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

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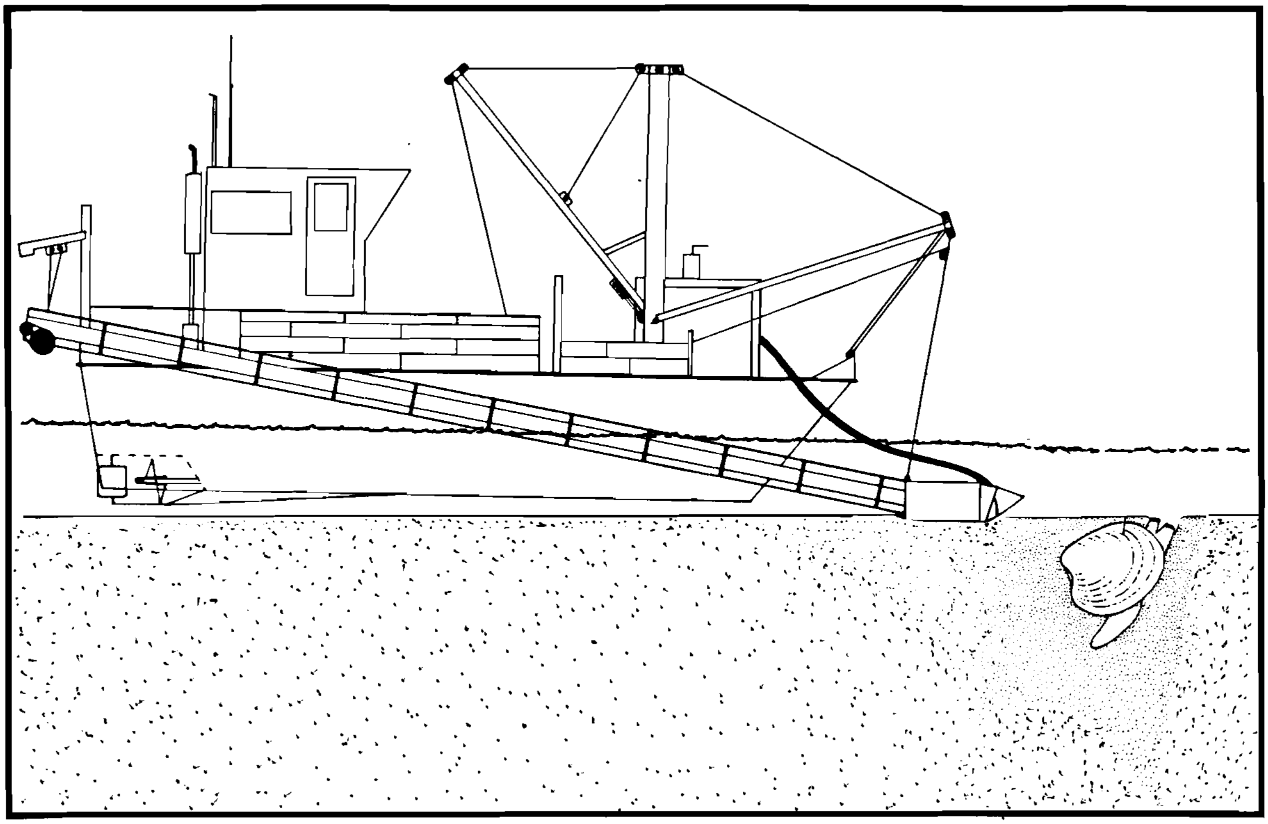

Fish and Wildlife Service
U.S. Department of the Interior

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 (South Atlantic)

HARD CLAM

by

Arnold G. Eversole
Department of Aquaculture, Fisheries and Wildlife
323 Long Hall
Clemson University
Clemson, SC 29634-0362

Project Manager
Carrol Cordes
Project Officer
David Moran
National Wetlands Research Center
U.S. Fish and Wildlife Service
1010 Gause Boulevard
Slidell, LA 70458

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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.

Users of this species profile should note that a Habitat Suitability Index (HSI) model is available for the hard clam. HSI models are designed to produce a numerical index of the relative value of a given site as fish or wildlife habitat. Those interested in obtaining copies of the model report should contact the Service's National Wetlands Research Center and request:

Mulholland, R. 1984. Habitat suitability index models: hard clam. U.S. Fish Wildl. Serv. FWS/OBS-82.77. 21 pp.

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

Information Transfer Specialist
National Coastal Ecosystems Team
U.S. Fish and Wildlife Service
NASA-Slidell Computer Complex
1010 Gause Boulevard
Slidell, LA 70458

or

U.S. Army Engineer Waterways Experiment Station
Attention: WESER-C
Post Office Box 631
Vicksburg, MS 39180

CONVERSION TABLE

Metric to U.S. Customary

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

U.S. Customary to Metric

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

CONTENTS

ACKNOWLEDGMENTS

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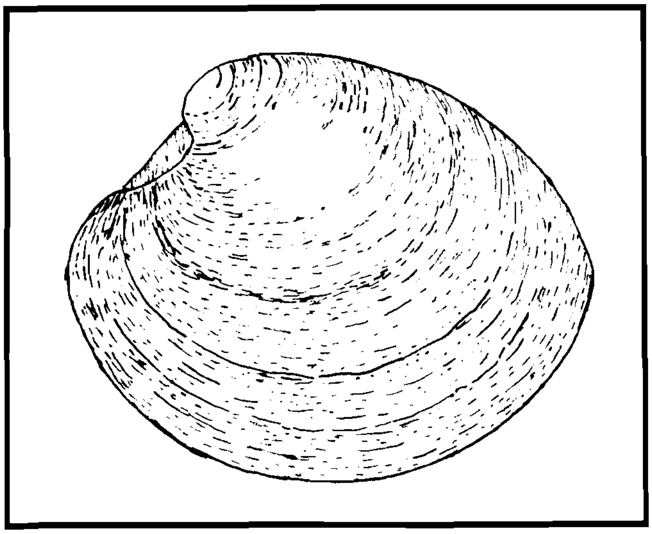

Figure 1. Hard clam, Mercenaria mercenaria.

HARD CLAM

NOMENCLATURE/TAXONOMY/RANGE

Scientific name............Mercenaria mercenaria (Linnaeus 1758). Initially known under the European genus Venus, it was recognized to be sufficiently different and reassigned to the generic name Mercenaria (Frizzell 1936; Wells 1957a). Venus mercenaria was incorrectly used for M. mercenaria up to the mid-1960s.

Preferred common name.....Hard clam in the Southern United States (Figure 1) and quahog in the Northern United States.

Other common names....Hard shell clam, hard-shelled clam, quohog, quahaug, cherrystone clam, little-neck clam, chowders, round clam

Class...........Bivalvia (Pelecypoda)

Order...............Eulamellibranchia

Suborder..................Heterodonta

Family......................Veneridae

Geographic range: Mercenaria mercenaria is distributed from the Gulf of St. Lawrence, Canada, to Texas (Abbott 1974). It has also been successfully transplanted to California (Loosanoff and Davis 1963; Crane et al. 1975) and Europe (Marteil 1956; Heppell 1961; Ansell 1964a). It is abundant from Virginia to Massachusetts and supports isolated breeding communities above Cape Cod (Turner 1953). Hard clams occur throughout the South Atlantic region (Figure 2) in estuaries from the intertidal zone to a depth of 15 m or more (Porter 1974; Fox and Ruppert 1985). M. mercenaria texana, the only subspecies recognized by Abbott (1974), extends south from Cape Canaveral, Florida, on the Atlantic coast and west from Northwest Florida, on the Gulf of Mexico coast to Texas and northern

