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Patrick Baker and Roger Mann

Special Scientific Report No. 125

Virginia Institute of Marine Science
The College of William and Mary
Gloucester Point, Virginia 23062
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ABSTRACT

Large populations of softshell clams persist only in relatively shallow, sandy, mesohaline portions of Chesapeake Bay. These areas are mostly in Maryland, but can also occur in the Rappahannock River, Virginia. In some other portions of the bay, especially polyhaline portions, sparse populations of soft shell clams persist subtidally. Restricted populations exist intertidally.

Softshell clams grow rapidly in Chesapeake Bay, reaching commercial size in two years or less. They reproduce twice per year, in spring and fall, but probably only fall spawnings are important in maintaining population levels. Major recruitment events do not occur in most years, despite heavy annual sets.

Softshell clams are a major food item for many predator species. Major predators on juveniles include blue crabs, mud crabs, flatworms, mummichogs, and spot. Major predators on adults include blue crabs, eels, and cownose rays. Some other species that may depend heavily on softshell clams include overwintering and migrating ducks, geese, and swans, and estuarine populations of muskrats and raccoons.

Diseases may play an important role in regulating populations of adult softshell clams, and hydrocarbon pollution is linked to increased frequency of disease. Oil pollution does the most widespread and persistent damage to softshell clams, and may also induce disease. Heavy metals, pesticides, and other contaminants can be extremely toxic, but the harmful effects to clams do not last when the contamination abates. The main concern with these toxin compounds is the chance of bioaccumulation by softshell clams, thereby passing the compounds on to predators or to humans.

Siltation, caused by storm events, dredging operations, or erosion, can smother clam populations. Eutrophication, enhanced by nutrient inputs from sewage or agriculture, is not yet known to have affected softshell clam populations, but the danger exists.
INTRODUCTION

Low salinity limits the upstream distribution of soft shell clams in most of the major tributaries of Chesapeake Bay. In shallow and mesohaline portions of the bay, clams have more time to grow to a relative size refuge. Predation pressure places an effective upper salinity limit to softshell clam distribution. Optimal areas are found on the Eastern Shore from Pocomoke Sound to Eastern Bay, and on the western side from the Rappahannock River to the Severn River, Maryland. Ideal conditions may exist in small areas in other portions of the bay also, and low population densities exist throughout most of the bay. Predators virtually eradicate softshell clams of all sizes in soft mud, so only sandy areas contain significant levels of clams (Pfitzenmeyer and Drobeck, 1963). Seasonal anoxia is normally restricted to deep waters, which do not support softshell clam populations, but periodic "seiching" events can temporarily inundate shallower areas with anoxic water.

Softshell clams spawn twice in most years. Juveniles that recruit in spring rarely survive because of predation pressure. A major recruitment event may occur only every ten to fifteen years. Severe temperature shifts for intertidal populations can eliminate large numbers of recent recruits in a short period.

Population levels of harvestable softshell clams have declined since exploitation began in 1953. Major harvesting of Maryland softshell clam stocks began in 1953, harvests climbed to 3,700,000 kg in 1964 and remained stable until 1971. Harvests in Virginia began in 1955, reached a peak of 180,000 kg in 1966, but ceased in 1968. Tropical storm Agnes in 1972 was responsible for poor harvests in Maryland in the early 1970s (Smith and Marasco, 1977), but stocks had apparently collapsed in Virginia prior to the storm. In 1973 harvests in Maryland were only 300,000 kg, but rebounded to 1,400,000 in 1988. There has been no significant harvest of softshell clams in Virginia since 1968.

Softshell clams are major components of the filter feeding benthic infauna of the mesohaline portion of the bay, consuming microscopic algae filtered from water drawn into their incurrent siphon. There is evidence from other systems that softshell clams are very important in removing particles from the water, even as small juveniles. A density of 3,000 juveniles averaging 2.5 mm long in an area of one square meter can filter one cubic meter of water per day, while 1,500 juveniles 5 mm long in the same area can filter 2.5 cubic meters per day. Filtering capability increases exponentially with shell length.

The abundance of soft shell clams in the bay underscores their importance as members of the benthic infauna, yet their documented variability in abundance (with resultant effect on the commercial fishery) suggests a possible role as indicator species of temporal and spatial change in the bay environment. With this in mind we offer this report to biologists, managers, and legislators as a brief introduction to the biology of the soft shell clam, and further comment on issues that affect its continued existence in the bay.
BACKGROUND

Nomenclature

Scientific name .................. Mya arenaria
Common names .................. softshell clam, mannose, steamer clam
Phylum .................. Mollusca
Class .................. Bivalvia
Subclass .................. Heterodonta
Order .................. Myoida
Family .................. Myidae

Geographical Range

The softshell clam is found in marine and estuarine waters, intertidally and subtidally to depths of nearly 200 m along the Atlantic coast of North America from northern Labrador to Florida, with maximum abundances from Maine to Virginia (Laursen, 1966; Theroux and Wigley, 1983). It is also found throughout Europe from northern Norway to the Black Sea (Laursen, 1966; Gomoiu, 1981) and has been successfully introduced to the west coast of North America from southern Alaska to southern California (Fitch, 1953).

Identification Aids

The softshell clam rarely exceeds 11 cm in shell length in Chesapeake Bay (Appeldoorn, 1983), and is elongate and oval in outline. The shells gape at both ends when closed, and in life the foot and the siphons protrude from either end. The fused siphons (also called the "neck") are covered with a leathery integument (see Figure 1). The shell is relatively brittle (hence the name "softshell clam"), and in life is at least partially covered with a thin grey or tan parchment-like periostracum, while dead shells quickly become bleached chalk-white. Inside the left-hand shell there is a spoon-like chondrophore attached to the hinge (see Figure 1).

LIFE HISTORY

Spawning and Fecundity

Softshell clams usually spawn twice per year in Chesapeake Bay; once in mid to late autumn, and once in late spring. The actual times depend on the temperature of the water, because the clams can spawn only in water between 10 and 20°C, and most efficiently at 12-15°C (Pfitzenmeyer, 1965; Lucy, 1976). Optimal temperatures occur for only a few weeks every year, and if the length of time that these conditions exist is too short, the clams may not spawn at all. This most often happens in spring (Shaw, 1964, 1965; Lucy, 1976).

