maintenance. Finally, although adult survival is most important, modeling also requires data on calf and subadult survival. With the possible exception of information collected at Blue Spring, existing data are inadequate for the estimation of survival of calves and subadults. Future research must address this need.

The working group noted that studies with tagged manatees will probably not be as useful as existing techniques with photo-identification for estimating survival or abundance. As for most databases of manatees, long-term efforts are required before information that is useful for an understanding of population biology can be obtained from tagging. Application of permanent tags, such as Passive Integrated Transponders (PIT), would require the logistically difficult marking of large numbers of manatees during several years to obtain useful estimates with band recovery models. Development of means to accurately read PIT tags without handling, however, may enhance future application of the technique with other capture-recapture models. These tags were tested and found harmless to manatees since the workshop (S.D. Wright and I. E. Wright, Florida Department of Environmental Protection, St. Petersburg, unpublished data). PIT tags may provide useful information for matching carcasses to known individuals, e.g., released rehabilitated captives, unscarred calves or subadults, and animals with potentially changing marks.

Integration of Life History Data and Population Modeling

First attempts at manatee population modeling were made in the mid-1980's (*Packard 1985b), but information on life history at that time remained incomplete. The synthesis reflected in these proceedings permits improvements of population modeling. One such approach is reported by Eberhardt and O'Shea (1995), who caution that despite advancements, further improvements are necessary to increase the effectiveness of modeling for the interpretation of the status of the Florida manatee population.

Future researchers should improve the quality of data from the field, investigate concordance among data sets, and attempt new approaches to modeling. Existing long-term databases should be maintained and improved. Like Eberhardt and O'Shea (1995), developers of new models may use regional approaches and use new information to refine validity and predictive capability.

Additional Recent Knowledge

Recent developments in manatee population biology occurred since papers in these proceedings were completed. A summary of these findings follows. Reynolds and Wilcox (1994) reported counts on manatees in selected power plants in Florida during a 10-year period ending in winter 1991–92. The number of calves that were seen and the percentages of counts that were calves showed an apparent decrease over time, particularly at Atlantic Coast aggregation sites. Reynolds and Wilcox

(1994) found these data worrisome in light of the rising number of deaths of perinatal manatees (Ackerman et al. 1995). Other aerial survey data sets should also be examined to further evaluate these findings. For example, recent synoptic surveys reported in these proceedings showed higher totals and percentages of calves (Ackerman 1995) that were comparable to those reported in the 1970's (Irvine and Campbell 1978), to pooled sightings reported in these proceedings from surveys of manatee distribution in Florida, and to data from surveys in Central America and the Caribbean (Rathbun et al. 1995).

Garrott et al. (1994) expanded the analyses of population-size trends in total counts at power plants by including years beyond those reported in the present study (Garrott et al. 1995). Findings were consistent with those reported in these proceedings. Counts at Atlantic Coast sites increased over this longer period, whereas counts at Fort Myers revealed no temporal trends. Although a linear model for the increase in manatee counts at Atlantic Coast sites was chosen as the most parsimonious, the analysis revealed a significant curvilinear trend. The latter suggests that any increasing trend in counts may have diminished in the most recent years (Garrott et al. 1994).

An additional effort at population modeling was made since the 1992 workshop. Marmontel (1993) conducted a population viability analysis (PVA) with reproduction and survival information from the carcass data set. Results of the PVA provided estimates of the probability of persistence of the Florida manatee population over a 1,000-year time scale under various scenarios of initial population size, environmental stochasticity, and levels of mortality and reproduction. Only a combination of factors that included a 10% reduction in adult mortality resulted in an acceptable probability of persistence and an increase over a hypothetical population size of 2,000 (based on the assumption that the minimum count of 1,856 during the 1992 synoptic survey was close to the true value). Estimates of survival and reproduction from carcass studies may be further revised, and whether the carcass sample reflects the age structure of the existing population is uncertain. However, of major importance, the results of the PVA by Marmontel (1993) show the great significance of adult mortality reduction to the persistence of Florida manatees. Current management aimed at reducing human-related deaths (summarized in part by O'Shea 1995) are well justified as the cornerstone for maintaining populations of Florida manatees in the future.

