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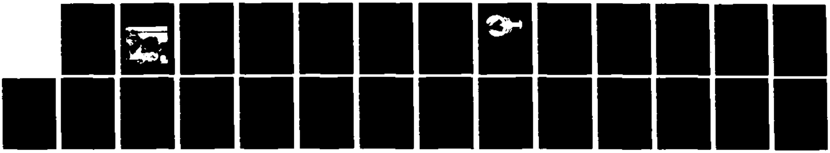

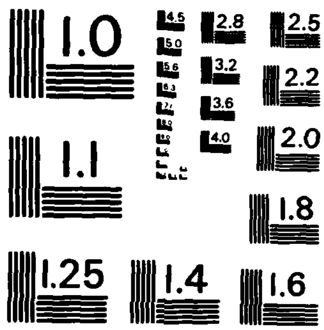
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Biological Report 82(11.33)
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Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (North Atlantic)

AMERICAN LOBSTER

Coastal Ecology Group
Waterways Experiment Station
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Fish and Wildlife Service
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Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (North Atlantic)

AMERICAN LOBSTER

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PREFACE

This species profile is one of a series on coastal aquatic organisms, principally fish, of sport, commercial, or ecological importance. The profiles are designed to provide coastal managers, engineers, and biologists with a brief comprehensive sketch of the biological characteristics and environmental requirements of the species and to describe how populations of the species may be expected to react to environmental changes caused by coastal development. Each profile has sections on taxonomy, life history, ecological role, environmental requirements, and economic importance, if applicable. A three-ring binder is used for this series so that new profiles can be added as they are prepared. This project is jointly planned and financed by the U.S. Army Corps of Engineers and the U.S. Fish and Wildlife Service.

Suggestions or questions regarding this report should be directed to one of the following addresses.

Information Transfer Specialist
National Coastal Ecosystems Team
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NASA-Slidell Computer Complex
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Slidell, LA 70458

or

U.S. Army Engineer Waterways Experiment Station
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Post Office Box 631
Vicksburg, MS 39180

CONVERSION TABLE

Metric to U.S. Customary

Multiply	By	To Obtain
millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters (m)	3.281	feet
kilometers (km)	0.6214	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	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	1.102	short tons
kilocalories (kcal)	3.968	British thermal units
Celsius degrees	1.8(C°) + 32	Fahrenheit degrees

U.S. Customary to Metric

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

CONTENTS

ACKNOWLEDGMENTS

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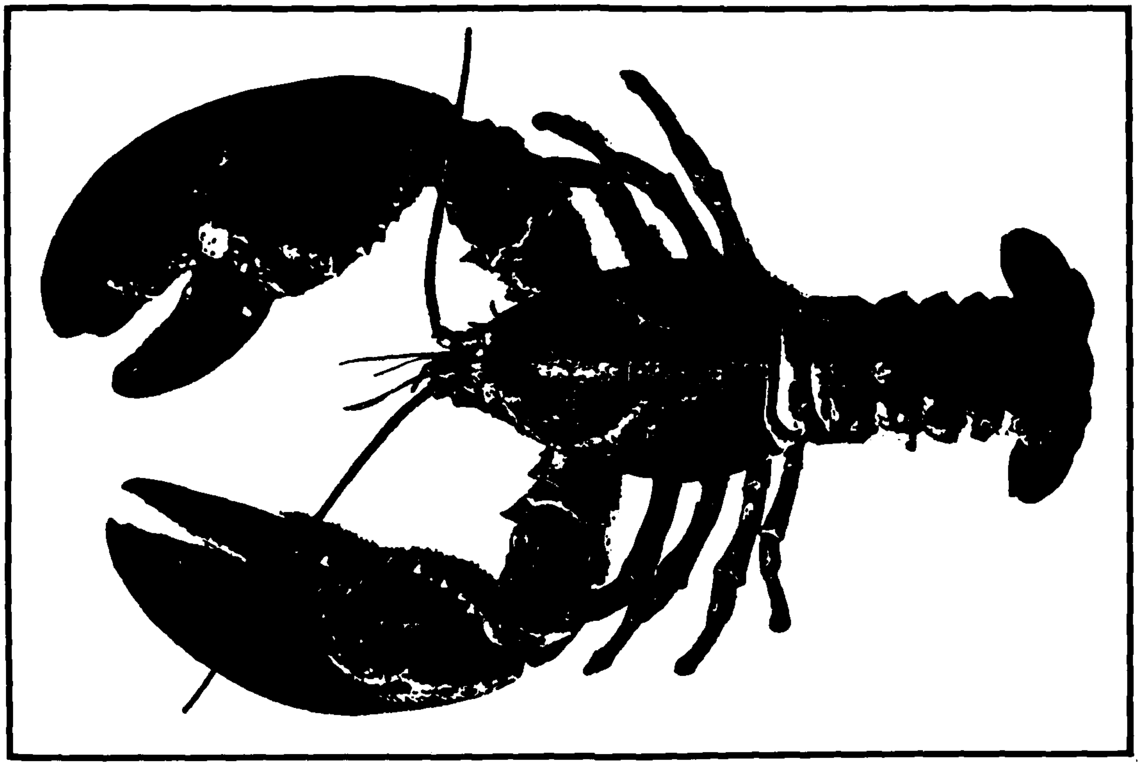

Figure 1. American lobster, _Homarus americanus_.

