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October 1983

TR EL-82-4

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

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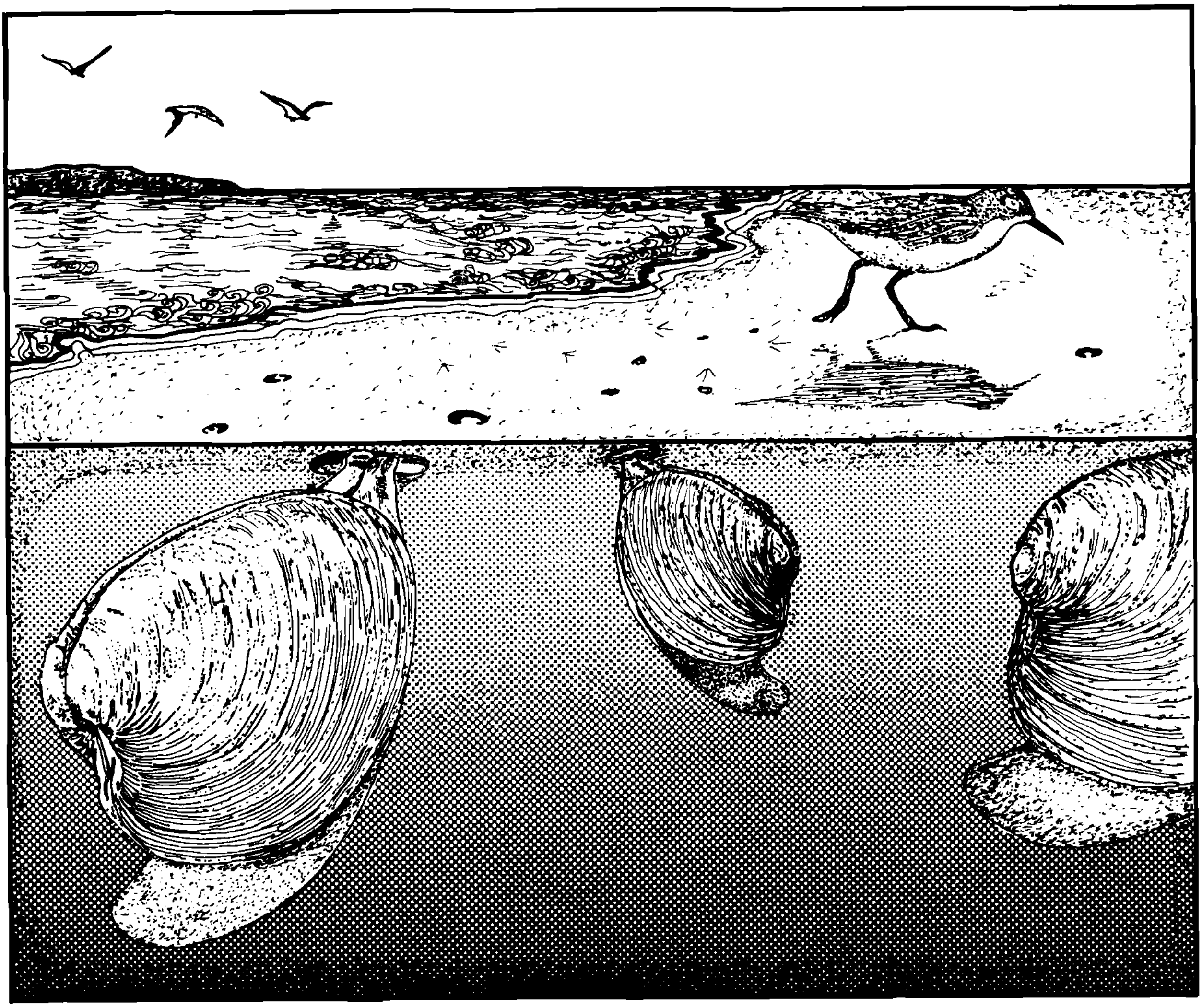

Fish and Wildlife Service
U.S. Department of the Interior

Coastal Ecology Group
Waterways Experiment Station
U.S. Army Corps of Engineers

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

HARD CLAM

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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.

A Habitat Suitability Index (HSI) model is being prepared by the U.S. Fish and Wildlife Service for the hard clam. HSI models are designed to provide a numerical index of the relative value of a given site as fish or wildlife habitat.

Suggestions or questions regarding this report should be directed to:

Information Transfer Specialist
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Attention: WESER
Post Office Box 631
Vicksburg, MS 39180

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CONVERSION FACTORS

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 (1)	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 (mt)	2205.0	pounds
metric tons	1.102	short tons
kilocalories (kcal)	3.968	BTU
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
BTU	0.2520	kilocalories
Fahrenheit degrees	0.5556(F° - 32)	Celsius degrees

ACKNOWLEDGMENTS

The cover is adapted from an illustration by Trudy Nicholson and is used with permission from Grass Medical Instruments and the artist. Figure 4 is reproduced with permission from the General Secretary of the Conseil International Pour L'Exploration de la Mer. We are grateful for the review by Robert L. Dow, Maine Department of Marine Resources, Augusta.

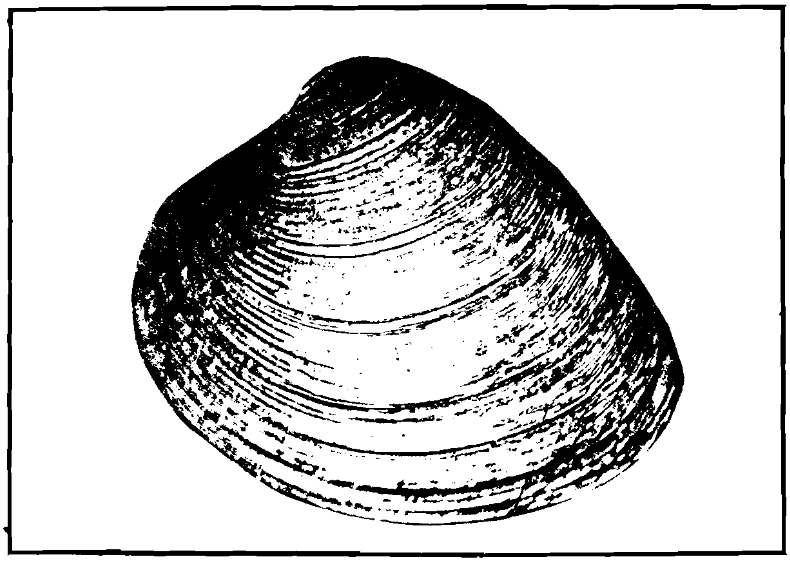

Figure 1. Hard clam.

