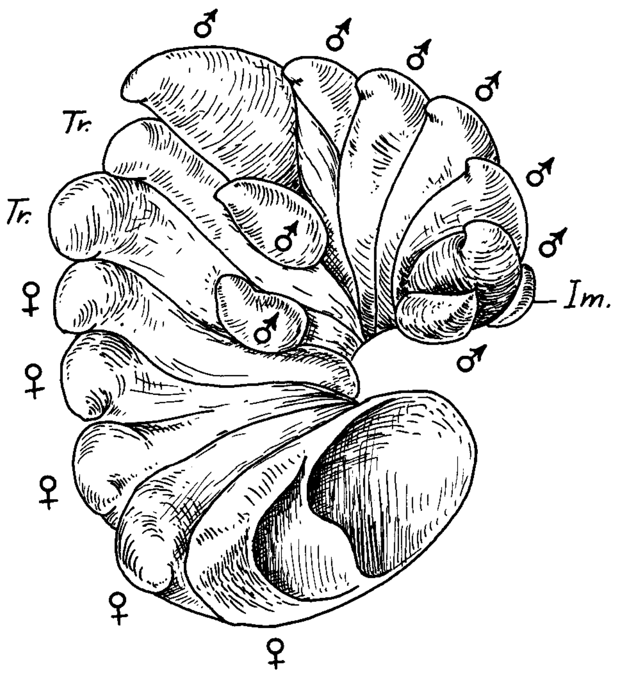

FIGURE 386.—Chain of *C. fornicata*. Female mollusks, the oldest of the group, are at the bottom; the males occupy the uppermost position with the hermaphrodites (tr.) between the two groups. From Coe, 1936.

Wadden Zee and the Limfjord in Denmark, where it successfully competed for space and settled on scattered shells, making it impossible for the larvae of *O. edulis* to set on them. Furthermore, a large amount of silt and soft mud was deposited by *Crepidula* and rendered the bottom unsuitable for oyster planting.

The story of *C. fornicata* is an excellent illustration of the possible danger of introducing a foreign species, which under new conditions, and in the absence of natural enemies and diseases, may reproduce and survive at a rate which upsets the natural balance of nature.

Other fouling organisms may be of a seasonal nature. Some of the oyster bottoms along the Atlantic coast of the United States are often covered with millions of tunicates of the species *Molgula manhattensis* (De Kay). This ascidian can be so abundant in a dredged sample that the oysters are hidden under the gray mass of tunicates. I observed this condition in the mouth of Chester River, Md.; undoubtedly it occurs in other places along the coast. The fouling by *Molgula* is seasonal; the organism dies and the remnants are sloughed off in the fall. Among the 29 species of invertebrates collected from oysters suspended from a raft in the water of Oyster River, Mass., four species constituted the largest portion of the biomass: *Molgula manhattensis*, *Botryllus schlosseri*, *Amphitrite ornata*, and *Balanus balanoides*. The worm *Amphitrite* was found in typical tubes of mud about one-quarter-inch or more in diameter.

At the height of the fouling season in August, the weight of the animals and plants and of sediment accumulated by them comprised 44 percent of the total weight of a string of oysters. The death of *Molgula* in October and the sloughing off of its cases reduced the weight to 11 percent. Later on in November the weight increased to about 17 percent because of the growth of the remaining organisms.

The shells of living oysters are frequently covered with encrusting Bryozoa. In New England waters and in Chesapeake Bay the appearance of Bryozoa usually precedes the time of setting of oyster larvae. When the oysters complete their development, the shell surfaces may be covered with Bryozoa colonies and unsuitable to receive the set of spat. There is a possibility, not fully substantiated, that a great many oyster larvae are eaten by Bryozoa, and Osburn (1932) thinks they are detrimental to the oyster beds in Chesapeake Bay. Marie Lambert made a faunistic study of the Bryozoa collected during the summer on live oysters in the Oyster River near Chatham, Mass. She recorded two species of Endoprocta and five species of Ectoprocta. The most common on oyster shells were *Bowerbankia imbricata* and *Schizoporella unicornis*. The latter is an encrusting bryozoan (fig. 387) commonly found on oyster grounds of Connecticut, part of Long Island Sound (Hutchins, 1945), and Chesapeake Bay.

Dense setting of barnacles on oyster shells is very common throughout the range of distribution of *C. virginica*. In many instances, the space that would have otherwise been available to oyster larvae is already occupied by barnacles, or the spat becomes covered with barnacles and fails to grow. Barnacles have no adverse effect on adult oysters.

The assemblage of invertebrate species found living in close association with the oyster reflects the fauna of the region and naturally differs from place to place. In some areas oysters may be almost entirely free of fouling organisms, while in others their shells are hidden under a heavy mass of siliceous sponges, hydroids, compound ascidians (*Botryllus*), and Bryozoa.

