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SPECIES PROFILES: LIFE HISTORIES AND ENVIRONMENTAL
REQUIREMENTS OF COASTA (U) MAINE SHELLFISH RESEARCH
AND DEVELOPMENT DAMARISCOTTA ME C R NEWELL ET AL

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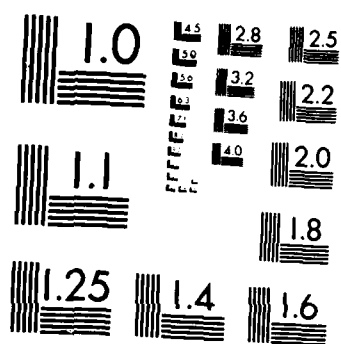
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Biological Report 82 (11.53)
June 1986

TR EL-82-4

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

SOFTSHELL CLAM

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Biological Report 82(11.53)
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June 1986

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

FISHES

SOFTSHELL CLAM

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Vicksburg, MS 39180

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Washington, DC 20240

This series should be referenced as follows:

U.S. Fish and Wildlife Service. 1983-19 . Species profiles: life histories and environmental requirements of coastal fishes and invertebrates. U.S. Fish Wildl. Serv. Biol. Rep. 82(11). U.S. Army Corps of Engineers, TR EL-82-4.

This profile should be cited as follows:

Newell, C.R., and H. Hidu. 1986. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (North Atlantic) -- softshell clam. U.S. Fish Wildl. Serv. Biol. Rep. 82(11.53). U.S. Army Corps of Engineers, TR EL-82-4. 17 pp.

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

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

U.S. Customary to Metric

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

	<u>Page</u>
PREFACE	iii
CONVERSION TABLE	iv
ACKNOWLEDGMENTS	vi
NOMENCLATURE/TAXONOMY/RANGE	1
MORPHOLOGY/IDENTIFICATION AIDS	1
REASON FOR INCLUSION IN SERIES	3
LIFE HISTORY	3
Spawning	3
Fecundity and Gametes	4
Larvae	4
Juvenile Seed Clams	5
Adult Clams	5
COMMERCIAL/SPORT FISHERIES	6
POPULATION DYNAMICS	6
GROWTH CHARACTERISTICS	7
ECOLOGICAL ROLE	8
Food and Feeding Habits	8
Predators	8
ENVIRONMENTAL REQUIREMENTS	9
Salinity	9
Temperature	9
Oxygen	10
Substrate and Current	10
Pollution	11
LITERATURE CITED	13

ACKNOWLEDGMENTS

Dana Wallace and Walter Foster, Maine Department of Marine Resources, Augusta, Maine, and John Moring, Maine Cooperative Fishery Research Unit, University of Maine, kindly reviewed the manuscript.

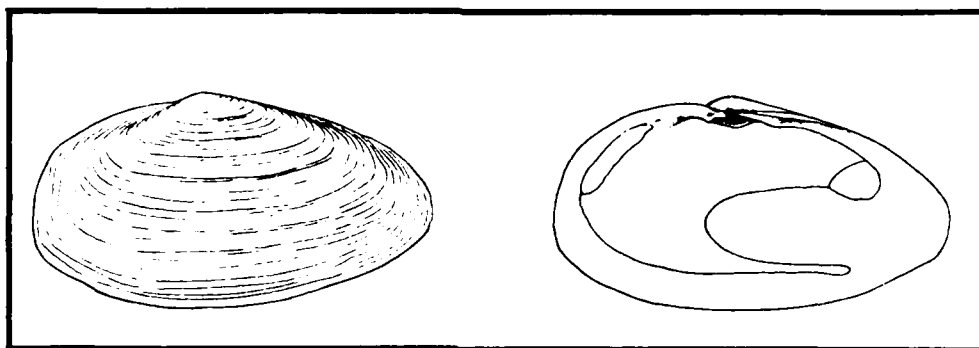


Figure 1. The softshell clam (figure courtesy of the Maine Sea Grant Program).

SOFTSHELL CLAM

NOMENCLATURE/TAXONOMY/RANGE

Scientific name *Mya arenaria* L.
 Preferred common names ... softshell clam, steamer clam, nannynose (Figure 1).
 Other common names sand gaper, long-necked clam
 Class..... Bivalvia (Pelecypoda)
 Order..... Eulamellibranchia
 Suborder..... Heterodonta
 Family..... Myidae

Geographical Range: Intertidal and subtidal to depths of 100-199 m along the Atlantic coast from Labrador to South Carolina and extending, in lesser abundance, south to Florida; throughout western Europe; successfully introduced in Pacific coastal waters of Alaska and California (Theroux and Wigley 1983). The softshell clam is most abundant intertidally along the New England coast (Figure 2) and subtidally in Chesapeake Bay.

MORPHOLOGY/IDENTIFICATION AIDS

The softshell clam sometimes exceeds 10 cm in length (all lengths in this report are shell lengths). The shape of the shell is elongate and elliptical. The clam has a large siphonal gape on the slightly pointed and elongate posterior end, and there is a small pedal gape on the anterior end (Stanley 1970). The shell exterior has numerous growth lines; each usually represents 1 year's growth or an environmental disturbance (Schuster 1951). On live specimens, the exterior of the shell is rugose and is covered with a protein layer called the periostracum. Empty shells turn chalk white after the periostracum erodes away. On large live specimens, the long contractile siphon may extend as far as 20 cm to reach the sediment surface. The foot is small and muscular and the mantle lobes are fused except at the pedal gape and at the ends of the siphon tubes. The end of the incurrent siphon has a ring of tentacles. The adductor muscles are unequal in size (anisomyarian).