HARD CLAM

NOMENCLATURE/TAXONOMY/RANGE

Scientific name . . . . Mercenaria mercenaria L. Widely known as Venus mercenaria before Wells (1957) reassigned the species to the genus Linneaus originally applied

Preferred common names . . Quahog in the Northern United States, hard clam in the Southern United States (Figure 1)

Other common names . . . . Quahaug, hard-shelled clam, round clam, cherrystone clam, little-necked clam

Class	Bivalvia (Pelecypoda)
Order	Eulamellibranchia
Suborder	Heterodonta
Family	Veneridae

Geographical range: The hard clam occurs in intertidal and subtidal areas to depths of 15 m along the Atlantic and gulf coasts from the Gulf of St. Lawrence to Texas. The hard clam is most abundant from Massachusetts to Virginia. It has been introduced to Europe and California. A similar species, M. campechiensis, occurs from North Carolina southward to Mexico and is also called the hard clam.

MORPHOLOGY/IDENTIFICATION AIDS

The hard clam has a thick shell with a violet border and short siphons (Verrill 1873; Stanley 1970; Morris 1973). The mean length of the thick solid shell is 60 to 70 mm, but some are 120 to 130 mm. The ratios of length (L), height (H) and width (W) are: L/H 1.25; H/W 1.52; L/W 1.90. The thickness index (ratio of shell volume to internal volume) is 0.60.

The external surface has numerous concentric lines, conspicuous and closely spaced near the ends, more widely spaced around the umbo, especially in younger shells. The center of each valve is smoother than the distal portion. The umbo is anterior and projects nearly to the front of the shell. The elliptical, somewhat pointed shell has a grayish-white exterior and a white interior with a dark violet border near the margins. The colored part of the shell was fashioned into wampum by the American Indians for use as money, hence the scientific name. The interior ventral margins are denticulate.

The internal anatomy also has distinctive characteristics. Short siphons are united from their bases to near the ends; the incurrent siphon has a short fringe of tentacles. The siphon tubes are yellowish- or brownish-orange toward the end and may be streaked with dark brown or opaque white. The foot is large, muscular, and plow shaped. The mantle lobes are separate along the front and ventral edges of the shell with thin edges folded into delicate frills, some of which are elongated near the siphons. Foot and mantle edges are white.

REASON FOR INCLUSION IN SERIES

Hard clams are the most extensively distributed commercial clam in the United States and have the greatest total market value (Ritchie 1977). Their occurrence in clean substrates accessible to the public makes the hard clam a popular recreational species. Their shore habitat is vulnerable to coastal construction projects and pollution from urban and industrial development. The absence of hard clam populations is an ecological indicator of disturbances. Because adults do not move, repopulation of annihilated hard clam beds depends on transport of larvae and several years growth. Hence, a temporary disturbance causes a long-term impact.

LIFE HISTORY

Spawning

The spawning season extends from May through August, dependent on latitude and temperature. In temperate latitudes the largest and densest spawns occur during July (Carriker 1961). In the York River, Virginia, the peak is in May, and is progressively later in Raritan Bay, New Jersey, and Narragansett Bay, Rhode Island (Jeffries 1964). Female hard clams require 2 to 2.5 months to spawn out completely, but the greatest release of eggs is during the initial spawning of the season (Ansell 1967a). Spawning is more intense during neap tides than spring tides, presumably because of higher temperatures during neap tides (Carriker 1961).

Temperature is the decisive factor for final gamete maturation. In a 2-year study in the Lower Little Egg Harbor, New Jersey, the median daily spawning temperature was 25.7°C with a range of 22° to 30°C (Carriker 1961). Seventy-three percent of the spawnings occurred during 2 to 3 days of rising temperatures. Kennish and Olsson (1975) cited 21° to 25°C as the required or preferred temperature range. Spawning in England takes places at 18° to 20°C (Mitchell 1974). When threshold temperatures are reached, males release semen that contains pheromones. The pheromones are carried by water currents to the females, which are then stimulated to release eggs (Nelson and Haskin 1949).

Sexual maturity usually is reached at 2 years of age (3 years in many areas in the North Atlantic region). The shell length at this age is between 32 and 38 mm. Size, not age, determines sexual maturity, so that slower growing individuals mature later than 2 years of age. The peak of reproductive potential is reached at 60 mm; larger, older hard clams gradually lose the reproductive capacity (Belding 1931).

Fecundity and Eggs

The average number of eggs released by a 60-mm female in the wild is about 2 million (Belding 1931). In laboratory tests, the average-sized female released 8 million eggs per season (Davis and Chanley 1956; Ansell 1967a). The fecundity of one large female was 16.8 million eggs, whereas small clams (33 mm) had far fewer eggs (Bricelj and Malouf 1980). About 2,000 spermatozoa are shed for each ovum.

The spherical eggs are 78 µm in diameter with closely packed yolk granules (Belding 1931). A large gelatinous capsule distinguishes the hard clam egg from the eggs of other mollusks. Eggs are released through the excurrent siphon, and the capsule swells after contact with water until it is 3.2 times the diameter of the egg. The gelatinous capsule imparts buoyancy, so that the eggs are pelagic and carried by tidal and coastal currents. Spermatozoa swimming in water come into contact with and penetrate the capsule, fertilizing the egg.

At about 10 hr the embryo developing within the capsule becomes covered with cilia. The lashing of the cilia tears the membrane and gelatinous capsule; the ciliated gastrula escapes into the water. The egg may be carried 2 to 25 km from the spawning site.

Larvae

The larva develops into a trochophore larva 12 to 14 hr after hatching (Belding 1931). The shape, like a top, and the cilia on the blunt anterior end result in spiral swimming with rotation around the long axis in either direction. A functional mouth develops and the larva commences feeding on suspended particulates, especially dinoflagellates. The larvae concentrate near the surface during daylight at about 1 m below the surface (Carriker 1952). At night the larvae are more evenly mixed in the water column.

A shell gland forms opposite the mouth by 24 hr after hatching, and a thin transparent shell is secreted; the larva is now called a veliger (Belding 1931). The veliger drifts in ocean and estuarine currents with limited ability to swim horizontally. The veliger is able to move 7 to 8 cm/min vertically by extending the ciliated velum (Mileikovsky 1973). Vertical swimming may enable the veliger to control horizontal displacement and thus travel to better areas (Mileikovsky 1973). Vertical migration is stimulated by turbulence, which could bring veligers into water currents for transport (Carriker 1961). Greatest numbers of veligers occur in the water column 3 hr after low tide (Moulton and Coffin 1954), which suggests differential tidal transport. By entering the water column on the incoming tide, the veligers would be transported up the estuary and thus be retained within the estuary. Veligers, however, also migrate upwards during daylight regardless of tide (Carriker 1961). Veligers are important zooplankters in estuaries during the summer (Carriker 1952; Moulton and Coffin 1954; Jeffries 1964). Densities may exceed 500/l.