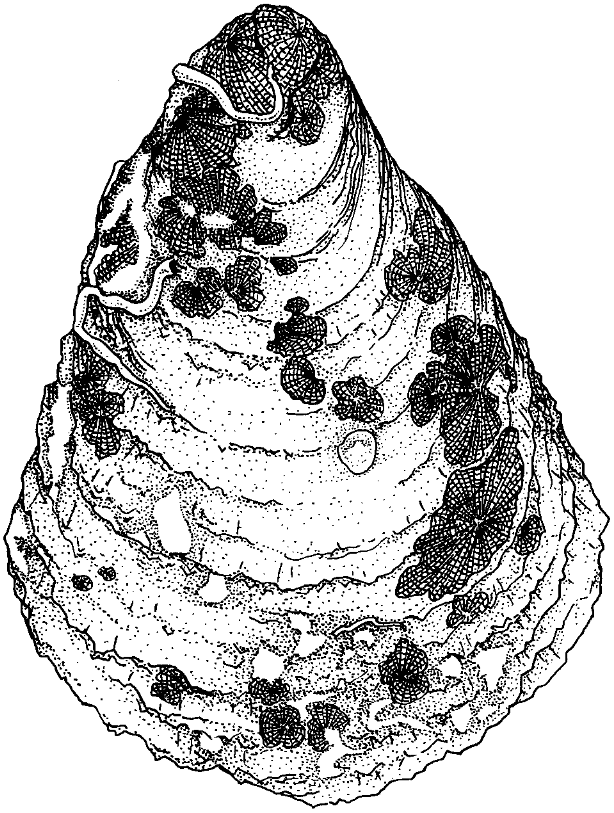

FIGURE 387.—Oyster from Oyster River, Chatham, Mass., covered in part by the colonies of the bryozoan *Schizoporella unicornis* and the compound ascidian (white spots) *Amaroucium constellatum.* Fouling is beginning; within a few days the surface of the shell may be completely covered with these two animals.

The fouling is always seasonal, and with the onset of cold weather many animals and plants die and slough off. Possibly because of the periodicity of fouling, the oysters survive and with few exceptions are not affected by the organisms growing on their shells. An exception is the invasion of oyster beds by mussels (*Mytilus edulis* L.), which in several situations may completely cover an oyster bed with a thick layer of mud mixed with excreta.

A number of annelids are commonly associated with oyster communities, living between clusters of oysters or in the shells. Sometimes a surprisingly large number of worms crawl out of the shell crevices when Epsom salt is added to the water in which oysters were kept. Hartman (1945) lists seven species of annelids inhabiting the spaces between clusters of living oysters. Korringa (1951b) describes more than 30 species of annelids which in Dutch waters live on or in the shell of *O. edulis.* Except for the boring Spionidae, the worms apparently cause no direct harm to oysters, but some of the mud-gathering species of Nereidae materially increase the deposition of sediment over an oyster bed. No evidence has been found of any other adverse effects of annelids on oyster communities.

Various siliceous sponges are very common members of the epifauna of oyster bottoms. With the exception of the boring sponges, they do not affect oyster populations. The red sponge, *Microciona prolifica,* is often found on highly productive oyster bottoms.

Of the protozoa that live on oyster shells, the stentorlike infusorian, *Folliculina* sp., commonly inhabits brackish water beds. This relatively large protozoan, measuring from 200 to 800 μ, lives in bottle-shaped cases attached to the leaves of *Elodea,* and *Potamogeton* found in the mouths of rivers and on shells of other mollusks. During the warm season it rapidly multiplies and appears swimming with other plankton. Mass occurrences of folliculinids in the Chesapeake Bay were recorded by Andrews (1915) and in Oosterschelde, Netherlands, by Korringa (1951a). Different species are widely distributed in the coastal waters of the United States (Andrews, 1944). The number of this infusoria found attached to a single oyster shell has varied from one to several hundred.

In many localities along the eastern shore of the United States, oyster beds are frequently overgrown by various algae. *Gracillaria confervoides* (Linnaeus) Greville is one of the species which sometimes completely covers an oyster bottom with its thick growth. Huge masses of the plant wash away from the home grounds and pile on beaches. Of the many other algae found growing on oyster shells, several are in some regions as abundant as *Gracillaria: Enteromorpha, Ulva, Griffitsia, Ceramium, Chondria, Champia,* and *Scytosiphon.* During experiments on raft culture in Oyster River near Chatham, Mass. in 1956 to 1959 (Shaw, 1962), the shells of young oysters suspended in water became covered with a very dense growth of *G. confervoides.* Since there was no noticeable ill effect on the oysters, an examination was made of the periphyton, the organisms living loosely attached to the plant's branches. The prevailing form was found to be a diatom *Lycosoma* sp., which was not present in the river plankton outside the immediate area occupied by *Gracillaria.* The stomach content of the oysters consisted of many *Lycosoma,* some half-digested, and of *Skeletonema,* which was also abundant among the branches. It is apparent that some constituents of the periphyton may be ingested and that the microscopic flora of the environment provides a substantial amount of food not available in true phytoplankton.

