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

SOFTSHELL CLAM

Fish and Wildlife Service
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Coastal Ecology Group
Waterways Experiment Station
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SOFTSHELL CLAM

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PREFACE

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

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

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CONVERSION TABLE

Metric to U.S. Customary

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

U.S. Customary to Metric

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

CONTENTS

ACKNOWLEDGMENTS

We are grateful to Victor Kennedy, Horn Point Environmental Laboratory, Cambridge, Maryland, for his helpful review of the rough draft of this manuscript.

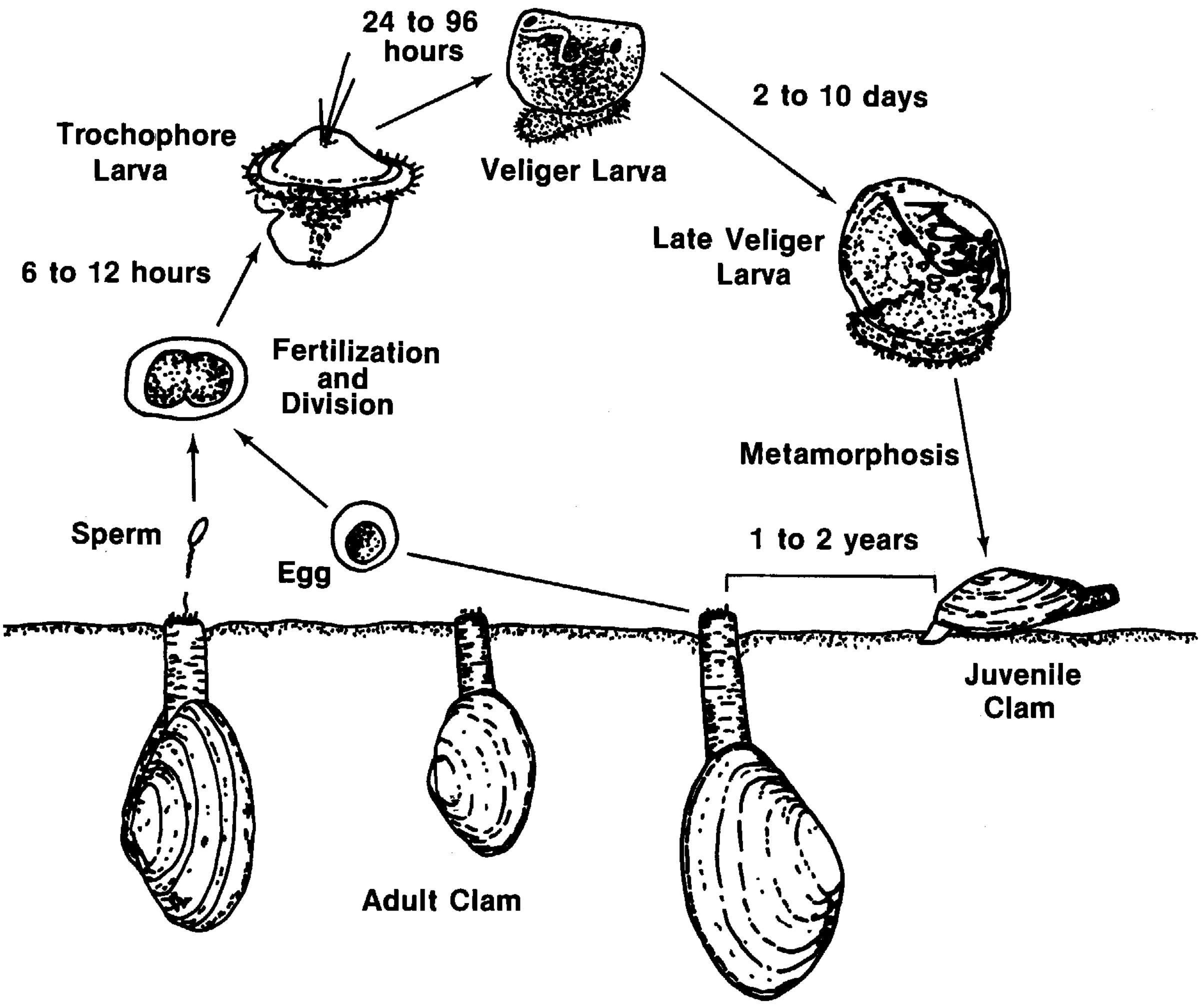

Figure 1. Life cycle of the softshell clam (after Anonymous 1983).

SOFTSHELL CLAM

NOMENCLATURE/TAXONOMY/RANGE

Scientific name	*Mya arenaria* L.
Preferred common name	Softshell clam (Figure 1)
Other common names	Steamer (New England), long clam, gaper (Gosner 1978); long-neck clam (Light 1967); manninose (Chesapeake Bay) (Pfitzenmeyer 1972)
Class	Bivalvia
Order	Eulamellibranchia
Family	Myacidae

Geographic range: along the Atlantic coast from the Subarctic to Cape Hatteras, less commonly to South Carolina (Figure 2); introduced on the west coast from Alaska to San Francisco (Pfitzenmeyer 1972; Lucy 1976).

