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**SPECIES PROFILES: LIFE HISTORIES AND
ENVIRONMENTAL REQUIREMENTS OF COASTAL
VERTEBRATES AND INVERTEBRATES
PACIFIC OCEAN REGION**

Report 5

THE PARROTFISHES, FAMILY SCARIDAE

by

R. E. Brock

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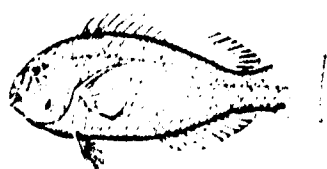
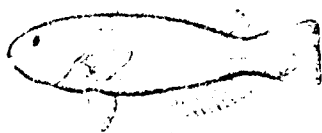
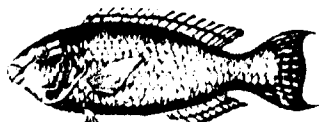
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Parrotfishes are highly colorful species inhabiting coral reefs of the world's tropical seas. They may usually be identified by the fused teeth forming a massive beak which is used in rasping the substratum for food materials. With growth, many species go through a number of color phases and adults usually have marked color and morphological sexual dimorphism. These characteristics have resulted in considerable confusion in the taxonomic literature; there are about 68 species of parrotfishes worldwide. Little is known about the life history of parrotfish; apparently many species spawn at discrete times and locations and eggs and larvae are pelagic, returning to the adult habitat after several weeks in the plankton. With growth these fishes display sex reversal and dichromatism; the largest fish are usually terminal-phase males. Parrotfishes are primarily herbivorous, feeding on microalgal resources. The heavy beak is used to rasp algal materials from the hard coralline substratum; once ingested all (Continued)					
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food passes to the pharyngeal mill, which is equipped with a set of opposing teeth that grind and pulverize all food materials. In feeding, parrotfishes consume microalgae as well as cryptobiota (small cryptic invertebrates) which provide a source of protein. Studies suggest that there is considerable overlap in the algal resources consumed by sympatric parrotfish species; however, competitive trophic interaction is low because of the high turnover characteristics of the microalgal resource. In feeding, parrotfishes ingest considerable carbonate material resulting in the production of 400 to 2,000 kg of calcium carbonate material per hectare per year. Thus these fishes are important in the production and redistribution of sediments on reefs.

Through their feeding activities, parrotfish clear the substratum of algae (which compete with corals for space) thus increasing the successful recruitment of corals as well as promoting the growth of encrusting coralline algal species. Studies suggest that parrotfishes play an important role in maintaining benthic community structure in their normal field densities, hence they are considered to be "keystone species" on coral reefs.

Parrotfish are caught and consumed by many fishermen; loss of these fishes may result in local changes occurring in benthic communities, shifting from coral-dominated to algal-dominated systems. It is suggested that conservation and management of these important fishery resources are probably best carried out by incorporating modern concepts with traditional management strategies developed by the local indigenous culture. The challenge confronting the modern resource manager is to integrate traditional and modern strategies into a format that is politically and culturally acceptable.

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PREFACE

This report is designed to provide coastal managers, engineers, and biologists with a brief comprehensive sketch of the biological characteristics and environmental requirements of the parrotfishes (Family Scaridae) and to describe how populations of the species in Hawaiian waters may be expected to react to environmental changes caused by coastal development. This report has sections on taxonomy, life history, ecological role, environmental requirements, growth, exploitation, and management.

This work was part of the Environmental Impact Research Program (EIRP), sponsored by Headquarters, US Army Corps of Engineers (HQUSACE), under EIRP Work Unit 31627. Technical Monitors were Dr. John Bushman, Mr. David P. Buelow, and Mr. David Mathis of HQUSACE.

This report was prepared by Dr. R. E. Brock of the SeaGrant College Program and Hawaii Institute of Marine Biology, University of Hawaii.

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CONVERSION TABLE

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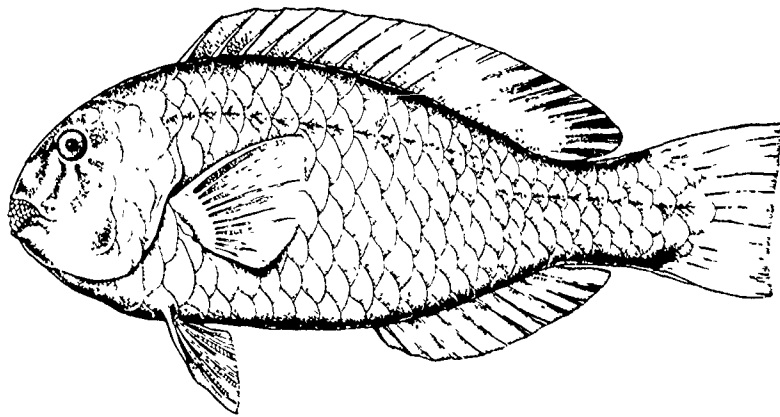
<u>Multiply</u>	<u>By</u>	<u>To Obtain</u>
millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters (m)	3.281	feet
meters (m)	0.5468	fathoms
kilometers (km)	0.6214	statute miles
kilometers (km)	0.5396	nautical miles
square meters (m ²)	10.76	square feet
square kilometers (km ²)	0.3861	square miles
hectares (ha)	2.471	acres
liters (l)	0.2642	gallons
cubic meters (m ³)	35.31	cubic feet
cubic meters (m ³)	0.0008110	acre-feet
milligrams (mg)	0.00003527	ounces
grams (g)	0.03527	ounces
kilograms (kg)	2.205	pounds
metric tons (t)	2205.0	pounds
metric tons (t)	1.102	short tons
kilocalories (kcal)	3.968	British thermal units
Celsius degrees (°C)	1.8(°C) + 32	Fahrenheit degrees

U.S. Customary to Metric

inches	25.40	millimeters
inches	2.54	centimeters
feet (ft)	0.3048	meters
fathoms	1.829	meters
statute miles (mi)	1.609	kilometers
nautical miles (nmi)	1.852	kilometers
square feet (ft ²)	0.0929	square meters
square miles (mi ²)	2.590	square kilometers
acres	0.4047	hectares
gallons (gal)	3.785	liters
cubic feet (ft ³)	0.02831	cubic meters
acre-feet	1233.0	cubic meters
ounces (oz)	28350.0	milligrams
ounces (oz)	28.35	grams
pounds (lb)	0.4536	kilograms
pounds (lb)	0.00045	metric tons
short tons (ton)	0.9072	metric tons
British thermal units (Btu)	0.2520	kilocalories
Fahrenheit degrees (°F)	0.5556 (°F - 32)	Celsius degrees