The compact hinge ligament is attached to the right valve and is

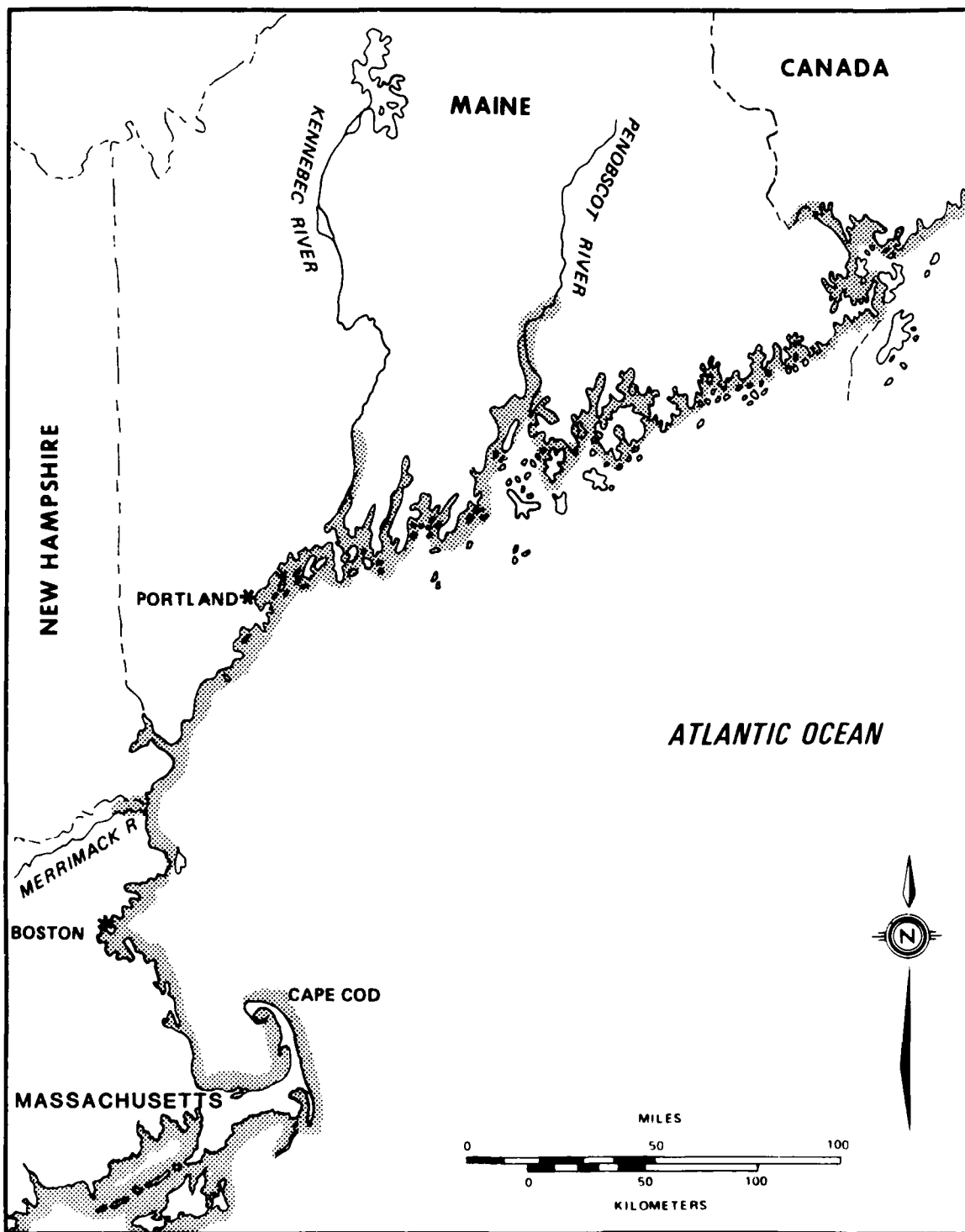


Figure 2. Distribution of the softshell clam in the North Atlantic Bight.

enclosed by the chondrophore of the left valve (Figure 1). The valves are thin, and mean ratios of length (L), width (W), and height (H) are: L/H-1.65, H/W-1 (Stanley 1970). Newell and Hidu (1982) observed mean L/W ratios of 2.6 in clams from gravel beds, and 3.2 in clams from sand beds.

REASON FOR INCLUSION IN SERIES

The softshell clam is a dominant member of many estuarine soft-bottom communities and is commercially important along much of the North Atlantic coast. In New England, it is the second most important commercial clam after the hard clam (*Mercenaria mercenaria*). In 1978, U.S. landings yielded about 4.6 million kg (10.1 million lb) of meats (Pileggi and Thompson 1979). Its inshore distribution, however, makes it vulnerable to contamination by municipal sewage, industrial effluent, and coastal construction projects. Also, the adults usually live in permanent burrows, so excessive siltation can suffocate them. The construction of piers and jetties that alter clam habitat is likely to have long-term adverse effects on clam populations.