During spawning both eggs and sperm are released externally. It has been found for other benthic invertebrates that spawn this way, that fertilization success decreases sharply with both sperm dilution and sperm age. Both of these factors increase with the distance between spawning adults, so low densities of adults results in low fertilization success (Pennington, 1985). Assuming that this holds true for softshell clams, it means that areas with high adult density produce proportionately more larvae per adult than areas with low adult density.
Figure 1. Top: living softshell clam, with siphons protruding. Bottom (left to right): dorsal view, interior view, and exterior view of softshell clam shell valves.
Sexes are separate in softshell clams, with an even male:female ratio (Lucy, 1976; Brousseau, 1978b), although Appeldoorn (1984) found a slight but significant bias towards females in Long Island Sound. Fecundity, or the number of eggs produced per female, increases exponentially with size (Brousseau, 1978b). This means that a clam with a shell 3 cm long can produce only about 1,300 eggs per spawning episode, while a clam 5 cm long can produce 9,300 eggs, and a clam 10 cm long can produce 85,100 eggs. Larger clams, therefore, are disproportionately important in maintaining population levels.

Eggs and Larval Development

Egg size varies from about 42 to 73 μm in diameter (Loosanoff and Davis, 1963; Brousseau, 1978b). An egg develops into a trochophore larva within a day, and becomes a veliger larva in several more days. The veliger metamorphoses into a juvenile clam at the size of about 200-300 μm in shell length (Loosanoff and Davis, 1963, Moeller and Rosenberg, 1983) in about one to three weeks, depending partly on temperature (Stickney, 1964b; Lucy, 1976). During their larval phase bivalve larvae are planktonic, swimming just strongly enough to maintain themselves at some level in the water column. When the larvae are ready to metamorphose they alternately swim near and crawl on the bottom for several hours before settling (Loosanoff and Davis, 1963). Gregarious settlement has been reported (Hidu and Newell, 1989). The newly settled clams, or spat, usually attach themselves to any available substrate with byssal threads secreted by the foot (Loosanoff and Davis, 1963).

Juveniles, Growth, and Adults

Although adult softshell clams are completely sedentary, small juveniles up to about 15 mm long can be very active. If hard substrate, such as shell, worm tubes, eelgrass, or coarse sand is available, they attach themselves to it with byssal threads. A clam may trail a byssal thread while crawling with its foot. It may also temporarily burrow during this time period (Smith, 1955; Loosanoff and Davis, 1963). Eventually the clam permanently burrows, and unless disturbed, spends the rest of its life in one place. Disturbance and redistribution by physical forces can occur during strong tidal or storm events. The depth of the burrow increases with age, so that the top of the shell can be 2 cm below the surface when shell length is only 1 cm, 4 cm deep at a size of 2 cm, and 12 cm deep at a size of 4 cm (Zwarts and Wanick, 1989).

Growth of softshell clams in Chesapeake Bay is relatively rapid. Under average conditions, they can reach the marketable size of 5 cm (shell length) in 1.5 to 2 years (Manning and Dunnington, 1956; Hanks, 1966). Growth rate depends on many things, including salinity and temperature, food abundance, sediment type, intertidal level, and pollution. High salinity and warm water, especially in spring, both favor growth (Matthiessen, 1960a; Stickney, 1964a; Appeldoorn, 1983). Food abundance, both as affected by actual abundance and by competition with other filter-feeders, affects growth (Stickney, 1964a). Fine sediments, such as mud, favor growth, while sand and gravel decrease growth rates (Newell and Hidu, 1982). (This does not mean mud is better softshell clam habitat, however; see HABITAT REQUIREMENTS.) Intertidal clams grow more slowly both because they have less time to feed, and because the sediment tends to be coarser (Jacques et al., 1984). Some types of pollution have been shown to decrease clam growth rates (see SPECIAL PROBLEMS: Contaminants). Growth is best in summer and poorest in late winter (Newell, 1984), and most growth is achieved within the first five years of life, because growth decreases exponentially with age, even though clams 28 years
old have been found (Brousseau, 1979; MacDonald and Thomas, 1980). There is no evidence that there are genetic differences between populations or subpopulations that affect growth rate (Spear and Glude, 1957).

Distribution, Population Status, and Trends

The distribution of softshell clams in Chesapeake Bay is restricted by several parameters. Low salinity limits the upstream distribution in most of the major tributaries: Hog Island in the James River; Tappahannock in the Rappahannock River; Mathias Point in the Potomac River; and Patapsco River in the mainstem of Chesapeake Bay. Sediment type does not affect survival directly, but predators virtually eradicate softshell clams of all sizes in soft mud, so only sandy areas contain significant levels of clams (Pfitzenmeyer and Drobeck, 1963). Soft sediments predominate in deeper water; water depth therefore imperfectly correlates with softshell clam distribution. Seasonal anoxia is normally restricted to deep waters (Taft et al., 1980; Kuo and Neilson, 1987), which do not support softshell clam populations, but periodic "seiching" events, or tilting of the density gradient, can temporarily inundate shallower areas with anoxic water (Tuttle et al., 1987).

There is no physiological reason why softshell clams cannot survive in deep water, and individuals in Chesapeake Bay have been collected from as deep as 15 m (Orth and Boesch, 1975), but populations persist mainly in depths of less than 5 meters. The reported persistence in shallow water may be a sampling artifact, since most sampling for adults has been done in less than 5 m (Pfitzenmeyer and Drobeck, 1963; Haven, 1970); however, the distribution is consistent with the general distribution of coarse sediments.

Although softshell clams survive well in high salinity, indirect factors limit sustained high population levels to mesohaline portions of Chesapeake Bay. High salinity increases the number of predator species that can exist near softshell clam populations. In shallow and mesohaline portions of the bay, clams have more time to grow to a relative size refuge. Predation pressure places an effective upper salinity limit to softshell clam distribution.

In Chesapeake Bay, optimal softshell clam areas are found on the east side of the bay from Pocomoke Sound to Eastern Bay, and on the west side of the bay from the Rappahannock River to the Severn River, Maryland. The northward "deflection" of this distribution on Eastern Shore may be due to the higher salinities on that side of the Bay. Optimal conditions may exist in small areas in other portions of the bay also, and low softshell clam densities exist throughout most of the bay. We have chosen the relatively arbitrary level of 1 adult softshell clam per square meter as a definition of high abundance; throughout most of the Chesapeake Bay abundance is much lower. Juvenile abundance may greatly exceed this temporarily in almost any part of the bay. Potential distribution, averaged for a variety of conditions, is shown in Figure 2. References for distribution information include: Maryland Department of Tidewater Fisheries (1950-1963); Pfitzenmeyer (1960); Pfitzenmeyer and Drobeck (1963); Maryland Department of Chesapeake Affairs (1964-1967); Haven (1970); Lipson (1973); Cory and Redding (1977); Mihursky and Boynton (1978); van Engel et al. (1978); Becker and Kaufman (1979); Holland et al. (1979); Dauer et al. (1984); U.S. Army Corps of Engineers (1984); Scott et al. (1988); Dauer and Ewing (1989); Dauer et al. (1989a, 1989b, 1989c, 1990); M. Castagna. Virginia Institute of Marine Science (pers. comm.). Multi-year trends in salinity, temperature, and anoxia may temporarily expand or contract this range. Within-year variations allow
Figure 2. Potential distribution of softshell clams in Chesapeake Bay.