MORPHOLOGY/IDENTIFICATION AIDS

The softshell clam has a thin, gray or chalky-white, egg-shaped shell

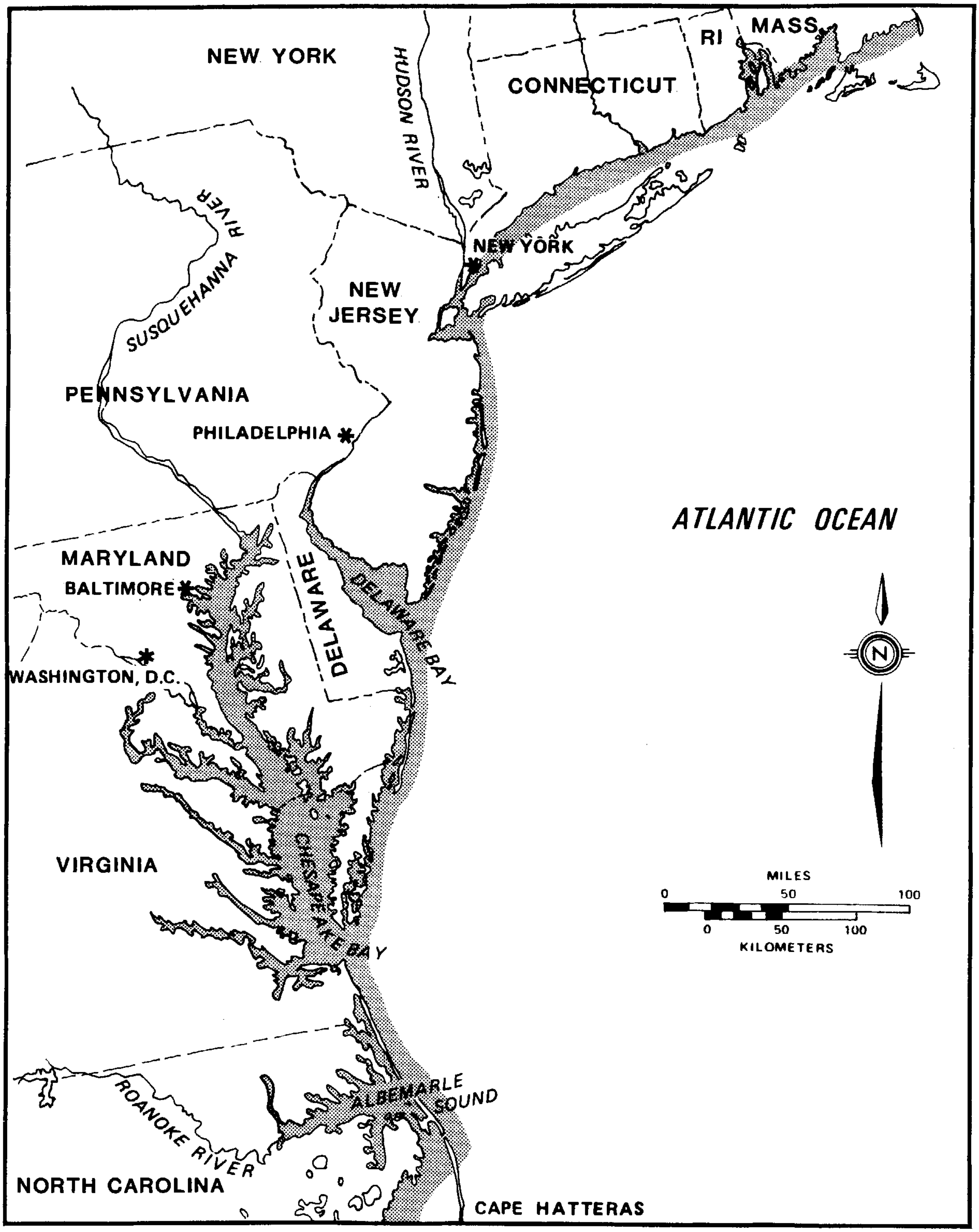

Figure 2. Mid-Atlantic coast distribution of softshell clams. This species is found the entire length of the mid-Atlantic region in bays and sounds, to a depth of about 9 m, in a minimum salinity of 5 ppt (Gosner 1978).

that gapes at both ends (Morris 1973; Gosner 1978). The brittle shell averages 75-100 mm in length, but sometimes reaches 150 mm. The valve surface is roughened and covered with a dark brown periostracum. The hinge of the left valve has an erect, spoon-like tooth, the chondrophore, which supports the resilium; the right valve has a corresponding heart-shaped pit (Gosner 1978). The siphons are fused into a rigid siphonal process that is too large to be completely withdrawn into the shell and is capable of great elongation (Purchon 1977).

REASON FOR INCLUSION IN SERIES

The softshell clam supplies the third most important commercial clam fishery in the United States. Meats of this species averaged 12% by volume, and 20% by value, of the commercial harvest from 1965 to 1975 (Ritchie 1976). In 1984, commercial landings totalled 7.9 million lb and were valued at $19.8 million. Maine landings were 5.2 million lb, Massachusetts had 1.4 million lb, and Maryland had 931,000 lb; the Maryland figure represents a decrease from 1.9 million lb in 1983. The 5-year average (1979-1983) for the east coast fishery was 8.4 million lb (Thompson 1985).

Overfishing can drastically reduce the value of clam beds (see also "Fisheries"). Because of its near-shore habitat, this valuable resource is easily endangered by pollution (see also "Environmental Requirements and Tolerances"). Mariculture efforts have been unsuccessful (Ritchie 1976).

During red tides caused by Gonyaulax tamarensis, paralytic shellfish poisoning (PSP) may result from consumption of softshell clams. The organisms do not harm the clams, but result in temporary loss of the fishery because they endanger humans. Red tides causing PSP seldom occur south of Cape Cod (Hanks 1963; Ritchie 1976).