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PARROTFISHES, FAMILY SCARIDAE

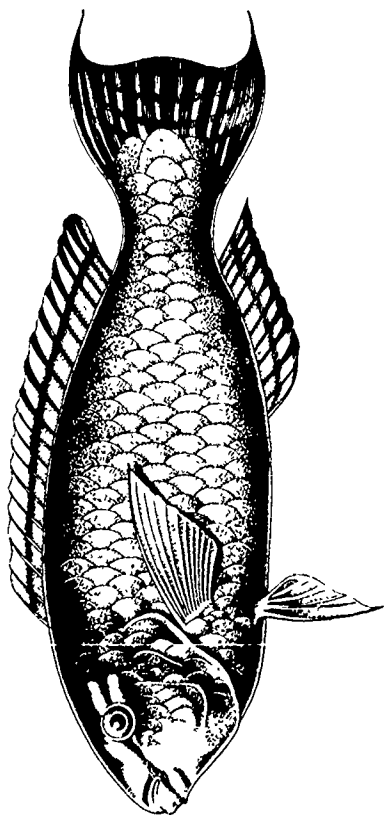
NOMENCLATURE/TAXONOMY/RANGE

For more than a century the parrotfishes have been known as one of the most difficult and confusing families of reef fishes in systematic ichthyology (Schultz 1958; Randall 1963a and b). The recognition of species is often uncertain and the descriptions provided in the literature are in many cases inadequate. Not until Schultz's (1958) monumental effort had anyone attempted a revision of the family on a worldwide basis. Since the publication of that revision, there have been a number of papers locally revising the parrotfishes. Because of the taxonomic confusion and apparent similar behaviors and influences in the coral reef community which are detailed below, this species profile was written to provide a general review of the parrotfish family Scaridae rather than focusing on a single species. Examples of Hawaiian parrotfishes are shown in Figure 1.

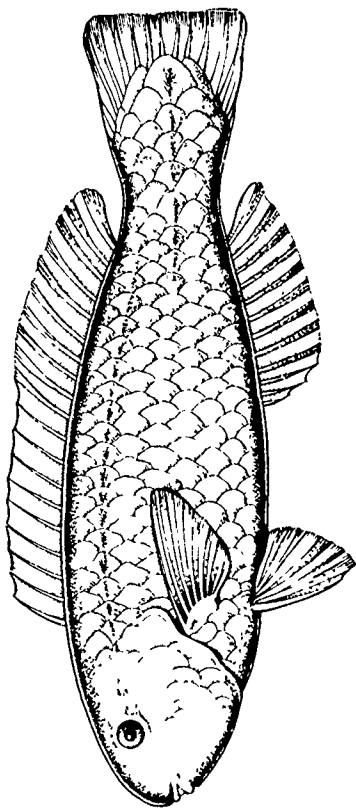
Characters that are of use in differentiating species of parrotfishes include (a) the number of rows of scales on the cheek, (b) the number of scales in the ventral row on the cheek, (c) the number of rows of teeth on the pharyngeal bones, (d) the number of median predorsal scales, (e) the number of pectoral rays, and (f) the color pattern. These alone are usually insufficient

as diagnostic features; fin ray, scale, and gill raker counts that are useful in identifying most fishes are of limited use in the recognition of many scarid species, leaving color as one of the few usable characters. However, the use of color complicates comparative work with long-preserved specimens (Schultz 1958). The use of color as an identifying character is further complicated by the sexual dichromatism that is found in many parrotfish species (Choat and Robertson 1975; Robertson and Warner 1978).

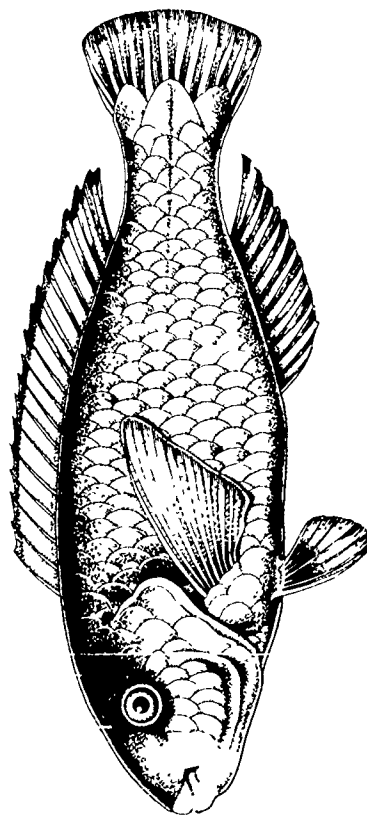
The value of color in distinguishing various parrotfish species has been recognized by a number of ichthyologists. Smith (1956) notes "...There is probably not a single work based on preserved material of the parrotfishes whose list of synonymy is worth any great consideration. It is ludicrous to expend time and effort in attempting to deduce what species earlier workers really had, and to attempt to fit material into their utterly inadequate definitions...In attempting to fit numbers of parrot fishes into existing species it became clear that adequate and accurate definition and portrayal of our material would be of far greater value than any names. In consequence every effort was made to prepare the fullest possible notes as well as sketches of the live colors and



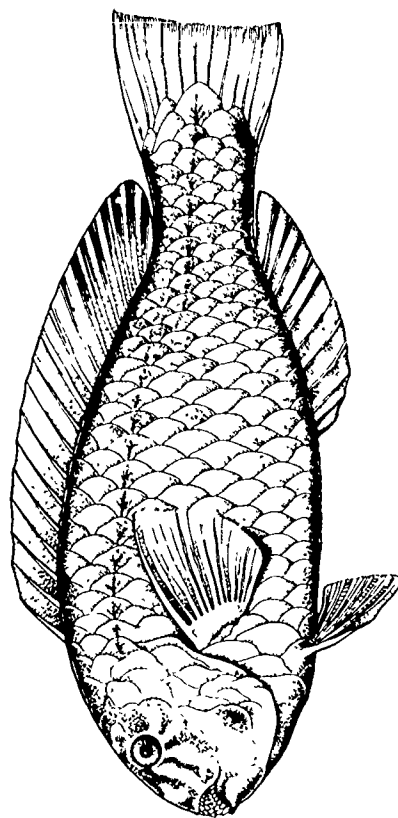
a. *Scarus forsteri*



b. *Scarus perspicillatus*



c. *Scarus sordidus*



d. *Calotomus carolinus*

Figure 1. Typical Hawaiian Parrotfishes

markings..." Thus recent taxonomic treatments of the parrotfishes often present the color photographs of the species. However as noted by Bruce and Randall (1985), the sexual dichromatism and color changes that occur with growth were not recognized until relatively recently. Thus duplication in names is common and the color descriptions often are not diagnostic.