AMERICAN LOBSTER

NOMENCLATURE/TAXONOMY/RANGE

Scientific name.... _Homarus americanus_
Preferred common name........ American lobster (Figure 1).
Other common names .... lobster, Maine lobster, northern lobster, blueshells (color variant), hard shell lobster, old shell lobster; blackshell, crack backer (lobsters preparing to molt); shedder, soft shell, new shell, shadow, rubber shell, paper shell, and buckle shell (recently molted lobsters) (Herrick 1895).
Class .... Crustacea
Order........................ Decapoda
Family.................... Nephropidae

Geographic range: American lobsters inhabit the coastal and oceanic waters of the Atlantic Ocean from Labrador south to North Carolina (Herrick 1909). They live from the intertidal zone out to a depth of 720 meters (McRae 1960). Major coastal concentrations of lobster are in the Gulf of Maine and the coastal waters of New Brunswick and Nova Scotia, Canada (Cooper and Uzmann 1980). American lobsters are widely distributed in most of the coastal waters of the northeastern United States. Major offshore concentrations are along the outer edge of the Continental Shelf and upper slope between the eastern part of Georges Bank and the offing of Delaware Bay (Schroeder 1959). Small numbers inhabit the outer edge of the Nova Scotian shelf (Cooper and Uzmann 1980).

MORPHOLOGY/IDENTIFICATION AIDS

The American lobster has five cephalic and eight thoracic segments fused together to form a cephalothorax, which is covered by a shield-like carapace (Figure 1). All the segments comprising the cephalothorax bear appendages. Beginning anteriorly, the appendages of the cephalothorax are the first antennae, second antennae, mandibles, first maxillae, second maxillae, first, second, and third maxillipeds and five pairs of walking legs, or pereiopods (Phillips et al. 1980). The first three pairs of pereiopods are chelate, the first pair modified into large claws. One claw of this pair, the crusher, is larger than the other claw, the cutter. American lobsters have compound eyes that are movable and stalked.

The six body segments posterior of the carapace make up the abdomen. Paired, biramous pleopods are located on the first five abdominal segments. The last abdominal segment consists of the telson flanked by uropods, which are modified pleopods. The broad tail fin, composed of the telson and uropods, is used for backward swimming, which is characteristic of lobsters.

The first pair of pleopods on male lobsters are modified into rigid structures, gonapods, which are used to convey sperm to the female (Cobb 1976). In females, the first pair of pleopods are similar to the others but are much smaller. There are two characteristics used to separate the sexes of mature lobsters. Males have sharp spines under the abdomen; female spines are blunt. The male's abdomen is narrower than the width of the carapace; those in the female are about equal (Cobb 1976).

American lobsters are normally greenish-brown but some specimens are blue, red, reddish-yellow, cream, black, or calico (Herrick 1895).

The largest American lobsters are males (Wolfe 1978). The largest male on record weighed 19.25 kg, and was 63.4 cm long. The heaviest female weighed 8.35 kg (Aiken 1980).

The total propodite length in relation to carapace length is a means of distinguishing between the larval stages of the American lobster and the European lobster, _Homarus gammarus_ (Gruffydd et al. 1975). The total propodite length is greater than the carapace length of the European lobster larvae. The opposite is true for American lobster larvae. Geographic isolation is the only character that distinguishes the adults of the two species (Corrivault and Tremblay 1948; as cited in Gruffydd et al. 1975).

REASON FOR INCLUSION IN SERIES

American lobsters support an important commercial fishery along the northeastern coast of the U.S. They are abundant in coastal and offshore waters. It is important that the impact of development projects on lobster populations be considered so that this important and valuable natural resource will be protected.

LIFE HISTORY

Spawning

Male American lobsters mature at shorter lengths than females. Most males carry viable spermatozoa when the carapace length (CL) (measured from tip of rostrum to the back of the carapace) is 40 to 45 mm. About 50% of the males examined along the Maine coast were physiologically mature at 44 mm CL; the smallest mature male was 41 mm CL (Krouse 1973). Females in Maine mature when they are about 90 mm CL (Krouse 1973) but in warmer waters (Long Island Sound), most mature at lengths of 70 to 74 mm CL (Templeman 1936b; Briggs and Mushacke 1979).

Small males usually cannot mate successfully with larger females (Templeman 1934, 1935). Males may be capable of producing mature spermatozoa when they are 40-45 mm CL but they may not be capable of mating until they are as large as the smallest mature females.

When spawning, lobsters pair for about 2 weeks (Atema et al. 1979). Females leave their solitary shelters about 7 days before molting and share the shelter of a dominant, territorial male.

A female sex pheromone is produced before or at the time of molting. This pheromone suppresses male aggression and induces courtship (McLeese 1970; Atema and Engstrom 1971). Pre-molt behavioral displays are also important in successful pair formation (Atema et al. 1979). Mating usually takes place 20-40 minutes after the female molts, but to be successful, mating must take place within a few hours (rarely more than one) after the female has molted. One female, however, was reported to have successfully mated 12 days after molting (Templeman 1936a). Successful mating of hard shelled female lobsters several months after molting has been reported (Dunham and Skinner-Jacobs 1978; Aiken and Waddy 1980a).