LIFE HISTORY

Reproductive Physiology and Strategy

Softshell clams are dioecious and nonprotandrous (Brousseau 1978a). Shaw (1965) found no hermaphrodites in a sample of more than 800 clams; Lucy (1976) found 2 in a sample of 2,400. The sex ratio of clams 25-95 mm long was 1:1 (Brousseau 1978a); Lucy (1976) also reported a 1:1 sex ratio in adult clams.

Brousseau (1978a) found that female body size and oocyte production were correlated. Females less than 40 mm long were never gravid. Brousseau reported that a 60 mm female produced a mean of about 120,000 oocytes during a single breeding season (two spawning periods) at Gloucester, Massachusetts; this would make a lifetime production of about 1.5 million oocytes.

Reproductive processes for both males and females have been described as "inactive," "active," "ripe," "partially spawned," and "spent" (Ropes and Stickney 1965; Shaw 1965). Brousseau (1978a) preferred to divide the developmental sequence into "active" and "inactive" stages. Her active stage included developing (= active of Ropes and Stickney), ripe, and partially spawned phases; the inactive stage included spent and indifferent (= inactive of Ropes and Stickney). Criteria for determining each phase corresponded to those of earlier authors.

Spawning

There are two cycles of gonadal development per year in both male and female softshell clams in Chesapeake Bay (Shaw 1965; Lucy 1976). These gonadal cycles result in two spawning periods. These are mid-March through

May and mid-October through November in the Chesapeake Bay in Virginia (Lucy 1976). Pfitzenmeyer (1965) described two periods of spawning in the Chesapeake Bay in Maryland, the first in May-June and the second in September-October.

Spawning depends upon water temperature; therefore its timing varies with latitude. Spring spawning in Chesapeake Bay occurs when the water temperature reaches 10 °C and may continue at water temperatures up to 20 °C; autumn spawning occurs when water temperature has fallen from the summer high of 25 °C to 20 °C (Lucy 1976).

According to Brousseau (1978a), temperature is more important in timing gonadal development than in triggering release of gametes. She found that at Gloucester, Massachusetts, spawning occurred at a surface (1 m) water temperature of 4-6 °C in March-April, but at 15-18 °C in June-July.

Lucy (1976) noted that rapid changes in water temperature in spring may be detrimental to gamete development. It takes about 60 days for the water to fall from the maximum summer temperature to the autumn spawning temperature; the time from minimum winter temperature to the spring spawning temperature may be as little as 40-42 days. Lucy recorded that 18%-23% of softshell clams spawned in the spring when water temperature rose over a 62-day period; only 2%-4% spawned when spawning temperature was achieved in 40 days. Shaw (1965) also reported a spring spawning failure in Chesapeake Bay, although he was not able to determine the limiting factor.

Larvae

The fertilized egg takes about 12 h to develop into the planktonic trochophore larva in cold New England waters, and probably less in the warmer waters of the mid-Atlantic Region (Hanks 1963). This top-shaped, ciliated larva feeds on suspended particles. Within the next 24-36 h the trochophore develops into the veliger larva, which has two calcareous valves. This stage remains suspended in the water column by means of a ciliated velum and drifts in estuarine and ocean currents feeding on phytoplankton. Veligers are important food for the larvae of a number of fish species. In samples collected at water depths of 1-17 m off the coast of Maine, the density of veligers was as high as 1,000 larvae/m^3 (Anonymous 1983).

The veliger stage lasts for 2-6 weeks, depending on water temperature. The mean period that larvae spend in the water column before setting is shorter during the spring spawning (4 weeks) than during the autumn (6 weeks) in Chesapeake Bay. The rate of larval development is faster in spring because the water temperature is at the warmer end of the spawning temperature range (Lucy 1976).

Juveniles

When the veliger reaches a length of about 200 μm, its shell thickens, a muscular foot replaces the velum, and a byssal gland develops (Hanks 1973; Perkins 1974; Lucy 1976). This late veliger (the "setting stage") settles to the substrate to become a juvenile clam. A byssus (sticky thread) is secreted to anchor the young clam to the substrate. This may be retained until the clam is 7 mm long (Perkins 1974). Adult habits are slowly acquired, and bysally attached young temporarily retain an active foot for locomotion (Green 1975). Although usually attached to the substrate by the byssus, the juvenile clam is able to move and attach itself in a more favorable location (Hanks 1963).

Eventually the byssus is shed and the adult lifestyle adopted: the young clam burrows and becomes sedentary. The final settling location is usually a sandy bottom with less than 50% silt. Very young softshell clams apparently cannot tolerate highly silted substrates (Pfitzenmeyer 1972). It took 35 days for a clam to grow to 2 mm and an additional 95 days to reach 12 mm at Gloucester, Massachusetts (Brousseau 1978a).

Clams up to 12 mm move about considerably over the substrate, and only burrow down 1-2 cm. This exposes them to wave action, and they are moved shoreward and concentrated at the break in the beach profile where the slope increases suddenly. The observed clumped distribution of juvenile clams is therefore, according to Lucy (1976), primarily due to hydrodynamics, rather than predation or other factors.

Young softshell clams may achieve a length of 30 mm by the first winter (Perkins 1974). Andrews (1970) reported that it takes 18 months from setting to steamer size in Chesapeake Bay; according to Hanks (1963), the acceptable commercial size of 5 cm is achieved in 1.5-2 years in the same area.

Adults

Maturity may be achieved in 5 years, and clams may reach 15 cm at an age of 8 years. The lifespan has been given as 10-12 years or, rarely, as many as 19 years (Perkins 1974; Brousseau 1978a). However, internal shell growth lines indicate a lifespan of as many as 28 years (MacDonald and Thomas 1980).