Within the parrotfishes two subfamilies have been defined: the Scarinae and the Sparisomatinae. Schultz (1969) recognized seven genera in the Sparisomatinae including *Calotomus*, *Leptoscarus*, *Cryptotomus*, *Nicholsina*, *Euscarus*, *Sparisoma* and *Scaridea*. Bruce and Randall (1985) treated the monotypic genus *Scaridea* as a synonym of *Calotomus*. Some authors (e.g., Bruce and Randall 1985) regard *Euscarus* as a synonym of *Sparisoma*. Most of the parrotfish species are found in the subfamily Scarinae under which Schultz (1958, 1969) noted four genera: *Scarops*, *Bolbometopon*, *Ypsiscarus* and *Scarus*. Randall (1981) has placed the monospecific genus *Scarops* under *Scarus*. Thus in the classification of parrotfishes, we find the following genera generally recognized: *Calotomus*, *Leptoscarus*, *Cryptotomus*, *Nicholsina*, *Bolbometopon*, *Ypsiscarus* and *Scarus*.

Parrotfishes are found in all tropical oceans of the world. The taxonomic confusion with the family makes the determination of geographic range of many species difficult; in his early work, Schultz (1958) noted 354 scientific names from the literature proposed for species in the family but found only 80 valid species. More recently, Schultz (1969) listed 68 species of parrotfishes; these are distributed across the tropical Atlantic, Indian, and Pacific Oceans as well as into the Red Sea. Many species appear to have wide

geographic distributions but others are apparently restricted indicating the occurrence of some endemism at the species level.

Recent regional taxonomic works encompassing parrotfishes include those for the Red Sea and Western Indian Ocean (Smith 1956, 1959, 1965; Jones and Kumaran 1980; Randall and Bruce 1983), the Eastern Pacific (Rosenblatt and Hobson 1969) the Central, Western, and South Pacific (Schultz 1960, 1969; Marshall 1964; Munro 1967; Bagnis et al. 1972; Yang 1979; Randall and Choat 1980; Randall 1981; Bruce and Randall 1985; Shao and Chen 1989) and the Caribbean (Randall 1968).

MORPHOLOGY/IDENTIFICATION AIDS

Members of the family may be recognized by the following characters: teeth fused or coalesced forming a pair of dental plates separated by an obvious midline suture; external canines may be present; gill membranes broadly joined to the isthmus; cheek scales in one to four rows; median predorsal scales three to eight in number; dorsal rays IX, 10; anal III, 9; pectoral rays ii, 11 to ii, 15; branched caudal rays 6 + 5; paired upper pharyngeal bones with one to three rows of molarlike teeth and a single lower pharyngeal bone bearing rows of molarlike teeth.

In the field, most scarids may be easily recognized by their fused teeth presenting an appearance similar to a parrot's beak, large scales, and often bright colors. These fish may travel in mixed schools or singly and are often seen browsing on the substrate. Because of the confusion in the taxonomy of the family, the appropriate aforementioned taxonomic works should be consulted in determining species locally present.

LIFE HISTORY

Reproduction

Parrotfishes typically show a sexual dichromatism as noted above; color changes with size were first noted by Parr (1930). Sexual dichromatism was established for a Hawaiian scarid species (*Scarus perspicillatus*) in 1954 where females are reddish brown and males are blue-green (Brock and Yamaguchi 1954). Protogynous sex reversal in scarids was first documented by Reinboth (1968) although earlier work had suggested that it may exist. In general the sex change in parrotfishes is similar to those seen in wrasses; at a cellular level, ovaries of functional females may possess spermatogenic cells along the ovarian lamellae which expand during sex reversal while oogonia degenerate. Males in many scarid species can be either primary (i.e., born male) or secondary (derived from females). Primary and secondary males differ in gonad structure where the testes of primary males lack any indication of having arisen from ovarian tissue while in secondary males remnants of ovarian lumen are present.

Sex reversal or sequential hermaphroditism may be responsible for the harem mating systems seen in many scarid species where large males keep a harem of smaller females, which favors a sex reversal from female to male with greater size (Warner 1984).

Reinboth (1968) noted protogyny in seven species of Western Atlantic and Eastern Pacific parrotfishes in the subfamilies Scarinae and Sparisominae. Sixteen Great Barrier Reef *Scarus* species were found to be protogynous (Choat 1969; Choat and Robertson 1975) as well as *Scarus sordidus* in Japan (Yogo, Nakazono, and Tsukahara 1980). Similarly, 10 Western Atlantic species in the

genera *Sparisoma*, *Scarus* and *Cryptotomus* were found to be protogynous (Robertson and Warner 1978). Apparently, the relative proportions of primary and secondary males may vary widely among species. Some are monandric where all males are derived from females by sex change while other species may lack the development of any secondary males.

The relationship between sex and color pattern in scarids is complex. The most common situation is where two adult color patterns exist in a species; terminal-phase males with bright colors (blues, greens, reds, and yellows) and initial-phase males and females that are characterized by drab combinations of greys, browns, and black. Examples of this dichromatism have been documented in *Scarus*, *Sparisoma*, *Nicholsina*, *Bolbometopon* and *Cryptotomus* (Thresher 1984). However, monochromatic species do exist (Randall 1968; Rosenblatt and Hobson 1969; Choat and Robertson 1975); large males in at least two species (*Scarus coeruleus* and *S. perrico*) may be differentiated by variation in morphological characters (i.e., larger forehead humps in large males than encountered in females; Rosenblatt and Hobson 1969). In other species such as *Scarus rubroviolaceus*, large males develop more lunate tails (elongated filaments on the caudal), a feature less obvious in females and smaller males (Thresher 1984). Finally, variation from the usual scarid pattern of dichromatism is the development of specific color patterns in large females of *Scarus compressus* (Rosenblatt and Hobson 1969; Thresher 1984).

Spawning in most parrotfishes appears to occur throughout the year but the peak is usually centered on the summer months (Randall and Randall 1963; Colin 1978; Robertson and Warner 1978). Watson and Leis

(1974) found that Hawaiian scarids appear to spawn in the period from April through July. In contrast Reeson (1983) noted that Caribbean scarids appear to spawn throughout the year with more intense spawning activity being confined to the cooler months of the year. However, non-ripe scarids may be present over the annual cycle suggesting that discrete non-spawning periods exist (Robertson and Warner 1978). Johannes (1978, 1981a) has noted that many coral reef fish species including scarids spawn on the lunar cycle but spawning may be associated with peak tides (Thresher 1984).