Some of the seaweeds cause unexpected damage to commercial oyster grounds. *Colpomenia sinuosa* (Toth) Derbes and Solier, a common seaweed in many parts of the word, is one of them. It grows along the Pacific Coast of North America from Alaska to southern California, along the eastern coast of Australia and in France. The thallus of *Colpomenia* is of a papery texture and hollow; it can grow attached to oyster shells to the size of a hen's egg or tennis ball. On sunny days at low tide in shallow water photosynthesis may be so intense that gas bubbles fill up the thallus, and on the return of the tide the inflated balloon floats out to sea carrying with it the young oysters. In 1906 *Colpomenia* became such a nuisance on the western coast of France at Vannes that the oystermen called it "oyster thief." The floating oysters carried out by the ebb current were not returned to shore with flood tide, and the losses were severe enough for local oystermen to organize the recapture of oysters with nets and to tear off the inflated algal ballons by dragging faggots over the bottom (Church, 1919).

In 1961 the seaweed, *Codium fragile* subsp. *tomentosoides* (Goor) Silva, was introduced to Cape Cod waters with oysters brought from Peconic Bay, Long Island, N.Y. This Pacific Ocean species, not indigenous to Massachusetts, occurs in abundance along the western coast of Europe. It is not known how the alga was introduced to Long Island where in January 1957 it was found at East Marion attached to dead *Crepidula* shells (Bouck and Morgan, 1957). In Oyster River, near Chatham, Mass., where the Long Island oysters were planted the shells were covered with a luxuriant growth and had to be thoroughly scrubbed before being shipped to market. The following year the plants were so large (fig. 388) that on sunny days they acted as "oyster thieves" by lifting the oysters from the bottom with gas-filled branches and floating them off with the tide.

Eel grass, *Zostera marina,* frequently covers the

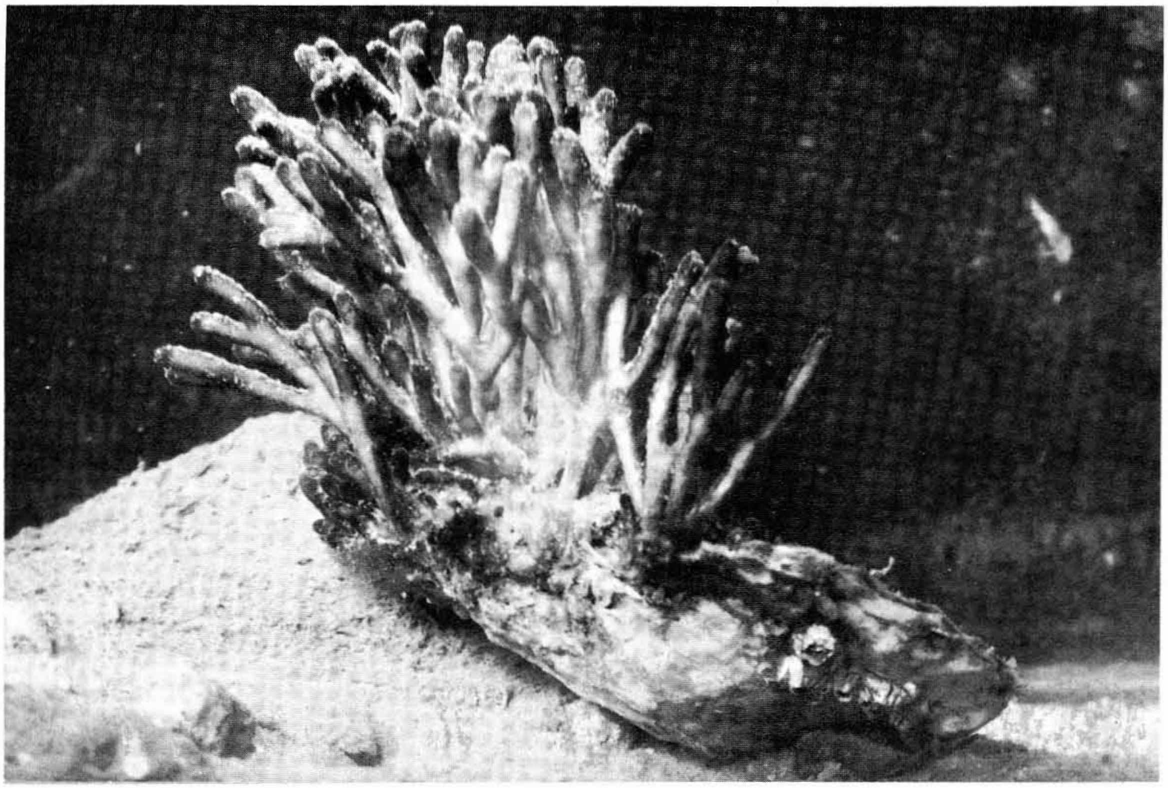

FIGURE 388.—*C. fragile* introduced into Oyster River, Chatham, Mass., with oysters from Long Island. Two-year-old plant.