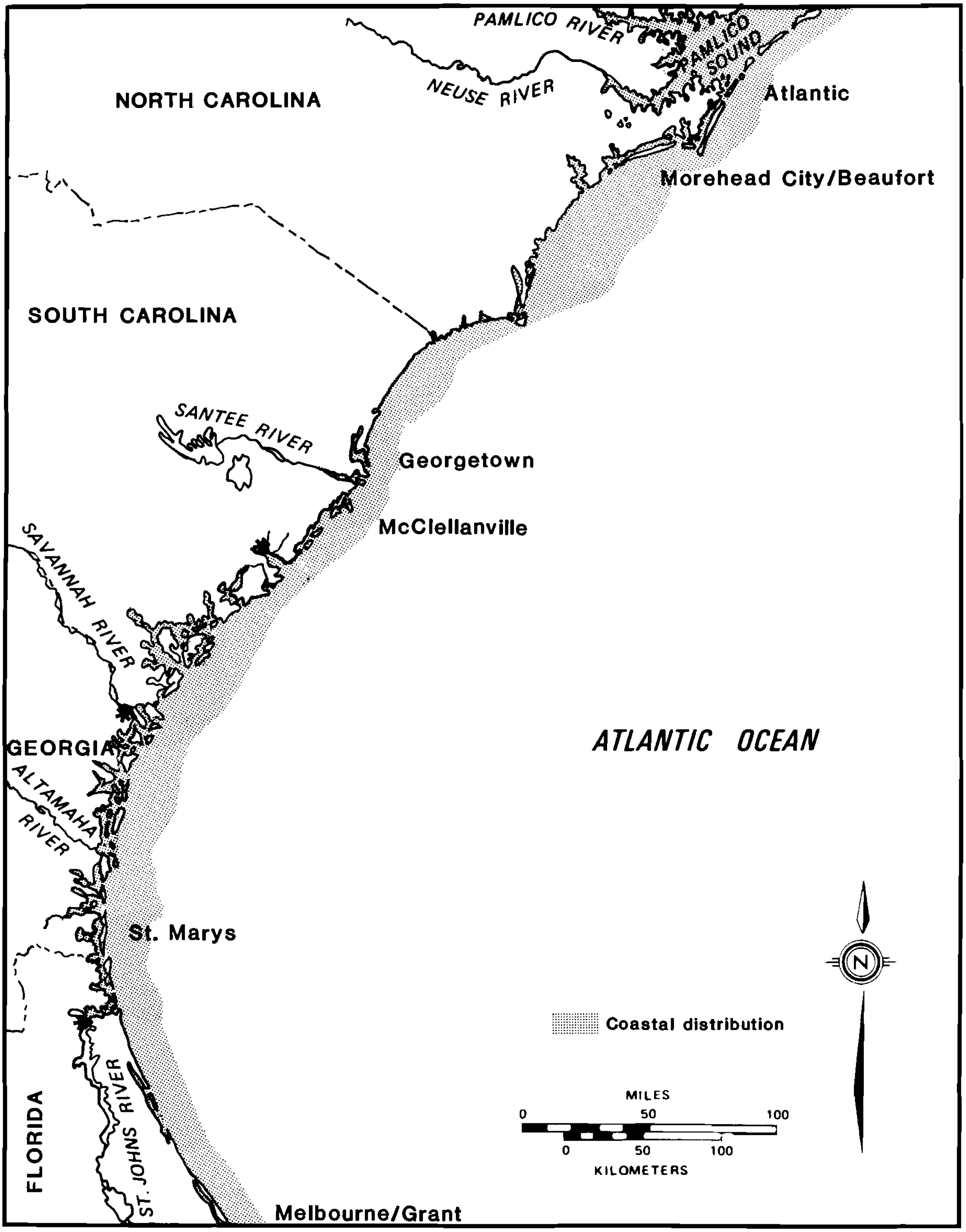

Figure 2. Distribution of hard clams in the South Atlantic, showing major clam fishing ports in North Carolina, South Carolina, Georgia, and Florida.

Mexico (Abbott 1974). The M. mercenaria notata "form," which Abbott (1974) does not recognize as a subspecies, occurs sympatrically with hard clams. The more conservative classification of Abbott (1974) is followed here. The very similar species M. campechiensis extends from Cape May, New Jersey (Merrill and Ropes 1967), south to Florida and Mexico (Abbott 1974). The distributions of M. mercenaria and M. campechiensis overlap; however, M. campechiensis is usually in deeper, more saline areas, e.g., offshore of barrier islands. Intergrades of the two species occur in shallow water south of Indian River, Florida.

MORPHOLOGY AND IDENTIFICATION AIDS

Hard clams undergo larval development and a series of morphological changes in their life cycle. Characteristics of early life history stages of hard clams are presented in the LIFE HISTORY section. The following information on the morphology of the adult was summarized primarily from Pierce (1950), Gosner (1971), and Abbott (1974).

The shell of the hard clam is composed of two equal-size valves with an ovate-trigonal shape. Valves are joined dorsally by a dark brown external ligament. Swellings or umbos occur on either side of the ligament. Conspicuous concentric lines of growth extend out from the umbo on each valve (Figure 1). Ventral and anterior to the umbo lies a heart-shaped configuration called a lunule. The exterior shell is fawn colored or off-white and has a very thin periostracum. Shells of the form notata are marked with brown, zigzag mottlings. Chanley (1959) reported the notata markings to be inherited in a simple Mendelian manner.

Interior shell color is white or pale yellow with noticeable purple markings near the shell margin. A prominent adductor muscle scar is near each end of each valve. The scars are connected by the distinct pallial line, which is parallel to the shell margin. The pallial line forms a triangular or pallial sinus at one end of the valve. Opposite the pallial line and anterior to the ligament are internal cardinal teeth.

The hard clam has two short siphons fused at the base; the inhalent siphon is ventral to the exhalent siphon and fringed with small tentacles. Ends of both siphons are pigmented, but color varies from opaque white or cream color to dark brown or black. The foot is large and somewhat hatchet-shaped. Mantle lobes, which cover the soft parts of the clam, are separate along the anterior and ventral edges of the shell, where the lobe borders are thickened and attached along the pallial line. The lobes of the mantle edge are fused at two points to form the siphons. Dissection guides are available for the hard clam (e.g., Pierce 1950; Sherman and Sherman 1976). Shuster (1969) also developed a three-ply representation of the hard clam so that sections of the inner and outer surfaces of the shell, mantle, and visceral mass can be cut out of a pamphlet and assembled to form a sequence of structures encountered when the hard clam is dissected.

REASONS FOR INCLUSION IN SERIES

Hard clams support an important commercial fishery along the Atlantic coast of the United States. Among the species of clams harvested in the United States, hard clams yield the highest dollar value, and are exceeded only by surf clams, Spisula solidissima, and ocean quahogs, Arctica islandica, in kilograms of meats harvested (Table 1). Less than 10% of

Table 1. Commercial clam landings in 1984 (U.S. Department of Commerce 1985).

Species	Landings (meats)		Ex-vessel value	
	1,000 kg	%	$1,000	%
Hard clam	6,704	11.10	49,849	42.79
Surf clam	31,929	52.85	34,334	29.47
Softshell clam	3,600	5.95	19,842	17.04
Ocean quahog	17,642	29.20	11,829	10.15
Other	545	0.90	637	0.55
Total	60,420	100.00	116,491	100.00

the total U.S. commercial harvest results from aquaculture, though the potential for aquaculture in the United States is high (Manzi 1985). Recreational harvests of hard clams are important; thousands of persons participate in the South Atlantic region. However, no scientifically derived estimates are currently available for recreational harvest of hard clams from this region. The estimated recreational harvest in Great South Bay, New York, was 4,796 bushels or 1.42% of the reported commercial summer harvest (Fox 1981). The hard clam is a delicacy of considerable nutritional value; it is low in calories but high in protein and essential minerals such as iodine and iron (Miller et al. 1975).

Hard clams occur extensively in estuarine systems throughout the region, and because of their distribution, they may be exposed to a myriad of environmental impacts. Because hard clams have a sensitive planktonic larval stage (Carriker 1961) and are long-lived sessile organisms as adults (Chestnut 1951; Lutz and Haskin 1984), they appear to be particularly vulnerable to the effects of pollution and coastal development.

LIFE HISTORY

Spawning

Mercenaria mercenaria exhibits consecutive hermaphroditism, going through a juvenile or preadult sexual phase when it is a few months old and 6-7 mm in shell length (Loosanoff 1936, 1937a). Although it functions mostly as a male during this juvenile sexual phase, close examination of the gonad reveals both male and female sex cells. These sex cells are differentiated, but because of continued proliferation of the spermatogonia, the gonad acquires a predominately male character. Hard clams in this phase can discharge sperm and function as males (Coe 1943a). Hard clams go through a sex change after the juvenile sexual phase and can function only as males or females. Loosanoff (1936, 1937a) established that sex change in *M. mercenaria* was protandrous, or male to female. Dalton and Menzel (1983) found that *M. campechiensis* and its *M. mercenaria* hybrids exhibited protandric sexual development similar to that of *M. mercenaria*.

Eversole (1986), using data from various literature sources, calculated an approximate shell length of 33 mm at which M. mercenaria reaches sexual maturity. Size at maturity tends to be smaller in males than in females (Eversole et al. 1980). Growth rate of young hard clams appears to be an important factor in determining early sexual maturity; faster-growing clams attain sexual maturity at an age of only 1 year in some localities (Eversole et al. 1980) and 2 years in others (Bricelj and Malouf 1980). Evidence from studies on the hard clam corroborate the hypothesis advanced by Quayle and Bourne (1972) that sexual maturity in clam species appears to be more a function of size than of age.