The most disconcerting new information on manatee populations is mortality. In 1993 the total number of deaths in Florida and in other southeastern states followed the downward trend of the previous two years (Ackerman et al. 1995); 147 deaths in all categories. In 1994, however, the total in Florida and in other states increased to 195, the highest on record except in 1990, which included 50 deaths from unusually cold weather (Ackerman et al. 1995). More anthropogenic deaths of manatees were tabulated in 1994 than in any other year on record. Considering the continued development of Florida's coastal areas and the changes in engineering that allow more powerful boat motors to achieve higher speeds and navigate in shallower areas (Wright et al. 1995), the most recent manatee mortality also underscores the need to reduce the number of manatee deaths from human activity.

Florida Manatee Population Status: Conclusions

Since the enactment of legislation for the protection of the Florida manatee in the 1970's and subsequent conservation and research, all counts of manatees at power plant outfalls in winter that have been analyzed revealed upward trends except at Fort Myers in southwestern Florida (Garrott et al. 1994, 1995). (Major increases in the number of recovered carcasses in southwestern Florida have also been reported; Ackerman et al. 1995.) Counts at Blue Spring, which are based on individual identifications, have increased steadily. Aerial counts at Crystal River and Tampa Bay have also risen over time (Ackerman 1995 and sources therein). Uncorrected composite and synoptic survey counts in the entire state also revealed increases (Irvine and Campbell 1978; Ackerman 1995).

Plausible reasons for such increases in numbers were discussed by Ackerman (1995), Garrott et al. (1994, 1995), Eberhardt and O'Shea (1995), and others. Redistribution from other areas accounts for a portion of the growth at Crystal River and Blue Spring (Ackerman 1995; Rathbun et al. 1995). Clearly, however, a major undocumented population source that accounts for simultaneous increases in counts of manatees at nearly all aggregations counted since the 1970's is improbable. Researchers have speculated that increases in counts could be from improvements in technique and observer skill, although arguments are mixed (Ackerman 1995; Garrott et al. 1994; Reynolds and Wilcox 1994), and that perhaps manatee behavior has changed, resulting in more aggregated individuals that can be counted (Garrott et al. 1994, 1995). Manatees have a predilection for warm water and consequences of exposure to cold can be lethal (O'Shea et al. 1985; Ackerman et al. 1995). They are roving and curious and have used power plant outfalls in winter for nearly half a century (Moore 1951, 1956). An influence of behavioral changes as a significant source of upward trends in counts therefore seems improbable. We believe that the increases in numbers of manatees counted in aggregation areas in winter reflected an increase in the Florida population from the 1970's through the 1980's but that the actual rates of the

increase may be less than those observed because of influences of factors similar to those noted above, which remain poorly understood. We are uncertain whether such a trend continued in the 1990's.

Eberhardt and O'Shea (1995) provide results based on data from direct observations of living manatees that suggest substantial population growth from internal recruitment at the Crystal River and at Blue Spring and slower growth or stability on the Atlantic Coast (but based on calculations from a less adequate database). Similar data (particularly on survival) were simply non-existent to extend modeling to other regions. Reproduction parameters revealed by studies presented in these proceedings (Marmontel 1995; O'Shea and Hartley 1995; Rathbun et al. 1995; Reid et al. 1995) indicated the potential for more rapid growth than previously recognized (*Packard 1985b). Eberhardt and O'Shea (1995), for example, calculated an annual population growth rate of 7%/yr at the Crystal River, an area where human-related mortality is low (Ackerman et al. 1995) and management is extensive. This higher potential for population growth makes the probability of true population growth in other areas during the 1970's and 1980's more plausible than previously thought (*Packard 1985b).

The information on potential population growth rates and increases in counts, however, demand reconciliation with the number of recovered carcasses. We believe that a number of variables influenced the increases in the number of recovered carcasses during the study by Ackerman et al. (1995) and that the influence of these variables may differ among cause-of-death categories. In addition to an increase in the number of dead manatees, other variables may include an increase in the probability of carcass discovery and reporting (from increased numbers of boats on the water, increased number of residents in coastal areas, and effective public education campaigns), and a probable increase of the manatee population (under a constant mortality rate this would result in a greater number of deaths). Much of the reported total mortality during this period was of calves and subadults (Marmontel 1993), which have less of an effect on population growth than deaths of adults (*Packard 1985b; Eberhardt and O'Shea 1995). The number of manatees that are killed by boats increased at the greatest rates, however, and these form a major component of mortality of adult manatees. Mortality from boat strikes can therefore have a major effect on population dynamics. However, this source of mortality also lends itself to straightforward management.