entire oyster bottom but apparently exerts no ill effect on oyster populations. This is not the case, however, with another aquatic plant, the Eurasian watermilfoil, *Myriophyllum spicatum*, which by 1933 was established on the Virginia and Maryland sides of the Potomac River; since 1959 it has increased rapidly in the Chesapeake Bay area, including the Potomac River, and is found also in the fresh and nontidal waters above Washington D.C. In recent years the growth of the plant has become spectacular and is a threat to brackish water oyster grounds, which may become covered with a heavy layer of decomposing leaves and stems of the milfoil (Beaven, 1960; Springer, Beaven, and Stotts, 1961).

The effect of commensals and competitors on the productivity of an oyster bottom can be evaluated for each species if the intimate relationship to the host is clearly understood and the relative abundance of a species is determined. A single species which appears to be innocuous under normal conditions may become destructive and dangerous because of its mass development. All these conditions should be evaluated in order to express their effect in numerical terms. Commensals such as bryozoans, barnacles, and tunicates so completely cover the shell surface that the settlement of young oysters upon it is prevented. Thus the negative effect of fouling may be considered in relation to the productivity of setting grounds. On the other hand, in southern waters where setting continues for the greater part of the year and oysters become overcrowded with successive generations of young, the reduction and prevention of settlement of spat may be beneficial because it reduces overcrowding and permits better growth and fattening of oyster stock. The struggle for space is an essential factor in the life of an oyster community.

PREDATORS

The list of many enemies that prey on oysters includes flatworms, mollusks, echinoderms, crustaceans, fishes, birds, and mammals. Not all of them are equally destructive to oyster populations. The most dangerous are those which prefer oyster meat to other types of food, and in search of it invade the oyster grounds.

Carnivorous gastropods

The deadliest enemies of oysters are various gastropods inhabiting coastal waters. The most widely distributed species is the common oyster drill, *Urosalpinx cinerea* (Say), which is found along the entire Atlantic Coast from Canada to Florida. With a shipment of *C. virginica* the common oyster drill was introduced to the Pacific Coast of the United States (1870 and the following decades), and to Great Britain (1920 and probably earlier) where the American oysters were planted at Brightlingsea and West Mersea. In a short time the drill became very abundant along the coast of Essex and across the Thames estuary. At present *Urosalpinx* is the most dangerous and the most widely distributed of all the predators of oysters in Europe.

Oyster planting by shellfish growers is the major factor in the wide dispersal of *Urosalpinx* in this country and its introduction into areas which formerly were free of the pest. The migration of drills is rather limited. When hungry, they may move at an average rate of 15 to 24 feet per day in the direction of food. To a certain extent the drills are dispersed by floating objects to which they may cling and by hermit and horseshoe crabs which have been seen bearing as many as 140 drills per animal (Carriker, 1955).

The drill is particularly destructive to young oysters. In Cape Cod coastal waters, which are infested by these snails, the oyster spat has very little chance of surviving the first year; often small seed oysters are wiped out before the end of the second year. Adult oysters with thick shells suffer less, and the losses sustained during 1 year by the 4 and 5 year classes are insignificant. There are many localities in Long Island Sound, on the eastern shore of Virginia between Chincoteague and Cape Charles, and in other regions where drills commonly kill 60 to 70 percent of the seed oysters and sometimes annihilate the entire crop.

Fortunately, brackish water effectively bars the drills from the upper parts of estuaries and tidal rivers. Survival of drills in water of low salinity depends on temperature and on the concentration of salts to which they were adjusted. It may be accepted as a general approximation that minimum survival salinities at summer temperatures vary from 12°/₀₀ to 17°/₀₀ in different regions.

Extensive literature on the biology and control of oyster drills has been critically reviewed by Carriker (1955), who has also made a detailed study of the structure and function of the proboscis and drilling apparatus of the drills (Carriker, 1943).

The maximum height of adult drills varies in different localities between 25 and 29 mm.; a giant form reaching 51.5 mm. in height is found in the area of Chincoteague Island, Va., and is considered a subspecies *U. cinerea follyensis* (fig. 389). As the common name indicates, the *Urosalpinx* attacks oysters and other mollusks by drilling a round hole in the shell. The hole, usually made in the upper (right) valve of the oyster, tapers toward the inner surface; the shape of the hole identifies the attacker, and the presence of drilled empty shells on oyster grounds is reliable evidence of the inroads made by the snail on an oyster population.