The gametogenic and spawning cycle of the hard clam in North America varies with latitude (Table 2). Populations in Connecticut (Loosanoff 1937b), New York (Kassner and Malouf 1982) and Delaware Bay (Keck et al. 1975) have an annual gametogenic cycle. Gametogenic activity and the period of ripeness in populations occur earlier in the year in Delaware Bay than in Connecticut and New York (Table 2). Populations in more south-

Table 2. Spawning times and temperatures (at the first major spawning peak) of populations of Mercenaria mercenaria in North America, based on histological evidence of gametogenic activity and gamete release. The solid lines show periods of peak spawning.

Location	Temp. (°C)	Months J F M A M J J A S O N D	Sources
Charles Island, Conn.	23-25	--- — ---	Loosanoff 1937b
Gr. South Bay, N.Y.[a]	20	--- — ---	Kassner and Malouf 1982
Gr. South Bay, N.Y.[a]	20	-- ——— --	
Delaware Bay, De.	25-27	-------- ———	Keck et al. 1975
Core Sound, N.C.	27-30	-- —— ---- —— --	Porter 1964
N. Santee Bay, S.C.	20	-- ——— ------ ———	Manzi et al. 1985
Clark Sound, S.C.	20-23	-- ——— ------ ———	Eversole et al. 1980
Wassaw Sound, Ga.	22-26	--- —— - -- —— ---	Pline 1984
Alligator Harbor, Fla.[b]	16-20	-- ——— ---------- ——— -	Dalton and Menzel 1983

[a] Observation at same locality in different years.
[b] Spawning cycle of young male clams less than 2 years old.

erly latitudes continue the trend of earlier and extended periods of gametogenesis until a second developmental and spawning period becomes possible. Porter (1964) observed two periods of gametogenic activity in North Carolina: a major redevelopment period in early spring after the fall spawning peak and a second minor redevelopment period after a June spawning (Table 2). Two separate gametogenic cycles were observed in hard clam populations from South Carolina (Eversole et al. 1980; Manzi et al. 1985) and Georgia (Pline 1984). Hard clams transplanted from northern latitudes to southern latitudes had a gametogenic cycle similar to that observed in native clams (Dalton and Menzel 1983). The trend of altering gametogenic activity toward a bimodal pattern in the more southerly latitudes appears to be linked to water temperature (Loosanoff 1937b).

The spawning cycle of the hard clam parallels its gametogenic cycle, varying with latitude. Like the gametogenic cycle, the time of spawning appears closely related to water temperature (Loosanoff 1937a; Carriker 1961; Ansell et al. 1964; Keck et al. 1975). Temperature has been considered the most important factor in spawning because a certain degree of gonad ripeness must be achieved before the clams can respond to a specific spawning stimuli. Hard clams can be artificially conditioned to develop ripe gonads for early spawning by gradually increasing water temperature to about 20 °C, and providing food (Loosanoff and Davis 1950). Similarly, they can be induced to spawn by rapidly increasing water temperature from 20-22 °C to 26-28 °C and then decreasing it to 20-22 °C, over a 30-min cycle (Loosanoff and Davis 1963; Castagna and Kraeuter 1981). Other factors such as the presence of food (Breese and Robinson 1981), sperm infusions (Loosanoff and Davis 1963), and weak injections of serotonin (Gibbons and Castagna 1985) trigger hard clams to spawn.

Porter (1964) suggested that differences in spawning temperatures of hard clams were expressions of racial differences or phenotypic responses to environmental factors (Table 2). Keck et al. (1975) observed that gonad developmental patterns for clams in Delaware were intermediate between those for clams in Long Island Sound and in North Carolina, and thereby provided evidence that different physiological races exist in these three areas.

Fecundity and Eggs

Estimates of fecundity of the hard clam vary. Belding (1931) reported that hard clams averaging 63.5 mm in shell length produced about 2 million eggs in a spawning season. Bricelj and Malouf (1980) observed induced spawning in hard clams of similar sizes to produce an average of 6.3 million eggs over a spawning season. These fecundity estimates are lower than the average fecundities (about 25 million eggs) reported by Davis and Chanley (1956). Some of the discrepancies in these estimates may be explained by differences in clam size and condition. Ansell and Loosmore (1963) detected a direct relationship between condition and spawning potential in the hard clam. Bricelj and Malouf (1980) found a general trend of increasing fecundity as shell size increased, some 15%-25% of the variance in total fecundity being accounted for by differences in shell length. Total fecundity varied significantly among the three commercial sizes of hard clams; number of eggs spawned were about equal in clams 36.5-41.3 and >41.3 mm shell length, and greater than the number spawned by clams 25.4-36.5 mm long (Bricelj and Malouf 1980). Other measures of relative fecundity (e.g., gonadal-somatic indices) varied significantly with shell length (Peterson 1983; Eversole et al. 1984).

Spawning clams release eggs through the exhalent siphon. The average diameter of the newly discharged eggs is 70-73 µm (Loosanoff and Davis 1963). The eggs are surrounded by a gelatinous envelope about 25 µm thick which swells after contact with water to a thickness of 95 µm, resulting in a total diameter of about 270 µm (Carriker 1961). Bricelj and Malouf (1980) observed that clams induced to spawn produced a wide range of egg sizes (50-97 µm), and that small eggs were most abundant late in the spawning season. Survival was much higher in large eggs cultured in the laboratory than smaller ones (Kraeuter et al. 1982). The gelatinous envelope provides buoyancy and enables water currents to carry eggs. Fertilization occurs in the water after actively swimming sperm come into contact with and penetrate the gelatinous envelope. To insure fertilization, numerous sperm must be available. Bricelj and Malouf (1980) calculated an optimum ratio of 1,800 sperm to 1 egg for successful fertilization under culture conditions and it is likely that higher gamete ratios are required in nature.

Fertilized eggs develop rapidly; cleavage begins within 30 min at 27-30 °C and after about 10 h a ciliated gastrula can be seen spinning within the gelatinous envelope (Belding 1931). Continuous beating of the cilia tears the surrounding envelope, permitting the embryo to escape. The embryo immediately changes from a sphere to a pear-shaped form called a trochophore, which is a nonshelled planktonic stage (Carriker 1961).

Larvae

The hard clam has two nonshelled larval stages, trochophore and early veliger (Carriker 1961). During these two larval stages, the shell gland and mouth develop and feeding begins. Both nonshelled larval stages propel themselves with a ciliated velum (Loosanoff and Davis 1950). At about 1 day of age, the organism enters the first shelled larval stage, called a straight-hinged veliger, or sometimes the prodissoconch I stage; it has a smooth shell secreted by the shell gland (Eyster and Morse 1984). Valves of this shell range from 90 to 140 µm in length and are slightly asymmetric (Carriker 1961). After about 3 days, the second shelled larval stage - the umboned veliger or prodissoconch II stage - begins. Minute striae appear on the shell surface, and a smooth arc appears near the hinge line at the point where the umbo forms (Carriker 1961). Age and shell length of umboned veligers are 3-20 days and 140-220 µm (Carriker 1961). The velum is well developed in both stages, enabling the veligers to swim well enough to move 7-8 cm/min (Mileikovsky 1973) and maintain themselves in the water column. Vertical distribution of the larvae in the water column is uniform at night and concentrated about 1 m below the surface during the day - possibly to keep larvae away from bottom-dwelling predators (Carriker 1952). Larvae may be stimulated to rise in the water column by turbulence resulting from water currents and waves (Carriker 1961). The horizontal distribution of larvae is patchy and is influenced by water movement and the temporal aspect of spawning (Carriker 1961). During the spawning seasons, larval hard clams are important members of the zooplankton community, reaching densities that exceed 500 larvae/l (Carriker 1961).

The next stage, near the end of planktonic life, is the pediveliger. At sometime after they are 6-20 days old and 170-220 µm long, clams develop a strong ciliated foot, but maintain use of the velum (Carriker 1954, 1961). The presence of both of these locomotor organs allows the clam to crawl, examine the substrate, and swim to another area. The pediveliger stage terminates when the velum is lost and the clam takes up a benthic existence; locomotion is then limited to crawling.