Possible increases in manatee population size since the mid-1970's may be attributable to intensified conservation. However, the threats to manatee survival and habitat loss have accelerated and are expected to increase. A turning point may soon be reached, if it has not already. This contention is supported by the possibility that upward trends in counts at power plants in winter may have diminished in the late 1980's and early 1990's (Garrott et al. 1994); by the lack of a notable increase of counts and a higher number of deaths in southwestern Florida (Ackerman et al. 1995; Garrott et al. 1994); by the high number of recovered carcasses in 1994; and by increased numbers of boats and the more complex technology of high-speed boating (Wright et al. 1995). Because of the lack of accuracy and precision in estimates of population size, the size of the Florida manatee population could decrease even while counts may seem to increase or be stable (*Eberhardt 1982; Lefebvre et al. 1995; Marsh 1995a). Given that negative effects on manatee populations will continue to increase with burgeoning human populations in Florida and that decreases in adult mortality can result in growth and long-term persistence of Florida manatee populations (Eberhardt and O'Shea 1995; Marmontel 1993), no prudent alternatives exist to maintaining proactive, vigorous management aimed at mortality reduction.

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Cited References[3]

Ackerman, B. B. 1995. Aerial surveys of manatees: a summary and progress report. Pages 13–33 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Ackerman, B. B., S. D. Wright, R. K. Bonde, D. K. Odell, and D. J. Banowetz. 1995. Trends and patterns in mortality of manatees in Florida, 1974–1992. Pages 223–258 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Beck, C. A., and J. P. Reid. 1995. An automated photo-identification catalog for studies of the life history of the Florida manatee. Pages 120–134 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

*Beck, C., R. K. Bonde, and D. K. Odell. 1981. Manatee mortality in Florida during 1978. Pages 76–85 *in* R. L. Brownell, Jr. and K. Ralls, editors. The West Indian manatee in Florida. Proceedings of a workshop held in Orlando, Fla., 27–29 March 1978. Florida Department of Natural Resources, Tallahassee.

*Brownell, R. L., Jr., and K. Ralls, editors. 1981. The West Indian manatee in Florida. Proceedings of a workshop held in Orlando, Fla., 27–29 March 1978. Florida Department of Natural Resources, Tallahassee. 154 pp.

*Brownell, R. L., Jr., K. Ralls, and R. R. Reeves. 1981. Report of the West Indian manatee workshop. Pages 3–16 *in* R. L. Brownell, Jr., and K. Ralls, editors. The West Indian manatee in Florida. Proceedings of a workshop held in Orlando, Fla., 27–29 March 1978. Florida Department of Natural Resources, Tallahassee.

*Eberhardt, L. L. 1982. Censusing manatees. Manatee Population Research Report 1. Florida Cooperative Fish and Wildlife Research Unit. University of Florida, Gainesville. 18 pp.

Eberhardt, L. L., and T. J. O'Shea. 1995. Integration of manatee life-history data and population modeling. Pages 269–279 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Garrott, R. A., B. B. Ackerman, J. R. Cary, D. M. Heisey, J. E. Reynolds, III, and J. R. Wilcox. 1995. Assessment of trends in sizes of manatee populations at several Florida aggregation sites. Pages 34–55 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Garrott, R. A., B. B. Ackerman, J. R. Cary, D. M. Heisey, J. E. Reynolds, III, P. M. Rose, and J. R. Wilcox. 1994. Trends in counts of Florida manatees at winter aggregation sites. Journal of Wildlife Management 58: 642–654.

Gerrodette, T. 1987. A power analysis for detecting trends. Ecology 68:1364–1372.

Hartman, D. S. 1979. Ecology and behavior of the manatee (*Trichechus manatus*) in Florida. American Society of Mammalogists, Special Publication 5. Lawrence, Kans. 153 pp.