The male mounts the female and turns her over with his walking legs and maxillipeds. The male places his gonapods in the female seminal receptacle (thelycum) and deposits a spermatophore (Herrick 1895; Hughes and Matthiessen 1962; Atema et al. 1979). Mating usually is completed in about 30 seconds; the longest in 3 minutes (Atema et al. 1979). Males larger than the female are most successful at copulation (Templeman 1934, 1935). Males protect females from predation and cannibalism for up to 7 days during the vulnerable post-molt stage. This "protection" by the male also ensures that other males will not copulate with his mate (Atema et al. 1979).

Eggs are normally extruded 11 to 13 months after mating. As ova are released, they are fertilized by part of the spermatozoa stored in the seminal receptacle (Templeman 1936a; Krouse 1973). Oviposition occurs on a two year cycle even if the female is not carrying spermatozoa. Evidence is strong that eggs are fertilized externally as they pass over the seminal receptacle (Aiken and Waddy 1980a), but Farmer (1974) believes that fertilization is internal.

Females are capable of fertilizing at least two successive batches of eggs from a single mating (Templeman 1936a; Aiken and Waddy 1980a; Campbell 1983). Large females do not molt or mate every year.

Eggs and Fecundity

Freshly extruded American lobster eggs are dark green and irregularly shaped. They soon become spherical and telolecithal, and are about 1.5 to 1.7 mm in diameter (Herrick 1909). As eggs develop, they increase in size and become elongated and lighter in color.

The number of eggs in a clutch ranges from 3,000 to 115,000 (Herrick 1909; Saila et al. 1969; Perkins 1971). The logarithmic relationship between average fecundity (Y) and carapace length (CL) of lobsters collected from inshore waters off Rhode Island and Massachusetts (Saila et al. 1969) is:

$$\log_{10} Y = -1.6017 + 2.8647 \log_{10} CL.$$

The estimated fecundity-length (CL) relationship of lobsters from the Continental Shelf off southern New England is: $\ln Y = -5.0231 + 3.1569 \ln CL$ (Perkins 1971). Individual variation in fecundity is large (Squires 1970).

After extrusion, fertilized eggs become firmly attached to pleopods, where they develop for 9-11 months (Aiken and Waddy 1980a). About 36% of the eggs are lost between extrusion and hatching (Perkins 1971). Temperature is a key factor that determines the length of time the eggs are carried on the pleopods (Templeman 1940; Aiken and Waddy 1980b). Eggs develop to the 16 cell stage in two days at 18.5°C, and 4.8 days at 10.5°C (Templeman 1940).

Lobster eggs hatch from May to October; the warmer the water the earlier the hatch. In Massachusetts, eggs begin hatching in mid or late May when water temperatures are about 15°C (Hughes and Matthiessen 1962). Peak hatching is in June and early July when water temperatures reach 20°C. The time required to hatch all the eggs within a brood depends on the water temperature. All eggs within a brood usually hatch in 2 to 3 days at 20°C, and in 10-14 days at 15°C (Hughes and Matthiessen 1962).

Females release larvae during a brief period at night by actively beating their pleopods (Ennis 1975). Females normally molt and mate within one month after their brood has hatched.

Prelarvae and Larvae

American lobsters pass through one prelarval and four free-swimming larval stages before settling to the bottom and molting into juveniles. Most prelarvae molt into the first larval stage before being released by females (Davis 1964). All larval stages are normally completed in 25-35 days, but the length of time is temperature dependent (Table 1). Herrick (1895, 1909) describes and diagrams each of the four larval stages.

The distribution and abundance of larvae are affected by the distribution of spawning females, surface current velocity and direction, temperature, salinity, light intensity, hydrostatic pressure, and larval mortality (Phillips and Sastry 1980). The larvae are planktonic from late May to October; they appear earlier in the plankton in southern New England than in the Gulf of Maine (Fogarty and Lawton 1983). Stage I larvae were collected from May to early July in Block Island Sound off Rhode Island (Bibb et al. 1983) and from June to early August off the coast of Maine (Sherman and Lewis 1967).

Vertical distribution is affected by light intensity (Templeman 1937, Scarratt 1973, Harding et al. 1982). At night the larvae seek deeper waters but return near the surface during day (Phillips and Sastry 1980). Phototactic responses observed in the laboratory differed among larval stages and within each larval stage (Hadley 1905, 1908). Stage I and IV larvae were originally positively phototactic but became negatively

Table 1. The approximate number of days required by larvae to pass through each larval stage at different temperatures (modified from data by Templeman 1936a in Aiken 1980).

Temp.	Larval stage				
(°C)	1	2	3	4	Total
8	20	26	42		
10	14	15	25	49	103
12	10	11	15	32	68
14	7	8	11	25	51
16	5	6	9	22	42
18	3	5	7	18	33
20	2	4	6	14	26
22	2	4	5	11	22

phototactic late in each stage. Stage II and III larvae were negatively phototactic but responses were highly variable.