Adult softshell clams inhabit sandy, sand-mud, or sandy-clay bottoms of bays and inlets. Density is usually six to eight clams per square foot; it is highest at depths of 3-4 m, temperatures less than 28 °C and salinities not less than 4-5 ppt (Pfitzenmeyer and Drobeck 1963; Lucy 1976). Adult clams burrow as far as 30 cm into the sediment, but the siphonal process extends to the sediment surface (Kennedy and Mihursky 1971).

COMMERCIAL AND SPORT FISHERIES

Fisheries

The softshell clam is a valuable commercial species (see also "Reason for Inclusion in Series") and is also harvested recreationally in New England. It is a popular delicacy when fried, steamed in broth, or baked in fire pits under seaweed (Hanks 1963; Lucy 1976).

Softshell clams have been harvested commercially by hand on the tidal flats of New England since the mid-1800's. The first commercial fishery began with a demand for salted clams to be used as bait by cod fishermen on the Grand Bank; more lately, fresh, frozen, and canned clams have been an important consumer item (Hanks 1963). The hydraulic escalator dredge, which efficiently harvests subtidal clams, was introduced in 1951 (Ritchie 1976). This allowed commercial harvesting in the Chesapeake Bay, and the Maryland fishery began to develop rapidly, reaching a peak of 7.9 million lb in 1969 (Lucy 1976; Ritchie 1976). A commercial fishery never developed in Virginia because the best clam beds are in oyster areas; oystermen claim that the escalator dredge silts over the oysters (Lucy 1976).

The New England beds were overharvested in the late 1940's, and declined from 15 million lb in 1940 to

2 million lb in 1958 (Lucy 1976; Ritchie 1976). The decline is also partly attributed to predation by crabs (Hanks 1963). Between 1956 and 1970 the Maryland catch exceeded that of New England, but in 1970 and 1971 the Maryland beds also showed signs of overfishing (Ritchie 1976; Lucy 1976). In June 1972 Tropical Storm Agnes decimated the Maryland clam beds (see also "Temperature" and "Salinity"); mortality was as high as 90% in some upper bay areas (Lucy 1976). A successful spawn in the autumn led to rapid recovery; however, Maryland closed its beds in 1973 because of high levels of bacteria (Chesapeake Research Consortium, Inc. 1976). In 1975 Maryland landed 1 million lb; New England harvested 7.5 million lb.

In the Maryland Chesapeake Bay acceptable commercial size for softshell clams is 51 mm (Hanks 1963), and the maximum allowable catch is 40 bu per day (Andrews 1970).

Population Dynamics

Larval softshell clams are among the more abundant plankters in estuaries. In sedentary bivalves, settlement of recently metamorphosed planktonic larvae is the only significant source of recruitment. Size-frequency distributions show that recruitment of young represents a large proportion of the population, but average settling rates of juveniles are low. Observed survivorship at Jones River, Massachusetts, was less than 0.1% of the estimated egg production (Brousseau 1978a); survivorship follows an exponential decline (Figure 3).

Therefore, in the life history of this species, high fecundity is offset by high mortality during pelagic life, metamorphosis, and early settlement (Brousseau 1978b). Because spawning cycles in which the greatest number of oocytes were released did not correlate with the periods of highest recruitment, Brousseau considered that sources of mortality (predation, disease) and the character of the substrate were more important in explaining fluctuations in recruitment than was variability in fecundity.

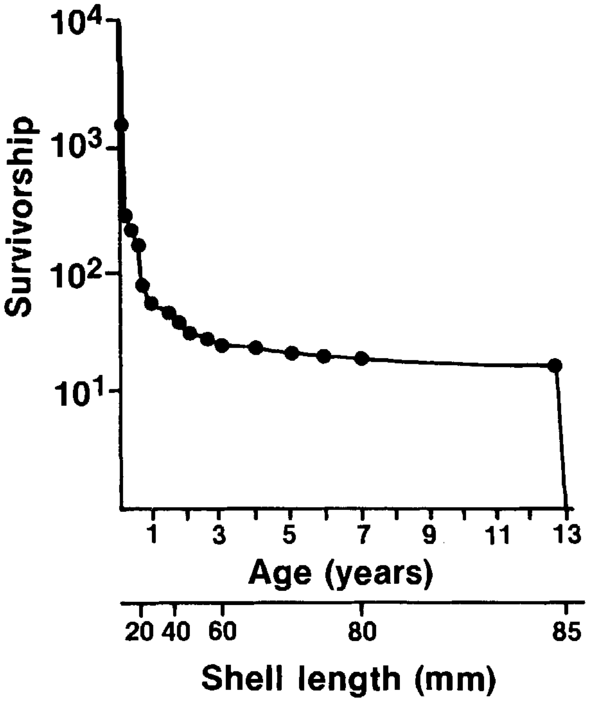

Figure 3. Survivorship curve for softshell clams at Gloucester, Massachusetts. (after Brousseau 1978b)

The numbers of seed clams that set at Gloucester Point and Fox Point, Virginia, were reported to be 114-431/m^2 and 133-578/m^2, respectively (Lucy 1976). A good set (3,000/m^2) yields sufficient clam densities (100-200/m^2) to be considered commercially productive. Lucy has shown that predation and stress from thermal and osmotic fluctuations exact heavy tolls on newly set bivalves. In the York River in Virginia, he found 65%-100% reduction in density of fall-spawned juveniles by the next summer; the lower figure occurred only once.