Solid fill indicate areas of potential adult distributions equal to or greater than 1 per m²; horizontal hatch indicates areas of potential adult distributions of less than 1 per m².
juveniles to settle in outlying areas, but these populations rarely survive more than a year (Scott et al., 1988; Dauer et al., 1989a). Juveniles often set in high abundances in areas with low adult abundance, but are virtually eradicated within months (Haven, 1970; Holland et al., 1979, 1980; Vörnstein, 1977). This is in contrast to Long Island Sound populations, where settlement is thought to be the critical factor in determining population levels (Brousseau and Baglivo, 1984). In addition, episodic events such as high summer temperatures, high predator abundance or low salinity can eradicate adults in small areas (Orth, 1975) or large areas (Cory and Redding, 1977; Haven et al., 1977). These areas can quickly be recolonized, when conditions once again become favorable (Hanks, 1968), but since bivalve larvae tend to be retained within their native subestuaries (Seliger et al., 1982; Mann, 1988), severely affected subestuaries would probably take longer to recover.

Although softshell clams reproduce twice most years, juveniles that recruit in spring rarely survive because of predation pressure, regardless of the magnitude of recruitment (Vörnstein, 1977; Holland et al., 1980). Only those that are spawned in autumn and grow in cold water when predators are inactive survive to a size large enough to avoid most predators (Ulanowicz et al., 1982). Even then major recruitment events may occur only every ten to fifteen years (Haven, 1976). Severe temperature shifts for intertidal populations can eliminate large numbers of recent recruits in a short period (present authors, pers. obs.). There is evidence that large amounts of drifting macroalgae can inhibit settlement of softshell clams (Olafsson, 1988). Attached macrophytes, on the other hand, enhance settlement by slowing currents (Jackson, 1986). Recruitment events within subestuaries are likely to be relatively independent because bivalve larvae tend to be retained within subestuaries (Seliger et al., 1982; Mann, 1988).

In lower regions of Chesapeake Bay, populations of softshell clams are low, except in intertidal areas. The high intertidal region may have greater than 20 adults per square meter when subtidal areas have virtually no adults (Lucy, 1976; present authors, pers. obs.). This distribution is probably due to the coarse sediments at this level and the limited time that they are exposed to predators (Matthiessen, 1960b; Scapati, 1984). If spawning success is affected by the density of adults (Pennington, 1985), these intertidal populations are probably vital in maintaining recruitment of juveniles subtidally.

Population levels of harvestable softshell clams have declined since exploitation began in 1953 (U.S. National Marine Fisheries Service, 1950-1988), but the reasons for this are unclear. In 1950 the hydraulic escalator harvester was invented, and in 1953 major harvesting of Maryland softshell clam stocks began. Prior to that the maximum harvest had been 730 kg (meat) in 1949 (Maryland Department of Chesapeake Affairs, 1966), but harvests rapidly climbed to a maximum of 3,700,000 kg in 1964, where they remained nearly stable until 1971 (U.S. National Marine Fisheries Service, 1950-1988). Harvests in Virginia began in 1955 and were much more irregular, reaching a peak of 180,000 kg in 1966, but ceasing in 1968. Extreme mortality of adult softshell clams in parts of Chesapeake Bay from tropical storm Agnes in 1972 was responsible for poor harvests in Maryland in the early 1970s (Smith and Marasco, 1977), but stocks had apparently collapsed in Virginia prior to the storm. In 1973 harvests in Maryland were only 300,000 kg, but rebounded to 1,400,000 in 1988. There has been no significant harvest of softshell clams in Virginia since 1968. All evidence in Virginia, which has limited populations in most areas, suggests that large settlements of juveniles can be
produced by small populations of adults (Haven, 1970; Dauer et al., 1989a, 1989b, 1989c, 1990). Softshell clams also appear to be resistant to domestic sewage and low levels of industrial pollution (Loi and Wilson, 1979; Appeldoorn, 1981; Hruby, 1981). So little is known about fisheries dynamics that we cannot say that there are not natural population trends on the scale of decades (Rothschild, 1986). Since virtually every exploited fishery stock for which data has been kept has shown a significant overall decline (Rothschild, 1986), the possibility exists that declines in softshell clam populations in Chesapeake Bay may in part be caused by exploitation.

In Long Island Sound, Brousseau (1978a) generalized size-specific mortality of softshell clams over a several-year period. Clams 2-5 mm in shell length suffered nearly 90% mortality, clams 5-10 mm suffered 68% mortality, and mortality steadily decreased to a minimum of 6% for clams attaining 50 mm in shell length. The age at 50 mm was about 2.3 years, slightly older than clams that size in Maryland (Manning and Dunnington, 1956; Hanks, 1966). Survival can vary significantly between sites, however, with a resulting egg-to-adult survival that varies by nearly a factor of ten (Brousseau and Baglivo, 1984).

ECOLOGICAL ROLE

Role as Filter Feeder

Softshell clams feed on microscopic algae which filtered from water drawn into their incurrent siphon. They consume small flagellated cells and diatoms in the 5-50 μm range (Matthiessen, 1960a; Eaton, 1983; Shumway et al., 1985), and can selectively reject non-food particles and toxic dinoflagellates such as Alexandrium (Gonyaulax) tamarensis (Eaton, 1983; Shumway and Cucci, 1987). Rejected particles are incorporated into pseudofeces, and therefore effectively removed from the water column. Free-living bacteria are too small to be filtered (Wright et al., 1982), but bacteria associated with detritus may be assimilated (Langdon and Newell, 1990). Although some invertebrate larvae are rarely drawn into the siphons (Ertman and Jumars, 1988), the presence of softshell clams affects the settlement of many species of infauna, enhancing some and inhibiting others. The mechanisms of these interactions are not known, but differential filtration may be one (Hines et al., 1989).

