Biological Report 82(11.41)
February 1985

TR EL-82-4

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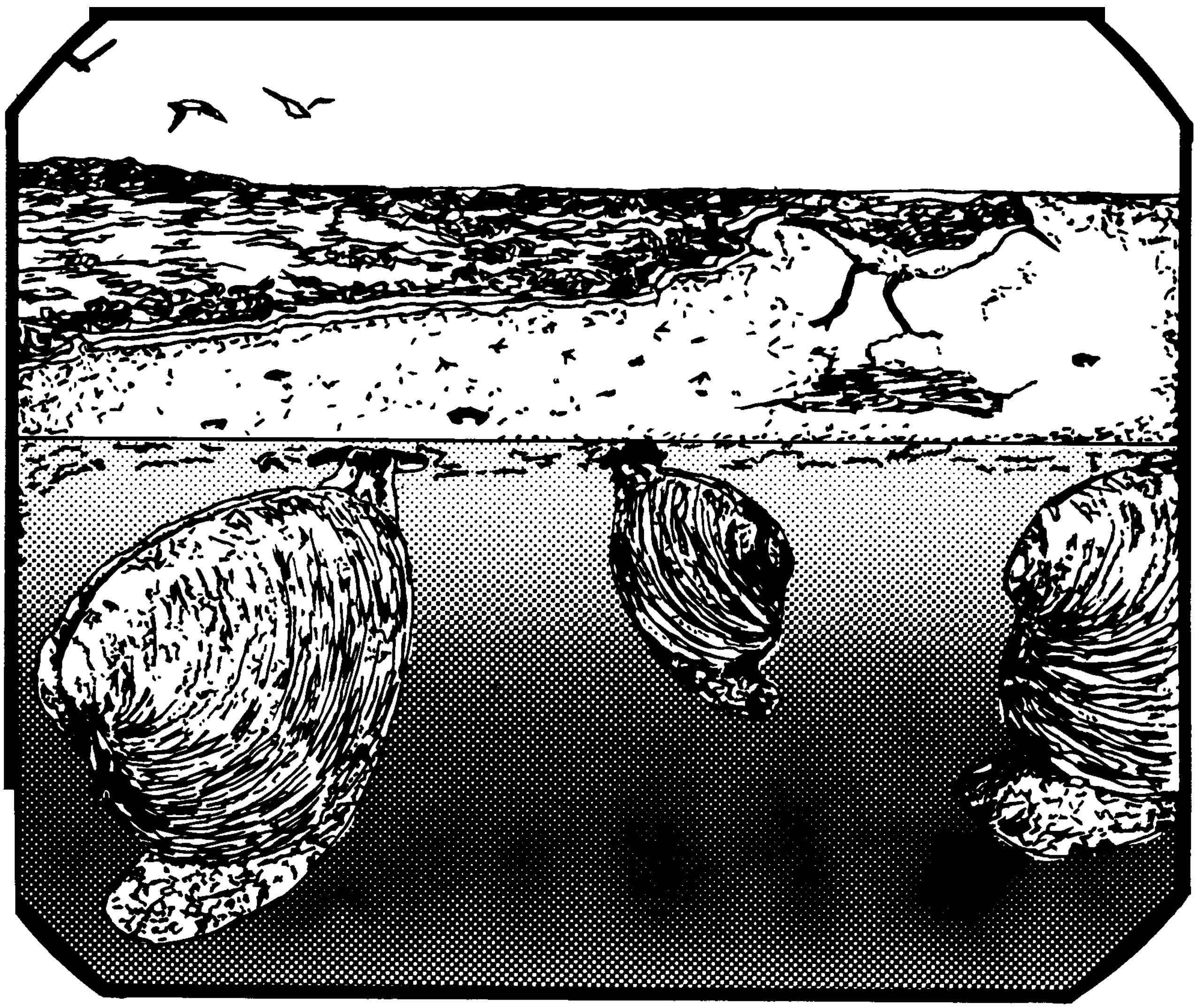

Fish and Wildlife Service
U.S. Department of the Interior

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

This is one of the first reports to be published in the new "Biological Report" series. This technical report series, published by the Research and Development branch of the U.S. Fish and Wildlife Service, replaces the "FWS/OBS" series published from 1976 to September 1984. The Biological Report series is designed for the rapid publication of reports with an application orientation, and it continues the focus of the FWS/OBS series on resource management issues and fish and wildlife needs.

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

HARD CLAM

by

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Performed for

Coastal Ecology Group
Waterways Experiment Station
U.S. Army Corps of Engineers
Vicksburg, MS 39180

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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.

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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 (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 (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

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

Thanks are due to Robert L. Dow, Maine Department of Marine Resources, Augusta, for helpful information; and Herbert Hidu, University of Maine, Michael Castagna, Virginia Institute of Marine Sciences, and John R. Moring, Maine Cooperative Fish and Wildlife Unit, University Of Maine, for reviewing the manuscript. McHugh et al. (1982) was a major source of information.

Figure 1 is used with the permission of Grass Medical Instruments and the artist, Trudy Nicholson. Figure 4 is reproduced with permission from the General Secretary of the Counseil International Pour L'Exploration de la Met-.

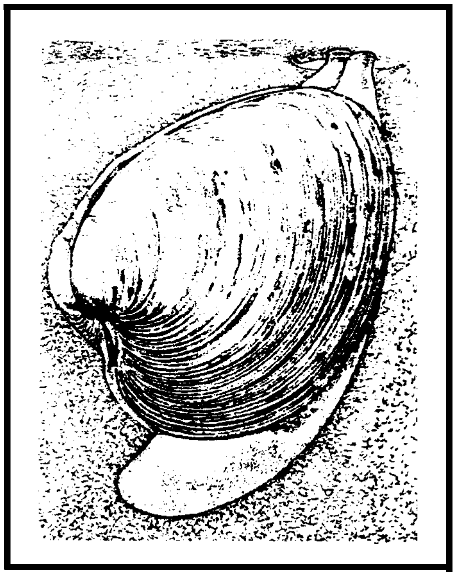

Figure 1. The hard clam.