Adult population densities vary according to natural mortality and commercial harvesting. Estimates of fishing mortality of adults in Massachusetts have been reported by Hruby (1981) to be 50%-60% of the total population, or 3.2 million animals (2,000 bu). In Massachusetts, any clam over 51 mm (2 inches) may be harvested; this effectively reduces the lifespan to 2 years and may endanger the long term stability of the resource (Brousseau 1978a). Natural mortality rates decrease with size and age. Mortality in fall and winter may be considerably lower than in summer, because predators become inactive (Brousseau 1978b).

Factors influencing growth of softshell clams include seasonal availability of phytoplankton, water currents, clam density, mudflat topography, sediment type, tidal level, water temperature, and spawning activity (Anonymous 1983). Most rapid growth occurs in sediments which are easily penetrated (not coarse gravel or hard clay), when clams are not spawning, and when density is less than 25 clams per square foot. Growth slows as clams get larger.

In addition to the use of annular ring measurements and mark-recapture methods for determining growth rates, Brousseau (1979) used the von Bertalanffy equation, which relates age and linear size:

$$L = a\,(1 - be^{-kt})$$

where L = linear size, t = age in any convenient time unit, and a, b, and k = constants. Plotted results (Figure 4) are decaying exponential curves.

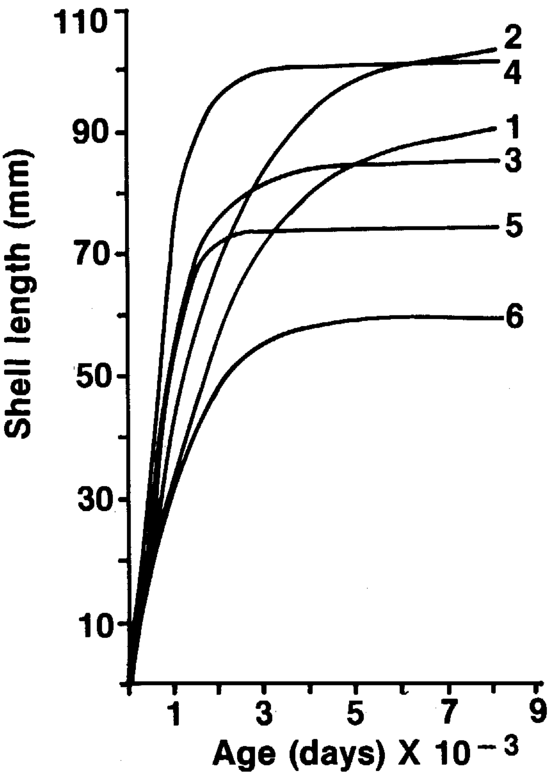

Figure 4. Von Bertalanffy growth curves for softshell clams from the Bay of Fundy (1), Georgetown Island, Maine (2), Gloucester, Massachusetts (3), Monomoy Point, Massachusetts (4), San Juan Island, Washington (5), and Roskilde Fjord, Denmark (6) (after Brousseau 1979).

ECOLOGICAL ROLE

Feeding Habits

Adult softshell clams feed by filtering microscopic particles of organic material, including detritus and plankton, suspended in seawater. Coe and Turner (1938) suggested that softshell clams depend on abundant plankton before and during spawning to produce adequate gametes. Softshell clams can also absorb and use dissolved organic material, although its importance has been difficult to estimate (Stewart 1978).

Organic materials are drawn in through the inhalent siphon where branched cilia strain out suspended particles as small as 2 µm in diameter. Mucus, secreted by the mantle, gills, and visceral mass, collects the incoming particles, which are carried to the mouth by cilia. At the mouth, the labial palps sort and reject large particles. Digestion begins in the stomach and continues intracellularly in the digestive gland. Waste materials are expelled through the exhalent siphon (Anonymous 1983).

Predators

Most predation on softshell clams is on the larvae and juveniles. In Chesapeake Bay, the jellyfish *Chrysaora quinquecirrha* and the comb jelly *Mnemiopsis leidyi* are efficient feeders on the planktonic larvae of infaunal bivalves (Holland et al. 1980). According to Andrews (1970) cyprinodont fishes are voracious feeders on bivalve larvae in ponds and shallow areas.

Serious invertebrate predators on juveniles in the lower Chesapeake Bay include the oyster drill *Urosalpinx cinerea*, the thick-lipped oyster drill *Eupleura caudata*, several kinds of crabs, and the flatworm *Stylochus ellipticus*. Less important predators in the mid-Atlantic Region include the starfish *Asterias*, the horseshoe crab *Limulus polyphemus*, the channeled whelk *Busycon canaliculatum*, and the lobed moon snail *Polynices duplicatus* (Andrews 1970; Lucy 1976; Ritchie 1976).

The most important invertebrate predator on softshell clams north of Cape Cod is the green crab, *Carcinus maenas* (Hanks 1963; Ritchie 1976; Anonymous 1983); this species ranges southward into New Jersey. The blue crab, *Callinectes sapidus*, which ranges southward from Cape Cod, replaces the green crab as a major predator on clams in Chesapeake Bay (Andrews 1970; Lucy 1976; Holland et al. 1980; Blundon and Kennedy 1982a).

Lucy (1976) strongly implicated blue crabs as the major factor contributing to mortality of juvenile clams. In one experiment, he took three 145-cm^2 cores and found the density of clams 4-18 mm long to be 4,360-6,000/m^2; 1 month later, four cores contained no clams, but broken shells were scattered on the sediment. Lucy considered the blue crab to be the most important predator on softshell clams for two reasons: abundance and ability to dig down 6-12 cm into the substrate.