There is evidence from other systems that softshell clams are very important in removing particles from the water, even as small juveniles. In San Francisco Bay, it was calculated that a density of 3,000 juveniles averaging 2.5 mm long in an area of one square meter can filter one cubic meter of water per day, and 1,500 juveniles 5 mm long in the same area can filter 2.5 cubic meters per day. The filtering capability of adults was not calculated, but it increases exponentially with shell length (Nichols, 1985). These densities are high for Chesapeake Bay (Lucy, 1976), but even much lower densities may be significant. In waters off western Sweden, it was estimated that infaunal bivalves, including high numbers of softshell clams, consumed nine times as much of the small plankton as did zooplankton grazers (Loo and Rosenberg, 1989). Filtering by benthic filter feeders is especially important in controlling microalgal biomass associated with eutrophication in shallow, well mixed bodies of water, such as Chesapeake Bay.

When compared to other common Chesapeake Bay filter feeders, softshell clams are equal to or higher than American oysters in weight-specific filtering rate, but lower than jackknife or razor clams. Ribbed mussels can
filter bacteria from the water, while softshell clams cannot (Kioerboe and Moelenberg, 1981; Shumway et al., 1985).

Role of Empty Shells
Despite its fragility, the shell of the softshell clam is relatively resistant to dissolution, and because of its light weight is less likely to be buried than many shells (Driscoll, 1970). This means that it is particularly suitable as substrate for many fouling organisms, especially in areas that lack other shell or rock. Most of these fouling species are small, but two bivalves make extensive use, directly or indirectly, of softshell clam shells. The jingle shell requires a smooth, hard surface, such as softshell clam shells, as a substrate, and the ark clam settles onto hydroids that grow on the shells (Driscoll, 1968).

Predators
Predation on softshell clams at all stages is very intense. Under most conditions, from 90% to over 99% of fertilized eggs and planktonic larvae are destroyed in the water column (Thorson, 1966; Yoo and Ryu, 1985). Jellyfish (hydromedusae and scyphozoans) and comb jellies are considered major predators of molluscan larvae (Pennington and Chia, 1985; Quayle, 1988). Sea nettles, although abundant part of the year, are not normally present when softshell clam larvae are abundant (Wass et al., 1972). Other potential predators on mollusk larvae include copepods, larval and juvenile fish, and filter-feeding fish such as anchovies and menhaden (Schumann, 1965; Checkley, 1982; Pennington and Chia, 1985; Quayle, 1988). As the larvae metamorphose and settle, they fall prey to benthic planktivores such as barnacles, sea anemones, and annelid worms (Breese and Phibbs, 1972; Steinberg and Kennedy, 1979; Young and Gotelli, 1988). Mortality of newly-settled juveniles is about 90% within the first several weeks (Powell et al., 1984).

Softshell clams provide an important, direct link between phytoplankton and predators of all sizes. The relative importance of a predator on juvenile or adult clams depends both upon the proportion of its diet that is made up by softshell clams and its overall abundance. For most predators one or both of these factors is not known, so their importance can only be estimated. Table 1 lists major and minor predators on juveniles softshell clams, and Table 2 lists major and minor predators on adult clams. "Major" predators are here defined as animals that are abundant throughout most of the softshell clam range in Chesapeake Bay and use softshell clams as a significant portion of their diet, while "minor" predators are those that are not abundant, or are restricted to a small proportion of the bay, or for which softshell clams are only a minor portion of the diet. "Juveniles" are here defined as clams with shell lengths of under 2 cm.

Mummichogs are limited to very shallow water (Hildebrand and Schroeder, 1928), but the other major predators are found in all water depths that sustain large softshell clam distributions. Their importance as clam predators relative to each other is not known. Submerged aquatic vegetation reduce predation of infaunal bivalves (Peterson, 1986). Polychaete worms certainly have the capability of preying on juvenile clams (Fauchald and Jumars, 1979; Lewis and Whitney, 1988), and Hidu and Newell (1989) review evidence that suggests that some polychaete worms are major predators.

Of the minor predators, horseshoe crabs, snapping shrimp, and oyster drills are abundant mainly in polyhaline areas. Although Botton (1982, 1984) considers horseshoe crabs to be major predators in Delaware Bay. Buckley
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<td>Lewis &amp; Whitney, 1988</td>
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<tr>
<td>Blue crab (<em>Callinectes sapidus</em>)</td>
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<td>Mud crabs (<em>Xanthidae</em>)</td>
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<td>Whetstone &amp; Eversole, 1978</td>
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<td>Shrimp (<em>Crangon septemspinosa</em>)</td>
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<td>Mummichogs (<em>Fundulus spp.</em>)</td>
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<td>Spot (<em>Leiostomus xanthurus</em>)</td>
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<td><strong>Minor Predators</strong></td>
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<td>Flatworm (<em>Stylochus ellipticus</em>)</td>
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<td>Polychaete worms (<em>Eunicidae, Nephtyidae, Nereidae</em>)</td>
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<td>Mud snails (<em>Ilyanassa obsoleta, Nassarius spp.</em>)</td>
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<td>Moon snail (<em>Polinices duplicatus</em>)</td>
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<td>Oyster drills (<em>Urosalpinx cinerea &amp; Eupleura caudata</em>)</td>
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<td>Horseshoe crab (<em>Limulus polyphemus</em>)</td>
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<td>Croaker (<em>Micropogonias undulatus</em>)</td>
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<td>Tautog (<em>Tautoga onitis</em>)</td>
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<td>Ducks (<em>Anas spp., Aythya spp.</em>)</td>
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Table 2: Predators on adult softshell clams in Chesapeake Bay.

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<td>Eel (<em>Anguilla rostrata</em>)</td>
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<td>Cownose ray (<em>Rhinoptera bonasus</em>)</td>
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<td>Moon snail (<em>Polinices duplicatus</em>)</td>
<td>Edwards &amp; Heubner, 1977</td>
</tr>
<tr>
<td>Whelks (<em>Busycon spp.</em>)</td>
<td>Heubner &amp; Edwards, 1981</td>
</tr>
<tr>
<td>Skates (<em>Raja spp.</em>)</td>
<td>Davis, 1981</td>
</tr>
<tr>
<td>Rays (<em>Dasyatis spp.</em>)</td>
<td>Hildebrand &amp; Schroeder, 1928; Smith &amp; Merriner, 1978</td>
</tr>
<tr>
<td>Black drum (<em>Pogonias cromis</em>)</td>
<td>Hildebrand &amp; Schroeder, 1928</td>
</tr>
</tbody>
</table>
(1974) believes them to be overrated as predators, and in any case, horseshoe crabs are less abundant in Chesapeake Bay than in Delaware Bay. Mud snails are abundant in Chesapeake Bay, but less so in sandy areas, and apparently affect only extremely small bivalves (Hunt et al., 1987). Ducks and geese affect only shallow areas, but are active in winter, when most other predators are inactive (Grandy and Hagar, 1971; Jorde and Owen, 1988).