For a long time boring was considered an entirely mechanical process. Observations made by Carriker (1961a) showed that both chemical and mechanical actions are involved. Secretion from the accessory boring organ, called ABO for short, softens the shell, probably by an enzyme acting on the conchiolin, and the softened material of the shell is removed by abrasive action of the radula. Active drilling continues for a few minutes and is followed by a long period lasting up to an hour of chemical action during which the ABO gland remains in contact with the shell.

The oyster is not the only victim of drills. They show preference, in fact, to barnacles, and usually stop drilling oysters if a rock covered with live barnacles is placed near by. A well-developed chemical sense permits the drills to distinguish between young and adult oysters. If both kinds are offered to hungry snails kept in a large tank with running sea water, the majority of active drills will choose the young oysters. The drills are positively rheotactic and in running water orient themselves against the current. The orientation is not, however, precise and the path of a moving drill is a meandering line only generally directed against the current.

Light has an effect on the orientation of drills. They move away from a strong source of light, but move toward it at lower intensities (Carriker, 1955). In dim light, the phototactic response is lost. In laboratory tests at Woods Hole, I noticed no orientation of drills toward the window side of the tank; the drills distributed themselves at random. They have a tendency to climb away from the bottom (negative geotaxis) and congregate on rocks, pilings, and on the wall

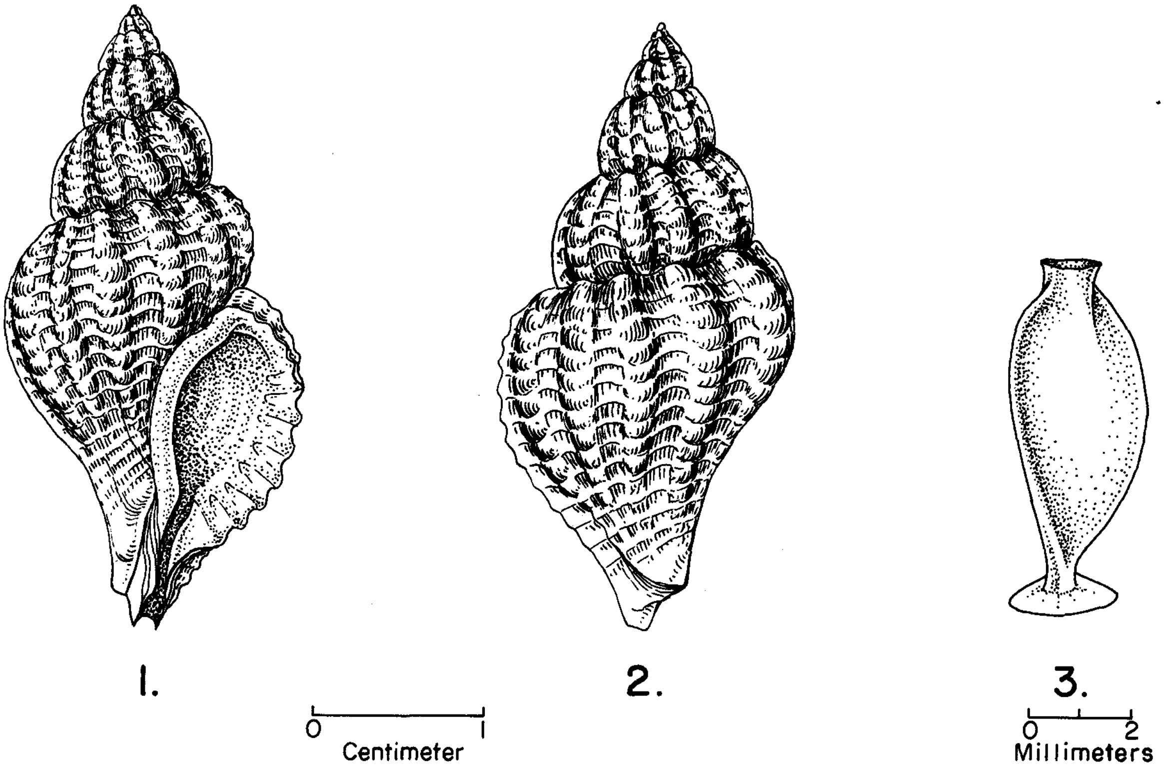

FIGURE 389.—*U. cinerea follyensis* from Chincoteague Island region, Va. 1—apertural view; 2—abapertural view; 3—egg cases.

of tanks. Drills put in the bottom of a vertical glass tube about 1 inch in diameter and 6 to 8 feet tall, filled with sea water, will climb to the top of the tube and remain there. Negative geotaxis is pronounced, particularly during the reproductive period. At this time drills climb on any objects above the bottom level and ascend rocks and various underwater structures to lay their eggs, which are deposited in tough, leathery capsules (fig. 389, 3). The egg-laying period depends on geographical location and local conditions. Summarizing the data from various sources, Carriker (1955) estimates that the number of egg cases deposited by one drill per season ranges from 0 (in an immature female) to 96 for older females. In Woods Hole harbor, the breeding season lasts from the end of June to the middle of August. The number of egg cases deposited by a single female kept in laboratory tanks varied from five to nine; the average number of eggs in each case was nine. The number of eggs per egg case varied in different localities from eastern Canada to Chesapeake Bay from 0 to 22 and from 1 to 29 in British oyster beds. (Cole, 1942).