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 lives in intertidal areas and subtidal waters to depths as great as 15 m along the Atlantic and Gulf coasts from the Gulf of St. Lawrence to Texas (Abbott 1974). It is most abundant from Massachusetts to Virginia and has been introduced to Europe and California. A similar species (*M. campechiensis*) that lives in coastal waters from North Carolina southward to Florida and Texas is also called the hard clam. Abbott (1974) stated that *M. campechiensis* may be a subspecies of *M. mercenaria* because they hybridize.

MORPHOLOGY/IDENTIFICATION AIDS

The hard clam has a thick shell, a violet interior border, and short siphons (Verrill 1873; Stanley 1970; Morris 1973). The mean length of the thick solid shell is usually 60 to 70 mm, but sometimes reaches 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 (3.60.

The external surface has numerous concentric lines that are conspicuous and closely spaced near the outer margins, but more widely spaced around the umbo, especially in younger shells. The center of each valve is smoother than the distal portion. The umbo is far anterior and projects toward the front of the shell. The shell is elliptical, somewhat pointed posteriorly, and 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 (Morris 1973). The interior ventral margins are denticulate.

The internal anatomy also has distinctive characteristics (Verrill 1873). 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, black, 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 and have thin edges folded into delicate frills, some of which are elongated near the siphons. Foot and mantle edges are white.

Theveliger larvae can be distinguished from other bivalves by the shape of the shell and hinge structure (Loosanoff et al. 1966; Chanley and Andrews 1971; Lutz et al. 1982). The margin of the shell is circular, tapering toward the hinge; the hinge is short and narrow.

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 abundance in clean substrates accessible to the public makes the hard clam a popular recreational species. Their habitat is vulnerable to coastal construction projects and pollution from urban and industrial development. Because adults do not migrate, repopulation of over-fished hard clam beds depends on the transport of larvae from other areas and several years for growth, maturation, and reproduction. Any disturbance, however temporary, may cause a long-term impact.

LIFE HISTORY

Spawning

The spawning season extends from March through November, depending on latitude and temperature. In temperate climates, spawning is heaviest in July (Carriker 1961). The peak is in May in the York River, Virginia, and is progressively later in Raritan Bay, New Jersey, and Narragansett Bay, Rhode Island (Jeffries 1964). Spawning begins in Greenwich Bay, Rhode Island, about the first of June and is completed by mid-July (Landers 1955). In Delaware Bay, spawning lasts from June to October but is most intense in August (Keck et al. 1975). In Chincoteague and Sinepuxent Bays, Maryland, spawning extends from early June through August (Sieling 1956). Individual female hard clams require 2.0 to 2.5 months to complete spawning, but the release of eggs is greatest during the initial spawning of the season (Ansell 1967). Spawning is more intense during neap than during spring tides, presumably because water temperatures are higher during neap tides (Carriker 1961).

Water temperature is the decisive factor governing final gamete maturation. In a 2-year study in Lower Little Egg Harbor, New Jersey, the median daily spawning temperature was 25.7°C and the range was 22" to 30°C (Carriker 1961). In Delaware Bay, clams spawn at 25° to 27°C (Keck et al. 1975). About 73% of the clams spawn during the first 2 to 3 days of rising water temperatures (Carriker 1961). The required or preferred water temperature range for spawning is 21° to 25°C (Kennish and Olsson 1975). In England, the clams spawn at a water temperature of 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 during the second year of life. Because size, not age, determines sexual maturity, slower growing individuals mature at an older age. Reproductive potential peaks at 60 mm, but then declines as the clams grow larger (Belding 1931).

Fecundity and Eggs

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

The spherical eggs are 78 µm in diameter and yolk granules are closely packed (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 seawater until it is 3.2 times the diameter of the egg. Because the gelatinous capsule imparts buoyancy, 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.

After 10 h the embryo developing within the capsule becomes covered with cilia. The lashing of the cilia tears the membrane and gelatinous capsule and the ciliated gastrula escapes into the water. Eggs may be carried as far as 25 km from the spawning site.

Larvae

Trochophore larvae are formed about 12 to 14 h after hatching (Belding 1931). The shape resembles a child's top, and the cilia on the blunt anterior end cause spiral swimming and rotation around the long axis in either direction. 4 functional mouth develops and the larva begins feeding on suspended particulates, especially dinoflagellates. The larvae concentrate about 1 m below the surface during daylight but at night are more evenly mixed in the water column (Carriker 1952).

About 24h after hatching, a shell gland forms opposite the mouth, a thin transparent shell is secreted, and the larva becomes a veliger (Belding 1931). The veliger drifts in ocean and estuarine currents, but it is able to move 7 to 8 cm/min vertically by extending the ciliated velum (Mileikovsky 1973). Vertical migration is stimulated by turbulence, which carries veligers into horizontal water currents for transport (Carriker 1961). The number of veligers is greatest in the water column 3 h after low tide (Moulton and Coffin 1954). By drifting with the incoming tide, the veligers are transported into the estuary and to sea. Veiigers of hard clams are abundant in the zooplankton in estuaries during the summer, where densities may exceed 500/l (Carriker 1952; Moulton and Coffin 1954; Jeffries 1964).

The veliger stage lasts 7 to 30 days, depending on temperature. Metamorphosis of the veliger of the hard clam is a gradual process that takes place 16 to 30 days after hatching 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 0.2 to 0.3 mm long, the shell thickens, a foot replaces the velum, and a byssal gland develops, indicating metamorphosis to the seed clam. Metamorphosis is inhibited at salinities below 17.5 to 20 parts per thousand (ppt) (Castagna and Chanley 1973), ensuring that seed clams avoid setting in an environment with salinities unsuitable for adults. Seed clams usually are most abundant in years when freshwater inflow into the estuary is below normal and salinity is above normal (Hibbert 1976).

The byssal gland of the seed clam secretes a tough thread, the byssus, which anchors the clam to the substrate. Seed clams set more densely in sand than mud (MacKenzie 1979); bits of shell or detritus may also serve as anchors. In the laboratory, sand is preferred to mud for setting, but the size of sand grains is not important (Keck et al. 1974). In Little Egg Harbor, New Jersey, the seed clams prefer to set 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): extraordinary sets may be as high as 270,000/m^2 (Dow and Wallace 1955). The density of the set is not necessarily related to adult concentrations because of movements and mortality of the seed clams. Seed clams seek a preferred habitat -- a sandy or silty bottom with small rocks and shells. They hide under shells or rocks to avoid predators (Lee 1977). The seed clams may reach their ultimate habitat in their-second year of life (Burbanck et al. 1956). A 25-mm clam may be tumbled along by currents of 25 cm/sec and deposited behind obstructions (M. Castagna, Va. Inst. Mar. Sci.; pers. comm.).