Adult softshell clams, if they can be excavated, are vulnerable to predators because their shells are fragile and do not close tightly. The method of predation by eels is unknown, but crabs can excavate to 20 cm or more (R. Lipcius, Virginia Institute of Marine Science, pers. comm.), and rays can, by means not well understood, excavate large pits to reach adult clams (R. Blaylock, Virginia Institute of Marine Science, pers. comm.). Of the minor predators, all but the black drum are limited to polyhaline portions of Chesapeake Bay.

Many species of predators eat mainly siphon tips of softshell clams, especially fish (Hildebrand and Schroeder, 1928; Wenner and Musick, 1975). This is usually non-lethal to clams, but reduces the fitness of individuals, so the effect on a population level is approximately equal to the effect of removing an equal biomass of entire individuals. A proportion of each affected clam's energy intake that could have gone into gamete production must be used to regenerate tissues.

Some populations of certain other species may depend heavily on softshell clams, even though they are not numerically important predators. These include ducks and geese, especially overwintering populations (Grandy and Hagar, 1971; Jorde and Owen, 1988), muskrats and raccoons (Triplet, 1983; J. Carlton, Oregon Institute of Marine Biology, pers. comm.).

Present evidence suggests that predation overall is the most important source of mortality for all juvenile and adult age classes. A high abundance of benthic planktivores can prevent settlement locally (Young and Gotelli, 1988). Predators can eradicate softshell clams from an area, whether newly-settled juveniles (Haven, 1970; Powell et al., 1984; Elmgren et al., 1986; Hunt et al., 1987), or older juveniles (Vîrnstein, 1977; Holland et al., 1979, 1980; Moeller and Rosenberg, 1983). Predation can keep populations from persisting in muddy substrates, where it is easier to dig down to the clam (Lipcius and Hines, 1986). Although larger clams are less vulnerable to predation, a high abundance of predators can destroy a local clam population (Orth, 1975).

There are four ways softshell clams can escape most predation pressure. The first is to grow larger, since larger clams are buried deeper, and deeper clams are harder for predators to excavate (Vîrnstein, 1977; Holland et al., 1979; Blundon and Kennedy, 1982; Zwarts and Wanick, 1989). The second is to live in coarser sediments, such as sand as opposed to mud, where predators have more difficulty excavating (Lipcius and Hines, 1986). It follows, therefore, that even though clams grow faster in soft mud (Newell and Hidu, 1982), large populations cannot persist there in Chesapeake Bay (Pfitzenmeyer and Drobeck, 1963). The third partial refuge is low temperature. Clams can survive and grow at low temperatures (Harrigan, 1956; Borget, 1983), at times when their predators are inactive. Consequently, they grow to a larger, less vulnerable size before their predators become active (Ulanowicz et al., 1982). The fourth partial refuge is tidal level. Intertidal areas are an exception to general softshell clam distribution. The slight tidal range in most of Chesapeake Bay limits intertidal areas to narrow bands near the shore, but softshell clams are well-adapted to intertidal existence (Anderson, 1978).
Intertidal areas provide a relative refuge from most predators, because there is limited time for predation (Matthiessen, 1960b; Scapati, 1984), and areas that do not support significant subtidal populations can sometimes support intertidal populations of adults (Haven, 1970; Lucy, 1976). Some predators, such as mummichogs (Fundulus spp.), ducks, geese, whistling swans and raccoons, are well-adapted to this zone, however, so the intertidal area is only a partial refuge. Recreational clam harvesting also occurs mainly in the intertidal region.

Low density is also thought to be a partial refuge from predation, because predators tend to seek out patches of high density prey, especially in areas of coarse sediment, where it is more difficult to excavate them (Lipcius and Hines, 1986). The value of this to the softshell clam, however, is probably at least partly offset by a loss of reproductive fitness, if reproductive success is related to sperm density and gamete age (Pennington, 1985), and therefore adult proximity (density).

**HABITAT REQUIREMENTS**

**Salinity, Temperature, and pH**

According to Matthiessen (1960a), adults cannot survive below 4 ppt salinity for more than a few days, and do not grow below 8 ppt, but Chanley (1958) reported survival after acclimation at 2.5 ppt. Probably the lower summer salinity limit is 8 ppt. Larval salinity tolerance varies, depending upon the salinity to which the adults are acclimated (Stickney, 1964b), but Chanley and Andrews (1971) give 5 ppt as a lower limit. There is no upper salinity limit, but there are more predator species in water of high salinities (see ECOLOGICAL ROLE: Predators). Large populations of softshell clams in Chesapeake Bay are therefore restricted to mesohaline areas. Salinities as low as 0 ppt can be survived by adults for about two days (Matthiessen, 1960a), but longer periods cause mass mortalities (Haven, 1976). Juveniles are more susceptible to low salinity, and warm temperature decreases tolerance to low salinity.

Softshell clams can survive temperatures as low as -12° C for long periods of time (Borget, 1983), so there is normally no lower temperature limit in Chesapeake Bay. Sudden and extreme temperature shifts may affect intertidal populations of juveniles, however, even though Kennedy and Mihursky (1972) reported that juveniles are more tolerant of temperature extremes. A sudden decrease in air temperature from 20° C to below 0° C in a few hours was followed by massive mortalities of intertidal juveniles within a day in the York River (present authors, pers. obs.). Only juveniles recruited the previous autumn were affected. Since these temperature shifts occur mainly in winter, it represents a major source of mortality for clams during a time when most predators are inactive. Only intertidal populations are likely to be affected, however.

Optimum temperatures for feeding are about 16-20° C, but feeding can take place at as low as 1.5° C (Harrigan, 1956), a temperature much lower than the minimum required for activity by most softshell clam predators. The upper limit for softshell clams is about 34° C (Harrigan, 1956), a temperature rarely encountered in Chesapeake Bay except in shallow embayments.
Temperature extremes do limit spawning, however, since spawning is restricted to temperatures between 10 and 20°C at the most (Lucy, 1976), and probably is even more restricted for optimal spawning (Pfitzenmeyer, 1965). These temperatures are required for a period of at least several weeks for gamete maturation and successful spawning, and some years, especially in spring, temperatures rise or fall too quickly for successful spawning (Shaw, 1965; Lucy, 1976). Larvae can evidently grow at a wide range of temperatures, and growth rate is independent of temperatures within certain limits (Lucy, 1976).