The veliger stage lasts 6 to 12 days, depending on temperature. Metamorphosis of the veliger occurs at 16 to 30 days at 18°C, 11 to 22 days at 24°C, and 7 to 16 days at 30°C (Loosanoff et al. 1951).

Juvenile Seed Clam

When the veliger becomes 2 to 3 mm long, the shell thickens, a foot replaces the velum, and a byssal gland develops, marking metamorphosis to the seed clam. Metamorphosis is inhibited at salinities below 17.5 to 20 parts per thousand (ppt) (Castagna and Chanley 1973), perhaps ensuring that seed clams avoid setting in an environment with salinities unsuitable for adults.

Good sets occur in years with low freshwater inflow into the estuary (Hibbert 1976).

The byssal gland secretes a tough thread, the byssus, which anchors the animal to the substrate. Seed clams set more densely in sand than mud (MacKenzie 1979); bits of shell or detritus may also serve as anchors. Distribution of adults suggests that the average size of substrate particles exceeds 2 mm diameter (Saila et al. 1967) although in the laboratory size of sand grains was not associated with setting (Keck et al. 1974). The seed clams prefer setting on a firm surface with a thin layer of detritus (Carriker 1952) or on shells coated with mud (Carriker 1961).

The set may exceed 125 clams/m^2 in good habitat (Carriker 1961) with extraordinary sets of 270,000/m^2 (Dow and Wallace 1955), but set is not necessarily related to adult concentrations because of movements and mortality. Seed clams seek a preferred habitat: a bottom with a few small rocks and shells. They discern between silt and sand in the laboratory (Keck et al. 1974), explaining the selection for sand in nature.

The seed clams begin a final migration to their ultimate habitat in their second summer (Burbanck et al. 1956). To move, the clam casts off the byssus and uses the foot for locomotion (Belding 1931). On finding desirable conditions, the young clam spins a new byssus and reattaches itself to a small object. Byssal fibers are used for anchorage for about a year, until the young clam is 10 mm long; the juveniles then metamorphose and assume the burrowing habits of the adults. A population in Maine was displaced an average of 30 m by a storm (Dow and Wallace 1955).

The habitat distribution of seed clams is altered by predation. Clams that set among oyster shells or stones are protected (Maurer and Watling 1973); without cover, seed clams largely disappear. Normally they do not occur in areas exposed to wave action or strong currents (Anderson et al. 1978), but in a saltwater pond they survived better on an unstable bottom because crab predation was absent (Carriker 1959).

Adult

The adult hard clam lives in the substrate and burrows with a muscular foot. It remains in essentially the same location for the remainder of its life. In 38 days adults moved laterally an average of 5 cm and a maximum of 15 cm from the place where seed clams first bedded (Chestnut 1951). Clams 20 to 30 mm long traveled up to 30 cm in 2 months (Kerswill 1941). Thus, the adult habitat is determined by where the juvenile beds.

Adults bury deeper in sand (mean depth 2 cm) than in mud (mean depth 1 cm), and small adults burrow deeper than larger ones (Stanley 1970). If dug up, the hard clam reburrows, and if covered, can escape upward (Belding 1931). A 6.8-cm long clam moved vertically at 44 cm/hr (Kranz 1974). A clam can escape 10 to 50 cm of overburden if the sediment dumped is the same as surroundings. Foreign sediment reduces escapability.

The adult is found in the intertidal and subtidal areas of bays and estuaries. Hard clams are most abundant in the lower estuary and are seldom found in the upper estuary (Turner 1953). In some locations they are absent above the mean tide line (Hibbert 1976). Greenwich Cove, Maine, had about three times more clams at the seaward end of the cove than in the upper cove (Tiller 1950). In Rand's Harbor, Massachusetts, about 50% of the population was on the gravel slope, 25% in the muddy channel, and 25% in the subtidal zone (Burbanck et al. 1956). In South Carolina, the hard clam is usually absent from open estuaries, but is present in small channels and protected areas (Anderson et al. 1978). In Georgia hard clams are largely in intertidal areas protected from wave action (Godwin 1968). Loosanoff (1946) also mentioned intolerance to rough waves. There are, however, oceanic populations, e.g., in the shoals of Nantucket Sound (Turner 1953). Several reviews (Belding 1931; Loosanoff 1946) state that hard clams occur to depths of 15 m; Burbanck et al. (1956) reported the maximum depth to be 8 m.

COMMERCIAL/SPORT FISHERIES

Fisheries

The hard clam is harvested for commerce and recreation. It is more widely distributed than any other clam species in U.S. waters and is the most valuable commercial species (Ritchie 1977). The fishery is located chiefly along the mid-Atlantic Bight. North of Cape Cod (Figure 2) and in the Gulf of Mexico it is important only in isolated areas (McHugh 1979). In Maine, for example, the only hard clam fishery was in Casco Bay with good year classes in 1937, 1947, and 1952 (Dow 1955); the catch is now insignificant (Table 1).

Hard clams are harvested commercially by bullrakes, hand tongs, and power dredges. The power dredge disturbs the substrate no more than bullraking, and all evidence of harvesting disappears within 500 days (Glude and Landers 1953). A power dredge with an escalator caused only temporary disturbance of the substrate and increased the catch of the more valuable small clams relative to larger clams (Godcharles 1971). Dredging, however, destroys seagrasses and benthic algae that recolonize dredged areas slowly; thus dredging has a long-term impact.

The annual landings of hard clam along the Atlantic seaboard average about 14 million pounds (McHugh 1979). All harvest reported is meat weight. The harvest in Massachusetts in 1970

Table 1. Hard clam landings in Maine and Massachusetts (*Current Fishery Statistics*, National Oceanic and Atmospheric Administration; Hutchinson and Knutson 1978; and R. L. Dow, Maine Department of Marine Resources, Augusta).

	Meat Weight (100 kg)	
Year	Maine	Massachusetts
1931	898	NA[1]
1932	611	NA
1933	53	NA
1935	8	NA
1937	60	NA
1938	250	NA
1939	2	NA
1940	17	NA
1941	540	NA
1942	555	NA
1943	358	NA
1944	140	NA
1945	1,367	NA
1946	763	NA
1947	437	NA
1948	1,310	NA
1949	2,675	NA
1950	2,283	NA
1951	2,580	NA
1952	1,924	NA
1953	1,520	NA
1954	1,323	NA
1955	1,133	NA
1956	1,306	NA
1957	1,635	NA
1958	1,146	NA
1959	727	NA
1960	290	6,355
1961	57	7,550
1962	5	5,983
1963	10	6,686
1964	10	6,532
1965	12	4,808
1966	>1	5,997
1967	NA	6,305
1968	>1	5,221
1969	40	5,257
1970	37	5,700
1971	29	5,330
1972	31	4,840
1973	14	5,611
1974	>1	4,922
1975	36	5,035
1976	14	4,296

[1] NA = Data not available.