High larval densities along windward coasts suggest that larvae are transported by surface currents (Fogarty 1983). Prevailing south-westerly winds along the New England coast in the summer may transport larvae from offshore to coastal waters (Fogarty 1983).

Late in stage IV, larvae settle to the bottom and burrow into the substrate. They molt into juveniles while sheltered in their burrows (Cooper and Uzmann 1980).

Juveniles and Adults

American lobsters in inshore waters excavate shelters under objects resting on the sea floor when there are no natural crevices available as shelter. Highest lobster densities are on sand substrate with overlying flattened rocks. Juvenile and adult lobsters are negatively phototactic and prefer dark shelters shaped so that the lobster can maintain contact with the roof and walls (Cobb 1971).

Lobsters inshore tend to be solitary. They rarely share shelters, and sharing behavior has only been reported in winter when bottom water temperatures are coldest (Cooper and Uzmann 1980). Lobsters offshore often share shelters or bowl-shaped depressions in the substrate. This behavior may be caused by the scarcity of shelters (Cooper and Uzmann 1980).

Juvenile American lobsters less than 35 mm CL rarely leave their shelters (Cooper and Uzmann 1977). When juveniles are 35-40 mm CL they venture just outside their shelters at night. When about 45 mm CL they begin nocturnal foraging away from their shelters. Adult and juvenile lobsters usually travel less than 300 m from the home shelter when foraging (Cooper and Uzmann 1980).

Lobsters inshore move from shoal water (< 10 m) to deeper water when storms generate heavy seas (Cooper et al. 1975). These horizontal movements are usually 100 m or less but involve an increase in depth up to 10 m. Lobsters along the Canadian east coast make short distance seasonal movements from relatively deep waters (15-18 m) in winter to shallower waters (7-9 m) in summer (Stasko 1980).

Lobsters inshore appear to have a limited home range. About 99% of the lobsters (81-123 mm CL) recaptured after tagging were within 2.2 km from the release site (Cooper 1970). From 74% to 98% of the lobsters (81-116 mm CL) recaptured after being released at sites along the coast of Maine were caught within 8 km from the release site (Krouse 1973).

In another study 22% of the large mature lobsters (127-200 mm CL) that were recaptured after being tagged and released in Penobscot Bay, Maine, were caught 137 km to 256 km from their release points (Dow 1974). Large lobsters apparently migrate farther than small lobsters.

Lobsters offshore migrate greater distances than their coastal counter-parts. Movements of up to 345 km in 71 days were reported by Uzmann et al. (1977). Ground speeds ranged from 0.18 to 10.2 km per day; the median was 1.7 km.

MOLTING AND GROWTH CHARACTERISTICS

The growth of lobsters is contin-uous, but it is greatest when they molt (Phillips et al. 1980). The growth rate depends on the molting frequency and the size increase at molting. With increasing age, American lobsters molt less frequently and grow proportionally less at each molt. Lobsters molt an average of 10 times in their first year, 3 or 4 times in the second and third years, twice in the fourth year, and once a year or less thereafter (Hughes and Matthiessen 1962).

Although salinity, dissolved oxygen, food availability, and crowding are factors that affect growth (Phillips et al. 1980), temperature appears to be the dominant factor (Huntsman 1924; Templeman 1936c; Hughes and Matthiessen 1962; Hughes et al. 1972; Gruffydd et al. 1975). For example, captive juveniles held two years in water with a constant temperature about 23°C weighed 454 g but those kept at ambient temperatures (2° to 24°C) took 5.5 years to reach the same weight (Hughes et al. 1972). The higher growth rate was due to a greater number of molts, not to a change in the rate of growth between molts.

The percentage increase in length per molt of larval lobsters collected in the Northumberland Strait, southern Gulf of St. Lawrence, was 33% from larval stage I to stage II, 32% from stage II to stage III, and 30% from stage III to stage IV (Wilder 1953).

Estimates of the average percentage increase in length per molt for juveniles and adults ranged from 7% to 20%; weight gains were 30% to 61% (Aiken 1980). Mature females have a slower growth rate than males because females molt less frequently. Growth between molts for the two sexes is similar (Wilder 1953). Other studies have indicated that the percentage increase in lengths of mature females between molts is less than that of mature males of the same size (Wilder 1963; Cooper and Uzmann 1971; Ennis 1972; Campbell 1983).

Lobsters offshore (90 mm CL) grow faster (18% length increase) per molt (Cooper 1970) than lobsters inshore (12%) that are the same size. The difference in growth of the two sexes is slight (2%) according to Cooper and Uzmann (1971). Lobsters offshore molt more often than lobsters inshore. The difference in growth rates of inshore and offshore lobsters may be explained by the migratory habits of the two populations. Each year offshore lobsters migrate between the outer Continental Shelf and upper slope waters (8° to 12°C) and shallower Continental Shelf waters (10° to 17.5°C) seeking optimum water temperatures for growth, molting, and extrusion of eggs (Cooper and Uzmann 1971, Uzmann et al. 1977) whereas inshore lobsters are nonmigratory and subject to winter temperatures (<5°C) that inhibit growth.