To move, the clam byssus is cast off and the foot is used for locomotion (Belding 1931). When the young clam reaches a desirable habitat, it spins a new byssus and reattaches to a small object. Byssal fibers are used for anchorage until the young clam is 10 mm long; it then metamorphoses and assumes the burrowing habits of the adult.

The distribution of seed clams is also altered by predation. Clams that set among oyster shells or stones are protected (Maurer and Watling 1973); without cover, seed clams are subject to heavy predation. Normally they do not live in areas exposed to wave action or strong currents (Anderson et al. 1978), but in the absence of predators, Carriker (1959) reported that survival on unstable bottoms was possible.

Adult

The adult hard clam lives in the substrate and burrows with a muscular foot. It remains in the location at which it first burrows for the remainder of its life. In the first 38 days after first burrowing, adults moved laterally an average of only 5 cm and a maximum of 15 cm from the point of origin (Chestnut 1951). Clams 20 to 30 mm long are known to travel as far as 30 cm in 2 months (Kerswill 1941).

Adults bury deeper in sand (mean depth 2 cm) than in mud (mean depth 1 cm), and small adults burrow proportionally deeper than larger ones (Stanley 1970). If dug up, the hard clam reburrows, and if covered with overburden it can escape upward (Belding 1931). A clam can escape through

10 to 50 cm of overburden, if the sediment dumped is similar to the local substrate (Kranz 1974). Foreign sediment reduces escapement.

The adult is most common in the intertidal and subtidal areas of estuaries and bays. Hard clams are most abundant in the lower estuary and are seldom found in the upper estuary where salinities are lower (Turner 1953). They are absent in places with salinity less than 15 ppt in upper Delaware Bay (Maurer et al. 1974) and in upper Chesapeake Bay (Sieling 1956; Lippson 1973). In Newport River, North Carolina, they are absent in the upper estuary at average salinities less than 19 ppt (Wells 1961). In Greenwich Cove, Maine, clams were about three times more dense at the seaward end of the cove than in the upper cove (Tiller 1950).

Hard clams tend to be found in protected locations within bays and estuaries (Loosanoff 1946). In Rand's Harbor, Massachusetts, about 50% of the population lived 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 usually avoids open estuaries, but lives in small channels and protected areas (Anderson et al. 1978). In Georgia, hard clams live largely in intertidal areas protected from wave action (Godwin 1968). Loosanoff (1946) also mentioned their intolerance to rough waves. In the Test and Itchen Rivers, England, they are absent above the mean tide line (Hibbert 1976).

Some populations are oceanic, e.g., those in the shoals of Nantucket Sound (Turner 1953). An offshore population of hard clams is located between Cape Lookout and Beaufort Inlet, North Carolina (Porter and Chestnut 1962). Reviews by Belding (1931) and Loosanoff (1946) state that hard clams live at depths up to 15 m, whereas Rurbanck et al. (1956) reported a maximum depth of 8 m. Hard clams were lacking in 9,000 bottom samples collected at depths greater than 24 m in the mid-Atlantic Bight (Theroux and Wigley 1983). The 1982 landings of about 13 million pounds were taken within 3 mi of the U.S. coast (Thompson 1983).

COMMERCIAL/SPORT FISHERIES

Shellfisheries

The hard clam is more widely distributed than any other commercial clam species in U.S. waters and is the most valuable commercial and sport species (Ritchie 1977). The fishery is located chiefly along the mid-Atlantic Bight (Figure 2). North of Cape Cod and in the Gulf of Mexico it is important only in relatively isolated waters (McHugh 1979).

Hard clams are taken commercially with hoes, bullrakes, hand tongs, and power dredges (Engle 1970). Of the commercial landings from Narragansett Bay, 90% are taken by handraking (Holmsen 1966), whereas in Chesapeake Bay, 95% of hard clams are taken with patent tongs (Haven and Loesch 1973). Although a power dredge is effective, it is not permitted in many areas, even though it 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 increases the catch of the more valuable small clams, but causes disturbance of the substrate (Godcharles 1971). Because dredging destroys seagrasses and benthic algae and recolonization is slow, dredging has a relatively long-term environmental impact.

About 6 million kg (meat weight) of hard clam are landed annually along the Atlantic seaboard (McHugh 1979; Thompson 1983). The fishery is