A second species of drill, *Eupleura caudata* (Say), (fig. 390), is found in the same waters as *Urosalpinx* but is usually less abundant. Various observers estimate that in different locations it comprises from 2 to 29 percent of the total drill population (Carriker, 1955). The behavior of *Eupleura* is similar to that of *Urosalpinx*. Its food habits have not been studied, but occasional observations in the laboratory indicate they are probably not different from those of *Urosalpinx*.

In the York River, Va., where the growth and reproduction of *Eupleura* were studied by MacKenzie (1961), the snail becomes active as the temperature rises over 10° C. Spawning begins late in May at 18° to 20° C., reaches a peak in June and early July at 21° to 26° C., and ends in early August. Mature females (kept in cages) deposit an average of 55 cases, each containing an average of 14 eggs. In the absence of mortality, each female *Eupleura* may produce over 700 young drills each season. The leathery egg capsules are vase-shaped with two distal projections (fig. 390, 3) and are easy to distinguish from the egg cases of *Urosalpinx* (fig. 389, 3).

Conchs of the genus *Thais* occur on both the Atlantic and the Pacific coasts. The snails have strong polymorphic tendencies and form local races which greatly complicate the taxonomy of the species. A review of the speciation problem of *T. lamellosa* Gmelin made by Kincaid (1957)

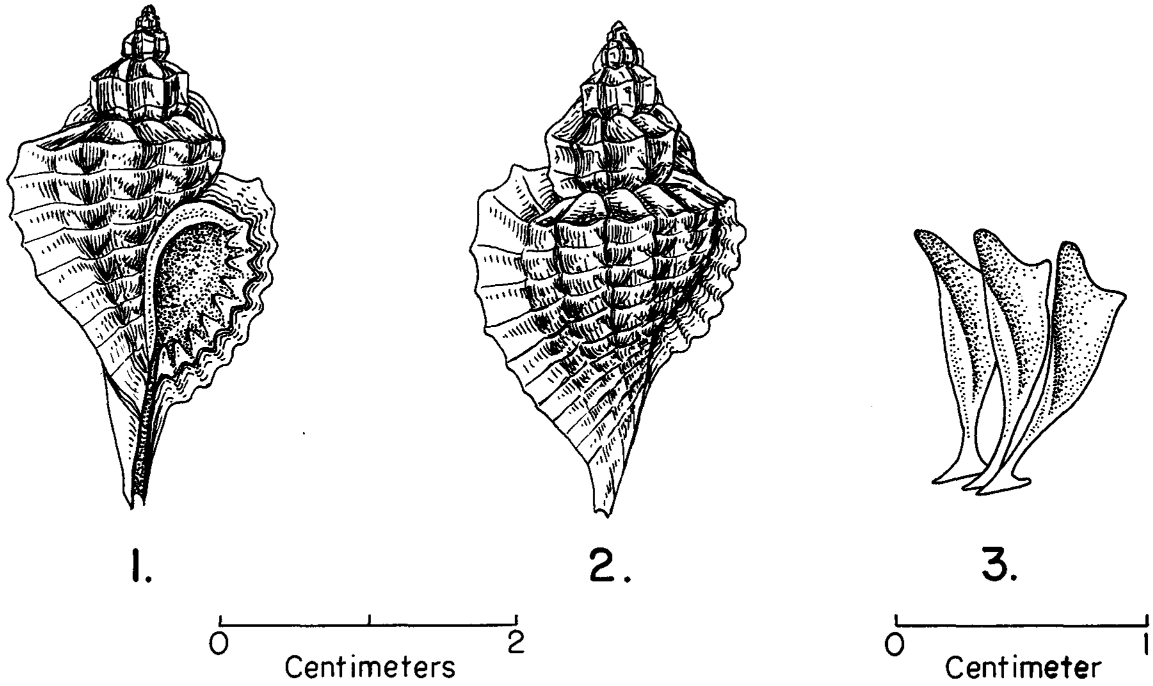

FIGURE 390.—*Eupleura caudata* (Say) from 1—apertural side; 2—from abapertural side, 3—egg cases.