Seawater is naturally buffered in the salinity ranges occupied by soft shell clams, so extreme pH values are unlikely to occur. Consequently there has been little study of the effects of changing pH. Physiological processes in soft shell clams occur without significant inhibition over a relatively wide range of pH (Stewart and Bramford, 1976).

**Habitat Characteristics**

Adult softshell clams removed from their burrow eventually die unless they can reburrow (Hidu, 1981), and they can reburrow quickly only into very soft sediments (Pfitzenmeyer and Drobeck, 1967). Although they grow most quickly in soft sediments (Newell and Hidu, 1982), they are also most vulnerable to predators there (Lipcius and Hines, 1986). Large populations in Chesapeake Bay persist only in muddy sand and sandy mud (Pfitzenmeyer and Drobeck, 1963). Softshell clams can survive in very coarse sediments (Newell & Hidu, 1982; present authors, pers. obs.).

**Anoxia and Depth**

Although softshell clams can survive near-anoxic conditions for as long as seven days (McCarthy, 1969). Seasonal anoxia in some deep portions of Chesapeake Bay (Taft et al., 1980; Kuo and Neilson, 1987) have minimal effect since softshell clam populations are largely restricted to shallow areas. If anoxia is extensive, however, and prolonged "seiching" events, or tilting of the density gradient, occur, anoxic deep water can inundate shallow areas (Tuttle et al., 1987) and cause mortalities of benthic organisms. It is not known to what extent anoxia in Chesapeake Bay is enhanced by domestic sewage and agricultural runoff, but these inputs correlate with anoxia and mass softshell clam mortalities in waters off western Sweden (Rosenberg and Loo, 1988). If eutrophication and the extent of seasonal anoxia in Chesapeake Bay are increasing, as suggested by Seliger et al. (1985) and Tuttle et al. (1987), the frequency and duration of shallow water anoxic events will also increase. A "catastrophic" anoxic event in 1984 apparently threatened shellfish beds in Maryland (Seliger et al., 1985).

**SPECIAL PROBLEMS**

**Contaminants: Toxicities of Heavy Metals and Pesticides**

Industrial pollution typically contains a suite of metal ions in various concentrations, termed "heavy metals." Table 3 lists some of these and their measured toxicities. Compared to other aquatic organisms, softshell clams are particularly vulnerable to copper and mercury. Copper is bioaccumulated slightly more in low salinity than in full seawater (Wright and Zamunda, 1987), so softshell clams in Chesapeake Bay are particularly vulnerable.
Table 3. Toxicity of metals to soft shell clams: LC-50 is concentration that is lethal to 50% of the sample in a 7 day time period. Data from Eisler (1977) and Eisler and Hennekey (1977).

<table>
<thead>
<tr>
<th>Metal</th>
<th>LC-50 (mg/L)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cadmium (Cd 2+)</td>
<td>0.15-0.7</td>
</tr>
<tr>
<td>Chromium (Cr +6)</td>
<td>8.0</td>
</tr>
<tr>
<td>Copper (Cu 2+)</td>
<td>0.035</td>
</tr>
<tr>
<td>Lead (Pb 2+)</td>
<td>8.8</td>
</tr>
<tr>
<td>Manganese (Mn 2+)</td>
<td>300</td>
</tr>
<tr>
<td>Mercury (Hg 2+)</td>
<td>0.004</td>
</tr>
<tr>
<td>Nickel (Ni 2+)</td>
<td>30</td>
</tr>
<tr>
<td>Zinc (Zn 2+)</td>
<td>3.1</td>
</tr>
</tbody>
</table>

Organotin (including tributyl tin, or TBT), until recently a component of most marine paint and still used on large vessels, is believed to be extremely toxic to most marine organisms, and is bioaccumulated at high rates by filter feeders such as softshell clams (Langston et al., 1987), but the toxicity of organotin to softshell clams has not been studied. Metallic aluminum particles are apparently nontoxic (Hanks, 1965).

Softshell clams sampled from areas with heavy metal pollution grow significantly more slowly than clams in unpolluted areas (Appeldoorn, 1981), and are in generally poor condition (Gardner and Yevich, 1988), but recovery is rapid when heavy metal pollution ceases (Appeldoorn, 1981).

A variety of pesticides, including DDT, endrin, dieldrin, and endosulfan have been shown to be toxic to softshell clams, but recovery is rapid when exposure ends (Roberts, 1975). Chlorine-produced oxidants, a byproduct of sewage treatment, in concentrations of as low as 0.3 ppm kill 50% of softshell clam larvae with only 16 hours of exposure (Roosenburg et al., 1980). PCB, a fire retardant formerly used in many industrial products, has been implicated as an agent of poor condition in softshell clams from polluted areas (Gardner and Yevich, 1988). Even in highly polluted areas, however, such as the Elizabeth River, Virginia, low populations of adult softshell clams persist (Richardson, 1971).

Contaminants: Petroleum and Petroleum Products

Petroleum, both crude and refined, and its by-products, including polycyclic aromatic hydrocarbons (PAHs), are toxic to softshell clams. Oil spills can be particularly damaging. In muddy sand, such as that found in Chesapeake Bay, spilled oil penetrates slowly but remains for years, and destroys increasingly larger clams over time, eventually eliminating most of the population (Dow and Hurst, 1975). Clams transplanted to oil spill areas are also killed by the oil (Dow, 1975). Depending on the dose and the type of oil, growth rate of survivors is significantly reduced. Bunker C and Number 6 fuel oil have been shown to reduce growth by as much as 50% in survivors (Gilfillan et al., 1976; Gilfillan and Vandermeulen, 1978; Appeldoorn, 1981; MacDonald and Thomas, 1982). Hydrocarbons extracted from polluted sediments are more than 10 times as toxic to softshell clams as they are to fish (Tsai et al., 1979). Not all oil pollution has been shown to have adverse effects (Anderson, 1972), but crude oil is bioaccumulated by softshell clams (Fong, 1976).
The role of hydrocarbon pollution in diseases of softshell clams has been debated, but in general high incidences of cancer-like diseases correlates with hydrocarbon pollution. Neoplasia, hyperplasia, and germinoma have all been correlated to hydrocarbon pollution of various types (Barry and Yevich, 1975; Harshbarger et al., 1979; Walker et al., 1981). Brown et al. (1979) did not find a correlation with total hydrocarbon pollution, but did find a correlation between neoplasia and total PAH levels. PAHs, some of which are known carcinogens, are common components of hydrocarbon pollution. This is an example of an indirect effect of human impact, and there are others that probably go unnoticed.