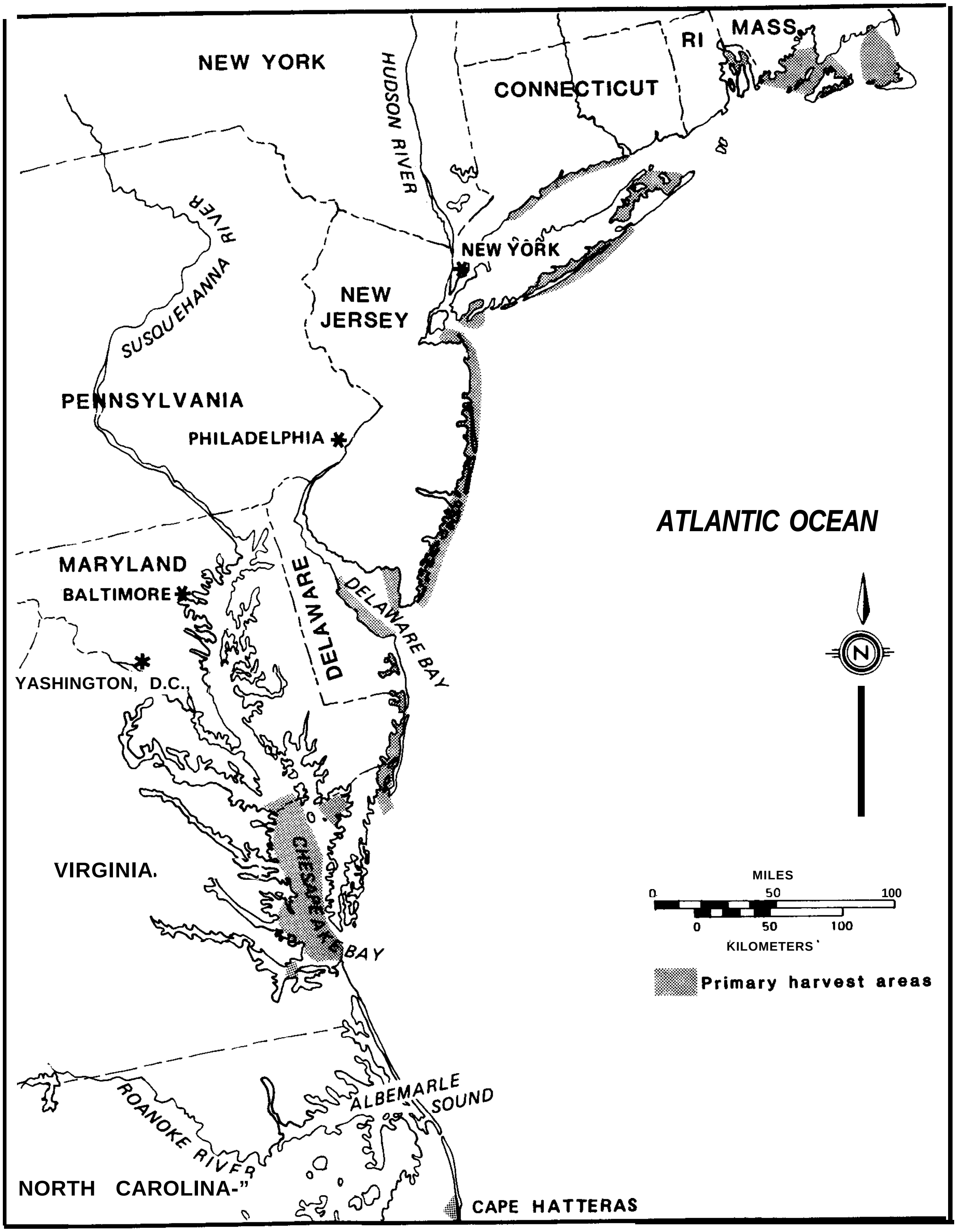

Figure 2. Primary areas of hard clam harvest in the mid-Atlantic coastal region.

characterized by large fluctuations. The landings in New York and New Jersey were high in the late 1800's, low in the early 1900's, and high again in the late 1940's and early 1950's (McHugh 1977). More recently, production in New York gradually increased from 1.8 million kg in 1960 to 4.1 million kg in 1976, and declined thereafter to 1.5 million kg in 1982 (Table 1). New Jersey had a period of moderate production of about 0.8 million kg from 1961 to 1965, a period of high production of about 1.1 million kg from 1966 to 1971, and a subsequent gradual decline to a low of 0.4 million kg from 1977 to 1982. Hard clam landings for Rhode Island are almost mirror images of those for New Jersey; high production in the early 1960's, low production from 1966 to 1977, and high production from 1979 to 1982.

The hard clam fishery in the mid-Atlantic region is most intense in a few bays with large populations. In the mid-1970's about 40% of the U.S. landings were from Great South Bay on Long Island (MacKenzie 1977). Other areas of high production are Greenwich Bay in Rhode Island (Stringer 1952); Little Egg Harbor, New Jersey (Figley and Townsend 1980); Raritan Bay, between New York and New Jersey (Jacobson and Gharrett 1967); and Chincoteague and Sinepuxent Bays, Maryland (Sieling 1956). The landings of hard clams in the mid-Atlantic region are about 83% of the U.S. total (Kinoshita and Vondruska 1980).

The value of U.S. landings has progressively increased. The U.S. landings (meat weight) declined between 1965 and 1975, but the value per unit increased (Zakaria 1979). The landings were 13.3 million lb valued at $29.7 million in 1978 (Pileggi and Thompson 1979), 18 million lb worth $51 million in 1981, and 12.9 million lb worth $43 million in 1982 (Thompson 1983).

The price of hard clams varies with size and the season (Ritchie 1977). Littlenecks (about 46 mm long) command a higher price ($60/bu) than cherrystones (77 mm, $22/bu), or chowder clams (97 mm, $13/bu). Prices in 1983 averaged about $26/bu. Hard clams are also processed and marketed as clam juice. The market for fresh hard clams is possible because the animals, if kept cool, live for 1 to 3 weeks out of water.

The recreational catch of hard clams is not included in the landing data. In New Jersey, one-third of the catch is taken by 21,600 shellfishermen with recreational licenses, and the rest by 1,000 commercial license holders (Figley and Townsend 1980). In the town of Islip, New York, 524,000 bu were taken commercially and 21,000 bu in the recreational fishery (Buckner 1979). Elsewhere, comparison with commercial fisheries is difficult because of differences in the way the catch is reported. In Rehoboth and Indian River Bays, Delaware, the commercial catch was 0.6 million kilograms in 1957 compared to a recreational catch of 1 million clams (Shuster 1959). In Massachusetts, the commercial fishery was worth $788,000 in 1975 and the recreational fishery was worth between $31,000 and $195,000 (Conrad 1979). In Great South Bay, New York, the recreational fishery was 4,806 bu in 1977 (Fox 1978), compared with a commercial fishery of about 8 million lb in 1976 (MacMillan 1978). Because a bushel of hard clams yields about 10 lb of meat (Shuster 1959), the recreational fishery in Great South Bay accounted for only 50,000 lb -- an insignificant amount.

In heavily fished areas, many clams are cropped about as soon as they reach a marketable size (Ritchie 1977), i.e., when 3 to 4 years old and 40 to 50 mm long. This method of cropping makes good use of the resource because it leaves the more valuable smaller clams and sufficient

Table 1. Hard clam landings (meat weight in thousands of kilograms) in the mid-Atlantic region (Kinoshita and Vondruska 1980). Data for 1980-82 are taken from unpublished records.