Migration to specific spawning sites seaward of the fringing reef is common among parrotfishes but is not a universal characteristic. The movement of scarids to spawning sites may occur throughout the day; however, spawning usually takes place in the afternoon (Randall and Randall 1963; Colin 1978; Robertson and Warner 1978). There is variability in the time of spawning which may be a function of local current patterns, i.e., at peak high tides for the dispersal of eggs by tidal currents (Choat and Robertson 1975; Yogo, Nakazono, and Tsukahara 1980).

Spawning in scarids may occur either by pairs or in groups. Pair spawning involves a single male and female and is probably universal in the family (Thresher 1984); pair spawning has been reported in most of the species that have been studied including members of the following genera: *Cryptotomus*, *Sparisoma*, *Bolbometopon*, and *Scarus*. Typically, terminal-phase males arrive at the spawning area and establish well-defended territories. Later, initial-phase males and females arrive and roam through the territories; some fishes are chased away (presumably males) and others are courted by the terminal-phase males. Courtship may involve circling the

female with the male's fins extended or displayed by "bob swimming" (Thresher 1984) around the female. Spawning occurs when the female moves from the bottom and the closely associated pair make a short and fast spawning ascent of about 3m, release their gametes at the apex of this rush, and quickly return to the substratum. Pair spawning in scarids has been described by Winn and Bardach (1960), Randall (1963a), Randall and Randall (1963), Rosenblatt and Hobson (1969), Buckman and Ogden (1973), Barlow (1975), Yogo, Nakazono, and Tsukahara (1980), and Thresher (1984).

Group spawning usually involves from 3 to 20 initial-phase fish and has been described for two *Sparisoma* and eight *Scarus* species (Randall and Randall 1963; Barlow 1975; Choat and Robertson 1975; Bruce 1978; Colin 1978; Robertson and Warner 1978; Yogo, Nakazono, and Tsukahara 1980). In group spawning, initial-phase males and females arrive at the spawning site and mill about in aggregations until some critical group size is attained. Within these aggregations, small numbers of individuals break away, forming tight schools; together these small groups accelerate upward several meters, release their gametes, and abruptly return to the bottom. Colin (1978) found that these tightly aggregated groups take as little as 0.45 sec to complete the spawning rush and swim at an average speed of 40 kmhr⁻¹.

For a given scarid species, both pair and group spawning will occur; the proportion of the population engaged in one type of spawning will vary widely (Warner 1984). *Sparisoma rubripinne* usually reproduces through group spawning in the Virgin Islands (Randall and Randall 1963) but pair spawning is the norm for this species off the Panamanian coast (Robertson and Warner 1978).

Apparently there is a basic flexibility in the scarid socio-sexual system; different behaviors may be manifested under different ecological conditions (Barlow 1975). Factors which may influence the local reproductive strategy include the availability of spawning sites, population density, seasonal effects, and water temperature. The relative success of the various sexual phases in scarids (i.e., primary, secondary, initial-phase and terminal-phase males) may be due to each being reproductively superior under a certain set of ecological conditions (Robertson and Warner 1978). The flexibility in scarid reproductive systems may, in part, explain the success of this family on coral reefs.

Eggs and Larvae

Little is known about the eggs or larvae of parrotfishes. Winn and Bardach (1960) noted that the pelagic eggs of two subfamilies (Scarine and Sparisomine) show morphological differences: Scarine eggs are spindle-shaped, 2.4 to 3.1 mm in length and are transparent with a yellow oil droplet. Watson and Leis (1974) provide a similar description. Sparisomine eggs are spherical, range in diameter from 0.6 to 1.1 mm, and have a single yellow to orange oil droplet (Randall and Randall 1963).

The eggs of *Sparisoma rubripinne* hatch in about 25 hours in a water temperature of 26°C (Randall and Randall 1963). These authors report that the newly hatched larva of *S. rubripinne* is about 1.7 mm long, has a prominent yolk sac, and lacks functional eyes, mouth, or anus. The larvae are weak swimmers and subsist on yolk reserves until those disappear and the mouth opens in about 3 days. Randall and Randall (1963) described 12 developmental stages over the 159 hours of observation.

Once hatched, larval scarids become part of the neritic plankton (Watson and Leis 1974; Young, Leis, and Hausfeld 1986). While in the plankton, scarid larvae (like the larvae of many other coral reef fish species) probably remain within a reasonable distance from the adult habitat through entrainment in ocean mesoscale eddies and currents (Lobel and Robinson 1983, 1986). This strategy presumably reduces predation on the larvae and allows for a return of individuals to the reef habitat (Johannes 1978). The length of larval life in scarids ranges from 41 to 48 days (Brothers, Williams, and Sale 1983).

Recruitment

Thus after about 7 weeks, scarid larvae recruit to the adult habitat. Many coral reef fishes at the time of settlement will undergo a metamorphosis, often gaining pigmentation and changing in body form to become a juvenile. Parrotfishes do so, with most species on settlement having a similar appearance: drab green to brown coloration, often with horizontal stripes (Matsuda and Tanaka 1962). The dearth of morphological variation confounds species identification of juvenile scarids (Bohlke and Chaplin 1968). Juvenile parrotfishes are often found in small foraging schools and are an important prey for many predatory reef fishes (Randall 1963b; Starck and Davis 1966; Brock 1972; Ogden and Buckman 1973; Reeson 1983).

Large variation in the abundance of fish recruiting to coral reefs is typical of many reef systems (Kami and Ikehara 1976; Luckhurst and Luckhurst 1977; Russell, Anderson, and Talbot 1977; deBoer 1978; Molles 1978; Talbot, Russell, and Anderson 1978; Williams 1980; Williams and Sale 1981; Kock 1982; Doherty 1983; Williams 1983; Walsh 1984). Data on the recruitment rates of

parrotfishes are few; Sale et al. (1984) note that recruitment rates in *Scarus sordidus* on Australian reefs varies from 2.6 to 17.3 individuals per 100 m². Such variability is an important factor influencing the fish community structure on reefs. Victor (1983) found that even with nearly continuous spawning in a labrid species, the recruitment was sporadic, suggesting that the pelagic environment has an unpredictable effect on recruitment.

In Hawaiian waters newly settled parrotfishes are seen from early February through October. Walsh (1984) found evidence of greater recruitment in scarids during the summer than at other times of the year on Kona, Hawaii reefs.