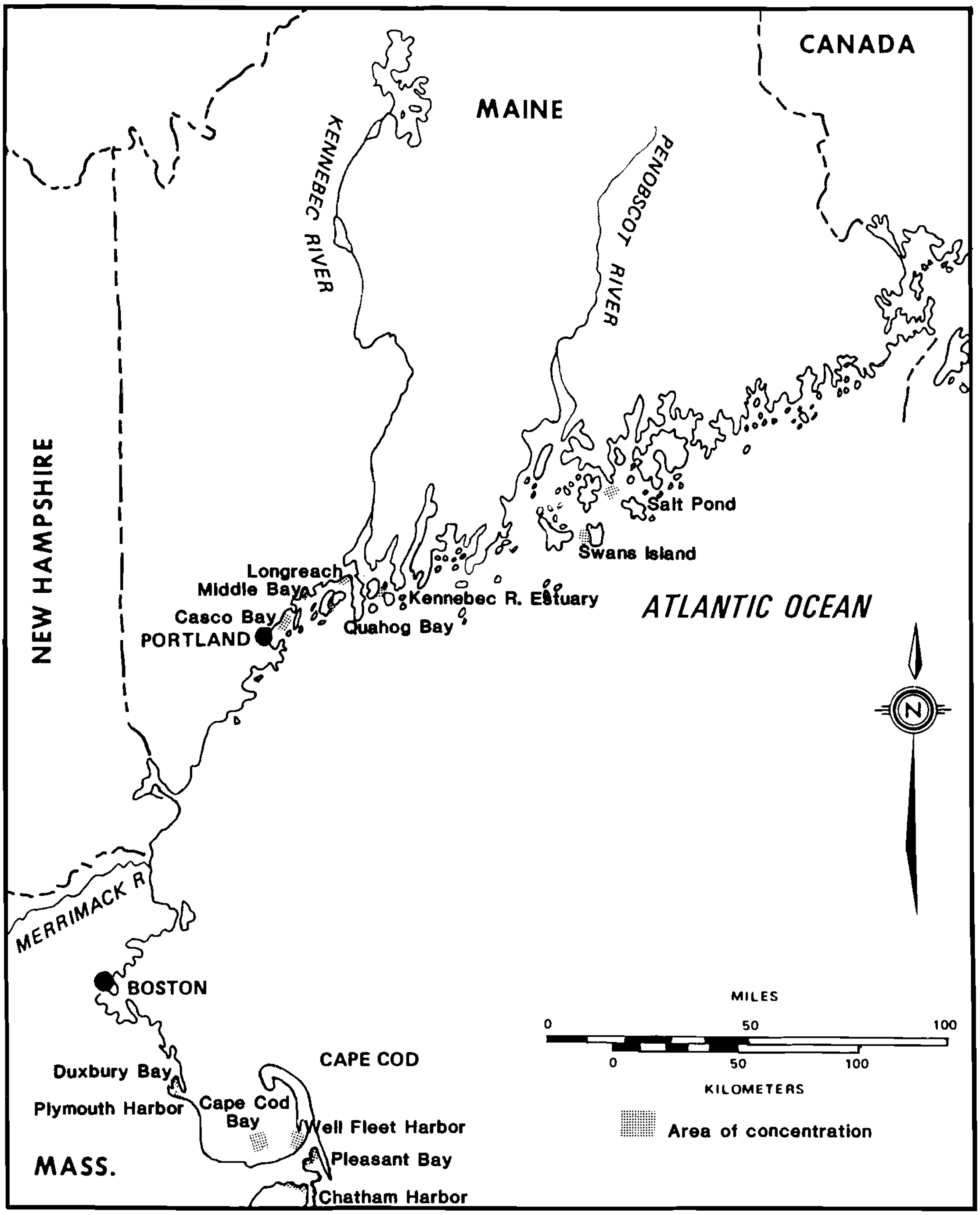

Figure 2. Major populations of hard clam in the North Atlantic region.

was 532,000 lb, worth $1,461,132 (National Marine Fisheries Service 1979). In the same year, Maine landed only 605 lb. Hard clam harvest peaked in New England in 1953, with 7.2 million pounds (Dow 1977). The U.S. landings declined between 1965 and 1975, concomitant with a 300% increase in value (Zakaria 1979). About 40% of the U.S. harvest is from Great South Bay on Long Island (MacKenzie 1977).

The price of the hard clam varies with their size and the season. The littlenecks (46 mm) command a higher price ($60/bu) than cherrystones (77 mm, $22/bu), or chowder clams (97 mm, $13/bu)(Ritchie 1977). Hard clams are also processed and marketed as clam juice. The market for fresh hard clams is made possible because the clams remain alive for 1 to 3 weeks out of water if kept cool. In contrast, Mercenaria campechiensis does not remain alive nearly as long out of water even though it too has a thick shell.

In heavily fished areas clams are harvested as soon as they reach a marketable size (Ritchie 1977), i.e., at 2 to 3 years old. Such harvest is the best use of the resource because the smaller clams are more valuable, and the larger clams grow more slowly. Older clams are found only in areas that are not actively fished (Greene 1979); here the maximum life span of 20 to 25 years may be reached (Belding 1931).

Population Dynamics

Larval hard clams may be one of the most abundant plankters in estuaries. Population densities of 25/l (Carriker 1952) and 572/l (Carriker 1961) have been measured. On the basis of these estimates and the bottom area, we calculated that there would be 50,000 to 1.1 million larvae/m^2 in an estuary 2 m deep. About 6 million larvae are produced from spawning of the three pairs of adults found on a typical 1 m^2 of bottom.

The number of seed clams that set in Little Egg Harbor, New Jersey was estimated to be 125/m^2 (Carriker 1961). Populations of seed clams in restricted locations in Casco Bay, Maine, may reach 270,000/m^2 (Dow and Wallace 1955).