	State								
Year	RI	NY	NJ	VA	NC	MD	CT	DE	Total
1960	1,456	1,764	1,158	753	NA[a]	NA	NA	NA	5,131
1961	1,183	1,946	765	844	NA	NA	NA	NA	4,738
1962	971	2,194	608	766	NA	NA	NA	NA	4,539
1963	1,462	2,409	718	951	NA	NA	NA	NA	5,540
1964	829	2,450	859	1,113	116	151	NA	NA	5,518
1965	920	2,698	850	1,128	142	108	68	165	6,079
1966	728	2,985	1,212	844	106	78	111	120	6,184
1967	575	3,205	1,305	a44	91	134	109	136	6,399
1968	585	3,169	1,158	848	92	360	109	108	6,429
1969	559	3,409	1,027	863	115	238	NA	NA	6,211
1970	490	3,586	1,168	604	128	257	NA	NA	6,233
1971	484	3,878	1,124	833	115	151	NA	52	6,637
1972	399	3,856	996	607	124	85	176	NA	6,243
1973	420	3,287	859	614	172	31	109	NA	5,492
1974	381	3,641	790	505	130	32	56	46	5,581
1975	508	3,932	735	494	129	34	54	15	5,901
1976	695	4,095	677	406	139	16	65	24	6,117
1977	719	3,869	484	463	335	11	65	la	5,964
1978	870	3,292	365	226	405	11	81	13	5,263
1979	992	2,606	407	281	70	9	82	19	4,466
1980	1,515	2,244	383	341	699	19	136	11	5,734
1981	2,041	2,068	419	504[b]	661	29	<1	11	7,524
1982	1,678	1,553	412	285	772	NA	136	18	4,854

[a] NA = Data not available.
[b] From State of Virginia records.

brood stock to repopulate the clam beds.

Population Dynamics

Larval hard clams may be one of the most abundant plankters in estuaries. Larval densities of 25/l (Carriker 1952) and 572/l (Carriker 1961) have been measured. Based on these densities, the author calculated that there would be 50,000 to 1.1 million larvae per square meter in an estuary 2 m deep. There were 50 larvae/l in Wickford Harbor, Rhode Island, which were reduced to 3 larvae/l hy the time of setting (Landers 1953). 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 Casco Bay, Maine, may reach 270.000/m^2 (Dow and Wallace 1955).

Adult population density varies widely. Populations in Greenwich Bay, Rhode Island, ranged from 2 to 12/m^2 (Stickney and Stringer 1957). At some places in Greenwich Bay hard clams densities averaged 215/m^2 (Stringer 1955). Populations elsewhere in Narragansett Bay ranged from 5 to 189/m^2 (U.S. Department of the Interior 1956); the highest average densities were in the Providence River Estuary (17/m^2) and Bristol Harbor (9/m^2). The population density in Nantucket Sound, Massachusetts, was about 0.06/m^2 (Ropes and Martin 1960). The population density in waters of the Town of Islip, New York, were 16/m^2 where fishing was permitted and 30/m^2 in closed waters (Buckner 1979). Population densities in Raritan Bay were 11/m^2 on the New York side and 5/m^2 on the New Jersey side (Campbell 1965). Biomass (meat weight) ranged from 1.6 g/m^2 in poor habitat to 36 g/m^2 in good habitat of Moriches Bay, New York (O'Conner 1972). Annual recruitment in the James River Estuary, Virginia, was 0.84/m^2 (Haven 1970). Along the Georgia coast abundance ranged from 0.1/m^2 to 21/m^2 (Godwin 1968). Hard clams introduced in Great Britain coastal waters reached densities of 6 to 8/m^2 (Ansell 1963). Densities of 110/m^2 and 540/m^2 in Casco Bay, Maine, were mentioned by Dow (1952).

Natural mortality is high in the larval and seed clam stages, but almost nil once the shell becomes thick enough to resist predators (Figure 3). Based on densities of different life stages in the field, I calculated monthly mortality coefficients (Z) of 1.7 for the eggs (monthly mortality = 81%) and 1.5 for the larvae (monthly mortality = 78%). In Rhode Island, observed mortality of larvae over the summer was 95% to 97% in Wickford Harbor and 94% to 99.7% in Greenwich Bay (Landers 1955). I calculated an annual mortality coefficient from seed clam to adult of 3.0 (annual mortality = 95%). In Chesapeake Bay, usually less than 10% of small clams survive for 1 year and in some locations none survive (Haven and Loesch 1973). On the basis of nine estimates of adult mortality in England, Hibbert (1976) calculated an average annual mortality coefficient of 0.8 (annual mortality = 55%). The mortality coefficient of adult clams held in trays and protected from Dredators in South Carolina was only' 0.13, or about 12%

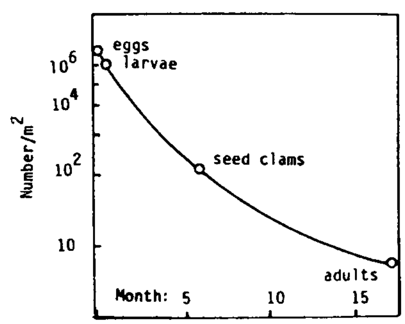

Figure 3. Abundance of hard clams at different life stages, from eggs to adult, based on a composite of the data cited in the text.

annually (Eldridge and Eversole 1982). These mortalities represent natural mortality, which was approximately equal to instantaneous total mortality Z in the absence of harvest. Overwinter mortality of hard clams in Maine was 40% (Dow and Wallace 1955).

Because hard clams tend to be completely harvested in any particular bed, it was not possible to arrive at a sound estimate of fishing mortality F. Mortality of hard clams smaller than the legal size was estimated to he 30% each time a flat was disturbed by digging (Dow 1953).

GROWTH CHARACTERISTICS

The hard clam grows rapidly in favorable environments. The veliger larvae grow from 10 μm to 200 μm in 7 days in Little Egg Harbor, New Jersey (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 as follows:

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

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%. Growth stops at temperatures below 9°C and above 31°C (Ansell 1968).

At the end of their first summer, seed clams are about 5 to 7 mm long in New York, and 16 mm long in Florida (Ansell 1968). Annual growth depends on the length of the growing season, which is largely a function of latitude (Figure 4). The average annual growth increments based on shell length, estimated from Figure 4 for ages 2 to 5 years, were about 10 mm in Canada, 13 mm in Maine, 14 mm in New Jersey, and 23 mm in North Carolina and Florida. Growth increment is about the same during the peak growth period of midsummer regardless of latitude (Ansell 1968).