Food and Feeding

Parrotfishes have received much attention in the literature on tropical reefs because of their purported role in feeding on corals (Randall 1974). There is, however, little quantitative data on food preferences for members of the family Scaridae. This is due in part to the difficulty of identifying and quantifying ingested food material because it is pulverized by the pharyngeal mill, a structure characteristic of the parrotfish family Scaridae. Parrotfishes typically have a rasping beak (Figure 1) comprised of teeth fused into upper and lower dental plates in all but the most primitive genera (Schultz 1958) and the beak is used in scraping hard substrata for food materials (primarily microalgae). Once ingested, all food passes into the pharyngeal mill consisting of two upper and one lower grinding surfaces into which are set the pharyngeal teeth. These opposing teeth form a concave-convex surface which grinds, pulverizes, and triturates all food materials. Strong muscles move the grinding surfaces over each

other reducing the size of ingested materials. The teeth set in the pharyngeal bones are constantly being produced in the alveolar cavity anterior to the mill. Posterior to the pharyngeal mill is the esophagus, separated from the intestinal tract (duodenum, ileum, and rectum) by a pyloric valve (Gohar and Latif 1959). Notably absent in parrotfishes is a stomach and the thin-walled gut is slightly acidic containing carbonic anhydrase (Smith and Paulson 1974, 1975).

There has been a long-standing controversy over whether scarids feed on live corals or just rasp algae and cryptofauna (organisms residing within coralline substrata) from the hard substratum. This controversy began with Darwin's (1845, 1890) observations at Cocos-Keeling Islands that these fishes feed on live corals. Forbes (1885) made the same observation at the Cocos-Keeling Islands. Finckh (1904) at Funafuti Atoll in Tuvalu determined that parrotfishes feed on algae only. Verwey (1931) noted that three scarid species at Batavia were algal feeders but Al-Hussaini (1947) listed four species of *Pseudoscarus* in the Red Sea as coral feeders. Suyehiro (1942) recorded one Japanese species as feeding only on algae. Newell et al. (1951) in the Bahamas and Newell (1956) found that Tuamotuan scarids fed on algae and took a layer of limestone in doing so; in Kiribati, Cloud (1952) noted the same thing. Emery (1956) at Johnston Atoll found that coral made up 25 percent of the stomach contents of *Scarus perspicillatus* and Hiatt and Strasburg (1960) in the Republic of the Marshalls recorded nine parrotfish species (including *Scarus sordidus*) feeding principally on corals. Gohar and Latif (1959) ascertained that coral was a major constituent of the food of three parrotfish species in the Red Sea. Stephenson and Searles (1960) on the Great Barrier Reef

found no coral in the stomachs of three scarids and Choat (1966) never saw parrotfishes at Heron Island (Great Barrier Reef) feeding on live corals. In the West Indies, Randall (1967) determined that of 10 species of parrotfishes examined, only two species had a very small amount of live coral present in their stomachs. Glynn (1973) has seen one scarid species feeding on live corals off the Pacific coast of Panama and Glynn, Stewart, and McCosker (1972) list three species from the same locality as coral feeders. Hobson (1974) found no evidence of coral feeding amongst scarids examined off the Kona, Hawaii coast; however, Randall (1974) and Brock (1979b) note that *Scarus perspicillatus* does occasionally feed on live coral in the Hawaiian Islands. In Barbados, Frydl and Stearn (1978) found that only one of six parrotfish species studied consumed live coral. In six species of Okinawan scarids examined by Sano, Shimizu, and Nose (1984) none were found to consume corals but rather fed on filamentous algae and detritus mixed with large amounts of calcareous powder.

Some quantitative information exists on what parrotfishes consume; the most pertinent summaries are found in Al-Hussaini (1947); Hiatt and Strasburg (1960); Randall (1967); Hobson (1974); Sano, Shimizu, and Nose (1984); Frydl and Stearn (1978); and Brock (1979b). Only the last two studies attempted to quantitatively discern food resource partitioning among these fishes. In his study of five Hawaiian parrotfish species, Brock (1979b) found that Hawaiian parrotfishes rasp algae from coralline substrata, but in doing so, also consume some animal tissue. Collectively among the five species, 6 percent of the identifiable remains were animal and 18 percent were algal in origin; however, calcium carbonate comprised over

60 percent of the volume of materials consumed for all species. Animal remains included harpacticoid copepods, mysids, amphipods, shrimps, sponges (*Cliona* spp.), bryozoans, tunicates, micromollusks, foraminiferans, and most commonly, polychaetes. On Caribbean reefs (Barbados) Frydl and Stearn (1978) found scarids consuming micromollusks, foraminifera, and echinoderm parts (*Diadema*) along with carbonate substratum. Randall (1967) noted that 6 of 10 Caribbean parrotfish species examined had consumed some animal remains including fragments of gorgonians, sponges, echinoids, corals, crustaceans, and mollusks as well as foraminifera. However, in none of these Caribbean species did the volume of animal material exceed 2.8 percent of the total. Many of the organisms consumed by parrotfishes are small, residing in the coralline substratum and are collectively known as the cryptobiota. The biomass of cryptobiota may range from 10 to 1,400 g (dry weight) m^{-2} of bottom with a mean value of 50 gm^{-2} in most Hawaiian and central Pacific reef areas (Brock and Smith 1982). The cryptobiotic resource is probably not directly tapped by many fish species besides the parrotfishes; few other fishes have the dentition and morphological adaptations necessary to get into the coralline substratum. Parrotfishes do rasp into coralline substratum as evidenced by tooth scars on the substratum in numerous published photographs (Cloud 1959; Bakus 1967; Hobson 1974) and by the presence of abundant calcium carbonate in the digestive tract.

Algae are the primary food resource of parrotfishes. In the Caribbean at least 31 genera of algae are consumed along with two seagrass species by 10 species of parrotfishes (Randall 1967). Algae comprise 84.7 percent and seagrasses make up 14.5 percent of the volume

of material ingested; important algal genera include *Acanthophora*, *Acrochaetium*, *Amphiroa*, *Anacystis*, *Bryothamnion*, *Calothrix*, *Centroceras*, *Ceramium*, *Cladophora*, *Coelothrix*, *Corallina*, *Dictyopteris*, *Dictyota*, *Enteromorpha*, *Gelidium*, *Halimeda*, *Herposiphonia*, *Jania*, *Laurencia*, *Lithothamnion*, *Lomentaria*, *Lyngbya*, *Microcoleus*, *Oscillatoria*, *Polysiphonia*, *Rhizoclonium*, *Spermothamnion*, *Sphacelaria*, *Spyridia*, *Ulva*, *Vidalia* and unidentified diatoms (Randall 1967). Many of these same genera have been found in central Pacific parrotfish stomach contents (Brock 1979b). Important microphytic algal genera consumed in Hawaiian waters included *Jania*, *Pocokielia*, *Liagora*, *Microdictyon*, *Neomeris*, *Laurencia*, *Herposiphonia*, *Polysiphonia* and *Chondria* (Brock 1979b). Part of the cryptobiota consumed by parrotfishes includes the boring algae, *Ostreobium* spp. Algal consumption rates by Hawaiian parrotfish (as experimentally measured by chlorophyll-*a* reduction) are in a range of 4.9 to 9 ug chlorophyll-*a* per gram (wet weight) of parrotfish per day (Brock 1979b).