LIFE HISTORY

The softshell clam has seven life history stages (Table 1).

Spawning

Sexual maturation of the soft-shell clam depends upon the size of the clam rather than its age. Clams longer than 20 mm in shell length are usually capable of spawning (Coe and Turner 1938). Clams from cold Maine waters may spawn at a smaller size than those from Massachusetts or Long Island Sound. Sexes are separate, the sex ratio is 50:50, and males are indistinguishable from females unless a gonad smear is examined under a microscope. A low incidence of hermaphrodites is common in most populations. The seasonal development of the gonads was summarized for the north Atlantic coast by Ropes and Stickney (1965). Gametogenesis begins in late winter and early spring, and spawning peaks from June to September, depending upon location.

Clams usually spawn once a year north of Cape Cod, and twice a year south of Cape Cod. The differences in

Table 1. The life stages and characteristics of the softshell clam.

Stage	Age or characteristic
Fertilized egg	0-12 hours old.
Trochophore	13-24 hours old, top-shaped.
Veliger	10-20 days old, has a shell and swims by using a velum.
Prodissoconch I	Has straight-hinged shell.
Prodissoconch II	Has umbo on shell.
Spat (Dissoconch)	Bottom-dwelling, after settlement and velum cast off.
Juvenile	Up to 20 mm shell length.
Adult	Sexually mature.

the spawning habits demonstrate the importance of water temperature on gonad maturation and spawning. In Maryland, the clams spawn in April when water temperatures reach 10 °C and the abundance of larvae peaks when the spring water temperatures are about 20 °C. Gametogenesis for the second spawning began when water temperatures dropped below 25 °C, according to Pfitzenmeyer (1965). Brousseau (1978a) observed an early spawn (March-April) in clams from Ipswich Bay, near Gloucester, Massachusetts, characterized by rapid maturation and gamete release. The clams spawned again in June and July, and the number of eggs and sperm released in the summer was greater than in the spring.

Food availability also is an important factor in determining the timing and intensity of spawning. In shellfish hatcheries, clams are exposed to slightly elevated temperatures and optimal algal diets to stimulate rapid gametogenesis and egg "ripeness." Exposure of broodstock to periods of alternating warm and cold temperatures stimulates spawning (Loosanoff and Davis 1963). On a Maine mud flat, spawning was observed when inshore seawater temperatures reached a seasonal maximum of 21 °C (Newell 1982). During the last week of June, water temperatures fluctuated between 13 °C (at high tide) and 21 °C (on a sunny day in shallow water at low tide). Males usually spawn first, releasing pheromone and sperm into the water, which cause the females to spawn.

Fecundity and Gametes

In Massachusetts, a female clam 63 mm long is capable of releasing as many as 3 million eggs a year (Belding 1930), but according to Brousseau (1978a), female clams from the middle intertidal zone at Cape Ann, Massachusetts, produce only 120,000 eggs a year. In an experiment in a

shellfish hatchery in Maine, females 60-70 mm long released about 1 million eggs (S. Chapman, Ira Darling Center, University of Maine, Walpole, pers. comm.). Fertilization is external. The egg, when released into seawater, is spherical, 66 microns in diameter, white, and gelatinous (Belding 1930). The sperm has a head which measures 4 microns in diameter and a long whiplike tail. The fertilized eggs may be carried by the current many miles from the spawning site. The percentage of energy that goes into the reproductive process increases with an increase in the size of the clam. The oldest and largest individuals in the population contribute most of the eggs.

Larvae

The larval stage lasts from 12 to 14 days in southern Massachusetts, about 14 days in Chesapeake Bay, and up to 21 days in Maine (Belding 1930; Pfitzenmeyer 1972). After hatching (in 9 h at 27 °C) the embryo quickly changes into a top-shaped, spinning trochophore (Belding 1930; Hanks 1969). Soon, the larva forms its first shell and a swimming organ (the velum) and becomes a prodissoconch I (or early veliger stage). It is about 80 microns long. When growth begins at the shell periphery, the prodissoconch II (or late veliger) larval stage begins. Loosanoff and Davis (1963) and Loosanoff et al. (1966) give measurements and pictures of development of the softshell clam up until settlement. The larvae may be identified by hinge structure (Lutz et al. 1982). Along the New Hampshire coast from June to October, the number of veligers in the plankton was as high as 1,000/m³ (Normandeau Associates Inc. 1978). Density peaked in late summer. Larval abundance was higher in inshore waters than offshore waters and higher at depths from 5 to 9 m than near the surface or at a depth of 13 m.

At the end of the larval stage, the clam attaches to the bottom. Then the velum is cast off and a foot develops as the clam metamorphoses into a bottom-dweller called a spat. Metamorphosis may be delayed later than usual, until the clam locates a suitable substrate for attachment.

Juvenile Seed Clams

After metamorphosis, the young spat (0.25 - 1 mm long) may undergo a floating - crawling stage for 2 to 5 weeks (Belding 1930). During this stage the clam spat sometimes holds on to the substrate using a byssal thread. The spat may first attach to eelgrass, filamentous algae, and other objects in the subtidal zone (Kellogg 1900), but as it continues to grow the spat drops to the bottom and burrows into the sediment. After the clam becomes large enough to be noticed by clam diggers (5 mm), it is referred to as clam "seed" until it reaches market size. Juvenile seed clams may migrate up to several hundred yards towards shore (Dow and Wallace 1961). The byssus is used for attachment while juvenile clams up to 13 mm long move or burrow.