The average increase in length for lobsters (68-110 mm CL) captured, released, and recaptured four to twelve months later along the Canadian east coast was 13% to 15% with an average weight increase of 43% to 54% (Wilder 1953). The average increase in length per molt for lobsters (20-176 mm CL) along the Maine coast was 8% (Thomas 1973). He found that the length relationship between premolt and postmolt for lobsters ranging in premolt sizes from 20 to 176 mm CL was linear.

Cooper and Uzmann (1980) determined the average growth increment per year for lobsters offshore that molt, and the annual probability of molting.

FISHERY

American lobsters have been harvested commercially since the 18th century. In the mid-19th century, the first large scale exploitation of lobster resources was induced by the canning industry (Dow 1980). By the end of the 19th century, the majority of lobsters were being sold to the live lobster industry. Storage facilities (or pounds) were constructed to hold live lobsters so that markets could be regularly supplied. Canada and the United States together have about 75 storage facilities with an estimated capacity of 75 million lobsters (Dow 1980).

Traditionally, lobsters are caught in baited traps (pots). Most lobsters are caught in shallow (5-30m) inshore waters (Cobb 1976).

Landings from the offshore fishing grounds (along the outer edge of the Continental Shelf and the upper slope from Georges Bank to Chesapeake Bay at depths from 100m to 600m) increased sharply from about 800,000 lb in 1958 to nearly 9 million lb in 1970 (Figure 2). Offshore lobster landings have declined since 1971 to about 5.6 million pounds in 1983. During the early years of the offshore lobster fishery, most vessels used otter trawls to capture lobsters, but since the late 1960's most vessels use large lobster pots set in long strings

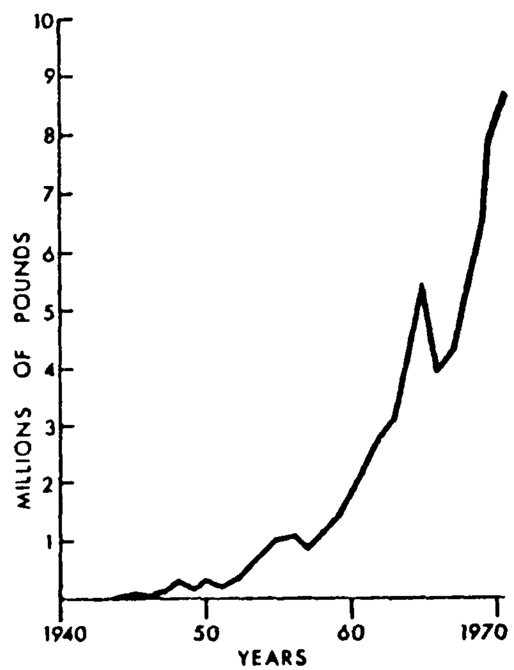

Figure 2. Estimated increase in catch of offshore lobsters, 1940-70 (Cobb 1976).

(Cobb 1976), something on the order of a longline.

Lobsters are caught throughout the year in New England except for a restricted area near Monhegan Island, Maine, which is closed to lobstering from January 1 to June 25. The catch in New England is highest from August to November.

Maine

Maine produces the greatest number of lobsters. Landings in 1982 were 22.5 million pounds with a dockside value of about $50 million (Table 2).

Lobsters may only be caught with traps that are vented to allow individuals smaller than legal size to escape. Neither the number of traps per fisherman nor the number of licenses is restricted. Minimum size is 3 3/16 inches (81 mm) CLM (carapace length measured from the back of the eye socket to the back of the carapace). Maine is the only state with a maximum size limit; all lobsters larger than 5 inches (127 mm CLM) must be released.

Female lobsters carrying eggs attached to their pleopods (berried) have been protected in all lobster producing states since the late 19th century (Dow 1980). Lobsters that extrude eggs while being held in holding pens in Maine are purchased by the State, marked with a "V"-notch in the telson, and released in the sea. "V"-notched lobsters are protected in Maine and must be released whether or not they are berried at the time of recapture.

New Hampshire

Lobsters in New Hampshire are taken by traps or trawl. The trawl fishery is not directed at lobsters but an incidental catch of lobsters is allowed. The 1982 commercial catch was 807,000 lb, valued at $1.8 million

Table 2. Landings (thousands of pounds) and dockside values (thousands of dollars) of American lobsters in Maine, New Hampshire, and Massachusetts from 1963-1982. (Fishery Statistics of the United States, 1963-64, 1969-70; New England Fisheries, 1971-76; N.M.F.S. unpublished data, 1977-82).