Lobel and Ogden (1981) experimentally found a preference hierarchy of algal species consumed for the Caribbean parrotfish *Sparisoma radians*. In the laboratory fish fed diets of single plants, a mixed plant diet, and starved controls showed a differential survival which paralleled the preference hierarchy with the consumption of the most preferred plants leading to longest survival. In the field, *S. radians* was found to deliberately feed on a variety of algae which did not directly relate to the preference rank established in the laboratory; in the natural setting, the consumption of a variety of plants presumably served to maintain a balanced diet.

It is difficult to separate scarid species by differences in food consumed because these fishes often feed together in mixed schools over the same substratum and presumably on the same benthic resources. Frydl and Stearn (1978) studied six sympatric Caribbean scarid species and noted some differences in feeding behavior of the species observed in the field were reflected in the gut contents. Differences were most obvious with species that fed over sand substrata having a greater proportion of benthic foraminifera in the stomach contents than the single species (*Scarus viride*) that foraged on hard coralline substrata which had consumed more encrusting (hard substratum) foraminifera species. Similarly in Hawaii, Brock (1979b) found little trophic separation amongst five parrotfish species. The most obvious differences were related to dentition. Generic separation of *Calotomus* from *Scarus* is based partially on differences in dentition (Schultz 1958); *Calotomus* has free, imbricate, incisor-like teeth whereas in *Scarus* the teeth are fully coalesced into a parrot-like beak. The dentition and jaw structure of *Calotomus sandvicensis* is not as heavy as that of *Scarus perspicillatus*, *S. sordidus*, or *S. taeniurus*. Differences in dentition suggest differences in food and feeding strategy. *Calotomus sandvicensis* was found to have the most divergent of diets of the species examined (the least calcium carbonate by volume and the greatest percentage of identifiable algae and animal material). A fifth species, *Scarus dubius*, has the typical fused beak of *Scarus*, however the teeth and jaw structure are less massive relative to *S. perspicillatus*, *S. taeniurus*, and *S. sordidus*. These differences were also reflected in the diet; *Scarus dubius* took in more identifiable plant material and less calcium carbonate than the other *Scarus* species. The data suggested that *Scarus dubius*

and *Calotomus sandvicensis* feed on similar materials which are probably more restricted to the surface of the coralline rock (more plant material and less calcium carbonate) than the food materials consumed by *Scarus perspicillatus*, *S. sordidus*, and *S. taeniurus*. The greater proportion of calcium carbonate slurry present in the gut contents of the latter species suggested that they utilize the cryptofaunal-*Ostreobium* layer to a greater extent than do other fishes. The lack of separation within this latter group suggests that (a) differential utilization of food materials by these species is very subtle, or (b) that the food resources are sufficiently great that there is no competitive interaction and hence no ecological separation by way of food (Brock 1979b).

Parrotfish are diurnally active (Bardach 1959; Randall 1967). Analysis of scarid stomachs collected late at night on Caribbean reefs show them to be empty; feeding commences at sunrise and continues through the day until sunset (Frydl and Stearn 1978). Feeding rates have been calculated for parrotfishes in some localities. In the Caribbean, Frydl and Stearn (1978) found that scarids spend 80 percent of their time feeding on surfaces covered by filamentous algae, about 20 percent on sand, and less than 1 percent on other (live coral, sponge, etc.) surfaces. While feeding, *Sparisoma viride* and *Scarus aurofrenatum* make about 10 bites min^{-1} on the substratum, while *S. taeniopterus*, *S. croicensis*, and *S. vetula* feed in bursts of about 30 bites min^{-1} separated by short (20-sec) intervals for repositioning (Frydl and Stearn 1978). In Hawaii, Brock (1979b) using polyvinyl chloride (PVC) panels and counting feeding scars, found scarids (four common species) to feed at a rate of 1.2 bites $\text{cm}^{-2}\text{day}^{-1}$. At normal Hawaiian field densities (0.8 fish

m^{-2} of planar reef surface) this translated into 168 bites fish $\text{m}^{-2}\text{hr}^{-1}$.

Hawaiian parrotfishes spend about 60 percent of the day engaged in feeding (Brock 1979b). Ogden and Buckman (1973) note that the Caribbean species *Scarus croicensis* spends about 8 hours, or 62 percent, of the day foraging. Similarly, other Caribbean scarids spend an estimated 75 to 80 percent of the day foraging. Juveniles pass food materials within 1 to 2 hr following ingestion, middle-sized fish (250-500 g wet weight) retain food materials for 3 to 5 hr, and larger fish (1 kg or more) turn over their intestinal contents only once a day (Bardach 1961). In contrast, Smith and Paulson (1974) estimate that 1-kg parrotfish will turn over their food materials twice a day and small parrotfish (i.e., 12 cm SL *Scarus croicensis*) have intestinal turnover rates of up to 15 times a day (Ogden 1977). Lobel and Ogden (1981) note that satiation occurs after 15 min of unrestrained feeding in *Sparisoma radians*. Considering a number of sizes, Frydl and Stearn (1978) obtained a mean turnover rate of about eight times day^{-1} . These data suggest that the considerable time spent feeding along with the short retention time is indicative of little energy derived on a per unit time basis from the coralline substratum food resources. There are, however, few other fishes that can use the coralline substratum and cryptobiota directly as a food resource.

Growth

Randall (1962) reported growth rates for several Caribbean scarid species from mark and recapture studies: rates varied from 3.5 to 20 mm per month. Both Randall (1962) and Reeson (1983) provide length-weight data for some Caribbean parrotfishes. Growth in the

species that have been studied is isometric (Reeson 1983).