Plantigrade (Dissoconch) Stages

Initially, the pediveliger metamorphoses into a byssal plantigrade that attaches to the substrate by means of a byssus (Carriker 1961). When larvae settle, they are commonly called spat and the stage is referred to as the setting or spatting stage. Byssal plantigrades are active during this period, breaking byssal attachments and crawling on or very close to the substrate surface to other attachment sites. Characteristics of this stage are a well-developed foot with a byssus gland (Belding 1912), the active development of siphons and fusion of the mantle, and the deposition of conspicuous concentric shell ridges (Carriker 1961). The byssal plantigrade develops into the juvenile plantigrade stage at a shell length of about 7-9 mm (Belding 1912; Carriker 1961). The foot shortens and the byssus gland becomes nonfunctional. Juvenile plantigrades maintain contact with water by means of two completely developed siphons, and hold their position in the substrate with a stout hatchet-shaped foot. Movement decreases as the clam grows, its siphons elongate, and it burrows deeper in the substrate.

The hard clam shows gregarious setting behavior (Keck et al. 1972). Clams often set along edges of sandbars or channels where differentials in water current occur (Carriker 1959). Concentrations of clams in these areas may be more of a mechanical sorting process than the selection of a site (Moulton and Coffin 1954; Carriker 1959). Keck et al. (1974) demonstrated in laboratory studies that clams preferred sand as a setting substrate rather than mud. They hypothesized that the organic matter (with its associated bacteria) was responsible for reduced setting in the mud substrate. Sand substrates treated with clam liquor resulted in higher sets than sand did without liquor (Keck et al. 1974). Presence of a pheromone on an appropriate substrate, possibly released by early setting larvae, may provide the necessary cue for metamorphosing larva to set nearby and lead to the aggregated distribution of clams.

Predation is an important factor in influencing the density and distribution of clams. Heavy sets of clams (e.g., 125/m^2) are often reduced to negligible quantities in areas without protection from predators (Carriker 1959, 1961). Bottoms with shell and subtidal grasses appear to have better conditions for spat survival than unstructured bottoms - probably because these bottoms offer some protection from predators, or because fewer predators are present (Kerswill 1941; Wells 1957b; MacKenzie 1977; Peterson 1982). Experimental areas with calico scallop shells had significantly greater numbers of juvenile hard clams than control areas (Parker 1975). Experimental exclusion of predators by caging illustrated that in unvegetated areas survival was higher in the absence of predation (Peterson 1982). The use of crushed stone, pens, and traps to protect clams from predators and reduce their impact on clam mariculture has been successfully demonstrated by Castagna and Kraeuter (1977) and Kraeuter and Castagna (1980).

Adults

Hard clams live in the substrate with the long shell axis 25-45° from vertical (Stanley 1970). Mean depths of clams average 2 cm in sand and 1 cm in mud (Pratt and Campbell 1956); smaller clams burrow deeper than large clams (Stanley 1970). I have noticed that very large clams lie on their side at the surface of firm substrates such as oyster bars. Horizontal movement of adult clams is limited and the distance traveled is generally correlated with the size of clams, the smaller clams being the more active (Chestnut 1952). Juvenile clams seemingly are able to change their habitat or correct for displacement caused by disturbances (e.g., wave action). The hard clam is a moderately rapid burrower (Stanley 1970) and can generally escape from a 15-50 cm burial with native sediment (Kranz 1974). Vertical movement of approximately 44 cm/h has been recorded (Kranz 1974). Burial in sediment different from native sediment (e.g., spoilage from dredging) radically diminishes the clam's ability to escape.

The spatial distribution of hard clams is aggregated and explained by a negative binomial distribution (Saila and Gaucher 1966; Anderson et al. 1978). Clams also occur at higher densities in certain bottom types. Densities are highest in sandy bottoms containing shell (Pratt 1953; Wells 1957b; Anderson et al. 1978; Walker et al. 1980; Walker and Rawson 1985). The clams are usually found in the intertidal and subtidal zones of estuaries and protected bays at depths less than 4 m (Godwin 1967, 1968b; Anderson et al. 1978; Walker and Rawson 1985). Hard clams in the South Atlantic region occur in beds along the outer edges of highly saline bodies of water (Godwin 1968b; Walker et al. 1980). Unlike hard clam populations in northern locations, clams are abundant (densities up to 101/m^2) in small tidal creeks, especially those with a prominent oyster bar at the mouth (Walker et al. 1980).

GROWTH CHARACTERISTICS

Relation of shell height (dorso-ventral axis), shell width (lateral axis), and the cube root of clam weight to shell length (anterior-posterior axis) is linear; thus, there are no changes in proportions with growth (Haskin 1950). Shell growth of hard clams is greater in the first year after metamorphosis than in succeeding years (Haskin 1950, 1952; Menzel 1963). The average length of hard clam seed, 3 mm long when planted in Alligator Harbor, Florida, was 28.1 mm after the first year of growth, 49.6 mm after the second, and 61.5 mm after the third (Menzel 1963). Monthly shell length increments averaged 2.47, 1.42 and 1.08 mm for the first, second, and third years of growth, respectively (Menzel 1963). In South Carolina, incremental growth declined similarly in hard clam seed planted at a greater shell length (13 mm) over a 3-year experimental period (Eldridge et al. 1979). Decreased incremental growth with increased shell length has been observed in the hard clam throughout its range (e.g., Belding 1931; Chestnut 1952; Gustafson 1955; Pratt and Campbell 1956; Crane et al. 1975). Growth of hard clams also appears to decrease with increasing age (Eversole et al. 1986). Older and slower growing clams thicken at the margin of the shell and become blunt as progressively more calcium is deposited (Belding 1931). Little incremental shell growth can be detected in these older clams, which are referred to as blunts. When two clams about 3 years old and 49 and 58 mm long were marked with a file between the years 1947 and 1951 and collected alive in 1980, they were only 87 and 99 mm long (Lutz and Haskin 1984). Annual growth in length had thus averaged about 17.8 mm for the first 3 years of life and 1.3 mm thereafter. Estimated ages of 36 and 33 years for these two clams are the oldest reported for the hard clam (Lutz and Haskin 1984).

Hard clams longer than 80 mm are common in unexploited populations such as that in Wassaw Sound, Georgia, where about 50% of the clams were reported to be >80 mm (Walker et al. 1980). Walford plots for hard clams grown in the York River, Virginia, and Clark Sound, South Carolina, predicted that clams would cease growing at lengths of 80 and 70 mm, respectively (Loesch and Haven 1973; Ng et al. 1982). These estimates of asymptotic sizes are not valid everywhere because hard clams >100 mm long have been reported in South Carolina and Georgia (Anderson et al. 1978; Walker et al. 1980).

Shell growth in hard clams is a dynamic process that is continually influenced by environmental, physiological, and genetic factors. Growth of veliger larvae of the hard clam is fastest at temperatures of 22.5-36.5 °C and salinities of 21.5-30.0 ppt (Lough 1975). The temperature-salinity conditions at which maximum growth occurs are somewhat higher than those at which survival is the highest (Lough 1975). Ansell (1968), who studied growth of adult hard clams throughout their geographical range from published literature, concluded that shell growth was fastest at 20 °C and stopped below 9 °C and above 31 °C. Annual growth increases progressively from the northern portions to the southern extreme of the range distribution (Ansell 1968). The number of years required to reach a commercial length of 45 mm (average minimum legal size calculated from data in Ansell, 1968) is about 5.5 in Canada; 4 in Maine, 3 in Massachusetts, Rhode Island and New York, 2 in South Carolina and Georgia, and less than 2 in Florida (Ansell 1968; Godwin 1968a; Menzel 1963; Eldridge et al. 1979). Ansell (1968) attributed these latitudinal differences in growth rate to differences in the length of the growing season, but stressed the importance of food availability within any range of water temperatures. Growth correlates well with available food (Pratt and Campbell 1956). Growth of hard clams in northern areas such as Canada and Maine is restricted principally to the summer months (Kerswill 1941; Gustafson 1955; Ansell 1968). The growing season is longer in southern areas, and extends throughout the year in South Carolina (Eldridge et al. 1976, 1979). However, growth was fastest during spring and fall when water temperatures approached 20 °C (Menzel 1963; Eldridge et al. 1979).

Hard clams store little food reserves (Ansell and Loosmore 1963). Growth and gonadal development in the hard clam therefore require continuous and substantial energy input (Ansell and Loosmore 1963; Eversole 1986). When gonadal development is most active (e.g., during oocyte formation), competition for food reserves may intensify and decrease growth rate. Data on interrelationships between growth and the physiological state of hard clams are rare.