Adult population density varies widely depending on numerous environmental factors discussed below. In Maine, populations in Boothbay Harbor ranged from 4/m^2 to 13/m^2 (Tiller 1950). In Rhode Island, populations in Greenwich Bay ranged from 2/m^2 to 12/m^2 (Stickney and Stringer 1957). Along the Georgia coast abundance ranged from 0.1/m^2 to 21/m^2 (Godwin 1968). Introduced populations in Great Britain reached densities of 6 to 8/m^2 (Ansell 1963). Biomass (meat weight) ranged from 1.6 g/m^2 in poor habitat to 36 g/m^2 in good habitat (O'Conner 1972). In Maine, populations of 2,000 bushels/acre (bu/A), 1,500 bu/A, and 1,250 bu/A were estimated in three areas (Dow 1952). Densities of 110/m^2 and 540/m^2 were mentioned.

Natural mortality is enormous in the larval and seed clam stages, but nil once the shell becomes thick enough to resist predators. Based on densities of different life stages, monthly mortality coefficients (Z) of 1.7 for eggs and 1.5 for larvae were calculated. The annual mortality coefficient from seed clam to adult was 3.0. Figures are available for calculating mortality coefficients of natural populations. Based on nine estimates of adult mortality in England, an average annual mortality coefficient was calculated to be 0.80 (Hibbert 1976). The mortality coefficient of adult clams held in trays and protected from predators in South Carolina was 0.13 (Eldridge and Eversole 1982). These mortalities represent natural mortality, which equals the instantaneous total mortality Z in the absence of harvest. Overwinter mortality of hard clams in two sites in Maine was 30% and 40% (Dow 1965).

Because of the method of fishing described above, it was not possible to arrive at a meaningful estimate of fishing mortality F. Hard clams tend to be completely harvested in any particular bed, resulting in instantaneous mortality of a different sort. Mortality of sublegal hard clams was estimated to be 30% each time a flat was disturbed by digging (Dow 1953).

Survivorship follows an exponential decay (Figure 3). Very few of the larvae successfully set, and few of the seed clams reach adulthood. The mortality rate appears to decrease slightly in the adults. Obviously survivorship depends on the microhabitat that individuals happen to occupy. Survival of hard clams planted in Casco Bay, Maine, was 91% over one summer (Gustafson 1954). There is little relationship between stock size and recruitment of young; a few adults produce sufficient offspring to sustain the populations.

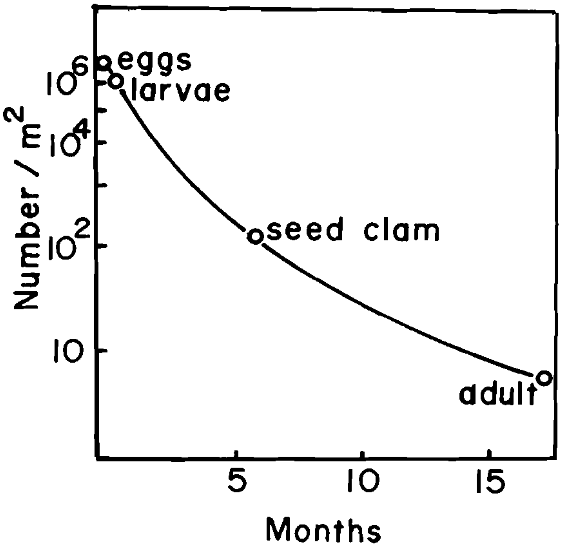

Figure 3. Survivorship of hard clams from eggs to adult, based on a composite of the data cited in the text.

GROWTH CHARACTERISTICS

The hard clam grows rapidly in favorable environments. The veliger larvae grow from 10 μm to 200 μm in 7 days (Carriker 1952). At 18°C the larvae increased from 105 μm to 183 μm in 20 days, whereas at 30°C they grew to this size in 12 days (Loosanoff et al. 1951). The daily percent growth rate of veligers as a function of temperature and salinity is:

$$\text{Growth} = -288 + 12.40T + 14.09S - 0.33T^2 - 0.37S^2 + 0.24TS$$

where T is the temperature in °C and S is the salinity in ppt (Lough 1975). At 20°C and 30 ppt, for example, the daily growth would be 68%.

Seed clams at the end of their first summer are 2 to 4 mm in Canadian waters, 5 to 7 mm in New York, and 16 mm in Florida (Ansell 1967b). The size reached depends largely on the length of the growing season.

The dependence of adult growth on the length of the growing season results in a pronounced latitudinal effect (Figure 4). The annual increment

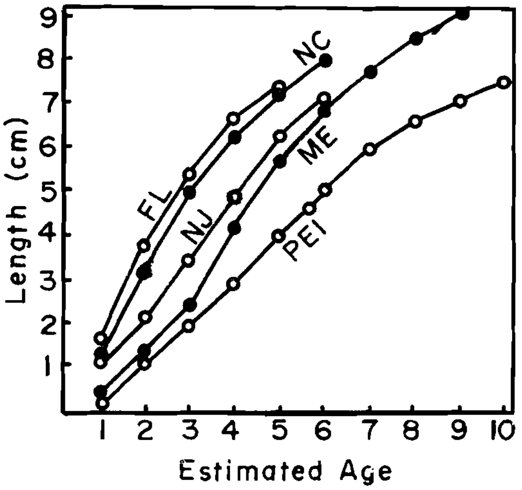

Figure 4. The increase in shell length with age of hard clams from Florida, North Carolina, New Jersey, Maine, and Prince Edward Island (Ansell 1967b).

in shell length, estimated from Figure 4 during the 2 to 5 years of linear increase, was 10 mm in Canada, 13 mm in Maine, 14 mm in New Jersey, and 23 mm in North Carolina. The annual rate of shell formation was about the same between North Carolina and Florida. In Casco Bay, Maine, 20- to 25-mm clams increased by 13 to 16 mm in one year, whereas 46- to 50-mm clams increased only 5 to 12 mm (Wallace 1952). The daily shell increment is about the same during peak growth regardless of latitude (Ansell 1967b), again suggesting that it is the length of the growing season that is decisive in determining annual growth.

Adult growth rate slows with increase in length. Clams of 35- to 39-mm length grow about three times as fast as clams that are 65 to 69 mm (Pratt and Campbell 1956).

Of interest to clam managers is the time required to reach the minimum legal size, which in most states is reached in about 3 years. In Massachusetts hard clams are about 3.5 years old by the time they reach the 50-mm legal size. In Rhode Island and Connecticut, where growth is faster, clams reach the 44-mm legal size in about 2.5 years. At the opposite extreme, Florida has a size limit of 56 mm, and clams reach this size in about 3 years. In Maine, however, the 51-mm size limit is not attained until about 5 years.