Years	Maine		New Hampshire		Massachusetts	
	Landings	Value	Landings	Value	Landings	Value
1963	22,804	$12,636	747	$ 388	4,505	$ 2,564
1964	21,413	14,182	850	544	6,021	3,316
1965	18,862	14,177	765	551	6,360	4,472
1966	19,916	14,905	807	585	4,828	3,697
1967	16,489	13,598	718	610	4,706	4,179
1968	20,502	14,932	755	597	4,817	4,250
1969	19,834	16,046	732	651	4,965	4,741
1970	18,172	17,202	688	722	5,685	5,853
1971	17,558	17,481	667	741	6,146	6,894
1972	16,257	18,588	674	809	8,032	10,276
1973	17,044	23,270	497	680	5,624	8,527
1974	16,458	23,213	499	703	5,263	8,665
1975	17,008	27,479	480	779	6,734	12,101
1976	19,001	29,238	477	668	6,586	11,620
1977	18,487	32,101	475	807	7,352	13,944
1978	19,130	33,878	469	820	9,802	19,187
1979	22,133	39,901	627	1,109	9,718	20,317
1980	21,981	41,705	711	1,315	9,700	21,144
1981	22,307	46,087	789	1,523	9,840	25,732
1982	22,438	49,783	807	1,804	11,176	25,596

(Table 2). The minimum size limit in New Hampshire is 3 3/16 inches (81 mm) CLM. There is no limit to the number of traps that can be set by commercial lobster fishermen. New Hampshire sells a recreational lobster license that allows the holder to set 5 traps.

Massachusetts

The State has a limited entry inshore commercial fishery. In 1983, the number of coastal lobster permits issued was limited to 1,608. Vented traps are used in the coastal fishery; there is no limit on the number of traps that can be set by each fisherman. An incidental catch of 100 lobsters per day is allowed for inshore trawlers. The number of permits for the offshore fishery is unlimited and both traps and trawls are legal gear. The minimum length in Massachusetts is 3 3/16 inches (81 mm) CLM.

Landings in 1982 had a dockside value of $25,596,000 (Table 2). Massachusetts has a large recreational fishery. About 11,000 non-commercial licenses were issued in 1983. Permit holders are allowed to set 10 lobster traps. Lobsters can be taken legally by skin or SCUBA-divers in Massachusetts but not in the other New England States.

The New England Regional Fisheries Management Council has developed a management plan for the offshore (3-200 miles) lobster fishery that will take effect on January 1, 1985. For example, the minimum length limit for offshore lobsters will be 3 3/16 inches (81 mm) CLM.

POPULATION DYNAMICS

Natural mortality is extremely high during the free-swimming planktonic larval stages of the American lobster. Scarratt (1964, 1973) used larval stage abundance to estimate the survival from stage I to stage IV of larvae in the southern Gulf of St. Lawrence, New Brunswick. Average annual survival was about 0.9% (range 0.1 to 2.5). The percentage survival may have been underestimated because of the difficulty in estimating the abundance of stage IV larvae. Larvae become negatively phototactic midway through stage IV and may not have been collected in surface tows that were used to estimate abundance (Scarratt 1973).

Estimates of mortality of juvenile and adult lobsters in United States waters were reviewed by Anthony (1980). Estimates of instantaneous total mortality (Z) from Maine, New Hampshire, Massachusetts, Rhode Island, New York, New Jersey, and Virginia averaged 1.84 (range 0.91 to 2.80). Estimates of instantaneous natural mortality (M) ranged from 0.02 to 0.35 with an average of 0.15. Mortality estimates of lobster populations in the Canadian Maritimes were reviewed by Campbell (1980).

Several methods were used to estimate the mortality of juvenile and adult lobsters along the coast of Maine (Thomas 1973). Instantaneous total mortality (Z) of commercial-size lobsters (> 81 mm) ranged from 1.1363 to 2.9188. Instantaneous natural mortality (M) for pre-recruit (less than commercial size) lobsters ranged from 0.0202 to 0.3467. Estimates of instantaneous fishing mortality (F) ranged from 0.7896 to 2.8986. These F values represent an annual exploitation rate of 54.6% to 84.5% of the lobsters vulnerable to the commercial fishery.

Annual exploitation rates of lobsters near Comfort Cove, Newfoundland, were as high as 95% (Ennis et al. 1982). For 1977-81, annual exploitation rates of lobsters near Notre Dame Bay, Newfoundland, varied from 80% to 95% (Ennis 1983).

Lobster movements usually are triggered by changes in water temperature (McLeese and Wilder 1958; Paloheimo 1963; Cooper and Uzmann 1971). A strong correlation between catch, fishing effort, and sea surface temperature was reported by Dow et al. (1975). Lobster yield predictions for Maine, based on sea surface temperatures, were calculated by Flowers and Saila (1972). Saila and Marchessault (1980) discuss other models that have been developed to predict the yield of lobsters and summarize the surplus-yield models that have been used.

ECOLOGICAL ROLE

Feeding Habits

American lobster larvae have been cultured on copepods and small lobster larvae but little is known about their feeding habits in nature. Larvae were raised on a diet of the copepods, Acartia, Tortanus, Eurytemora, and Pseudocalanus, and grew well on a diet of smaller lobster larvae (Templeman 1936c). Two larvae collected in Vineyard Sound, Massachusetts, contained parts of crustacea, diatoms, and algae (Herrick 1895).

Juvenile and adult lobsters are omnivorous. They are primarily predators, catching live prey, but they also scavenge for food (Ennis 1973). The bulk of their diet consists of bottom invertebrates, crabs, sea urchins, mussels, polychaetes, periwinkles, and sea stars (Herrick 1895, 1909; Miller et al. 1971; Ennis 1973). Fish and plants also contribute to the diet (Herrick 1895; Ennis 1973). In a report by Ennis (1973) crabs, Cancer irroratus and Hyas araneus, made up 50% of the volume of food in the stomachs of lobsters collected in Bonavista Bay, Newfoundland. Sea urchins, Strongylocentrotus droebachiensis, were the next most important food (7%).