Some variation in growth among hard clams may be attributed to genetic factors. In one generation, hard clams selected for fast growth were 60% larger than wild stock after 15 months (Chanley 1959). Natural hybridization of _M_. _mercenaria_ and _M_. _campechiensis_ appears to occur where the species overlap (e.g., Indian River, Florida). Growth of hybrids in Gloucester Point, Virginia, and Beaufort, North Carolina, was considerably better than that of _M_. _mercenaria_ (Chestnut et al. 1957; Haven and Andrews 1957). _M_. _campechiensis_ suffered high winter mortalities at these two locations, suggesting inability to withstand low temperatures. In more southerly areas, _M_. _campechiensis_ survives the winter and outperforms _M_. _mercenaria_; growth of hybrids is intermediate (Menzel 1964). Recommendations for hybridization programs provided by Menzel (1977) appear suitable to environmental conditions in the South Atlantic region.

COMMERCIAL/RECREATIONAL FISHERIES

Fisheries

Three of four commercial grades of hard clams are harvested legally in the United States (Table 3). Littlenecks or "necks" are sold as part of the live shell trade and are the most expensive. Price per bushel of clams varies, but usually that of littlenecks averages 4.5 times and 2.7 times that of a bushel of chowders and

Table 3. Commercial hard clam categories (Anderson et al. 1978).

Commercial grade	Shell length (mm)
Seed[a]	<50
Littlenecks	50-65
Cherrystones	66-79
Chowders	>80

[a] Minimum legal length varies by State along the Atlantic seaboard, but averages about 45 mm (Ansell 1968).

cherrystones, respectively (Ritchie 1977). Chowders, the largest and least valuable clams marketed, are frequently processed or made into chowder.

Commercial harvesting of clams in the United States is dominated by four species (Table 1): hard clams, ocean quahogs (Arctica islandica), softshell clams (Mya arenaria) and surf clams (Spisula solidissima). Hard clams yield the highest dollar value of the commercial catch, producing 11.1% of the clam meats landed in United States (Table 1). The Middle Atlantic region (New York, New Jersey, and Delaware) has long been the leading producer of hard clam meats (U.S. Department of Commerce 1984). Production of meats in the South Atlantic region (North Carolina, South Carolina, Georgia, and Florida east coast) was less than that in the New England region, similar to that in the Chesapeake region, but more than that in the Pacific region (U.S. Department of Commerce 1984). In the South Atlantic region, North Carolina is the leading producer. Production throughout the South Atlantic region has increased over the last 6-10 years (Table 4), partly in response to greater demand, higher value, and the evolution and use of mechanized harvesting equipment (Rhodes et al. 1977; Guthrie and Lewis 1982). Official harvest statistics of hard clams are underestimated, probably because the industry is diffuse,

Table 4. Mean annual commercial landings of hard clams (1,000 kg meats) and the percentage of the harvest in the South Atlantic region (calculations based on data from volumes of the U.S. Department of the Interior's and the U.S. Department of Commerce's Fishery Statistics of the United States, various years).

State	1928-32		1950-54		1973-77		1979-83[a]	
	1,000 kg	%	1,000 kg	%	1,000 kg	%	1,000 kg	%
North Carolina	146.8	92.7	280.5	97.5	181.5	61.1	681.7	78.8
South Carolina	0.9	0.6	4.9	1.7	67.5	22.7	145.5	16.8
Georgia	0.9	0.6	0.0	0.0	1.5	0.5	1.6	0.2
Florida[b]	9.7	6.1	2.3	0.8	46.8	15.7	36.5	4.2
Total	158.3		287.7		297.3		865.3	

[a] Unofficial statistics.
[b] East coast of Florida only.

and recreational harvests are not included in the landings.

There are no comprehensive records of recreational harvesting. A creel-census-type survey of the recreational hard clam fishery in Great South Bay, New York, indicated that about 2,000 persons harvested 2,200 kg (4,800 bushels) of clam meats in 1977 (Fox 1981). Estimates of recreational harvest range from less than 1% to about 25% of the commercial harvest (Conrad 1979; Fox 1981). The impact of the recreational harvest on hard clam resources is undetermined, and is probably less significant in the South Atlantic region than in the New England and Middle Atlantic regions, where recreational clamming is very popular. Recreational clamming is administrated by state governments in the South Atlantic region and is less restricted than the administration of shellfish grounds in either the New England or Middle Atlantic regions. For example, for recreational harvesting in South Carolina, no license is required, and clams may be harvested in season from state and public shellfish grounds throughout the state (Moore 1979).

Traditionally, most clams have been harvested with rakes or tongs. In North Carolina, a unique method of legally harvesting clams called "kicking" is practiced. Guthrie and Lewis (1982) outlined the evolution of this technique. Essentially, in clam kicking, the wash from the boat's propeller dislodges clams, shells, and other objects from the substrate. An otter trawl, or similar net, is pulled behind the vessel to collect the clams. Clam kicking is a very effective fishing method and a topic of some controversy in North Carolina (Hart 1982). Clams harvested by kicking are listed as taken by trawl in Fishery Statistics of the United States (U.S. Department of Commerce).

The use of hydraulic escalator harvesters has significantly increased hard clam production in South Carolina. Average annual meat yield increased from 37,050 kg in 1971-73, before the escalator harvester was introduced, to 95,400 kg in 1974-76 after its use became legal in South Carolina (Rhodes et al. 1977). Mechanization of clam harvesting equipment appears more acceptable to administrative and legislative bodies in the South Atlantic region than in other fishery regions.

Population Dynamics

In South Carolina, the hard clam begins spawning during the second year of life at a length of about 25-30 mm (Eversole et al. 1980). Females can spawn millions of eggs twice a year for approximately 2 years before they reach commercial size. The fecundity of hard clams is tremendous, but so is preadult mortality. Larval hard clams are abundant in the plankton, reaching maximum population densities of 672/l in Little Egg Harbor, New Jersey (Carriker 1961). Larvae survive in sufficient numbers to provide thousands of spat per square meter, yet the highest density of spat recorded by Carriker (1961) in the Little Egg Harbor was 125/m². Hard clam larvae are carried and concentrated by water currents and in some areas set at densities up to 270,000/m² (Dow and Wallace 1955). However, many larvae are lost from the system, eaten by filter feeders and predatory zooplankton, or set in unsuitable substrate.

Mortality of spat and seed clams is often many times higher than that of adults. Mortality reached 100% in experimental plantings of hard clam seed in unprotected plots in Florida and Georgia (Menzel and Sims 1964; Godwin 1968a). Mortalities among hard clams averaging 20.0 mm shell length were significantly lower than among those averaging 10.5 mm length when they were exposed to crab predation (Whetstone and Eversole 1981). Clams that survive and grow become less vulnerable to predation, probably because the shell thickens and predators are less able to open, crush, or bore into larger clams (Carriker 1959; MacKenzie 1977; Whetstone and Eversole 1978). Whetstone and Eversole (1978) observed an inverse relationship between percentage mortality and shell length of hard clams grown in experimental culture units in South Carolina. Data also indicated that predators selected smaller clams (Whetstone and Eversole 1978). The degree of predation on small clams (< 20 mm long) often determines their relative abundance in a habitat (MacKenzie 1977). Seed clams appear to suffer significant mortalities in summer when predators are active and abundant (Whetstone and Eversole 1978).

Mortality of hard clams in the absence of predation appears low. Annual mortality rates of 1.43% and 4.06% have been calculated for hard clams grown in trays, protected against predation, in South Carolina (Eldridge and Eversole 1982; Eversole et al. 1986). Predation on large hard clams >50 mm long is very low (MacKenzie 1977). The natural mortality of the hard clam is expected to decrease after it becomes 50 mm long; however, fishing mortality may be extensive beyond this size. Crane et al. (1975) observed hard clam densities of 53/m^2 to decrease to 1 to 2/m^2 after only 1 year of clamming. Some mortality among the smaller sublegal clams is associated with exploitation (e.g., breakage and burial). Dow (1953) estimated that these mortalities may reach 30% under some circumstances. The generalized survivorship curve of hard clams approximates the classical Type IV concave curve (Slobodkin 1962), where mortality is extremely high in the early life stages (larvae and spat) until the clams reach a certain shell size, and then mortality greatly decreases.

Calculated estimates of the bioenergetics of a hard clam population on an intertidal mudflat in Southampton, England, indicated that of the annual food intake of 1,292 kcal/m^2, 71% was deposited as feces and pseudofeces (59%) or excreted (12%), and 29% was assimilated (Hibbert 1977). The largest proportion of the 374 kcal assimilated was used for respiration (65%) and approximately equal amounts were allocated to tissue growth (19%) and gamete production (16%). Hard clams contribute annually 884 kcal/m^2 to other trophic levels in Southampton waters (Hibbert 1977). The largest amount of energy leaving the hard clam population passed in the form of biodeposits to the decomposers. Net annual production of the Southampton, England, population was comparable to production values (3-8 g/m^2, ash-free dry weight) reported for sites in Wassaw Sound, Georgia (Walker and Tenore 1984).