The movement of seed clams 2-15 mm long on a Massachusetts beach was studied by Matthiessen (1960b). Clams 2-3 mm long that set in late summer remained in the seaward portion of the sampling area for 8-10 months (until April, May, or June) and grew to 5 mm or more, and then moved shoreward. This movement was attributed to hydrodynamic forces such as sediment sorting by shoaling waves. During spring storms, clams 5-15 mm long showed a net horizontal displacement shoreward along with coarse sediment particles (Matthiessen 1960b). The movement of first-year juveniles peaked in September and October during early growth, and again in May after growth resumed in the spring (Dow and Wallace 1961).

Because adult softshell clams are sedentary, maintenance of each population depends upon the settlement of spat or the movement of juvenile seed clams. Because of the influence of oceanographic conditions on recruitment, the abundance of settling clams (the set) may be irregular in some locations; for example, enormous quantities of seed clams may be concentrated in a small area. A clam set of 538,000/m² was reported in an eddy adjacent to a sand bar in Plum Island Sound, Massachusetts (Belding 1930). The density of seed clams usually is greatest in eddies, along the sides of sand bars or islands, at the mouths of rivers or streams emptying into shallow water, or in slack water adjacent to a swift current. Because of their small size and shallow burrowing depth, juvenile clams are subject to intense predation. The density of juvenile clams approached 6,000/m² in the subtidal zone in Virginia, but dropped to zero 1 month later, presumably due to predation (Lucy 1976); however, clams in Chesapeake Bay were able to avoid most predators by burrowing as deep as 10 cm (Blundon and Kennedy 1982). Vegetation reduced predation of softshell clams in the subtidal zone. The movement of juveniles from subtidal areas to the intertidal zone in New England also reduces predation. For example, experimental plantings of seed clams at different intertidal elevations along the Maine coast revealed that growth is slowest but survival is the greatest in the upper intertidal zone (Newell 1982).

Adult Clams

In suitable habitat, the softshell clam makes a substantial contribution to the biomass of the benthic community. For example, 1 ha of mudflat containing clams about 62 mm long at a density of 269/m² contains 1,442 bushels of clams in the

shell, and 21,635 lb of meats (D. Wallace, Maine Dep. Marine Resources, Augusta, pers. comm.).

COMMERCIAL/SPORT FISHERIES

The softshell clam is a valuable sport and commercial species. The sport fishery is locally important to coastal resort towns, where clam ordinances strictly regulate the catch. In New England, where the resource is primarily intertidal, the commercial instruments are generally constrained by law to hand implements. Clam forks and hoes are common instruments, although dredges are sometimes used in subtidal areas in Massachusetts and experimentally in Maine. In Chesapeake and Delaware Bays, where the resource is subtidal, clams are harvested with a hydraulic escalator dredge. Damage to clams is less from dredges than from forks and hoes (Kyte and Chew 1975). Burial and breakage of clams during hand harvesting sometimes reduces production in New England (Glude 1954). Hydraulic clam rakes have been used in Canada (Bourne 1967) and Maine to collect seed clams for transplanting. Annual U.S. commercial landings of softshell clams from 1977 to 1981 averaged 4.2 million kg (9.3 million lb), worth \$15 million. At one time, sewage polluted many of the clam beds along the New England coast, so they were closed to diggers and dredgers. In the 1970's, the construction of municipal sewage treatment plants sharply increased and pollution decreased, so some of the beds have been reopened and production has proportionately increased.

POPULATION DYNAMICS

Because the mortality of eggs, larvae, and seed clams is extremely high, clam populations are maintained only because of a tremendous fecun-

dity. Less than 0.1% of the eggs produced in a spawning season result in a successful settlement, and about 1% of the settled spat must mature and reproduce in order to sustain the populations. Mortality is heavy in the planktonic stage and immediately after settlement, and decreases as the clam grows older. As the shell becomes thicker and the clam digs deeper, its survival rate increases. Survival rate follows an exponential decay, leveling off after 3 years of age. Mortality rates are highest in summer when predators are most abundant (Brousseau 1978b). Fecundity increases with clam size, so the intrinsic rate of natural increase is high. The high mortality of larvae is offset by the high intrinsic rate of natural increase (Brousseau 1978b).

Densities of larvae ranged from 0.1 to 1,000/m³ in New Hampshire waters of the Gulf of Maine (Normandeau Associates, Inc. 1978) and the late veliger larval densities ranged from 0 to 1,400/m³ in Chesapeake Bay (Pfitzenmeyer 1962) during the summer months. In one study, settlement densities as high as 107,600/m² (10,000/ft²), decreased to 21,500/m² (2,000/ft²) 2 months later, and then to 0 after 1 year (Turner 1953).

In Chesapeake Bay, spat (less than 10 mm long) densities decreased from 500/m² in December to less than 10/m² by June (Blundon and Kennedy 1982). In New Hampshire, densities of young-of-the-year spat ranged from 21/m² to 8,200/m² from 1971 to 1980. High larval densities (530/m³ in the summer of 1975) were followed by high spat densities (8,200/m²) in 1976; adults of the 1975 year class produced a strong fishery from 1978 to 1980 (Savage 1981).