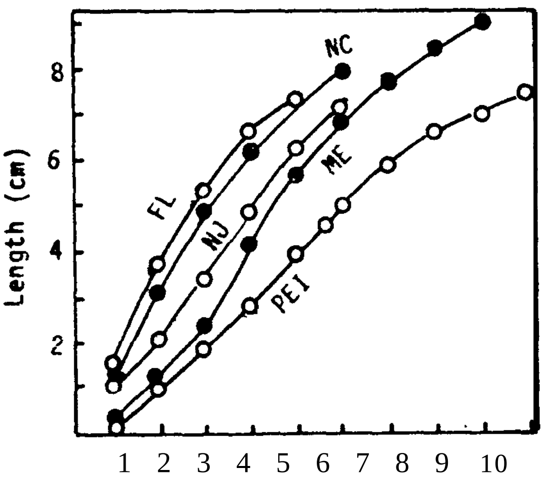

Figure 4. Shell lengths of hard clams of different ages from Florida, North Carolina, New Jersey, Maine, and Prince Edward Island, Canada (Ansell 1968).

The growth rate of adults slows with increase in length. Clams 35 to 39 mm long grow about three times faster than clams 65 to 69 mm long (Pratt and Campbell 1956).

Of interest to resource managers is the time required for clams to reach the minimum legal size (based on shell length), which in most States is reached in about 3 years (Ansell 1968). In Rhode Island and Connecticut, clams reach the 44-mm legal size in about 2.5 years. In New York, the 50-mm minimum size is reached in 3.0 years, whereas in New Jersey the minimum size is reached in 3.3 years. In Chesapeake Bay off Gloucester Point, hard clams require 4 to 5 years to grow to commercial sizes of 38 to 50 mm (Haven 1970). At the extremes of the U.S. range, the legal size is attained in 3 years in Florida at a size of 57 mm and in 5 years in Maine at a size of 51 mm.

ECOLOGICAL ROLE

Food and Feeding Habits

Adult hard clams feed by filtering out plankton and micro-organisms that are carried along the bottom by currents (Chestnut 1951). Hard clams depend on plankton for food before and during spawning to furnish sufficient energy to ripen the gonads (Ansell 1967). If the food supply is inadequate, spawning is diminished or nil. In the laboratory, food densities of 300 mg/l of carbon are optimal for deposition of biomass (Tenore and Dunstan 1973).

Food and other materials are taken in by the clam through the incurrent siphon. Tentacles on the siphon detect excessive concentrations of 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 is 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 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). The clams are preyed on hy fish, birds, starfish, crabs, and other mollusks. For defense they burrow or live among shells or rocks. Without shell or rock cover, the juvenile hard clam may be exterminated by predators. In one experiment, survival in penned sites was 94% compared with 9% in an unpenned area (Kraeuter and Castagna 1980).

Crabs are the most serious predators of hard clams; in one study 88% of the predators were crabs (Whetstone and Eversole 1978). The crabs crush smaller clams with their claws and chip the edges of the shells of larger clams. A rock crab (*Cancer irroratus*) consumes up to 30 small clams/h, and a mud crab (*Neopanope sayi*) consumes up to 14 clams/h (MacKenzie 1977). In some areas, mud crabs may be as dense as 50/m^2. Mortality of young clams parallels the frequency at which shell bits occur in the stomachs of the mud crab *Panopeus herbstii* (Whetstone and Eversole 1978). Crabs are effective predators because they can pry the clam out of the sediment. The rock crab, blue crab (*Callinectes sapidus*), and green crab (*Carcinides maenas*) dig up the clams, whereas mud crabs bury themselves in the sediment to crush the clam in place (MacKenzie 1977). Hard clams longer than 7 mm are not vulnerable to mud crabs, and those longer than 15 mm are not vulnerable to rock crabs (MacKenzie 1977).

Mollusks are the next most important predator. 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 (Buckley 1974). Hard clams larger than the predator are thick enough to withstand being drilled by moon snails (Kitchell et al. 1981). 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 long (MacKenzie 1977). In addition, the adult hard clam may destroy its own larvae by ingestion.

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) and reduce activity (Doering 1982c). Fish, such as flounder, and waterfowl also feed on larvae and young clams (Belding 1931).

ENVIRONMENTAL REQUIREMENTS

Temperature

Water 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 highly significant correlation between mean annual sea temperature and populations of adult hard clams.

Hard clams spawn at temperatures of 22" to 30°C in Little Egg Harbor, New Jersey (Carriker 1961) and from 21° to 25°C in Barnegat Bay, New Jersey (Kennish and Olsson 1975). They spawn in Delaware Bay at 25" to 27°C (Keck et al. 1975). Spawning is triggered by rising temperatures.

The optimum temperature range for larval growth is 22.5" to 25°C in brackish water and 17.5" to 30°C at a higher salinity (Davis and Calabrese 1964). According to Carriker (1961) larvae tolerate water temperatures of 13" to 30°C. Eggs require temperatures above 7.2°C, but larval survival is highest between 19" and 30°C (Lough 1975). Growth is greatest from 22" to 36°C. Embryos and veliger larvae develop abnormally and die at 15°C and 33°C, but straight hinged larvae tolerate these temperature extremes (Loosanoff et al. 1951). The minimum temperature for growth when clams are fed naked dinoflagellates is 12.5°C, but higher temperatures are needed to digest algae (Davis and Calabrese 1964).

Adult hard clans tolerate temperatures from below freezing to about 35°C. Adults survive at -6°C, but die when 64% of the water in the tissues has changed to ice (Williams 1970). Hard clams located in bars elevated above the gradient of the mud -flats usually suffer 100% winter mortality, almost surely caused by freezing (Dow and Wallace 1951). Summer temperatures as high as 34°C are tolerated (Van Winkle et al. 1976; MacKenzie 1979).

Growth is reduced at water temperatures below 10°C (Pratt and Campbell 1956) and growth stops at 8°C (Belding 1931). Hard clams hibernate at temperatures below 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 is 1° to 34°C (Van Winkle et al. 1976).