American lobsters apparently prefer to eat crabs. The responses of lobsters to the waterborne odors of crabs (Carcinus maenas), sea urchins, and mussels (Mytilus edulis) demonstrate that lobsters are attracted by crab odor more than the other two (Hirtle and Mann 1978). Lobsters prefer rock crabs (Cancer irroratus) over sea urchins when both are present in aquaria (Evans and Mann 1977).

Sea urchins and sea stars contribute a much larger proportion of the diet during the molting season than at other times of the year (Ennis 1973). This change in diet during molting may be one of selectivity for prey high in calcium, an important element in hardening the exoskeleton.

The diets of female and male lobsters (47-113 mm CL) are similar (Ennis 1973). Feeding activity declines in the fall as water temperatures decrease, and remains low in winter.

Predation

Juvenile and adult American lobsters are consumed by many bottom feeding fishes. Atlantic cod stomachs often are filled with juvenile lobsters (Herrick 1895). Most lobsters eaten by fish are less than 50 mm CL, but larger lobsters are eaten by Atlantic cod, sharks, wolffish, pollock, and goosefish (Herrick 1895; Cooper and Uzmann 1980). Skates, rays, cunner, tautog, striped bass, black sea bass, sea ravens, haddock, tilefish, conger eels, and weakfish sometimes prey upon juvenile lobsters (Herrick 1895; Cooper and Uzmann 1977). Predators of lobster larvae have not been identified but the planktonic larvae probably are consumed by surface-feeding planktivorous fishes.

Diseases and Parasites

Few diseases are known at the present time which affect the American lobster. Gaffkemia (Aerococcus viridans var. homari) and "shell" disease are two bacterial diseases that cause high mortality in holding pens (Stewart 1980). Incidence of gaffkemia in lobsters from natural populations along the Maine coast averaged 7% (Vachon et al. 1981). Lobsters also are infected with fungal diseases and epibiotic growths. Mussels, barnacles, marine algae, filamentous bacteria, stalked protozoans, and diatoms sometimes may completely cover the exoskeleton (Herrick 1909; McLeese and Wilder 1964). A trematode (Stichocotyle nephropsis), copepod (Unicaleuthes), Acanthocephela, and protozoa (*Porospora gigantea*, *Anophys* sp.) are parasites of the lobster (Stewart 1980).

ENVIRONMENTAL REQUIREMENTS

Temperature, salinity, and substrate are the most critical factors influencing lobster distribution and abundance. Also there is some evidence that lobster activity and feeding may be light dependent. Critical environmental factors are discussed below.

Temperature

Eggs of American lobsters hatch at water temperatures as low as 8°C in northern New England (Fogarty and Lawton 1983). At the Massachusetts State Lobster Hatchery the lowest temperature at which hatching was observed was 9.4°C (Hughes and Matthiessen 1962). Hatching usually begins when water temperatures are about 15°C and peaks near 20°C.

The average surface water temperatures during peak larval densities in Boothbay Harbor, Maine, range from 13.7° to 15.0°C (Sherman and Lewis 1967). These water temperatures are the maximum for the region. Larval densities in Buzzards Bay, Massachusetts, peaked when the surface water temperature was about 19°C and the bottom water temperature was about 17°C (Lux et al. 1983). Surface water temperatures ranged from 10.3 to 25.5°C when larvae were collected in Cape Cod Canal, Buzzards Bay, and Cape Cod Bay, Massachusetts (Collings et al. 1983).

The development of larvae is temperature dependent. Larvae attained stage V (which marks the end of the pelagic larval period) within 28 days after hatching at a water temperature of 19°C. Stage V was achieved in 50 days at 14°C, and 100 days at 10°C (Templeman 1936c). Lobster larvae are less tolerant to low temperatures than juveniles or adults. In one experiment all larvae died prior to molting at 5°C (Huntsman 1924).

Juvenile and adult American lobsters tolerate sea water temperatures ranging from -1 to 30.5°C (Huntsman 1924, McLeese 1956). Molting and growth cease when water temperatures drop below 5°C (Aiken 1980). The upper lethal temperatures (LD_{50} in 48 h) of lobsters (16 to 34 cm total length measured from tip of rostrum to tip of telson) acclimated to 27 combinations of temperature (5°, 10°, 15°C), salinity (20, 25, 30 ppt), and dissolved oxygen (2.9, 4.3, 6.9 mg/l) were reported by McLeese (1956). Acclimation conditions significantly affected the upper lethal temperature. Upper lethal temperatures ranged from 20.6°C for lobsters acclimated at 5°C, 20 ppt salinity, and 2.9 mg/l O_2 to 30.5°C for lobsters acclimated at 25°C, 30 ppt salinity, and 6.4 mg/l O_2 (Table 3).