In Casco Bay, Maine, standing crops in 1979 averaged 90 to 120 bushels of clams per acre. The total inventory of the bay was 107,500 bushels (Card 1980).

Adults have an aggregated distribution, limited primarily to intertidal and shallow subtidal areas (Saila and Gaucher 1966; Commito 1982). The degree of aggregation may depend upon the slope of the intertidal area and current (Newcombe 1936). Juveniles may concentrate near a steep shore profile (Matthiessen 1960b). Aggregation also may be caused by predation, by hand harvesting or dredging, and by the concentration of spat by hydrographic conditions.

GROWTH CHARACTERISTICS

The softshell clam grows rapidly in a favorable environment. Clams usually reach market size (2 inches long) in 1.5 years in Chesapeake Bay, (Pfitzenmeyer 1972), in 2 to 3 years in Rhode Island and Massachusetts (Turner 1948; Brousseau 1979), in 3 to 6 years in Maine, and in 5 years in New Brunswick, Canada (Turner 1948; Spear and Glude 1957; Commito 1982). Growth may be modeled using the exponential von Bertalanffy growth equation, expressed by the following formula: $\text{Shell length} = a(1 - e^{-kt})$ where a , b and k are constants derived from growth data, and t = time. Growth rate constants of clams from different geographic areas were calculated by Brousseau (1979). Data fit to the growth equation using best fit computer-generated curves demonstrate widespread differences in growth rates among locations. Seasonal variations in growth rates can be incorporated into the von Bertalanffy equation by adding temperature, in day-degrees (Munch-Peterson 1973).

Seasonal variations in growth rates have been attributed in part to food availability by Newcombe (1935), Matthiessen (1960a), and Stickney (1964); to temperature by Belding (1930), Dow and Wallace (1961), Stickney (1964), and Munch-Peterson (1973); and to spawning by Brousseau

(1979). In New England, softshell clams generally grow fastest in late spring and early summer, and slowest in the cold winter months (Belding 1930; Brousseau 1979). The months of rapid clam growth are coincident with rising abundance of phytoplankton and seawater temperature in the Gulf of Maine (Bigelow 1917; Petrie 1975). Also, rapid clam growth in a salt pond in Martha's Vineyard, Massachusetts, was coincident with a high abundance of flagellates (Matthiessen 1960a). Seasonal variations in growth rates are positively correlated with seasonal changes in biochemical (glycogen) levels and condition indices (measurements of shellfish "fatness"). Glycogen levels and meat yields are high in the spring; the glycogen is converted to gametes with a subsequent drop in meat yields during the spawning season, and the meat yield recovers after spawning (Newell 1982). In Maine, glycogen in shellfish of good market quality peaks in late spring and is lowest in winter.

Growth rates are also closely related to current, sediment type, and intertidal height. Clams grow the fastest in soft sediments on the lower shore (where food is relatively abundant) under good current conditions in New England (Belding 1930; Newell 1982). In a laboratory experiment, clams grew faster in soft mud or sand than in gravel (Newell and Hidu 1982). Similarly, shell form and percent shell weight varied with growth rate, sediment type, and intertidal height. Slow-growing clams from coarse sediments and from the upper shore (where food is relatively scarce) have higher percent shell weights and larger shell length-depth regression slopes (greater shell globosity) than fast-growing clams from the lower shore and from soft sediments.

Excessive density can also limit growth rates because of competition for food and space. Mature clam

densities of 161-269/m² are generally considered favorable for good growth (Belding 1930).

ECOLOGICAL ROLE

Food and Feeding Habits

Clam larvae, juveniles, and adults feed by filtering seawater. Postmetamorphic clams draw in through the incurrent siphon by beating the gill cilia. The water passes through the gills, where food particles are removed, trapped in mucus, and swept to the mouth. Particles too large for ingestion, inorganic particles low in nutrition, and particles of any type in dense concentrations in seawater are usually rejected by ciliated structures called the labial palps. These particles are expelled through the incurrent siphon as pseudofeces by a rapid contraction of the adductor muscles. Phytoplankton cell concentrations greater than 30,000/ml of seawater cause a reduction of filtration rates and the formation of pseudofeces as undigested algae and mucus (Stickney 1964).

Flagellates and diatoms are the preferred diet, although clams can obtain nutrition from bacteria and organic detritus in resuspended mudflat sediments (Eaton 1981) and dissolved organic molecules (Stewart and Bamford 1976). In a salt pond in Massachusetts, clams grew faster on a diet of flagellates than on diatoms (Matthiessen 1960b).

Food filtration rates are influenced by water temperature, seawater particle densities, and particle type (Eaton 1981). In Maine, Eaton found that clams filter and assimilate higher quantities of algae in the summer (14-20 °C) than in the spring (3-8 °C). Clams are discriminatory feeders and increase filtration rates when algae are added to diets of suspended silt particles. Clams are well-adapted to handling resuspended

silts in high concentrations, and may sort algal cells from inorganic particles prior to ingestion. Clams of 0.3 g dry meat weights continue to filter even if seawater silt particle densities exceed 300 mg/l (Eaton 1981). High levels of oil pollution in sediments (hydrocarbon levels over 1,500 ppm) caused a reduction in food filtration rates and a lower carbon flux in clams from Maine (Gilfillan et al. 1976). According to Matthiessen (1960b), filtration rates of clams declined when exposed to salinities between 8 and 15 ppt and stopped when salinities were below 4 ppt. Clams continue to filter when seawater temperatures are below 3 °C, but food assimilation is low.