Estimates of the optimum temperature for hard clam growth vary from about 20°C (Ansell 1967) to 23°C (Pratt and Campbell 1956). Other biological activities 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 (Van Winkle et al. 1976). Storr et al. (1982) reported two optima for shell calcium deposition: 13° to 16°C, and 24°C. Optimum temperatures for burrowing are 21° to 31°C (Savage 1976).

Hard clams are adversely affected by rapid temperature changes. A rapid temperature increase of + 5°C in the discharge from a nuclear power plant stopped shell growth (Kennish 1976). The summer growth of hard clams was reduced 60% to 90% when the clams were transplanted to the warmer waters of the discharge site.

Salinity

The salinities at which hard clams are found usually range from about 10 ppt to 35 ppt, allowing for possible geographic differences. Belding (1931) reported 23 to 32 ppt as the general range of tolerance. In Wellfleet Harbor, Massachusetts, salinity in clam beds ranged from 20 to 34 ppt (Curley et al. 1972). The range of salinities in a New York clam'habitat was 15 to 35 ppt (MacKenzie 1979). In New Jersey, clams are found only in bays where salinity is above 15 ppt (Figley and Townsend 1980). Hard clams do not live in salinities below 19 ppt in the Newport River Estuary, North Carolina (Wells 1961), or at salinities below 18 ppt in South Carolina (Anderson et al. 1978). The salinities of natural clam beds range from 10 to 28 ppt in the mid-Atlantic region (Loosanoff 1946).

Salinity is 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% develop (Davis 1958). Veliger survival is low during high rainfall (Carriker 1961). Veliger growth is best at 20 to 27 ppt. Larvae apparently require higher salinities than adults, and metamorphosis to seed clams is rare below 18 ppt (Castagna and Chanley 1973). Embryos develop normally between 20 and 35 ppt; the optimum is about 28 ppt. The minimum salinity at which larvae survive was 15 ppt. In Southampton Water, England, young clams were abundant only in years of low freshwater inflow from the River Test (Mitchell 1974).

Juvenile and adult clams close their shells when exposed to diluted seawater to increase their tolerance to low salinities. Juveniles can live in freshwater for 22 days in the laboratory (Chanley 1958). At 10 ppt they begin dying at 28 days and at 10 and 15 ppt there is little feeding or burrowing. Adult hard clams exposed to salinities as low as 0.3 ppt in the Santee River system in South Carolina survived for 14 days (Burrell 1977). Laboratory tests showed that pumping ceased below 15 ppt and above 40 ppt, and that the rate of pumping was highest between 23 and 27 ppt (Hamwi 1968). In the laboratory, siphons are rarely extended at salinities below 17 ppt or above 38 ppt (Van Winkle et al. 1976). The optimum salinity range for siphon extension is 24 to 32 ppt.

The optimum salinity for larval survival is about 27 ppt (Davis and Calabrese 1964). At about 22 ppt, the temperature tolerance was reduced. A strong interaction between temperature and salinity was reported by Lough (1975). The maximum survival of eggs was above 28 ppt and above 7.2°C. For larvae, survival was highest between 21 and 29 ppt at 19" to 29.5°C. The larvae grew best between 22 and 30 ppt at 22" to 36°C.

Dissolved Oxygen

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

Adults tolerated low oxygen in the laboratory, but their metabolism became depressed. The hard clam can tolerate less than 1 mg/l for 3 weeks and still be capable of reburrowing (Savage 1976). Growth is suppressed when oxygen concentrations are low. 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 because of accelerated eutrophication and reduced oxygen in coastal waters near a duck rearing area on Long Island, New York (O'Conner 1972).

Substrate

Numerous studies have shown that hard clams are more likely to live on a sandy bottom than on a mud bottom (Allen 1954: Maurer and Watling 1973; Mitchell 1974). Because water currents sort bottom substrates, there is a high correlation between currents and bottom type; consequently, water circulation may be the decisive element in the distribution of hard clams (Greene et al. 1978).

Clam larvae set more frequently and more densely on sand than on mud (MacKenzie 1979). There also appears to be some correlation between grain size and the density of setting (Keck et al. 1974). In a laboratory test, 781 larvae set on mud particles 0.05 mm in diameter whereas 2,083 set on sand particles 0.50 mm in diameter. There was little difference in the densities of setting on sand grain diameters of 0.25, 0.50, 0.71, and 1.00 mm. Larvae much prefer sand (0.25 mm) over mud (0.50 mm), yet the highest concentration of seed clams was on shells coated with mud (Carriker 1961). Seed clams can emerge from a depth of sediment at least five times their shell height.

Abundance also is related to other substrate. Twice as many hard clams live in gravelly substrate than in mud (Burbanck et al. 1956). The biomass of living clam tissue is related to the type of substrate in Moriches Ray, New2 York, as follows: 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). The presence of shells was more important than particle size in determining clam abundance in Greenwich Ray, Rhode Island. The abundance was as follows: $16/m^2$ in mud, sand and shell; $10/m^2$ in sand and shell; $6/m^2$ in mud and shell, or mud and sand, or sand; and $3/m^2$ in mud (Stringer 1955). The density of hard clams was correlated to the abundance of particles with diameters greater than 2 mm (Saila et al. 1967).

Not all reports agree. For example, in the Woods Hole region, Allee (1923) reported a relative density (per m^2) of 19 in mud, 14 in sand, 4 in rockweed, 2 in gravel, and 1 in eelgrass. Hard clams in Bogue Sound, North Carolina, tended to be in finer sediments (Brett 1963).

The growth of hard clams sometimes reflects the substrate type. Clams grew 50% faster in sand than in mud in Great South Ray, New York (Greene 1975). Clams placed *in* sand in Narragansett Bay, Rhode Island, 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 in Little Bay, New Jersey (Johnson 1977).

Currents

Water movement is important to all life stages of the hard clam. Currents transport eggs and larvae and bring food to the adults. Hard clams of Wickford Harbor, Rhode Island, live in current velocities less than 0.5 m/sec (Landers 1953).