ECOLOGICAL ROLE

Feeding Habits

The adult hard clam feeds by filtering out plankton and microorganisms that are carried along the bottom by currents (Chestnut 1951). Ansell (1967a) suggested that hard clams depend on plankton abundance before and during spawning to furnish sufficient energy to ripen the gonads. If the food supply is inadequate, spawning will not occur. Food densities of 300 mg/l of carbon are optimal for feeding (Tenore and Dunstan 1973).

Food and other materials are taken in through the incurrent siphon. Tentacles on the siphon detect excessive concentrations or oversized particles in the water and cause the siphon to close. The mantle, visceral mass, and gills are ciliated and secrete mucus. Particles brought in through the incurrent siphon attach to the mucus. Deposits on the gills are collected by the cilia and carried towards the mouth (Kellogg 1903). The palps at the mouth entrance determine, by volume, whether the particle mass will be ingested or rejected. Only small masses are selected for digestion. Complex patterns of cilia movement remove the waste, called pseudofeces, from palps and gills. Eventually all waste materials are collected on the mantle and carried to the base of the incurrent siphon, avoiding the stream of incoming seawater. When sufficient waste has been collected, the adductor muscle suddenly contracts, forcibly ejecting a stream of water containing the waste mass from the incurrent siphon (Kellogg 1903).

Predation

Predation is the primary natural control of hard clam populations (Virstein 1977). It is preyed on by fish, birds, starfish, crabs, and other mollusks. Its defenses are burrowing and setting among shells or rocks. Without shell or rock cover the juvenile hard clam is nearly exterminated by predators. Survival in penned sites was 94% compared to 9% in an unpenned area (Kraeuter and Castagna 1980).

Crabs are the most serious predators of hard clams. The crabs crush smaller clams with their claws, but chip the edges of the shells of larger clams. A rock crab (Cancer irruratus) may consume 30 small clams/hr; a mud crab (Neopanope sayi), 14 clams/hr (MacKenzie 1977). Mud crabs may be as dense as $50/m^2$. One reason crabs are effective predators is that they extract the clam from the sediment. The rock crab, blue crab (Callinectes sapidus), and green crab (Carcinides maenas) dig up the clams, whereas mud crabs bury themselves to crush the clam in place (MacKenzie 1977). Hard clams greater than 7 mm long are not vulnerable to mud crabs, and clams longer than 15 mm are not vulnerable to rock crabs (MacKenzie 1977).

Mollusca are the next most important predators. Oyster drills (Urosalpinx cinerea and Eupleura caudata) and the moon snails (Polinices duplicata and Lunatia heros) drill holes in the shell and remove the clam's body tissues. The whelks (Busycon canaliculatum and B. caria) chip off the outer edge of the shell to make a hole through which they insert their proboscises and ingest the clam's soft parts by alternately rasping and swallowing (Carriker 1951). Hard clams are vulnerable to oyster drills until 20 mm long and to moon snails until 50 mm (MacKenzie 1977). In addition, the adult hard clam may destroy its own larvae by taking them through in the incurrent siphon.

The sea star (Asterias forbesi) pulls the valves of adults apart with its tube feet and inverts its stomach into the body cavity (MacKenzie 1979; Doering 1982a). If a sea star is present, hard clams bury deeper (Pratt and Campbell 1956; Doering 1982b). Fish, such as flounder, and waterfowl feed on larvae and young (Belding 1931).

ENVIRONMENTAL REQUIREMENTS

Temperature

Temperature is the most important factor in growth and reproduction. The harvest of the hard clam in Maine was highly correlated (r = 0.80) to the August sea temperature 2 years previously (Sutcliffe et al. 1977). Dow (1977) recorded a high significant correlation between mean annual sea temperature and populations of adult hard clams.

Spawning occurred over the range 22° to 30°C median daily temperature in Little Egg Harbor, New Jersey (Carriker 1961) and 21° to 25°C in Barnegat Bay, New Jersey (Kennish and Olsson 1975). Spawning generally occurred during periods of rising temperature.

The optimum temperature for larvae was 22.5° to 25°C in brackish water and 17.5° to 30°C at a higher salinity (Davis and Calabrese 1964). Carriker (1961) stated that larvae tolerated 13° to 30°C. Lough (1975) found that eggs required temperatures above 7.2°C, but that larval survival was highest between 19° and 29.5°C. Maximum growth occurred at 22.5° to 36.5°C. Embryos and veliger larvae developed abnormally and died at 15°C and 33°C; hinged larvae tolerated these temperature extremes (Loosanoff et al. 1951). The minimum temperature for growth when clams were fed naked dinoflagellates was 12.5°C, but higher temperatures were needed to digest algae (Davis and Calabrese 1964). Thus, temperature, salinity and food are all interrelated.

The adult hard clam tolerates temperatures from below freezing to about 35°C. The adult can survive to -6°C, but dies when 64% of the tissue water has changed to ice (Williams 1970). Hard clams located in bars elevated above the gradient of the mud flats had 100% winter mortality, probably because of freezing (Dow and Wallace 1951). Summer temperatures of 33° to 34°C are tolerated (Van Winkle et al. 1976; Mackenzie 1979).

Sublethal effects of temperature include little growth below 10°C (Pratt and Campbell 1956). Shell growth ceases below 8°C (Belding 1931). The hard clam hibernates at temperatures of 5° to 6°C (Loosanoff 1939). Pumping water required for feeding ceases below 6°C and above

32°C (Hamwi 1968). The extension of the siphon also indicates pumping; the temperature range for siphon extension was 1° to 34°C (Van Winkle et al. 1976). The limits for growth also may depend on the type of food.

Estimates of the optimum temperature for hard clam growth vary from about 23°C (Pratt and Campbell 1956) to about 20°C (Ansell 1967b). An optimum mean annual temperature of 10°C was cited by Dow (1977). Other biological activities may indicate thermal optima. Hamwi (1968) found maximum pumping at 24° to 26°C. Siphon extension was greatest in the range of 11°C to 22°C (VanWinkle et al. 1976). There were two optima for shell calcium deposition: 13° to 16°C, and 24°C (Storr et al. 1982). The optimum range for burrowing is 21° to 31°C (Savage 1976).

Hard clams are adversely affected by rapid temperature changes. Rapid temperature fluctuations of + 5°C in the discharge from a nuclear power plant have caused breaks in shell growth (Kennish 1976). Summer growth was reduced 60% to 90% in hard clams transplanted to this discharge site.

Salinity

The hard clam occurs in environments with salinities ranging from about 10 ppt to about 35 ppt, with possible geographic difference. Belding (1931) cited 23 to 32 ppt as the general range of tolerance. In Wellfleet Harbor, Massachusetts, salinity ranged from 20 to 34 ppt (Curley et al. 1972). The normal range of salinities given by MacKenzie (1979) was 15 to 35 ppt. In South Carolina hard clams do not usually occur below 18 ppt (Anderson et al. 1978). Natural beds occur at salinities of 10 to 28 ppt (Loosanoff 1946).