Predators

Predation is one of the most important factors in the control of natural populations of softshell clams. Planktonic larvae are subject to predation by other planktors, fish, and filtering invertebrates; young spat may be devoured by birds, fish, shrimp, worms, crabs, snails and flatworms. As the juvenile clam grows, it burrows deeper into the substrate, where it finds protection from most predators. The rapid juvenile growth and postponement of gametogenesis are considered to be adaptations for survival (Commuto 1982). In one instance, it was estimated that in Massachusetts the mummichog (Fundulus heteroclitus), a small fish, consumed as many as 546,000 softshell clams (<12 mm long) per km of shoreline per day (Kelso 1979). In a laboratory experiment, sandworms (Nereis virens) consumed softshell clams <15 mm long (D. Dean, Department of Zoology, University of Maine, Orono; pers. comm.). In Massachusetts, Belding (1930) reported that major predators are the blue crab (Callinectes sapidus), lady crab (Ovalipes ocellatus), horseshoe crab (Limulus polyphemus), and especially moon snails (Lunatia spp.).

The green crab (*Carcinus maenas*) is one of the most destructive clam predators. For example, periodic declines in clam production in Maine coincided with increases in the abundance of green crabs when seawater temperatures were unusually high (Welch 1969). A green crab may consume as many as 15 clams per day. When abundant, green crab densities can exceed 24,700/ha (Spear 1953). Moon snails (*Lunatia* spp.) preferentially prey on clams 20 to 50 mm long and prefer softshell clams over other foods (Edwards and Heubner 1977). The moon snail feeds by drilling a hole in the clam shell with a rasping organ and eating the contents. A single snail may consume up to 100 clams a year (Edwards and Heubner 1977). Clams over 60 mm long are not usually attacked by crabs or moon snails. The blue mussel (*Mytilus edulis*) and another clam (*Gemma gemma*) compete with the softshell clam for space and food in the lower intertidal zone in some coves in Maine (Dow and Wallace 1961).

ENVIRONMENTAL REQUIREMENTS

Salinity

The salinities of softshell clam habitat decrease from north to south. Preferred salinities were 20-32 ppt in Maine (Dow and Wallace 1961; Gilfillan et al. 1976), 10-33 ppt in Massachusetts (Belding 1930; Brousseau 1978b), and 4-15 ppt in upper Chesapeake Bay (Pfitzenmeyer 1972). When clams were planted in salinities near their lowest tolerated level, they showed signs of distress and reduced their pumping rates. The rate of pumping was sharply reduced when the salinities were reduced to the stress point. The stress point is about 15 ppt for Massachusetts clams (Matthiessen 1960a), 22-24 ppt for Medomac River, Maine, clams (Welch and Lewis 1965), and 5 ppt for Chesapeake Bay clams (Schubel 1973). Larvae are more sensitive to low salinities than

adults (Belding 1930). The lowest tolerable salinity for adult softshell clams is about 5 ppt.

Growth rates of clams in Massachusetts are positively correlated with salinities from 3 to 14 ppt in Massachusetts (Matthiessen 1960a). Mortalities were as high as 90% in Chesapeake Bay when salinities dropped to 2 ppt because of the freshwater runoff after Hurricane Agnes (Shaw and Hammons 1974). Softshell clam survival at extremely low salinities is inversely related to water temperature (Allen and Garrett 1971). For example, softshell clams in the Bay of St. Lawrence survived salinities below 1 ppt for as long as 1.5 days at low temperatures. However, at higher water temperatures, clams acclimate faster to moderately decreasing salinities (Creaser and Clifford 1977). For example, in an experiment in Maine, acclimation time for a change from 30 ppt to 22 ppt was reduced from 60 hours at 4 °C to 10 hours at 10 °C. The tolerance of clams 2-25 mm long to low salinities is somewhat positively correlated with their size (Matthiessen 1960a). Amino acids regulate the osmotic characteristics of the clam hemolymph (blood) in different salinities.

Temperature

Water temperature regulates the time of spawning and influences the distribution of clams along the north Atlantic coast. The range of soft-shell clams is limited in the north by temperatures too low (12 °-15 °C) for spawning; the range in the south is limited by excessively high temperatures (Lawson 1966). Clams do not usually survive water temperatures above 28 °C in Chesapeake Bay; high temperatures restrict their distribution and abundance there (Pfitzenmeyer 1972). In 1-day bioassays, the LT_{50} (lethal temperature for 50%) was 32.5 °C for adult clams from Chesapeake Bay and

34.4 °C for juveniles (Kennedy and Mihursky 1972). Clams from the subtidal zone and the high intertidal zone better withstood high temperatures (> 25 °C) than clams from low and middle intertidal levels. Water temperatures regulate the length of larval life (low temperature-long life); optimal temperature for maximum growth is about 20 °C (S. Chapman, Ira Darling Center, Univ. of Maine, Walpole; pers. comm.). In a study of softshell clams from Maryland to Nova Scotia, water temperature was the dominant environmental factor affecting 68% of the observed growth rate fluctuations (Appeldoorn 1982). Food availability, water current velocity (Belding 1930), and sediment type (Newell and Hidu 1982) contribute to local fluctuations in growth rates, which sometimes mask the general latitudinal trend (Dow and Wallace 1961).