Larvae prefer currents from 12 to 130 cm/sec (Carriker 1952). Densities of larvae were low near the inlet of an estuary where tidal exchange was greatest and currents fastest (Carriker 1961). The planktonic abundance distribution of larvae is not affected by individual tidal stages, but observations suggest that the abundance was highest 3 h after low tide (Moulton and Coffin 1954).

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

Turbidity

Because hard clams filter water to obtain food material, they also trap other suspended material. Discharging this material reduces energy available for growth (Pratt and Campbell 1956). Excess turbidity can clog the filtering apparatus and cause-death. Eggs and larvae are also sensitive to turbidity.

Embryos develop normally if suspended silt or sediment are present, unless concentrations are unusually high (Davis 1960). Silt above 3 g/l impedes development, but some embryos develop normally in waters with 4 g/l of clay, chalk, or Fuller's earth. Embryo development is normal at 2 g/l of particles between 5 and 50 µm diameter. Sand had little effect on eggs except for the smallest particles at the highest concentrations (Davis and Hidu 1969).

Larvae are more sensitive than embryos to turbidity. In a laboratory study, 90% 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). Larvae tolerate silt up to 4 g/l, and even grow faster in low concentrations of silt than in silt-free water. Larval growth is depressed by concentrations of clay 0.5 g/l and higher (Davis and Hidu 1969).

Although turbidity may have profound effects on adult clams, the limits of the reaction of the clams to turbidity is not well defined. Menzel (1963) reported that high turbidity in summer may inhibit the growth of adults in Florida. Another view is that clearing of particles from the filtering apparatus reduces growth in muddy habitats (Pratt and Campbell 1956). Adults expelled pseudofeces produced when clams clear the filtering apparatus 107 times/h in mud, 19/h in fine sand, and 7/h in coarse sand. Rhoads et al. (1975) believed that a turbid layer near the bottom in Buzzards Bay, Massachusetts, enhanced the growth of hard clams because it contained detrital food.

Habitat Alteration

Dredging of coastal waters reduces the abundance of hard clams in the area of impact. For example, hard clams in the path of a dredged channel through a lagoon on Long Island, New York, were destroyed, and those on either side of the path were adversely affected by sedimentation (Kaplan et al. 1974). Hard clams 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 its previous abundance 13 years after dredging (Taylor and Saloman 1965).

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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. They spawn offshore in summer when water temperatures are between 18° and 30°C. The eggs and larvae are carried by currents into estuaries, where 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 and particulate material. Adults survive temperatures of -6" to 30°C and salinities of 10 to 35 ppt, and can withstand freshwater for several days by closing their 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	Temperature requirements
Mercenaria mercenaria	Spawning
Habitat	Fisheries
Salinity requirements	

c. COSATI Field/Group

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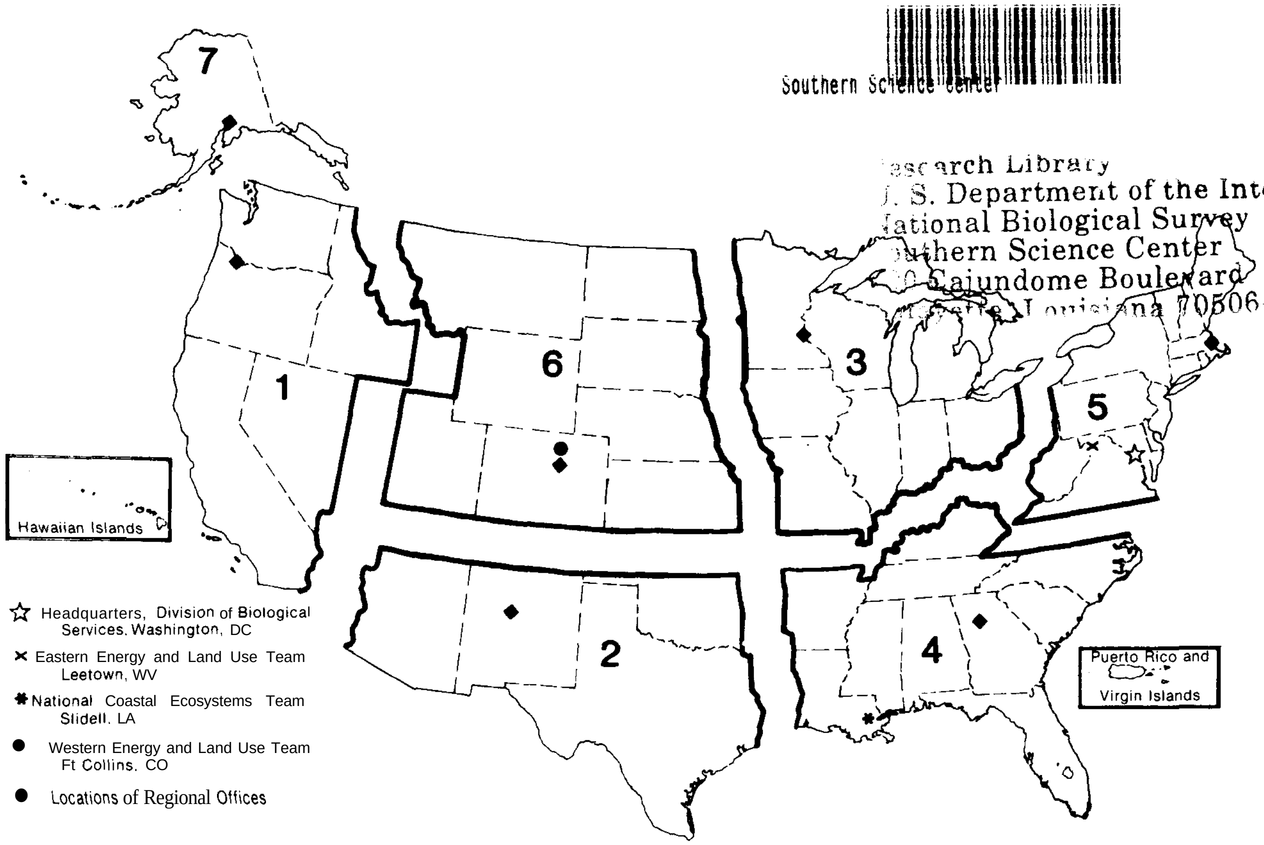

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