Salinity appears to be most critical during the egg and larval stages. The embryos in Long Island Sound develop only in the range of 20 to 32 ppt; at 35 ppt only 10% developed (Davis 1958). Veliger survival was low during high rainfall (Carriker 1961). Veliger growth was best at 20 to 27 ppt. Castagna and Chanley (1973) stated that larvae required higher salinities than adults and noted that metamorphosis to seed clams did not occur below 17.5 to 20 ppt. Embryos developed normally between 20 and 35 ppt, with an optimum at 27.5 ppt. The minimum salinity for larvae was 15 ppt. In Southampton Water, England, young occurred only in years of low freshwater inflow from the River Test (Mitchell 1974).

Juveniles and adults close their shells during episodes of diluted seawater and hence tolerate low salinities. Juveniles remained alive in freshwater for 22 days in the laboratory (Chanley 1958). At 10 ppt they began dying at 28 days; at 10 and 15 ppt there was little feeding or burrowing. Burrell (1977) reported that adult hard clams exposed to salinities as low as 0.3 ppt in the Santee River system, South Carolina, survived for 14 days; less than 5% died because of heavy freshwater runoff. Pumping in the laboratory ceased below 15 ppt and above 40 ppt, with maximum pumping at 23 to 27 ppt (Hamwi 1968). The siphons were rarely extended in the laboratory at salinities below 17 ppt and above 38 ppt (VanWinkle et al. 1976). The optimum salinity range for siphon extension was 24 to 32 ppt. The slightly different findings noted above are probably a result of temperature-salinity interactions. Davis and Calabrese (1964) reported an optimum salinity for larvae of 27 ppt. At reduced salinities, e.g., 22.5 ppt, the temperature tolerance was reduced. Lough (1975) also measured a strong interaction between temperature and salinity; maximum survival of eggs was above 28 ppt and above 7.2°C and of larvae, between 21 and 29 ppt at 19° to 29.5°C. The larvae grew best between 21.5 and 30 ppt at 22.5° to 36.5°C.

Dissolved Oxygen

Changes in dissolved oxygen do not affect hard clams as much as changes in temperature and salinity. All life stages tolerate nearly anoxic conditions for long periods, but may cease growing. Embryos require only 0.5 mg/l dissolved oxygen and die only at oxygen levels below 0.2 mg/l (Morrison 1971). Embryos at 0.34 mg/l fail to develop to the trochophore stage. Larval growth is nearly zero at such low oxygen levels. Growth occurs at 2.4 mg/l but is best at 4.2 mg/l.

Adults have tolerated low oxygen in the laboratory, but metabolism was depressed. The hard clam can tolerate less than 1 mg/l for 3 weeks and still be capable of reburrowing (Savage 1976). Growth is surpressed at low oxygen. Below 5 mg/l, oxygen consumption progressively declines and an oxygen debt is incurred (Hamwi 1969). The oxygen debt is rapidly repaid in a few hours after return to aerobic conditions. Ultimately, hard clams succumb to hypoxic environments. Hard clams nearly disappeared from a eutrophic environment near a duck rearing area on Long Island, New York (O'Conner 1972).

Substrate

Substrate is obviously important to a species that burrows, and numerous studies have shown that hard clams are associated with a sandy bottom rather than a mud bottom (Allen 1954; Maurer and Watling 1973; Mitchell 1974). Water circulation may be the decisive element in the distribution of hard clams (Greene et al. 1978). Because water currents sort bottom substrates, the correlation between currents and bottom type is high. Without attempting to determine whether substrate or current is more important, we will review the relationships between each and hard clam distribution. Even if substrate per se is not critical, it does serve as an index to water currents.

A series of studies indicate that larvae prefer to set on sand rather than mud. Larvae set more densely on sand than on mud (MacKenzie 1979), and Keck et al. (1974) found an association between grain size and setting; 781 set on mud of 0.05-mm diameter, whereas 2,083 set on sand of 0.50 mm. There was not much difference in setting between sand grain sizes of 0.25, 0.50, 0.71, and 1.00 mm. Larvae discriminated between sand (0.25 mm) and mud (0.05 mm). The highest concentration of seed clams was on shells coated with mud (Carriker 1961). The young can emerge from a depth of sediment at least five times their shell height.

Abundance is related to substrate type. Twice as many hard clams were in gravely substrate as in mud (Burbanck et al. 1956). The biomass of clams depended on substrate: sand, 25.5 g/m^2; sand without vegetation, 34 g/m^2; sand with vegetation, 11.3 g/m^2; and sand with clayey silt, 1.6 g/m^2 (O'Conner 1972). Allee (1923), however, reported a relative distribution of hard clams of 14 in sand, 19 in mud, 2 in gravel, 1 in eelgrass, and 4 in rockweed. Dow (1955) found hard clams only in sand-clay-silt, and states that in the North Atlantic region sand substrate is not the usual habitat for the hard clam; they are more often found in mud.

The growth of the hard clam is reflected by the substrate type. Clams grew 50% faster in sand than in mud (Greene 1975). Clams placed in sand grew 24% faster than those placed in mud (Pratt 1953). There was a high correlation (r = 0.88) between shell length and substrate particle size (Johnson 1977). The distribution of hard clams has been related to abundance of particle size greater than 2 mm (Saila et al. 1967).

Currents

Water movement is important to all life stages of the hard clam. Currents transport eggs and larvae and bring food to the adult.

Larvae occur in currents of 12 to 130 cm/sec (Carriker 1952). Carriker (1961) found lower densities near the inlet of an estuary where tidal exchange was greatest. The planktonic distribution of larvae was not affected by individual tidal stages, but summing all observations suggested greatest numbers 3 hr after low tide (Moulton and Coffin 1954).

The growth of adults is correlated with tidal currents (Kerswill 1949; Haskin 1952; Wells 1957). Hard clams grew better at a velocity of 7.5 cm/sec than in a sluggish slough (Kerswill 1949). Very strong currents, however, may scour the bottom and reduce habitat quality (Wells 1957).

Turbidity

Because hard clams filter water to obtain food they also collect other suspended material. Processing this material requires energy and clogs the filtering apparatus (Pratt and Campbell 1956). Turbidity can thus reduce the growth of hard clams. The eggs and larvae are also sensitive to turbidity.