ECOLOGICAL ROLE

Behavior

Parrotfishes, like other herbivorous species, are diurnally active. At dusk they seek shelter to rest and commence activity at about the time of sunrise (Hobson 1972, 1973; Collette and Talbot 1972; Starck and Davis 1966). A number of parrotfish species (primarily *Scarus*) produce mucous envelopes while "asleep" on the reef. Mucous envelopes have anterior and posterior openings and are produced by opercular glands (Byrne 1970). These envelopes form a cocoon around the body of the fish and are believed to reduce predation by nocturnal predators such as muraenid eels (Winn and Bardach 1960). Rosenblatt and Hobson (1969) note that only small individuals of *Scarus* in the eastern Pacific regularly produce the mucous envelope which supports the predation hypothesis (e.g., small individuals are probably subjected to greater predation than are larger fish).

Scarids undertake daily migrations between their diurnal feeding areas and nocturnal resting sites. As dusk approaches many tend to aggregate in shallow water, then move to resting sites in deeper areas. Ogden and Buckman (1973) were able to identify specific routes that *Scarus croicensis* utilize in their daily movements. Some *Scarus* species apparently use sun navigation to return to specific resting sites (Winn, Marshall, and Hazlett 1964). It has not been established whether parrotfishes utilize the same sleeping site each night (Reeson 1983). In the Caribbean some scarid species appear to be associated with the same area or "home reef" for variable periods of time but will traverse several

hundred meters while feeding (Bardach 1958; Randall 1961; Winn, Marshall, and Hazlett 1964). Although home ranges have been identified for some scarids, considerable variation in local dispersion within a species may exist (Colton and Alevizon 1981; Alevizon and Landmeir 1984). Buckman and Ogden (1973) and Ogden and Buckman (1973) have noted three behavioral patterns in *Scarus croicensis*: (1) both striped-phase and terminal-phase fishes may repeatedly be found in the same area of reef and use these areas for feeding, (2) striped-phase and terminal-phase fish may actively defend a territory which contrasts to (3) large foraging groups of these fishes that are seen to move and feed over the reef all day.

Scarids will school both monospecifically, with other parrotfish species, or in mixed aggregations (Winn and Bardach 1960; Starck and Davis 1966). There may be certain selective advantages to the formation of these groups: they may serve an antipredator behavioral function (Hobson 1969; Ehrlich and Ehrlich 1973) or allow access to otherwise unavailable food resources (Vine 1974; Alevizon 1976). In the latter case, schools of herbivorous fishes are able to forage on benthic algal resources in actively defended pomacentrid territories by large numbers of grazing fishes overwhelming the defending pomacentrid.

Sediment Production

As noted above, it has been well established that parrotfishes ingest considerable amounts of carbonate material in their feeding. Emery (1956) examined two specimens of *Scarus perspicillatus* from Johnston Atoll and found that about 90 percent (by volume) of the digestive tract materials were composed of calcium carbonate. Cloud (1959) stated that parrotfishes contribute between 4.25 to 6.18 metric tons of

calcium carbonate sediment per hectare of reef per year. Similarly Bardach (1961) found the total non-nutritive component of grazing and rasping fish gut contents to be 2 to 4 percent of their body weight in the Caribbean. He estimated that these reef raspers produce 2,300 kg of calcium carbonate sediment per hectare per year. Similarly, the Caribbean species, *Sparisoma viride*, produces 2,088 kg of calcium carbonate sediment per hectare per year (Gygi 1975). Ogden (1977) concluded that on the Caribbean coast of Panama *Scarus croicensis* produces 4,900 kg of sediment $\text{ha}^{-1}\text{yr}^{-1}$. Frydl and Stearn (1978) found actual sediment production by Caribbean scarids to be less, ranging from 400 to 1,700 kg $\text{ha}^{-1}\text{yr}^{-1}$; these fishes primarily turn over existing sediment. Data presented by Frydl and Stearn (1978) show sediment turnover to range from 3,400 to 5,900 kg $\text{ha}^{-1}\text{yr}^{-1}$. Nevertheless, the impact of the production and redistribution of all this material on coral reefs is large and must have an impact on the surrounding communities in which it occurs.

Interaction With Other Herbivorous Species

Herbivorous fishes are a common element of most coral reef fish communities, comprising 15 to 25 percent of the biomass and species diversity (Ogden and Lobel 1978; Brock, Lewis, and Wass 1979). On central Pacific reefs fishes in the families Kyphosidae, Acanthuridae, Pomacentridae, and Pomacanthidae all have species that are primarily herbivorous. The parrotfishes are often the most abundant family (Randall 1963b; Bakus 1967; Goldman and Talbot 1975; Jones and Chase 1975). The other major herbivorous group on coral reefs is the sea

urchins. These species are all potential competitors with scarids for available benthic algal resources but few studies have attempted to define the potential for interaction. It is usually difficult to separate the effects of sea urchins from those of fishes (Ogden and Lobel 1978); as urchins are more easily manipulated they have received more attention from field ecologists (Ogden 1976).

Ogden, Brown, and Salesky (1973) found an increase in population sizes of juvenile parrotfishes and surgeonfishes following the removal of all sea urchins (*Diadema antillarum*) from a St. Croix patch reef. Hay and Taylor (1985) noted that the removal of sea urchins on sections of Caribbean reefs resulted in significant local increases in herbivorous fishes including parrotfishes. The natural die-off of *Diadema* in the Caribbean (Lessios, Robertson, and Cubitt 1984) led to significant increases in the population sizes of parrotfishes and surgeonfishes within 9 months of the event (Carpenter 1985, 1986; Ogden and Carpenter 1987). These data suggest that competitive interactions do occur among sea urchins, parrotfishes, and surgeonfishes.

In a field manipulation, Brock* introduced sea urchins to an isolated Hawaiian patch reef that previously had lacked urchins but had maintained a stable assemblage of herbivorous fishes. Major shifts in the benthic community of the experimental reef occurred: macroalgae disappeared and within a year, coral coverage had significantly increased. Monitoring the fish populations on the experimental and nearby control reefs showed a decline in the abundance of fishes on both reefs but there were no

* Brock, R. E. (in preparation) Sea urchins and coral reef fish community structure. 26 pp.

significant differences. The lack of significant change in the herbivorous fish populations between the two reefs (experimental and control) suggests that the benthic community on the manipulated reef accommodated the increased grazing pressure (herbivore biomass 27 times greater on the experimental reef) through an increased rate of primary production. These "algal turfs" result from high grazing pressure and may be three to five times more productive than high biomass algal communities that previously existed there (Carpenter 1986). Thus, in some situations, benthic algal communities are able to respond to a wide range of grazing pressures, rapidly accommodating and supporting fluctuations in the abundance and diversity of herbivorous forms and thereby reducing competitive interactions.