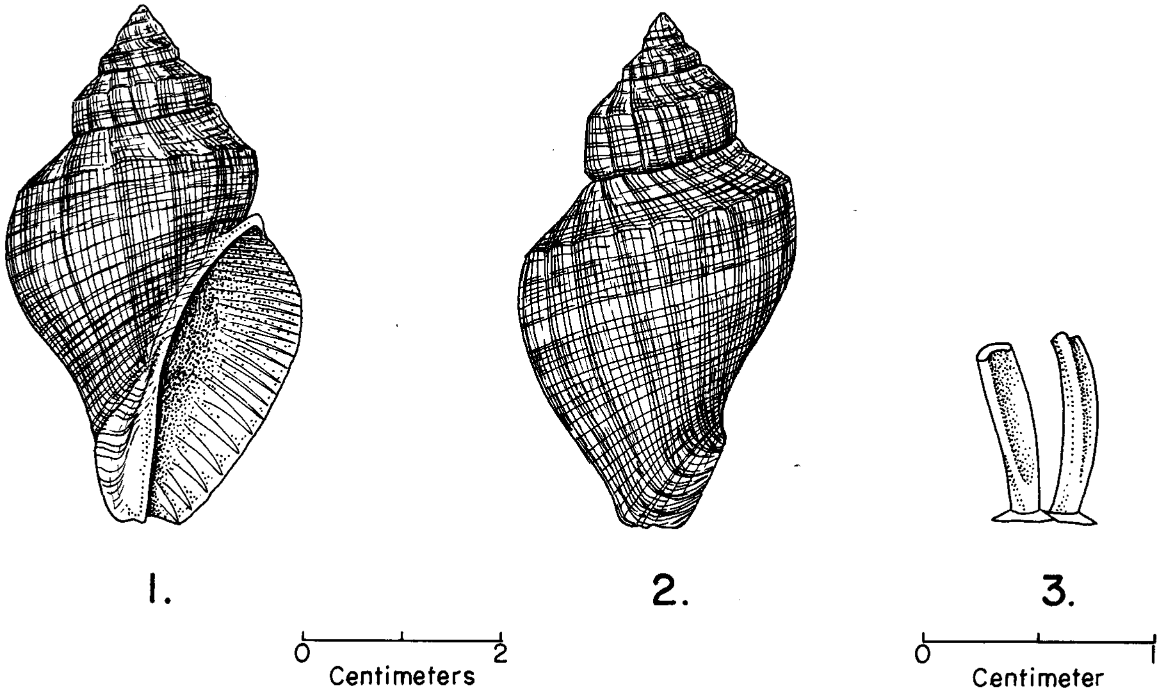

FIGURE 391.—*T. haemastoma floridana* Conrad from the shores of Pensacola Bay, Fla. 1—apertural view; 2—abapertural view; 3—egg cases.

contains interesting material regarding this and other species of the genus.

T. haemastoma is a common oyster predator in the waters of the South Atlantic and Gulf states. There are two subspecies, *T. haemastoma floridana* Conrad, which occurs from North Carolina to Florida and the Caribbean (fig. 391), and *T. haemastoma haysae* Clench (fig. 392), common on oyster grounds of northwest Florida, Louisiana, and Texas (Clench, 1947). *T. haemastoma floridana* is a medium-size gastropod with a relatively smooth shell and a single row of low spines. *T. haemastoma haysae* is a large, rugged snail, sometimes measuring 4½ inches in height. It can be distinguished from the other subspecies by double rows of prominent spines around the whorls and spire.

The behavior of the two varieties apparently is similar. The conchs feed on oysters and other mollusks, penetrating their shells from the edge by using the ABO gland or by drilling holes in the shell (Burkenroad, 1931; Carriker, 1961a). The entrance at the edge of the valves is often inconspicuous and may be easily overlooked.

Conchs multiply very rapidly because of their great fecundity and high survival rate of larvae. *Thais haemastoma* lays eggs in groups of about 800 to 975 enclosed in each egg case, with each female depositing more than 100 cases. These figures refer to my laboratory observations on conchs kept in captivity. The eggs are deposited in horny and transparent egg cases of a creamy color, which becomes brownish and finally turns reddish-purple. The breeding season in Louisiana waters begins by the end of March and reaches its peak in April and May. There is usually a rapid decline of egg laying in June and a complete cessation of reproduction in July. At the beginning of the breeding period the conchs become very active and develop a strong tendency to climb on structures and rocks to attach their egg cases above the bottom. Because of this behavior they can be trapped during the breeding season on stakes which the oyster growers erect on the grounds. Gregariousness is very pronounced, and many conchs can be trapped in this way in a relatively short time. The number of egg cases attached to a single stake may be enormous. One stake which I obtained as a sample was covered with a solid mass of egg capsules over a 5-foot length; the estimated number of cases was about 8,000. The incubation period is not known definitely, but judging from the growth of hydroids and other fouling animals on the conch cases, I believe it is not less than 2 weeks.