Although blue crabs bury themselves in the mud during the winter, which allows the fall spawn to establish in their absence, the juveniles cannot dig deeply enough to avoid predation the following spring. Lucy found juveniles of length 22-49 mm in July to be buried 6-16 cm.

Working in the Maryland Chesapeake Bay, Blundon and Kennedy (1982b) found the fall set to be buried below 10 cm by the next May, and to achieve maximum burial (25 cm) by June-July. They showed that clams below 10 cm were foraged by blue crabs less efficiently than were those closer to the surface.

Although invertebrate predation has been cited as the major factor determining post-settling survival of softshell clams, predation by fish may also be important. Kelso (1979) showed that on intertidal mudflats in Essex Bay, Massachusetts, predation by mummichogs (*Fundulus heteroclitus*) may equal or exceed that by invertebrates for clams less than 12 mm long.

Bottom-dwelling fish also prey on softshell clams. Spot (*Leiostomus xanthurus*) are the most abundant predacious fish which feed on infauna of mesohaline regions in the Chesapeake Bay (Holland et al. 1980). As shown by stomach content analysis, softshell clams are the preferred food of the cownose ray (*Rhinoptera bonasus*; Merriner and Smith 1979). The American eel (*Anquilla rostrata*) was found to subsist substantially on young softshell clams (Wenner and Musick 1975); winter flounder

(*Pseudopleuronectes americanus*) also eat them (Gosner 1978).

Birds and mammals that prey on clams in the mid-Atlantic region include herring gulls (*Larus argentatus*), diving ducks such as the canvasback (*Aythya valisineria*) and the oldsquaw (*Clangula hyemalis*), tundra swans (*Cygnus columbianus*), and raccoons (*Procyon lotor*; MacGinitie and MacGinitie 1968; Gosner 1978; Holland et al. 1980).

Competitors

No data concerning intraspecific competition among softshell clams are available. Since adults are randomly distributed, there seems to be no territoriality (Perkins 1974).

On a Maine tidal flat, *Gemma gemma* has occurred with *Mya* for more than 1,000 years (Bradley and Cooke 1959). *Mya* is numerically dominant in the muddy areas, *Gemma* in the sandy areas. Bradley and Cooke found the two species to be incompatible because of competition for food "or for some other reason." Sanders et al. (1962) thought that in Massachusetts, large populations of this small species excluded the larger softshell clams by consuming all available food. Kennedy and Mihursky (1971) noted that the greater resistance of *Gemma* to high temperature might allow this species to occupy habitat vacated by the less tolerant *Mya*, thus precluding resettlement. Thermal discharge from power plants into Chesapeake Bay in summer might therefore influence *Gemma*-*Mya* competitive interaction.

Holland et al. (1980) suggested that competition has a relatively unimportant role in determining the structure of Chesapeake Bay infaunal communities, because he thought that resources are probably rarely, if ever, limiting.

Parasites

Observed incidence of parasites is low (Hanks 1963). The pea crab, usually considered an internal commensal, has been reported to be an endoparasite of adult softshell clams (Ricketts and Calvin 1968). MacGinitie and MacGinitie (1968) reported *Malacobdella grossa*, a small, white, fluke-like nemertean, in the mantle cavity. Other parasites include the sporocyst and cercaria stages of various trematodes such as *Cercana myae*, *Gymnophallus*, and *Himasthla quissetensis* (Sinderman 1970), and a ciliate, *Trichodina myicola* (Hanks 1963).

The incidence of observed disease is low and probably does not affect clam production (Hanks 1963; Ritchie 1976). Several pathological conditions have been observed: "water belly," which causes watery, thin meats unfit for market and may be due to a nutritional deficiency, parasite, or disease (Hanks 1963); neoplasia, an uncontrolled new growth of tissue which may be benign or malignant; haemocytic proliferation, an increase in blood cells; hypoplasia, defective or incomplete development; hyperplasia, an increase in the number of cells which ceases when the stimulus is removed; and lipofucsin, fatty pigments which may be related to degenerating parasites (Walker et al. 1981).

Recent investigators have been interested in a possible correlation between pollution and increased disease. Walker et al. (1981) compared the incidence of five pathological conditions (neoplasia, haemocytic proliferation, hypoplasia, hyperplasia, lipofucsin) in softshell clams from 17 areas on the U.S. east coast. They could not infer cause and effect from their data, which seemed to indicate a relationship between the pollution histories of the areas and the incidence of pathology in softshell clams. Although neoplasia was found in both clean and polluted environments, occurrence of both neoplasia and hyperplasia affecting more than 10% of the clam population was found more often in areas impacted with refined petrochemicals.

Brown (1978) reported on a survey of diseases, which he divided into three categories: disturbances of growth (neoplasia, hyperplasia, hypoplasia); reaction to injury (haemocytosis, inflammation); and parasites (bedsonia, protozoa, metazoa, "accumulation of orange-brown bodies"). Prevalence of these conditions varied between sites, suggesting an environmental influence.

ENVIRONMENTAL REQUIREMENTS AND TOLERANCES

Temperature

The most important factor in growth and reproduction of softshell clams is temperature (see also "Life History"). Stewart and Bamford (1976) found that uptake of the dissolved amino acid L-histidine by clams 80-100 mm long increased with increasing temperature. Respiratory rate also varied directly with temperature; however, high temperatures (30 °C) depressed metabolism of cold-acclimated clams (Kennedy and Mihursky 1972).

In a principal components analysis, Appeldoorn (1983) found "northness" to account for the most variation in clam growth among 25 sites from Nova Scotia to Maryland. He found a distinct latitudinal trend, with growth decreasing toward the north. Temperature, tidal height, tidal position, and substrate all systematically varied with latitude, but temperature was the dominant factor.