The pumping rates of softshell clams increase with increasing temperature up to 16 °C (Harrigan 1956). At lower temperatures (1-2 °C), clams continue to pump but rates of food assimilation are low (Gilfillan et al 1976). Water temperatures of -1.7 °C are tolerated in New England. During icing, clams survive by utilizing glycogen energy reserves (Newell 1982).

Rafting of the surface sediment and the destruction of shallow burrowing juveniles by ice have been observed in mudflats in Maine.

Changes in temperature regulate the rate of burrowing. In Chesapeake Bay, burrowing was greatest at 18 °C, moderate from 9 to 21 °C, and greatly reduced at higher or lower temperatures (Pfitzenmeyer and Drobeck 1967).

Oxygen

Oxygen utilization by softshell clams is governed largely by body

size, water temperature, rate of metabolism, and oxygen concentrations in the water. A positive linear relation between oxygen consumption and wet weight was reported by Fong (1976). Oxygen intake in softshell clams is independent of oxygen concentration down to about 2.8 mg/liter (van Dam 1935). Oxygen intake is greatest at about 20 °C (Kennedy and Mihursky 1972). Intertidal softshell clams can function as facultative anaerobes (Collip 1920), switching to anaerobic metabolic pathways at low tide. Calcium carbonate from the shell is used to buffer the acidic products of anaerobic respiration. Upon reimmersion, clams undergo rapid ventilation to oxidize the end products of anaerobic respiration. Excessively low oxygen concentrations cause increased stress and heartbeat rates (Lowe and Trueman 1972). Softshell clams survive periods of anaerobiosis longer at low temperatures, for example, during icing. High respiration rates in the spring have been attributed to warm water acclimation (Gilfillan et al. 1976) or metabolic costs of active gametogenesis.

Substrate and Current

Clams live in soft muds, sands, compact clays, and coarse gravel, and between stones. Sediment type is important in controlling growth rate and shell allometry. Under identical current conditions, clams grow faster in fine sediments than in coarse sediments (Newell and Hidu 1982), and grow fastest in sand or sandy mud (Belding 1930; Dow and Wallace 1961), though few live in shifting sand. Slow-growing clams from gravel have more globose shells than those from mud or sand, and clams in sand are longer and narrower than those in mud. Differences in growth rates and shell form are attributed to the physical properties of the sediment and its resistance to burrowing. Sediment particle size also affects the

reburrowing of clams. Clams had difficulty burrowing in sediments larger than 0.5 mm (Pfitzenmeyer and Drobeck 1967).

The characteristics of the sediments reflect the rates of the bottom currents and establish, from a physical standpoint, the suitability of the bottom for clams. Coarser sediments usually reflect faster currents, which support greater population densities and cause faster growth (Appeldoorn 1982). If the currents are too slow, the sediments usually have a high silt-clay content, which, in excess, can clog the gills of the clams, reduce growth rates, and in extreme cases cause smothering (Dow and Wallace 1961). Most clams in Chesapeake Bay thrive in a substrate that is less than 50% silt (Pfitzenmeyer 1972). Clams may continue pumping when total suspended solids exceed 300 mg/l, but the production of mucus and the loss of energy during the ejection of pseudofeces strain the energy budget of the clam (Eaton 1983).

Coarse sediments and mats of vegetation help protect clams from most predators (Blundon and Kennedy 1982). During winter months when phytoplankton populations are lowest,

resuspended bottom sediments are an important food source for softshell clams.

Pollution

Softshell clams in polluted water accumulate pesticides (Dow 1972), oil (Mayo et al. 1975), heavy metals (Eisler 1977), and sometimes the bacteria and viruses in municipal sewage. Toxic materials are most damaging to fertilized eggs and larvae, and less damaging as the clams grow larger. Oil pollutants can cause a reduction in the carbon flux of clams (Gilfillan et al. 1976). More refined petrochemicals may have a greater effect on the incidence of pathological tumors in clams than unrefined oils and heavy metals (Walker et al. 1981). Clam larvae are sensitive to chlorine-produced oxidants but in general adult clams are relatively tolerant of pollution (Brown et al. 1977). Despite the tolerance of softshell clams to pollution, bacteria and viruses from municipal effluent accumulate in the clam's body tissues, and if eaten, are a threat to public health. Until municipal pollution is adequately abated, clamming in some waters will continue to be prohibited.