Bioaccumulation

From a human viewpoint, the most serious aspect of pollution in a fishery species is bioaccumulation. Many pollutants are bioaccumulated, or concentrated, by softshell clams, some of which are thought or known to be extremely toxic to humans. An indirect danger is that sublethal quantities of toxic compounds will be further accumulated by predators of softshell clams, such as blue crabs, which are also fishery species.

Two studies on bioaccumulation of heavy metals and organochlorine residues in Maryland (Eisenberg and Topping, 1984a, 1984b) showed no dangerous levels, but all compounds examined were bioaccumulated to some extent. Most are bioaccumulated by softshell clams less than or equal to accumulation by oysters, but arsenic, which was increasing over time in sediments, was bioaccumulated greater than by oysters. Mercury and cadmium were not bioaccumulated in high amounts, probably because of their toxicity to softshell clams, but they were accumulated more by blue crabs, which feed on softshell clams.

Organotin (including TBT) is accumulated by softshell clams far more than by non-filter feeders, and more than 50 times the accumulation by sediments (Langston et al., 1987). An herbicide, Diquat* (registered brand name), however, was present in lower amounts in softshell clams than in sediments (Haven, 1969). Chrysene, DDT, and napthalene were not bioaccumulated from sediments, while diethyl ether and dioctyl phthalate were accumulated from sediments in trace amounts only (Foster et al., 1987), but this does not mean they were not bioaccumulated from the water. Butler (1971) found that softshell clams accumulate all pesticides tested (aldrin, DDT, dieldrin, endrin, heptochlor, lindan, and methoxychlor) to a greater extent than hard clams but also flushed them better when exposure stopped. Both crude oil and PAHs are bioaccumulated by softshell clams, even when levels in the water are very low (Gilfillan et al., 1976; Mix and Schaffer, 1983). Copper and zinc, on the other hand, are accumulated far less than by oysters (McFarren et al., 1962).

Pathogens and Parasites

Softshell clams in the Mid-Atlantic Bight area are subject to a variety of cancer-like diseases, which may be directly caused by a viral agent (Cooper and Chang, 1982). The agents of these diseases are not known, and there are not standard descriptions of most of these, but at least four cancer-like diseases have been described. These include: neoplastic proliferation of tissue (usually mantle) that invades other tissues; hematocytic neoplasia, or leukemia (Smolowitz et al., 1989); or extreme increase in the number of hemolymph cells; hyperplasia, or proliferation of gill tissue; and germinoma, or proliferation of gonadal tissue (Harshbarger et al., 1979; Walker et al.,
1981). Only one of these, described as an epizootic sarcoma, and probably synonymous with neoplasia, has been studied in Chesapeake Bay. This was implicated in mass mortalities in parts of the Maryland Eastern Shore, where up to 65% prevalence was found in sampled populations, with 100% mortality of diseased clams (Farley et al., 1986). Hematocytic proliferation, however, has been found with up to 40% incidence in Rhode Island, with 50% mortality of diseased clams (Cooper et al., 1982).

Other diseases include hypoplasia, or defective gonadal development, and lipofuscin deposits, or brown pigmented areas (Walker et al., 1981). No mortalities have been reported for hypoplasia, but if the incidence is high, a significant proportion of the population could be effectively castrated. Lipofuscin deposits are not known to be pathogenic, but are more prevalent in polluted areas (Brown et al., 1977). The role of pollution in many of the above diseases, especially neoplasia, is fairly well established. Although pollution may not cause these diseases, certain forms of pollution are well-correlated with incidence of neoplasia (Barry and Yevich, 1975; Brown et al., 1977, 1979; Harshbarger et al., 1979; Walker et al., 1981). This is discussed later.

A series of softshell clam mass mortalities in 1970 and 1971 in Maryland lead to an investigation of pathogenic bacteria, and eight pathogenic bacteria were discovered. Whether any of these caused the mortalities is not known, but it demonstrated that bacterial diseases may be important ecological factors in softshell clam populations (Kaneko et al., 1975). The role of disease in regulating softshell clam populations has not been widely studied, but the information that exists suggests that diseases of all sorts may be as important as environmental factors or predators in adult clam population dynamics.

The most alarming softshell clam pathogen from a human viewpoint is paralytic shellfish poisoning, caused by the planktonic dinoflagellate Alexandrium (Gonyaulax) tamarensis. This species is apparently toxic to softshell clams, so they reduce feeding and reject the dinoflagellates when they are present. This means that for a period of up to ten days after the start of a bloom, there is no significant accumulation of the toxins by softshell clams (Shumway and Cucci, 1987). Fortunately, A. tamarensis does not bloom frequently in Chesapeake Bay. Paralytic shellfish poisoning is not therefore considered a problem in this location.

Although parasites are probably present, they have not been studied in softshell clams in Chesapeake Bay. Probably the most serious parasite is the cercaria stage of the trematode Himasthia leptosoma, which replaces muscle tissue in clams and uses mud snails and various shore birds as hosts for the other life stages. A number of other trematode species have been identified in softshell clams in New England and Canada (Cheng, 1967). A turbellarian flatworm, Paravortes gemellipara, has been found in softshell clams, but it is apparently not clear whether or not it is parasitic. The commensal nemertean Macrobodella grossa is probably not parasitic. A ciliate protozoan, Ancistrocoma pelseneeri, has been identified as a parasite, but does not appear to be common (Cheng, 1967). Two copepods, Myocheres major and Myicola metensis, have been identified as occasional parasites in softshell clams. The parasitic pea crab, is strictly polyhaline (Williams, 1984), as are the ectoparasitic snails, Odostomia spp. (Wass et al., 1972), so they do not affect most softshell clams in Chesapeake Bay.
Sewage and Eutrophication

Softshell clam populations can persist in areas with high domestic pollution (Hruby, 1981), but a high organic content, characteristic of sewage-polluted sediments, correlates with reduced growth rate of softshell clams (Nayak, 1964). One effect of sewage, however, is eutrophication, which can enhance regional anoxia (see HABITAT REQUIREMENTS: Anoxia and Depth).

Disturbance

Heavy siltation can occur from dredging operations or storms. The survival of adult softshell clams buried by sediments varies with the kind of sediments. Burial by up to 24 cm of coarse, mud-free sand can be survived, but only 6 cm of fine sand and only 3 cm of silt can be fatal (Turk and Risk, 1981).

Hydraulic escalators, used to harvest softshell clams in Chesapeake Bay, do relatively little damage to surviving clams. Incidental mortality of unharvested clams is about 7%, incidental catch of fish and crabs is largely nonlethal, and oysters more than 30 meters away are unaffected (Manning, 1959; Medcof, 1961; Pfitzenmeyer, 1972). This compares to about 50% mortality of unharvested clams by hand methods used in New England (Medcof and MacPhail, 1967). Delicate burrow systems and submerged aquatic vegetation are totally eradicated by the hydraulic harvesters, however (Manning, 1959). The use of the hydraulic dredge has been reviewed by Kyte and Chew (1975).