Softshell clams are eurythermal (have a wide tolerance range for temperature; Perkins 1974; Loi and Wilson 1979). Overwintering clams can survive temperatures below freezing (Ricketts and Calvin 1968). The 24-h LC_{50} values for summer-acclimated clams were 32.5-34.4 °C (Kennedy and Mihursky 1971). As temperature approached the upper lethal limit, a 1 °C increase often made the difference between total mortality and none (Kennedy and Mihursky 1971).

Juveniles up to 15 mm long have significantly higher heat tolerance than do adult clams (Kennedy and Mihursky 1971, 1972). This tolerance is an adaptation for surviving at or near the sediment surface, where temperatures are higher. During times of short-term natural heat stress, adult clams survive by withdrawing the siphons and living anaerobically in the cooler mud (Kennedy and Mihursky 1971). In the Virginia Chesapeake Bay at Gloucester Point, the summer water temperature is potentially lethal near the low watermark (33-35 °C), but the temperature 15 cm into the sediment is never over 30.6 °C (Lucy 1976). It is partly due to high temperature stress on the juveniles that softshell clams in the southern part of their range are not intertidal as in the northern part (Pfitzenmeyer and Drobeck 1963).

Anderson (1978) found that subtidal clams in Maine, if acclimated to warm water, were metabolically temperature independent from 10-25 °C. He also found that subtidal and high intertidal clams were better able to withstand high (25 °C) temperature than low to mid-intertidal clams. Kennedy and Mihursky (1972) also found temperature compensation; at nonstress temperatures, older clams compensated as effectively as did younger.

Salinity

According to Holland et al. (1980), salinity is the major environmental factor controlling presence of Chesapeake Bay infaunal species. Softshell clams are widely euryhaline

(Perkins 1974), being primarily marine in the northern part of their range and estuarine in the southern (Pfitzenmeyer 1965).

The estuarine habitat in which the softshell clam lives is constantly exposed to changes in salinity from about 10 to 25 ppt, mainly as a result of freshwater runoff. Under normal conditions, salinity fluctuations do not have a deleterious effect on softshell clams, which are isoconformers (Stewart and Bamford 1976). No softshell clams died when they were held at 27 ppt, then conditioned to 12.5 ppt, and finally subjected to a reduction in salinity of 2.5 ppt per week to a final salinity of 2.5 ppt (Lucy 1976). However, rate of feeding decreased as salinity fell from 31 ppt and ceased at 4 ppt (Perkins 1974). Stewart and Bamford (1976) reported a significant reduction in uptake of two amino acids by adult clams when salinity was reduced to 75%, 50%, 25%, and 10% of the 34 ppt in which they had been collected.

Small clams are less tolerant of low salinity than larger ones. When placed in freshwater, clams 2-4 mm succumb within 30-40 h, but clams over 20 mm survive more than 50 h. Within their tolerance limit of 4 ppt, clams can survive a change of 18 ppt in a few minutes (Perkins 1974).

Low salinity coupled with high temperature can cause mass mortality of softshell clams. This was seen in 1972, after Tropical Storm Agnes dropped large amounts of rain (over 12 cm throughout the watershed; 45 cm in isolated areas) and brought high air temperature, killing an estimated 90% of the clam population in some areas of the Chesapeake Bay (Chesapeake Research Consortium 1976; Merrimer and Smith 1979). Lucy (1976) measured salinities of 2-6 ppt for 1 week at various locations in the Virginia portion of the bay; subsurface water temperatures in the nearshore zone were 24-25 °C.

Substrate

Within a salinity zone, substrate is a primary determinant of the distribution and abundance of infaunal species (Holland et al. 1980). Softshell clams inhabit stiff sands and muds which will not collapse against the shell valves when they are closed (Perkins 1974; Lucy 1976; Purchon 1977). Appeldoorn (1983) found that sediment coarser and grainier than silt or clay was beneficial to growth; it allowed ample water percolation and drainage and was associated with a good current regime. Loi and Wilson (1979) reported more clams on substrate with a high sand/clay ratio and low organic content than on substrate with high clay and organic content.

In laboratory flow-through experiments on mud, sand, gravel, and in nets, Newell and Hidu (1982) found significant differences in shell length, dry meat weight, chondrophore growth increment, and percent shell weight. Growth was more rapid in finer sediments than in coarser sediments or in nets; this might have been partly due to food availability.

Oxygen and pH

The softshell clam is little affected by oxygen fluctuations. Juvenile and adult stages are able to withstand long periods of anaerobiosis. At 14 °C, adult clams use 30-40 µl of oxygen per gram of body weight per hour. Under experimental conditions they can live for 8 days in a medium lacking free oxygen; they show no adverse effects after being placed back into normal environmental conditions, except for a decrease in stored glycogen and an increase in metabolic rate (Ricketts and Calvin 1968).

Clams normally use 3%-10% of available dissolved oxygen, but after 21 h of anaerobiosis, as may occur during low tide, the ventilation current increases. Normal levels are not restored for 3-4 h; meanwhile, oxygen debt causes oxygen use to increase to 25% (Van Dam 1935, cited by Nichol 1967).

Digestion and absorption are not adversely affected by decreasing pH when the shell is closed for periods of time (Stewart and Bamford 1976). In laboratory experiments, uptake of L-alanine was not significantly different over a pH range of 6.2-8.8.