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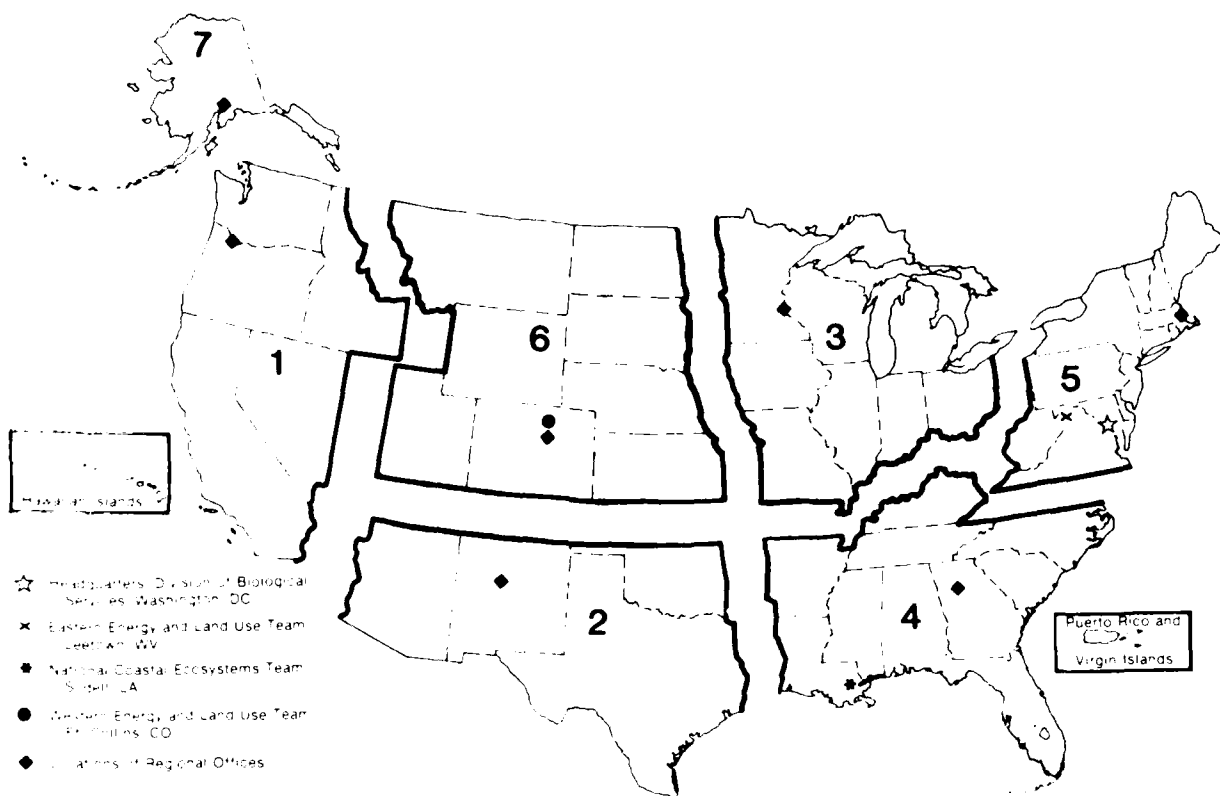
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REPORT DOCUMENTATION PAGE		1. REPORT NO. Biol. Rep. 82(11.53)*	2.	3. Recipient's Accession No.
4. Title and Subtitle Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (North Atlantic)--Softshell clam				5. Report Date June 1986
7. Author(s) Carter R. Newell and Herbert Hidu				6.
9. Performing Organization Name and Address Maine Shellfish Research and Development Damariscotta, Maine 04543 and Department of Animal and Veterinary Sciences University of Maine, Orono, ME 04469				8. Performing Organization Report No.
12. Sponsoring Organization Name and Address National Coastal Ecosystems Team U.S. Army Corps of Engineers Fish and Wildlife Service Waterways Experiment Station U.S. Dep. of the Interior P.O. Box 631 Washington, DC 20240 Vicksburg, MS 39180				10. Project/Task/Work Unit No.
				11. Contract(C) or Grant(G) No. (C) (G)
13. Type of Report & Period Covered				14.
15. Supplementary Notes *U.S. Army Corps of Engineers Report No. TR EL-82-4				
16. Abstract (Limit: 200 words) ➤ The softshell clam, <u>Mya arenaria</u>, is a commercially and recreationally important invertebrate that inhabits the bottom sediments of subtidal and intertidal waters of moderate to high salinity. Its range is limited by water temperatures too low for reproduction in the north and by lethal warm temperatures in the south. Clams feed by siphoning seawater and removing food particles, especially phytoplankton, with their gills. Clams are therefore sensitive to factors affecting water quality, including suspended sediments, salinity, water temperature, oxygen, and waterborne pollutants. The clam life cycle consists of mass spawning and external fertilization, the development of pelagic larvae, settlement and metamorphosis into spat, and rapid juvenile growth to maturity. Clam recruitment and the migration of spat are dependent upon inshore currents. High mortality of eggs, larvae, and spat is largely offset by high reproductive potential. As the clam grows, it finds refuge from most predators deep in the sediments, but it also loses its ability to burrow and is subject to suffocation by siltation. Sediment types, currents, and tidal heights all affect clam growth rates. <i>Kay...</i>				
17. Document Analysis a. Descriptors → Estuaries, Growth Feeding habits, Fisheries, Salinity, Life cycles Shellfish, Temperature, Contaminants, Sediments, Suspended sediments, Oxygen. b. Identifiers/Open-Ended Terms Softshell clam <u>Mya arenaria</u> Habitat requirements Spawning c. COSATI Field/Group				
18. Availability Statement Unlimited		19. Security Class (This Report) Unclassified		21. No. of Pages 17
		20. Security Class (This Page) Unclassified		22. Price



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