Hernandez, P., J. E. Reynolds, III, H. Marsh, and M. Marmontel. 1995. Age and seasonality in spermatogenesis of Florida manatees. Pages 84–97 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Irvine, A. B., and H. W. Campbell. 1978. Aerial census of the West Indian manatee, *Trichechus manatus*, in the southeastern United States. Journal of Mammalogy 59:613–617.

*Irvine, A. B., D. K. Odell, and H. W. Campbell. 1981. Manatee mortality in the southeastern United States from 1974 through 1977. Pages 67–75 *in* R. L. Brownell, Jr., and K. Ralls, editors. The West Indian manatee in Florida. Proceedings of a workshop held in Orlando, Fla., 27–29 March 1978. Florida Department of Natural Resources, Tallahassee. 154 pp.

Lefebvre, L. W., B. B. Ackerman, K. M. Portier, and K. H. Pollock. 1995. Aerial survey as a technique for estimating trends in manatee population size—problems and prospects. Pages 63–74 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Marmontel, M. 1993. Age determination and population biology of the Florida manatee, *Trichechus manatus latirostris*. Ph.D. dissertation, University of Florida, Gainesville. 408 pp.

Marmontel, M. 1995. Age and reproduction in female Florida manatees. Pages 98–119 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

*Marmontel, M., T. J. O'Shea, and S. R. Humphrey. 1990. An evaluation of bone growth-layer counts as an age-determination technique in Florida manatees. National Technical Information Service Publication PB91-103564. Springfield, Va. 104 pp.

Marsh, H. 1995a. Fixed-width aerial transects for determining dugong population sizes and distribution patterns. Pages 56–62 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Marsh, H. 1995b. The life history, pattern of breeding, and population dynamics of the dugong. Pages 75–83 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Moore, J. C. 1951. The range of the Florida manatee. Quarterly Journal of the Florida Academy of Sciences 14: 1–19.

Moore, J. C. 1956. Observations of manatees in aggregations. American Museum Novitates, 1811: 1–24.

*Odell, D. K., D. J. Forrester, and E. D. Asper. 1981. A preliminary analysis of organ weights and sexual maturity in the West Indian manatee (*Trichechus manatus*). Pages 52–65 *in* R. L. Brownell, Jr., and K. Ralls, editors. The West Indian manatee in Florida. Proceedings of a workshop held in Or-

[3] An asterisk denotes unpublished material.

lando, Florida, 27–29 March 1978. Florida Department of Natural Resources, Tallahassee.

Odell, D. K., G. D. Bossart, M. T. Lowe, and T. D. Hopkins. 1995. Reproduction of the West Indian manatee in captivity. Pages 192–193 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

O'Shea, T. J. 1995. Waterborne recreation and the Florida manatee. Pages 297–312 *in* R. L. Knight, and K. J. Gutzwiller, editors. Wildlife and recreationists: coexistence through management and research. Island Press, Washington, D.C. 384 pp.

*O'Shea, T. J., B. B. Ackerman, and H. F. Percival, editors. 1992. Interim report of the technical workshop on manatee population biology. Manatee Population Research Report 10, Florida Cooperative Fish and Wildlife Research Unit, University of Florida, Gainesville. 83 pp.

O'Shea, T. J., C. A. Beck, R. K. Bonde, H. I. Kochman, and D. K. Odell. 1985. An analysis of manatee mortality patterns in Florida, 1976–81. Journal of Wildlife Management 49:1–11.

O'Shea, T. J., and W. C. Hartley. 1995. Reproduction and early age survival of manatees at Blue Spring, upper St. Johns River, Florida. Pages 157–170 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

O'Shea, T. J., and C. A. Langtimm. 1995. Estimation of survival of adult Florida manatees in the Crystal River, at Blue Spring, and on the Atlantic Coast. Pages 194–222 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

*Packard, J. M. 1985a. Development of manatee aerial survey techniques. Manatee Population Research Report 7. Florida Cooperative Fish and Wildlife Research Unit. University of Florida, Gainesville. 68 pp.

*Packard, J. M. 1985b. Preliminary assessment of uncertainty involved in modeling manatee populations. Manatee Population Research Report 9. Florida Cooperative Fish and Wildlife Research Unit. University of Florida, Gainesville. 19 pp.