Pollutants

The shallow water habitat of the clam is especially vulnerable to pollution from urban and industrial development. Because the adults are sedentary, repopulation of destroyed clam beds requires several years for sufficient larval recruitment and growth. In southern New England, urbanization and pollution have resulted in the closure of numerous tidal flats to shellfishing (Whitlach 1982). For example, 30% of softshell clam beds at Gloucester, Massachusetts, were nonharvestable in 1980 because of discharge of untreated sewage. This was estimated as a $332,400 per year loss to the community (Hruby 1981). Maryland's Chesapeake Bay beds were also closed in 1973 because of a high coliform count; it is not known whether this was due to Tropical Storm Agnes or sewage pollution (Chesapeake Research Consortium, Inc. 1976).

Chlorine is used as a disinfectant of sewage effluent and as a biocide to combat fouling of condenser tubes in steam electric power plants. Modern facilities are frequently located near estuaries and the ocean, and meroplankton such as clam larvae may be circulated through the cooling systems, thus coming into contact with this chemical. Larvae near the outfall may also be exposed. Roosenburg et al. (1980) reported direct relationships between mortality and both increasing concentration of chlorine-produced oxidants (CPO) and increasing exposure time. Setting (pediveliger) larvae were more tolerant than were young (straight-hinge veliger) larvae.

Baltimore Harbor, a tributary of the northern Chesapeake Bay, has received and is receiving large quantities of chemical pollutants. Tsai et al. (1979) found lead, chromium, zinc, copper, arsenic, PCB's, and hexane extracts in the harbor sediments. At five stations the sediments were toxic enough to produce 50% mortality in softshell clams within 24 h. These investigators reported that clams can contract for a finite time to reduce the surface area exposed to a toxin or reduce the rate of pumping water through the gills.

Bioassays were conducted for copper, zinc, nickel, manganese, and lead in raw seawater under ambient summer conditions (30 ppt salinity, 22 °C, pH 7.95, dissolved oxygen above 4.0 mg/l) by Eisler (1977). The 168-h LC_{50}'s (mg/l) were as follows: Cu, 0.035; Cd, 0.150; Zn, 1.55; Pb, 8.80; Mn, 3.00; and Ni, 50.00. Additional tests for zinc and cadmium at 30 ppt at 17.5 °C in winter showed that survival of clams increased with decreasing temperature.

The hydrocarbons DDT, dieldrin, endrin, α-endosulfan and β-endosulfan all affect the rate of contraction of isolated clam ventricles. Effects range from reduction of amplitude to complete arrest, depending on the concentration and chemical (Roberts 1975).

Softshell clams are more seriously affected by oil pollution than other co-occurring commercial shellfish. Effects may be outright death, gonadal tumors, or stunting of growth. The threat is most serious in the Chesapeake Bay because of thermal stress at the southern limit of their distribution (Rose 1974).

Ecological, morphological, and behavioral characteristics make softshell clams particularly subject to the deleterious effects of oil spills. They tend to live in fine sediments, in a low-energy environment where oil persists for long periods after a spill. An immediate consequence of spilled oil is the smothering of clams' burrows, which reduces oxygen levels and promotes bacterial action (Thomas 1973). The siphons of the softshell clam prevent it from completely closing its shell; consequently the mantle and gills are constantly exposed to sediments and interstitial water. Since food is obtained from the boundary water, which is in intimate contact with the sediment surface, any oil leaching from the sediment is taken in by the clam (Gilfillan and Vandermeulen 1978).

In 1972 at Casco Bay, Maine, oiled clams showed marked reduction in metabolism and growth for 3 years after a spill. In Seaport, Maine, growth, survival, and recruitment were reduced for up to 5 years after a spill (Gilfillan and Vandermeulen 1978). Shortly after a Bunker C oil spill, MacDonald and Thomas (1980) compared clams in the polluted area with those in an unpolluted area. They repeated the comparison 9 years later and found growth to be retarded by 2-5 years in the oiled clams.

Petroleum hydrocarbons at rates up to 200 µg/g tissue were found in clams by Gilfillan and Vandermeulen (1978). When compared to controls, these clams exhibited decreased tissue and shell growth and carbon flux. Crude and refined hydrocarbons in increasingly greater concentrations increase mucus secretions and decrease tactile response. Increased mucus production drains the energy reserves of clams, clogs the gills and mantle cavity, and disrupts the normal feeding mechanism. Petroleum hydrocarbons also affect respiration; very low concentrations cause a doubling of the respiratory rate, but high concentrations cause depression of the rate. Gill cilia can remove oil globules of 1,030 µm in diameter from sea water, and handle the globules in the same manner as food and detritus particles (Fong 1976). An increase in respiratory rate increases filtration and therefore mortality.

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16. Abstract (Limit: 200 words)

The softshell clam supports the third most valuable commercial clam fishery in the United States. Density is highest at depths of 3-4 m, temperatures less than 28 °C, and salinities greater than 3 ppt. Its near-shore habitat makes it easily threatened by pollution. Clam beds in some places have been closed because of contamination by bacteria. Softshell clams are more sensitive to oil pollution than are the other clams that share its habitat.

The softshell clam spawns in spring (sometimes in early summer) and again in fall. In 36-48 h after fertilization, a pelagic veliger larva develops and persists for 2-6 weeks. Then it settles out of the plankton. It attaches to the substrate and can move and reattach itself. Eventually, it adopts the adult lifestyle and occupies a permanent burrow, usually in sandy bottom with less than 50% silt.

Adult clams feed by filtering small particles from the water column. Predators of adult clams include crabs, fish, birds, and raccoons.

The 24-h LC_{50} values for summer-acclimated clams have been reported as 32.5-34.4 °C. Juveniles and adults can withstand long periods of anaerobiosis.

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