Embryos developed normally in the presence of silt or sediment except at high concentrations of these suspensions (Davis 1960). Some embryos developed normally with 4 g/l of clay, chalk, or Fuller's earth, but the number developing decreased as the concentration increased above 0.75 g/l. Silt above 3 g/l impeded development. Sand had little effect on eggs except for the smallest particles at the highest concentrations (Davis and Hidu 1969). Development was normal at 2 g/l of particle sizes between 5 and 50 µm diameter.

Larvae are more sensitive to turbidity than are embryos. Ninety percent of the larvae died at concentrations of chalk above 0.25 g/l and of Fuller's earth above 0.5 g/l (Davis 1960). The larvae, however, tolerated silt of 4 g/l, and in fact, grew faster in low concentrations of silt than did controls in silt-free water. Growth was depressed by 0.5-g/l clay (Davis and Hidu 1969).

Little is known about the effects of turbidity in adults, despite the postulation of adverse effects on theoretical grounds. Menzel (1963) mentioned that high turbidity in summer may have inhibited growth in Florida. Pratt and Campbell (1956) hypothesized that processing of particles accounted for the reduced growth they observed in muddy habitats. Adults in mud expelled pseudofeces 107 times/hr; in fine sand, 19 times/hr; and in coarse sand, 7 times/hr. Rhoads et al. (1975), however, believed that a turbid layer near the bottom in Buzzards Bay, Massachusetts, enhanced the growth of hard clam. The layer probably contained detrital food utilized by the clams.

Habitat Alteration

Dredging may reduce populations of hard clams. Hard clams in the path of a dredged channel though a lagoon on Long Island, New York were destroyed (Kaplan et al. 1974). Hard clams that were not directly disturbed and were further than 400 m from the dredge site were unaffected. Commercial clammers in this area reported no noticeable reduction in harvest the following year, whereas scientists found a significant reduction in standing crop. In Boca Ciega Bay, Florida, the hard clam population failed to return to previous population level after dredging (Taylor and Soloman 1968).

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16. Abstract (Limit: 200 words)

Species profiles are literature summaries on the taxonomy, morphology, range, life history, and environmental requirements of coastal aquatic species. They are designed to assist in environmental impact assessment. The hard clam, Mercenaria mercenaria, is the most extensively distributed commercial clam in the United States, but at the northern end of its range in the North Atlantic region it has large fluctuations in population. Spawning occurs in summer at 18° to 30°C. Eggs and larvae are carried by currents in estuaries for 6 to 12 days, and then seed clams set on sand or pebbles. Seed clams that lack cover of shells or stone largely perish because of predation. Adults filter feed on phytoplankton. Adults survive temperatures of 17° to 30°C and salinities of 10 to 35 ppt, but can withstand freshwater for several days by closing the shell. When the shell is closed they must tolerate anoxic conditions, and they survive less than 1 mg/l oxygen in the water for several days. Even the larvae tolerate 0.5 mg/l of oxygen.

17. Document Analysis a. Descriptors

Estuaries
Clams
Growth
Feeding

b. Identifiers/Open-Ended Terms

Hard clam
Mercenaria mercenaria
Habitat
Salinity requirements
Temperature requirements
Spawning
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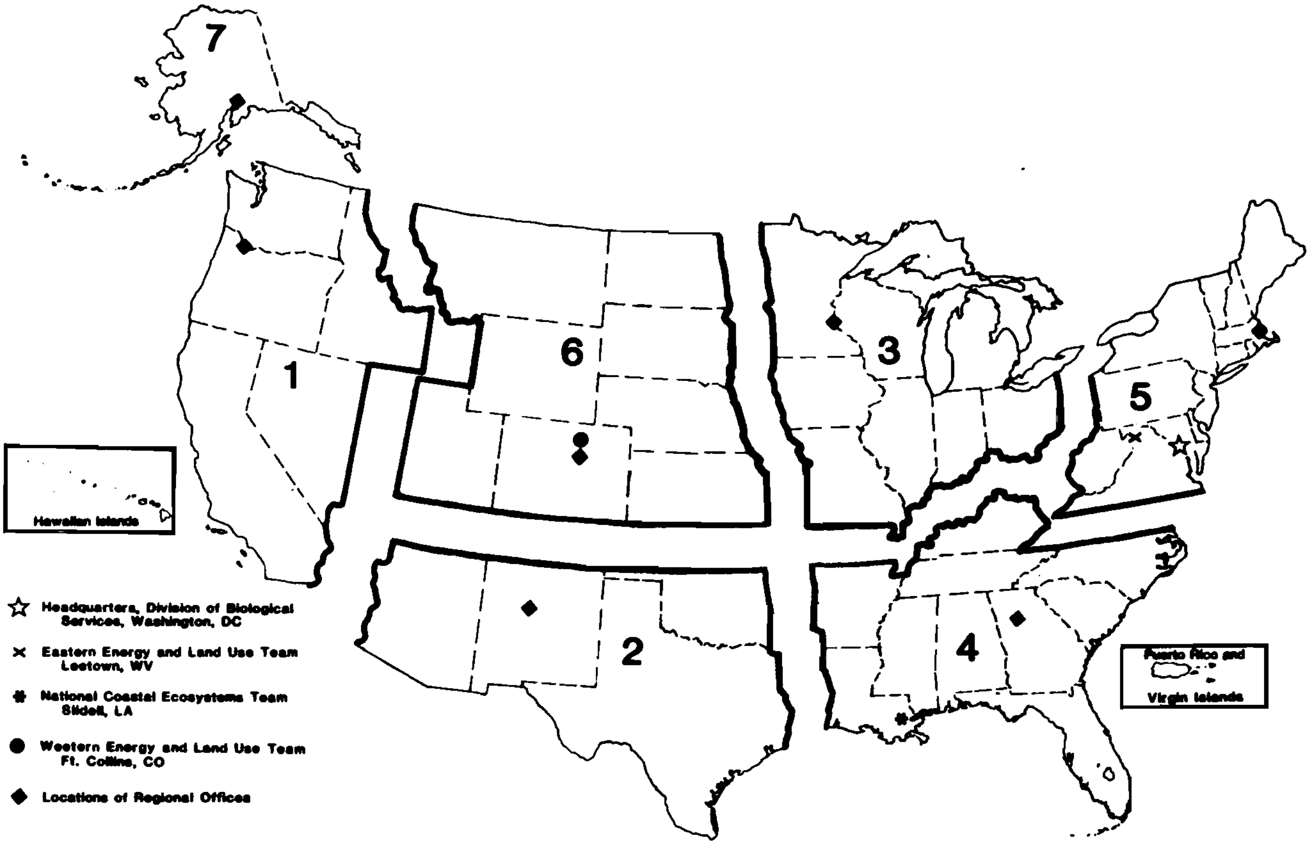

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