ECOLOGICAL ROLE

Feeding

Suspension-feeding bivalves such as the hard clam obtain food by filtering suspended particulate matter and absorbing dissolved organics from the water. Water enters through the ventral inhalent siphon, passes through the gills to an exhalent cavity and out the dorsal exhalent siphon. Food particles suspended on the inhalent surface of the gills are sorted and passed to the gill edges and then moved anteriorly to the labial palps. Large particles are rejected from the gill and palp surfaces and periodically voided from the mantle cavity into the water. This rejected material is usually called pseudofeces. Spasmodic contractions of the adductor muscles act to force pseudofeces out through the inhalent siphon (Kellogg 1903). Food becomes entangled in a mucus strand and is passed to the mouth by cilia on the palps. Food particles passed through the digestive system of the hard clam are expelled by feeding currents from the exhalent siphon into the water as compact rod-shaped fecal pellets, 1.4-4.2 mm long (Haven and Morales-Alamo 1972).

Larval and adult forms of hard clams are capable of selective feeding, regulating the quality and quantity of food ingested. Larvae of the hard clam offered a mixture of algal cells, selected the relatively larger cells of Chlamydomonas and rejected the cells of Porphyridium (Loosanoff and Davis 1963). When the concentration of food cells exceeded an optimum level, larval clams rejected cells and their stomachs contained less food than did those of larvae kept at lower cell concentrations (Loosanoff and Davis 1963). Mortality was considerable among larvae exposed to high concentrations of food for long periods, apparently from clogged feeding apparatus and bacterial fouling (Guillard 1959; Loosanoff and Davis 1963). In adult hard clams, feeding rate increases with increasing food concentrations to a maximum, followed by decreased feeding when food is further concentrated (Tenore and Dunstan 1973). Growth of hard clams correlates better with the presence or absence of particular algal species than with gross chemical or amino acid compositions of algal diets (Epifanio 1979). Feeding in the hard clam appears well adapted to changing food levels and is sensitive to the algal species composition. Hard clams also eat suspended detritus and its associated bacteria, and absorb dissolved organic matter directly from the water to help meet their energy requirements (DiDomenico and Iverson 1977).

Parasites and Disease

Literature on clam parasites and disease is sparse, particularly in comparison with the literature available on the American oyster, Crassostrea virginica. Few diseases of M. mercenaria have been identified. Tubiash et al. (1965) described a bacillary necrosis in larvae of the hard clam that was probably caused by a species of Vibrio and Davis et al. (1954) described a fungal invasion of larval clams as that of Sirolpidium zoopthorum. In culture conditions, S. zoopthorum sometimes causes significant mortality to both larvae and juveniles.

Mercenaria mercenaria are infested by few faunal parasites. Uzmann (1955) reported the trematode Aimasthala quissetensis, pathogenic to humans, in hard clams in New York. Cake (1977) found heavy infestations of the larval cestode Tylocephalum sp., which reduces the quality of meats, in clams in the Gulf of Mexico. Styloccus ellipticus, a free-living turbellarian flatworm, has been found in hard clams in Virginia and may be parasitic (Andrews 1970). Other parasites include nemerteans, Malacobdella grossa (Coe 1943b); mudworms, Polydora websterii (Davis 1969); and parasitic copepods, Leptinogaster major, Mytilicola spinosa, and M. porrecta (Pearse 1947; Humes 1954; Humes and Cressey 1960). Diagnosis and control of parasites and diseases in shellfish were reviewed by Sindermann (1974).

Predators

Predators of larval hard clams have not been identified; however, many zooplanktivores, as well as bottom dwelling filter feeders including adult clams, have been suggested as consumers of larvae (Belding 1931; Carriker 1961). The list of predators of the bottom-living hard clam over its geographical range is long (Table 5). Abundance and importance of any particular predator varies among locations with the time of year.

Crabs appear to be the major predators of the hard clam in the South Atlantic region. The blue crab, Callinectes sapidus, is probably the most destructive predator among crabs; mud crabs and stone crabs prey less on hard clams (Menzel and Sims 1964; Godwin 1968a; Whetstone and Eversole 1978). Crabs, especially the mud

Table 5. Predators of hard clams.

Common name	Scientific name	Source[a]
Horseshoe crab	*Limulus polyphemus*	l,u
Snapping shrimp	*Alpheus heterochaelis*, *A. normanni*	a
American lobster	*Homarus americanus*	v
Blue crab	*Callinectes sapidus*	c,d,f,g,h, l,m,o,y
Stone crab	*Menippe mercenaria*	y
Green crab	*Carcinus maenas*	e,l,t
Rock crab	*Cancer irroratus*	m
Mud crabs	*Eurypanopeus depressus*, *Neopanope sayi*, *N. texana*, *Rhithrapanopeus harrissi*, *Panopeus herbstii*	e,h,k,l,m, y
Calico crab	*Ovalipes ocellatus*	h
Moon snails	*Polinices duplicatus*, *Lunatia heros*	b,c,e,l,m,u
Oyster drills	*Urosalpinx cinerea*, *Eupleura caudata*	c,e,g,h,j, l,m,u
Whelks	*Busycon carica*, *B. canaliculatum*, *B. contrarium*	b,h,m,n,r
Atlantic murex	*Murex fulvescens*	w
Banded tulip	*Fasciolaria hunteria*	x
Sea star	*Asterias forbesi*	b,m,s,u
Rays	*Dasyatis centrura*, *Gymnura micrura*, *Rhinoptera bonasus*	f,m,p,q
Flounders	*Paralichtys dentatus*, *Pseudopleuronectes americanus*	h,m
Tautog	*Tautoga onitis*	m
Puffer	*Sphaeroides maculatus*	m
Herring gull	*Larus argentatus*	i
Waterfowl	not identified	e

[a] Sources: a-Beal 1983; b-Belding 1931; c, d, e-Carriker 1951, 1959, 1961; f-Castagna and Kraeuter 1977; g-Chestnut 1951; h-Flagg and Malouf 1983; i-Hibbert 1977; j-Kellogg 1903; k, l-Landers 1954, 1955; m-MacKenzie 1977; n-Megalhaes 1948; o-Menzel and Sims 1964; p-Menzel et al. 1976; q-Nelson 1947; r-Peterson 1982; s-Pratt and Campbell 1956; t-Ropes 1968; u-Ropes and Martin 1960; v-Saila and Pratt 1973; w, x-Wells 1958a,b; y-Whetstone and Eversole 1978.

crabs, usually feed on the smaller hard clams (Whetstone and Eversole 1978). Crab attacks on hard clams >50-60 mm long are less successful than those on smaller clams (MacKenzie 1977; Whetstone and Eversole 1978; Walker et al. 1980). Whetstone and Eversole (1981) observed that the percentage of mud crabs, Panopeus herbstii, that opened clams increased as crab size increased. Large crabs also were more successful in opening larger clams. Hard clams >35 mm long were not opened by any size of mud crab tested (10-40 mm carapace width). Mud crabs are an important source of mortality to hard clams because they are ubiquitous and abundant throughout the range of the clam (Carriker 1961; Whetstone and Eversole 1978).

Gastropods of the genus Busycon can open hard clams 20-75 mm long at the rate of about one per week (Carriker 1951). Busycon preys preferentially on the larger size classes of hard clams (Peterson 1982). Knobbed whelks (B. carica) and lightning whelks (B. contrarium) have similar feeding behaviors. These whelks grasp the clam shell with their muscular foot in such a way that when the columellar muscle contracts, the whelk shell crashes against the ventral edge of the clam shell. When enough of the clam shell is chipped away, the whelk either wedges open the shell or inserts its proboscis into the shell and the clam's soft parts (Megalhaes 1948; Carriker 1951). The chipping behavior characteristic of these species appears to be poorly developed in B. canaliculatum, which usually inserts its shell between the valves of an unsuspecting clam and wedges it open (Carriker 1951). Other carnivorous gastropods (Urosalpinx, Eupleura, Polinices, and Lunatia) use their radulae to rasp holes in the shell to gain entrance to the soft parts of the clam (Carriker 1981).

It is not known how detrimental other species of predators are to hard clams in the South Atlantic region. Starfish appear to be important predators in the Northeast (MacKenzie 1977) and rays cause significant mortality to clams in the Chesapeake Bay area (Castagna and Kraeuter 1977).