Changes in water temperature stimulate migrations of offshore lobsters which tend to seek bottom water temperatures from 8 to 14°C (Uzmann et al. 1977). During the spring, lobsters offshore move from the outer Continental Shelf and upper slope to shallower water along the southern New England Continental Shelf, including Georges Bank and the coastal waters of New York, Rhode Island, and southern Massachusetts. It is possible that bottom water temperatures (8 to 14°C) in the shallower waters are more suitable for the extrusion of eggs, molting, and mating than are the summer bottom temperatures over the outer Continental Shelf and upper slope (Cooper and Uzmann 1971). Return lobster migrations to the outer shelf and upper slope waters begin in late summer and continue through November as inshore bottom water temperatures drop. By December the lobsters offshore have returned to the outer

Table 3. Upper lethal temperatures and lower lethal salinity and oxygen concentrations for American lobsters acclimated to 27 combinations of temperature, salinity, and oxygen (McLeese 1956).

Acclimation conditions: Temperature (°C)	Acclimation conditions: Salinity (ppt)	Acclimation conditions: Oxygen (mg/l)	Upper lethal temp.	Lower lethal salinity (ppt)	Lower lethal oxygen (mg/l)
5	20	2.9	20.6	11.0	0.72
		4.3	22.0	9.0	0.77
		6.4	23.7	9.0	0.72
5	25	2.9	22.4	12.0	0.57
		4.3	22.1	12.4	0.51
		6.4	24.6	9.2	0.24
5	30	2.9	24.0	10.8	0.29
		4.3	25.2	11.5	0.33
		6.4	25.7	6.0	0.20
15	20	2.9	27.3	9.0	0.86
		4.3	27.7	9.0	0.79
		6.4	27.8	8.2	1.20
15	25	2.9	27.5	10.7	0.80
		4.3	28.2	10.7	0.90
		6.4	28.0	9.5	1.00
15	30	2.9	27.8	10.6	0.66
		4.3	28.2	11.0	0.83
		6.4	28.4	11.2	0.83
25	20	2.9	28.5	11.5	1.72
		4.3	29.0	11.5	1.58
		6.4	29.3	11.1	1.26
25	25	2.9	29.0	14.3	1.17
		4.3	29.5	14.8	1.20
		6.4	29.6	14.0	1.60
25	30	2.9	28.7	15.4	1.30
		4.3	29.5	16.0	1.25
		6.4	30.5	16.4	1.17

shelf and upper slope waters where bottom temperatures are 8 to 12°C (Uzmann et al. 1977).

Salinity

Studies of American lobster larvae exposed to various salinities in water temperatures of 15.0 to 17.5°C, revealed that survival was highest at a salinity of 30 ppt and salinities as low as 21 ppt were only slightly less suitable (Templeman 1936). Survival of larvae to stage IV decreased as salinities dropped below 21 ppt, and no larvae survived less than 17.0 ppt. Larvae attempted to avoid salinities as low as 21.4 ppt at water temperatures near 22°C (Scarratt and Raine 1967). There is no information on survival rates of lobsters at unusually high salinities.

The lower lethal salinity levels (LD_{50} in 48 hours) of juvenile and adult lobsters acclimated to 27 combinations of salinity, dissolved oxygen, and water temperature were reported by McLeese (1956). Lower lethal salinities ranged from 6 ppt for lobsters acclimated at 5°C, 6.4 mg/l O_2, and 30 ppt salinity to 16.4 ppt for lobsters acclimated at 25°C, 6.4 mg/l O_2, and 30 ppt salinity (Table 3). Due to osmoregulatory stress, molting lobsters are less resistant to low salinities than hard-shelled lobsters.

Dissolved Oxygen

American lobsters can survive relatively low dissolved oxygen concentrations. McLeese (1956) reported that the lower lethal oxygen concentration was 0.2 mg/l for lobsters acclimated at 5°C and 30 ppt salinity and rose to 1.7 mg/l at acclimation conditions of 25°C and 20 ppt salinity (Table 3). Acclimation levels of temperature and salinity significantly affected the lower lethal oxygen concentration whereas acclimation level of oxygen did not have a significant effect (McLeese 1956).

Substrate

Juvenile and adult American lobsters occupy substrates characterized by sand-rock, bedrock-rock, mud-rock, mud-silt, and clay-silt (Thomas 1968; Cobb 1971; Cooper et al. 1975; Cooper and Uzmann 1980). The most common substrate occupied by inshore lobsters is sand with overlying boulders. This substrate is uncommon in offshore areas where it is usually restricted to the heads of submarine canyons (Cooper and Uzmann 1980). The most common substrates in offshore areas are mud or clay with overlying silt. Lobsters burrow or excavate bowlshaped depressions into these soft substrates for cover and protection (Cooper and Uzmann 1980).

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16. Abstract (Limit: 200 words)

Species profiles are literature summaries of the taxonomy, morphology, distribution, life history, and environmental requirements of coastal aquatic species. They are designed to assist in environmental impact assessment. The American lobster (*Homarus americanus*) is a valuable commercial shellfish. After spawning, lobsters undergo a series of molts; as adults they live in coastal and offshore waters. Lobsters are captured in baited traps and incidentally in trawls. About 5-6 million pounds were captured commercially in 1983, a downward trend from 1971. Major environmental factors affecting reproduction, growth, and survival are water temperature, oxygen concentration, salinity, and substrate.

17. Document Analysis a. Descriptors

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