Packard, J. M., D. B. Siniff, and J. A. Cornell. 1986. Use of replicate counts to improve indices of trends in manatee abundance. Wildlife Society Bulletin 14: 265–275.

Packard, J. M., R. C. Summers, and L. B. Barnes. 1985. Variation of visibility bias during aerial surveys of manatees. Journal of Wildlife Management 49:347–351.

*Powell, J. A. 1981. The manatee population in Crystal River, Citrus County, Florida. Pages 33–40 *in* R. L. Brownell, Jr., and K. Ralls, editors. The West Indian manatee in Florida. Proceedings of a workshop held in Orlando, Fla., 27–29 March 1978. Florida Department of Natural Resources, Tallahassee.

*Powell, J. A., and J. C. Waldron. 1981. The manatee population in Blue Spring, Volusia County, Florida. Pages 41–51 *in* R. L. Brownell, Jr., and K. Ralls, editors. The West Indian manatee in Florida. Proceedings of a workshop held in Orlando, Fla., 27–29 March 1978. Florida Department of Natural Resources, Tallahassee.

Rathbun, G. B., J. P. Reid, and G. Carowan. 1990. Distribution and movement patterns of manatees (*Trichechus manatus*) in northwestern peninsular Florida. Florida Marine Research Publication 48. 33 pp.

Rathbun, G. B., J. P. Reid, R. K. Bonde, and J. A. Powell. 1995. Reproduction in free-ranging Florida manatees. Pages 135–156 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Reid, J. P., G. B. Rathbun, and J. R. Wilcox. 1991. Distribution patterns of individually identifiable West Indian manatees (*Trichechus manatus*) in Florida. Marine Mammal Science 7:180–190.

Reid, J. P., R. K. Bonde, and T. J. O'Shea. 1995. Reproduction and mortality of radio-tagged and recognizable manatees on the Atlantic Coast of Florida. Pages 171–191 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

Reynolds, J. E., III, and J. R. Wilcox. 1994. Observations of Florida manatees (*Trichechus manatus latirostris*) around selected power plants in winter. Marine Mammal Science 10:163–177.

*Rose, P. M. 1981. A preliminary report on the aerial census of the West Indian manatee, *Trichechus manatus*, in and around several "once-through cooling" power plant effluents; December–March 1977–78. Pages 22–24 *in* R. L. Brownell, Jr., and K. Ralls, editors. The West Indian manatee in Florida. Proceedings of a workshop held in Orlando, Fla., 27–29 March 1978. Florida Department of Natural Resources, Tallahassee.

Shane, S. H. 1983. Abundance, distribution, and movements of manatees (*Trichechus manatus*) in Brevard County, Florida. Bulletin of Marine Science 33:1–9.

*U.S. Fish and Wildlife Service. 1989. Florida manatee (*Trichechus manatus latirostris*) Recovery Plan. U.S. Fish and Wildlife Service, Atlanta, Ga. 98 pp.

Wright, S. D., B. B. Ackerman, R. K. Bonde, C. A. Beck, and D. J. Banowetz. 1995. Analysis of watercraft-related mortality of manatees in Florida, 1979–1991. Pages 259–268 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. National Biological Service Information and Technology Report 1.

*Zeiller, W. 1981. The management of West Indian manatees (*Trichechus manatus*) at the Miami Seaquarium. Pages 103–110 *in* R. L. Brownell, Jr., and K. Ralls, editors. The West Indian manatee in Florida. Proceedings of a workshop held in Orlando, Fla., 27–29 March 1978. Florida Department of Natural Resources, Tallahassee.



Endpiece: *Counties of Florida.*

NOTE: The mention of trade names does not constitute endorsement or recommendation for use by the Federal Government.

U.S. Department of the Interior
National Biological Service

As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This responsibility includes fostering the sound use of our lands and water resources; protecting our fish, wildlife, and biological diversity; preserving the environmental and cultural values of our national parks and historical places; and providing for the enjoyment of life through outdoor recreation. The Department assesses our energy and mineral resources and works to ensure that their development is in the best interests of all our people by encouraging stewardship and citizen participation in their care. The Department also has a major responsibility for American Indian reservation communities.