Intertidal populations of softshell clams are the only significant pool of adults in some parts of Chesapeake Bay (Haven, 1970; Lucy, 1976), so these areas are particularly vulnerable to shoreline construction, erosion, landslides, or other factors that cover or erode the intertidal zone. The effects of shoreline destruction, as well as bottom disturbance, by wakes and propeller wash from the increasing number of recreational boats, has not been studied in this context, but at this point effects are probably minor and local.

Miscellaneous

"Extensive" mortalities of softshell clams were reported in the Patuxent River, Maryland after the Chalk Point power plant was constructed, presumably from heated effluent (Mihurskey and Boynton, 1978). Studies specifically designed to study the effect of heated water near Calvert Cliffs, Maryland, however, failed to show any harmful effects to softshell clams (Holland et al., 1979, 1980; Loi and Wilson, 1979). This is a complex issue, in part because spawning, which is temperature-related, may also be affected by heated effluent.

CONCLUSIONS AND RECOMMENDATIONS

Fishery Recommendations

Evidence from Virginia populations of softshell clams indicates that small or restricted populations can give rise to heavy juvenile recruitment. Evidence from other bivalve species in Chesapeake Bay indicates that most juveniles within a subestuary come from adults in that estuary. For populations further north, settlement density and early survival are more important even than abundance of spawning adults. Taken together, this suggests that as long as each subestuary has reserved a small but sustained pool of adult softshell clams, and as long as care is taken not to destroy
newly settled clams by disturbance or sedimentation, harvesting will have no long-term population effects. Since more dense populations probably have better spawning success, for optimum effect the reserve population of adults in each subestuary should be in an area that traditionally sustains high densities of adults. Since domestic sewage apparently has no serious direct effects on softshell clams, one possibility is to use areas condemned for shellfish harvesting because of domestic sewage as adult reserve areas.

Hydraulic escalators used to harvest softshell clams in Chesapeake Bay do relatively little damage to unharvested softshell clams and incidental catch of mobile fauna, but submerged aquatic vegetation and oyster reefs are destroyed completely. The preservation of submerged aquatic vegetation and oyster reefs, because of their importance in the ecology of Chesapeake Bay, should in all cases take precedence over softshell clam harvesting; however, harvesting can occur within about 100 m of these communities with little harm.

Pollution Recommendations

The dangers of heavy metals, pesticides, detergents, and herbicides are well known, and for the most part do not need reiteration. Of the common ions, copper is the most deadly to softshell clams, and any pollution monitoring in areas where softshell clams are a concern should include measurements of copper ion levels.

Historically, the worst pollution problems with softshell clams have been from crude and refined petroleum. Oil spills lead to massive clam mortalities and, in areas with sublethal pollution, reduced growth rates. Chronic pollution from refined petroleum is implicated in increased disease incidence and resulting heavy mortality.

So far eutrophication has not been a problem for softshell clam populations, even though seasonal anoxia exists in some parts of Chesapeake Bay. Evidence from Sweden indicates that domestic sewage and agricultural runoff can catastrophically enhance eutrophication and lead to widespread anoxia, with total eradication of infauna, including softshell clams, so the danger probably exists also in Chesapeake Bay.

Development Recommendations

Two main types of development, both resulting in siltation or burial of softshell clams, pose threats. The first is dredging and spoil disposal. Channels are occasionally dredged in shallow areas, such as for creation of marinas, with obvious direct effects on any clams in the path of the channel, but most often existing channels, which do not support significant clam populations, are deepened or widened. If the dredged material is very fine, much of it may drift over adjacent areas and bury softshell clams, which are susceptible especially to burial by fine sediment.

The second form of disturbance is shoreline development that leads to landslides, especially in areas with significant tides. Such disturbance is worthy of further study. In much of Chesapeake Bay, intertidal softshell clams make up a significant portion of local populations, so destruction of intertidal areas by landslides can have a disproportionately large effect on local softshell clam populations. Conversely, landslides can help create habitat for soft shell clams in the intertidal and shallow subtidal regions of the bay if they replace unsuitable sediment with suitable sediment.
SPECIES LIST

Throughout the preceding text common names have been predominantly used. The following is an alphabetical cross reference list to latin names used in the scientific literature.

<table>
<thead>
<tr>
<th>COMMON NAME</th>
<th>LATIN NAME</th>
</tr>
</thead>
<tbody>
<tr>
<td>American oyster</td>
<td>Crassostrea virginica</td>
</tr>
<tr>
<td>anchovies</td>
<td>Anchoa spp.</td>
</tr>
<tr>
<td>annelid worms</td>
<td>Polydora spp.</td>
</tr>
<tr>
<td>ark clam</td>
<td>Anadara transversa</td>
</tr>
<tr>
<td>barnacles</td>
<td>Balanus spp.</td>
</tr>
<tr>
<td>comb jellies</td>
<td>Mnemiopsis leidyi</td>
</tr>
<tr>
<td>commensal nemertean</td>
<td>Ancistrocoma pelseneeri</td>
</tr>
<tr>
<td>ciliate protozoan</td>
<td>Odostomia spp.</td>
</tr>
<tr>
<td>ectoparasitic snail</td>
<td>Mercenaria mercenaria</td>
</tr>
<tr>
<td>hard clams</td>
<td>Ensis directus</td>
</tr>
<tr>
<td>jackknife or razor clam</td>
<td>Ectopleura dumortieri</td>
</tr>
<tr>
<td>jellyfish</td>
<td>Nemopsis bachei</td>
</tr>
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<td>jingle shell</td>
<td>Obelia spp.</td>
</tr>
<tr>
<td>menhaden</td>
<td>Aurelia aurita</td>
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<td>mud snails</td>
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<tr>
<td>muskrats</td>
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<td>Ondatra zibethica</td>
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<td>submerged aquatic vegetation</td>
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<td>toxic dinoflagellate</td>
<td>Diadumene laeacolena</td>
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<tr>
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<td>Edwardsia elegans</td>
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<td></td>
<td>Chrysaora quinquecirrha</td>
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<td>Zostera marina</td>
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<td>Ruppia maritima</td>
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<td>Protogonyaulax tamarensis</td>
</tr>
<tr>
<td></td>
<td>Paravortes gemellipara</td>
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ACKNOWLEDGMENTS

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