Role In Structuring Benthic Communities

Qualitative observations suggest that parrotfishes are important to the observed community structure of sessile benthic forms through feeding activities (Bakus 1966, 1969, 1972). Indiscriminant rasping of the substratum may serve to reduce benthic species dominance, creating patchiness leading to an increased local diversity in these communities. Caging experiments have shown that the standing crop of algae is inversely related to the number of herbivorous fish present (Stephenson and Searles 1960; Randall 1961; Earle 1972). Territorial herbivorous species (e.g., pomacentrids) may, by defending a territory, allow a greater standing crop of fleshy algae to develop within these territories than is present in other areas exposed to herbivorous fishes. This thicker algal mat hinders coral growth and development (Kaufman 1977; Potts 1977) as well as the settlement and growth of other invertebrate species (Vine 1974).

These fleshy algal mats also retard the growth of more herbivore-tolerant coralline algal species which cement the substratum (John and Poole 1973; Vine 1974). Birkeland (1977) demonstrated that herbivorous fishes enhance the survival of coral recruits on settlement plates in the Caribbean.

Experimentally, grazing parrotfishes have been shown to have a tremendous impact on the structure of benthic communities. Brock (1979a) has shown that parrotfishes in densities of 0.6 to 1.5 individuals per m^2 or 9 to 17 g wet weight of fish per m^2 of feeding surface were found to have an optimum effect resulting in greatest benthic species richness and biomass on two-dimensional surfaces. The presence of refuges (three-dimensional habitats), however, had a greater impact on benthic community structure (number of species and biomass) than did just the number of parrotfishes in such an experimental system. Coral recruitment was enhanced by the presence of refuges and, like coralline algae, was more successful under increased parrotfish grazing pressure. The optimum densities of scarids in the experiments were found to relate well to observed field densities in Hawaii. These experimental data suggest that scarids, much like some sea urchin species, may play an important role in benthic community development and structure through their feeding activities. Furthermore, these results lend support to the field observation that exposed benthic invertebrate species other than corals are rare on tropical Pacific reef flats (Bakus 1966) and that grazing parrotfish may be partially responsible for this (Bakus 1964).

ENVIRONMENTAL REQUIREMENTS

Some reef fish species are specific in their habitat requirements.

Thus a small change in a coral reef community due to an environmental stress may result in the loss of certain fish and invertebrate species. In many instances, human-induced environmental perturbations in Hawaiian reef systems has not led to the local disappearance of parrotfishes. Indeed, experimental removal of all fishes (including parrotfishes) from an isolated patch reef led to a rapid recolonization by parrotfishes in large numbers (Brock, Lewis, and Wass 1979). Such successful recolonization by parrotfishes may be related to the probable wide patterns of movement of both juveniles and adults on Hawaiian reefs. However, extreme fishing activity, changes in the substratum resulting in the loss of appropriate food resources or the reduction of available cover may cause local loss of parrotfishes. At present, there are no hard data to substantiate and link environmental change to the local disappearance of parrotfishes. Brock (1979b) reports that drastic habitat changes (nutrient enrichment through sewage and beach improvement by sand introduction) may have resulted in the local reduction and scarcity of parrotfish at two Hawaiian localities.

In general, parrotfishes are found on coral reefs where the water is relatively clean, has good circulation characteristics, and is well-oxygenated. In the coral reef environment, parrotfishes appear to favor areas that have a considerable amount of open hard substratum; this and the presence of appropriate shelter is a prerequisite to their success. Some parrotfish species show specific habitat preferences with size where juveniles may be spatially separated from adults. Juveniles of the Hawaiian species often form mixed schools which may range in size from a few to more than 1,500 individuals. Under these circumstances, adult *Scarus sordidus* and subadult *S. perspicillatus* will

often travel with these schools. Adults of all Hawaiian *Scarus* species may form small, mixed aggregations but adult terminal males are frequently solitary preferring habitats seaward of the fringing reef.

FISHERY

Parrotfishes are important to many artisanal fisheries. In the Caribbean they are taken in traps (Reeson 1983); in the Pacific Islands they are usually captured by net and spear (Johannes 1981a). On some Pacific Islands, fishermen take advantage of the spawning aggregations of parrotfishes that form seaward of the reef at specific times to make their catch (Johannes 1981a). Despite the frequent appearance of parrotfishes in catches, little is known of their contribution to local fisheries. Reported commercial catches of parrotfishes in Hawaii are small (from 1.2 to 15.1 metric tons per annum over the last 20 years) but the non-documented recreational catches must be large. Hawaiian parrotfishes are sought after and are particularly susceptible to spearfishing methods when asleep in the coral at night. Reeson (1983) presents length-frequency distributions of parrotfishes from Caribbean reefs (both unexploited and subjected to fishing).

RECOMMENDATIONS FOR CONSERVATION

Experimentally scarids have been shown to be important to the maintenance of coral reef systems through their feeding activities (Brock 1979a). It has been suggested that both parrotfishes and certain sea urchin species may be serving in a "keystone species" role (sensu Paine 1966) fostering the recruitment success and growth of corals and coralline algae (Brock 1979a; Ogden and Carpenter 1987). These

carbonate producers are important to the geological structure of reefs, elevating the need for conservation of these keystone species.

With population and economic growth in the tropical insular settings, many coral reefs and the species inhabiting them are coming under increasing pressure. Parrotfishes as part of the reef fauna have likewise received increased exploitation. Methods to counter degradation of habitat and overfishing are limited; effective management strategies for these systems and species are few. The manager of coral reef resources is faced with numerous biological, political, cultural, and economic constraints of a magnitude and complexity as to render sound scientific management a near impossibility (Johannes 1981b). These insular settings have no continental shelves and seafood stocks are largely confined to nearshore reefs and lagoons; thus, these areas are particularly vulnerable to over-harvesting.

Because of their dependence on reef resources, the people of Oceania over a millenia of trial and error devised methods of resource management that, in many instances, have fallen into decay due to the introduction of a cash economy and

Western ideas. Johannes (1978, 1981a, 1981b, 1982) presents a number of traditional management and conservation measures that have been practiced in Oceania and apparently work well. These include strategies for reef and lagoon tenure as well as limited entry. Other restrictions are or were tied to religious or superstitious beliefs.

All of these methods serve to conserve resources; these management regimes are based on localized control over access, and relative to a common property regime, offer the potential for a more rational use of the resources. Because they are decentralized these management methods may closely match the diffuse nature of many coral reef fisheries. Where the resources of a central governing body are limited, a diffuse management strategy may be an effective alternative (Dahl 1988).

The challenge confronting the modern resource manager is incorporation of these proven management strategies into a format that is politically and culturally acceptable today. In the modern context, marine parks and reserves may provide one solution, particularly if the local general public participates in the establishment of these areas.

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