Predation can substantially reduce clam abundance. Mortalities reached 100% in experimental plantings of hard clam seed in Florida and Georgia (Menzel and Sims 1964; Godwin 1968a). Over 90% of the losses at these two locations were due to predation by blue crabs. An increase in recruitment of hard clams in Great South Bay, New York, was linked to the decline of blue crabs after a severe winter (Greene and Becker 1978). Densities of hard clams increased seven- to eight-fold after predator numbers were reduced by a single application of a pesticide (MacKenzie 1977). Peterson (1982) demonstrated by exclusion experiments that hard clam survival is high in the absence of predators. Predation appears to be the most important biotic factor in limiting hard clam populations (Virstein 1977; MacKenzie 1979).

ENVIRONMENTAL REQUIREMENTS

Temperature

Temperature has been considered the most important factor in determining time of spawning, because a certain degree of gonad ripeness or maturation must be attained before hard clams can respond to specific spawning stimuli (Loosanoff 1937b: Ansell et al. 1964). Once an appropriate level of ripeness is reached, a critical temperature level or increase may trigger spawning (Loosanoff and Davis 1963). Gonadal development appears to begin at 10 °C and spawning occurs between 16 and 30 °C (Table 2). Because water temperatures in the South Atlantic region are relatively high, gametogenesis can occur year around and spawning occurs from early spring to late fall (Porter 1964;

Eversole et al. 1980; Manzi et al. 1984; Pline 1984).

Hard clams were cultured from the egg to the spat stage at constant temperatures ranging from 18 to 30 °C (Loosanoff et al. 1951). Larvae ingested food at temperatures as low as 10 °C, but did not grow (Davis and Calabrese 1964); minimum temperature for larval growth was 12.5 °C. Growth was generally more rapid at higher temperatures, peaking at 25-30 °C (Davis and Calabrese 1964). Abnormal larval development and heavy mortality occurred at temperatures above 33 °C (Loosanoff and Davis 1963). Response surface estimations (the response surface technique is a statistical method for determining the maximum biological response to more than one independent variable) of the temperatures and salinities yielding maximum larval growth and survival were 21.5-33.0 °C and 22-31 ppt (Lough 1975). In Little Egg Harbor, New Jersey, larval hard clams grew to setting size in about 8 days at water temperatures of 23.4-26.2 °C (Carriker 1961). High temperatures had more effect on the growth and survival of developing embryos than those of straight-hinged larvae (Kennedy et al. 1974; Lough 1975).

Ansell (1968), who summarized the growth rates of the hard clam over its geographical range, found that growth was optimal at 20 °C and ceased at 9 and 31 °C. Loosanoff (1939) demonstrated that hard clams became progressively less active as temperature decreased to 9 °C and became inactive at about 4 °C. Water temperatures rarely reach 4 °C and almost never remain at this low temperature for long periods in the South Atlantic region - one reason why hard clams grow there throughout the year (Menzel 1963, 1964; Godwin 1968a; Eldridge et al. 1976, 1979). Shell growth (length) is fastest in spring and fall, slower in winter, and the slowest in summer, when water temperatures often exceed 30-33 °C (Menzel 1963, 1964). Kennish and Olsson (1975) observed decreased growth in hard clams when thermal effluent was discharged in the summer from a power plant in Barnegat Bay, New Jersey. Hatchery-reared hard clams raised in warm-water upwelling systems in tropical St. Croix, Virgin Islands, grew little and nearly all died (Sunderlin et al. 1975). The upper lethal temperature of the hard clam is 45.2 °C (Henderson 1929); however, temperatures above 30 °C adversely affect its behavior and physiology (Hamwi 1968; Savage 1976; Van Winkle et al. 1976). Adult hard clams survive below-freezing temperatures to -6 °C and succumb to low temperatures only when a majority (64%) of the tissue freezes (Williams 1970). Hard clams covered by flowing water or sediment survive low temperatures better than those exposed in intertidal areas (Dow and Wallace 1951).

Salinity

The hard clam is an osmoconformer and moderately euryhaline. It has been found growing in waters of 4 to over 35 ppt salinity (Chestnut 1951; Wells 1957b, 1961; Godwin 1968b; Anderson et al. 1978), but growth is optimal at 24-28 ppt (Turner 1953; Chanley 1958). Native clam beds are known to occur at salinities of 10-28 ppt in North Carolina, 4-35 ppt in South Carolina, and 18-35 ppt in Georgia (Chestnut 1951; Godwin 1968b; Anderson et al. 1978). Minimum salinity conducive to favorable hard clam growth and survival is 12.5 ppt (Castagna and Chanley 1973). Hard clams can close their shells tightly during periods of stress, as when freshets occur, and respire anaerobically (Lutz and Rhoads 1977). Mortality was less than 5% in hard clams in the Santee River system, South Carolina, exposed to low salinities (<10 ppt,) during 2- and 3-week periods while mortality in oysters averaged about 50% (Burrell 1977). The lower hard clam mortalities were attributed to their ability to remain closed longer than oysters. Hard clams cease pumping at salinities below 15 ppt and above 40 ppt (Hamwi 1968).

Eggs of hard clams developed into normal straight-hinged larvae at salinities of 20.0-32.5 ppt (Davis 1958), but larvae did not metamorphose to byssal plantigrades (spat) at salinities below 17.5-20.0 ppt (Castagna and Chanley 1973). Larvae appeared less tolerant of low salinities than adults: minimum salinity for survival was about 12.5 ppt for adults and 15.0-17.5 ppt for larvae (Davis 1958; Castagna and Chanley 1973). Similarly, eggs require higher salinities than larvae for development: no eggs developed at 17.5 ppt salinity and only 16%-21% at 20 ppt (Davis 1958). Optimum salinity for egg development and larval growth and survival is 26-27 ppt (Davis 1958; Davis and Calabrese 1964; Castagna and Chanley 1973).

The range of temperatures tolerated by larval hard clams was reduced considerably when salinity was reduced. Lough (1975) reevaluated the combined effects of temperature and salinity, using response surface techniques, and noted that some of the differences between studies may be due to the temperature-salinity interaction.

Water Quality

Dissolved oxygen (DO) concentrations of 6.8-7.4 mg/l are recommended for successful culture of the hard clam (Hartman et al. 1974). Morrison (1971) reported that eggs developed at 0.5 mg/l DO, but mortality was high and growth was nonexistent at levels less than 0.3 mg/l. He observed that prolonged exposure to low DO lengthened the larval life stage and decreased the probability of survival. Growth rate of larvae returned to normal and metamorphosis proceeded when larvae were returned to higher concentrations of DO. Larval growth and metamorphosis appeared normal at DO levels higher than 4.1 mg/l (Morrison 1971). Hourly oxygen consumption by larvae was about 4.5-4.8 ml/g of dry weight (Marinucci 1975).

Adult hard clams encounter a wide range of DO concentrations and have apparently evolved several metabolic mechanisms to handle conditions such as anoxia (Greenfield and Crenshaw 1981). Hamwi (1969) observed that hard clams decreased oxygen consumption as DO concentrations decreased below 5 mg/l. Hard clams incurred an oxygen debt when deprived of oxygen (Hamwi 1969). Little correlation was observed between the growth of hard clams and DO concentrations in Narragansett Bay, Rhode Island (Pratt and Campbell 1956). Hard clams exposed to oxygen-impoverished conditions (<1 mg/l) for up to 3 weeks maintained the ability to burrow (Savage 1976). They appear not to be severely affected by low DO, and associated stresses apparently had no long-lasting effect (Savage 1976).

The hard clam usually lives in well-buffered areas; however, pH may decrease below 7.0 in tide pools and estuaries with poor circulation, heavy siltation, pollution, and hydrogen sulfide production. In laboratory experiments, Calabrese and Davis (1966) demonstrated that embryos of hard clams developed normally over a pH range of 7.0-8.75. The range for normal larval growth and survival was 6.75-8.50 and 7.25-8.75, respectively (Calabrese and Davis 1966). Hard clams appear to require that the pH not be below 7.0 nor above 9.0 for successful recruitment (Calabrese and Davis 1966; Calabrese 1972).

In addition to the effect of reduced pH associated with high concentrations of silt, silt itself appears to be directly detrimental at high concentrations to eggs and larvae of the hard clam. Egg development was adversely affected by silt concentrations above 0.75 g/l, and no eggs developed normally at concentrations of 3 g/l or higher (Davis 1960).

Growth of larvae was retarded at 1-2 g/l and stopped at 3-4 g/l (Davis 1960). Larvae are affected differently by various suspended-solid producing substances; e.g., larvae were more adversely affected by kaolin than by silicon dioxide (sand) of the same particle size (Davis and Hidu 1969). The particle size of silt is also an important factor in the survival of larvae. Hard clam larvae in the presence of a high concentration of smaller particles of kaolin eventually exhausted their sorting apparatus; as a result their stomachs became packed and they died (Davis and Hidu 1969). Eggs appear to tolerate higher levels of suspended solids than do larvae, which can tolerate higher levels than those normally encountered in natural waters (Davis and Hidu 1969). Although several hypotheses have been postulated, no clear relationship has been demonstrated between levels of suspended solids and the growth and survival of adults (Pratt and Campbell 1956; Rhoads et al. 1975). Cabelli and Heffernan (1971) noted a marked reduction in the number of coliform bacteria in hard clams at higher levels of suspended solids.

Hard clams tolerate wide ranges in different water quality variables such as ammonia, nitrite, nitrate, phosphates, and sulfur compounds. Epifanio and Srna (1975) reported that the 96-h median tolerance limit of the hard clam was 110-172 mg/l for ammonia and 1,863-1,955 mg/l for nitrite ion. Tolerance to nitrate and orthophosphate was so high that even clams cultured in effluents of secondarily treated domestic sewage would rarely be exposed to these levels. They concluded that hard clams are unlikely to be exposed to acute or chronic levels of ammonia, nitrite ion, nitrate ion, or orthophosphate in the natural environment. However, Calabrese (1972) showed that hydrogen sulfide production and its potential to reduce pH levels in some systems may have a negative effect on hard clams.

Hard clam embryos and larvae exposed to a variety of pollutants and toxicants have a wide range of responses; however, among almost all the 52 compounds tested, slowed shell growth was the first symptom of toxicity (Davis 1961; Davis and Hidu 1969). It was also apparent that the life stages of hard clams responded differently to toxicants; at some concentrations, larval growth was reduced significantly but embryonic development was little affected (Davis and Hidu 1969). Sublethal concentrations of many pollutants such as petroleum products have detrimental effects; hard clams exposed to only 0.6 mg/l of the water-soluble fraction of Nigerian crude oil exhibited decreased feeding rates, use of food consumed, and growth (Keck et al. 1978). Once exposed to a pollutant (e.g., petroleum hydrocarbons), hard clams retain a fraction of pollutant until it can be depurated. Persistence of the pollutant is related to duration of exposure and chemical qualities of the pollutant (Boehm and Quinn 1977). Ansell (1964b) observed that hard clams are relatively tolerant of pollution; however, organic pollution may include some microbes pathogenic to humans and toxicants that limit the commercial harvest of clams without extensive depuration.

Water Current

Water current that provides adequate circulation is essential for good growth and recruitment of hard clams. Water current performs several services: provision of food; maintenance of acceptable water quality; removal of biodeposits; and transportation of eggs and larvae (Belding 1931). Kerswill (1949) observed that hard clams grew more rapidly in areas with substantial flow (7.5 cm/sec) than in areas with little water circulation. He attributed this better growth to the increased water circulation and hence increased food availability. One kg of seed clams in an upflow nursery system utilizing a vertical flow of water increased its biomass 126% during the fall at a flow rate of 15 l/min, compared with 213% increase at a flow of 29 l/min (Manzi et al. 1986). Growth was positively correlated with flow rate in this culture system during most of the year. Strong tidal currents, however, may scour the bottom and displace clams (Wells 1957b).

Saila et al. (1967), after studying several environmental factors in an attempt to explain the distribution of hard clams, concluded that current, vegetation, predation, and sediment properties all affect clam distribution. Abundance of the larvae is uneven; densities are highest in the central basin of Little Egg Harbor, New Jersey, and away from the inlet, where tidal exchanges diluted larval density (Carriker 1961). In Orr's Cove, Maine, the abundance of hard clam larvae was highest 3 h after high tide; lowest abundance was near low tide (Moulton and Coffin 1954). Hard clams appear to set where differentials in water current exist; larval densities may be high there because of mechanical sorting and concentration by water currents (Moulton and Coffin 1954; Carriker 1961).

Substrate

Substrate type and the degree of sorting among the sediments are determined in part by water current (Newell 1970). Obviously, the interaction confounds any conclusions as to clam distribution, growth, and survival being related to substrate type.

Sediment appears to be an important factor influencing setting of hard clam larvae. Keck et al. (1974) observed in the laboratory that hard clams preferred to set in sand rather than in mud; 2,083 clams set in 500-μm sand compared to only 781 in 50-μm mud. Carriker (1959) recommended firm substrate free of organic mud for optimal setting of larval hard clams in culture. Adult hard clams occur at highest densities in sandy bottoms with shell (Pratt 1953; Wells 1957b; Anderson et al. 1978; Walker et al. 1980). In Georgia, averages of 22 hard clams/m^2 were found in sandy bottoms with shell, 12/m^2 in sandy bottoms, and 3/m^2 in mud bottoms (Walker et al. 1980). Although sandy bottom with shell is not the dominant substrate type in South Carolina, it was the source of 68% of the total hard clams collected and supported the highest density of clams recorded during a statewide survey of the resource (Anderson et al. 1978). When hatchery-reared seed clams were planted in South Carolina, survival was highest in substrates with the greatest fraction of shell (Eldridge et al. 1976). Pratt and Campbell (1956) observed less shell growth of hard clams in sediments with a high silt-clay content. Hard clams planted in sand grew faster than clams planted in mud (Pratt 1953) and a significant correlation existed between clam shell size and particle size of the substrate (Johnson 1977).

Ecosystem Alteration

Major alterations of the ecosystem, such as the rediversion of 80% of the flow from the Cooper River to the Santee River, South Carolina, are expected to affect the hard clam resource (Kjerfve and Greer 1978). About 80% of the commercial clam harvest in South Carolina came from the Santee River (Rhodes et al. 1977). Rediversion is expected to reduce salinity to such low levels that it may destroy this clam resource (Kjerfve and Greer 1978). Water is being rediverted from the Cooper River to help alleviate the problem of shoaling in Charleston Harbor and the consequent need for continued dredging. Dredging itself may reduce clam numbers in Charleston Harbor and the Atlantic Intercoastal Waterway. Average densities decreased from 7.5-12.1 to 0.3-2.9 clams/m^2 after a navigation channel was dredged through a lagoon on Long Island, New York

(Kaplan et al. 1974). Hard clams not exposed to the mechanical disturbance of dredging exhibited little immediate mortality; however, some delayed mortality, possibly due to dredging, occurred in adjacent clam beds (Kaplan et al. 1974). Burial in sediment different from the clam's native sediment, such as some dredged materials, radically reduces a clam's ability to escape (Kranz 1974). Disposal areas resulting from dredging may also contribute to the loss of valuable habitat for hard clams.

An annotated bibliography with over 2,200 cross-referenced titles on the hard clam was prepared by McHugh et al. (1982). This bibliography will help save time in searching past literature and in checking details of publications cited in this species profile.

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16. Abstract (Limit: 200 words)

Species profiles are literature summaries of the taxonomy, morphology, range, life history and environmental requirements of coastal species. They are designed to assist in environmental impact assessment. The hard clam, Mercenaria mercenaria, supports an important commercial fishery in the South Atlantic, averaging about 1 million kg of meats annually from 1979 to 1983. It also is an important constituent of estuarine systems throughout the region. Spawning occurs in the spring and the fall at 16 to 30 °C. Planktonic eggs and larvae are carried by water currents, and larvae set sometime after 6 days of age. Mortality is highest in egg and larval stages, the most sensitive part of the life cycle. Spat display gregarious setting behavior and appear to select sand over finer substrates. Highest densities of clams occur in sandy bottoms with shell. Crab predation is an important factor influencing the density and distribution of clams. Blue crabs and mud crabs appear to be the most important predators. Hard clams are infested by few parasites. Adult clams feed by filtering suspended particulate matter from the water. Growth of clams decreases with size and age. Growth occurs year-round with peaks in spring and fall. Growth of adult hard clams occurs at 9-31 °C and at 4-35 ppt (optima near 20 °C and 24-28 ppt). Hard clams mature in 2 years and reach commercial size in 3 years in the South Atlantic. Tight-fitting shells permit hard clams to survive poor water quality for short periods.

17. Document Analysis a. Descriptors

Shellfish
Growth
Salinity
Temperature
Fisheries
Suspended sediments
Sediments
Feeding habits
Life cycles
Oxygen
Contaminants

b. Identifiers/Open-Ended Terms

Mercenaria mercenaria
Hard clam
Quahog
Habitat requirements

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National Wetlands Research Center
NASA-Slidell Computer Complex
1010 Gause Boulevard
Slidell, LA 70458