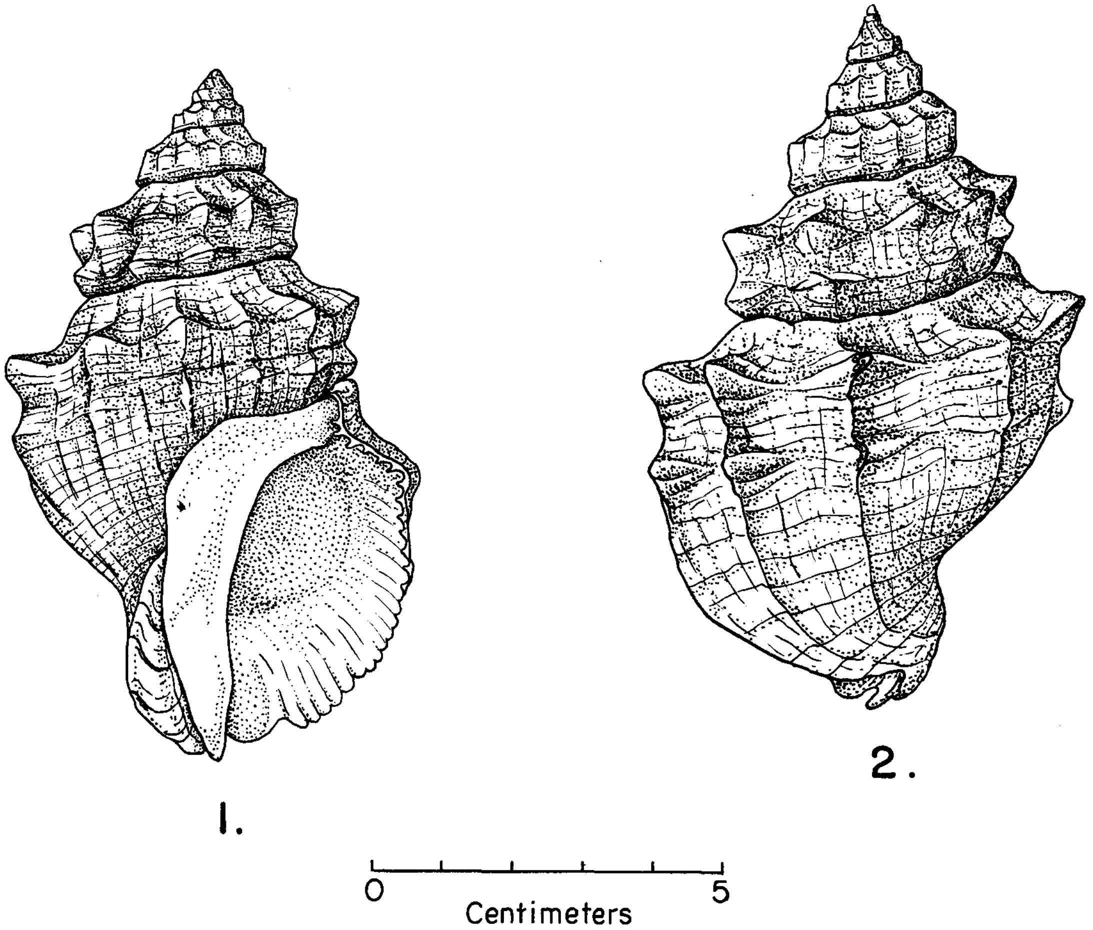

FIGURE 392.—*T. haemastoma haysae* Clench from Bastian Bay in the lower part of the Mississippi River delta. 1—apertural view; 2—abapertural view. Natural size.

The larvae that escape from the egg capsules are veligers, which pass through a free-swimming period of unknown duration, and are widely dispersed by tidal currents before they settle on the bottom and begin attacking small oysters and other bivalves.

The distribution of *Thais* is checked by fresh water. The conch is immobilized by a salinity of 10°/oo, and a 1- or 2-week exposure to a salinity of 7°/oo kills them (Schechter, 1943).

The effect of sudden changes in water salinity on the rate of crawling of *Thais* was corroborated by my observations at the Bureau of Commercial Fisheries Biological Laboratory at Gulf Breeze in northwestern Florida. The crawling of these snails in the tanks was automatically recorded on a kymograph. The movements stopped immediately when the salinity of the water was artificially reduced from 15°/oo or 17°/oo to 8°/oo or 9°/oo. The snails became active again when the salinity returned to the former level.

Two species of conchs found on oyster grounds of the Pacific coast are *Thais lamellosa* Gmelin (fig. 393), a native snail, and *Ocenebra* (*Tritonalia*) *Japonica* Dunker (fig. 394), introduced from Japan. *T. lamellosa* has been considered by some fishery biologists as a predator on *O. lurida*, but Kincaid (1957) discards this view as not substantiated by his 50 years of familiarity with the marine fauna of the region. He states that since *T. lamellosa* feeds mainly upon barnacles and mussels, the snail should be classified as "the only invertebrate friend" of the oyster, presumably because it destroys its competitors. Chapman and Banner (1949) found that under experimental conditions *T. lamellosa* drilled some *O. lurida*, but that in a natural environment it showed a preference for mussels (*Mytilus edulis*).

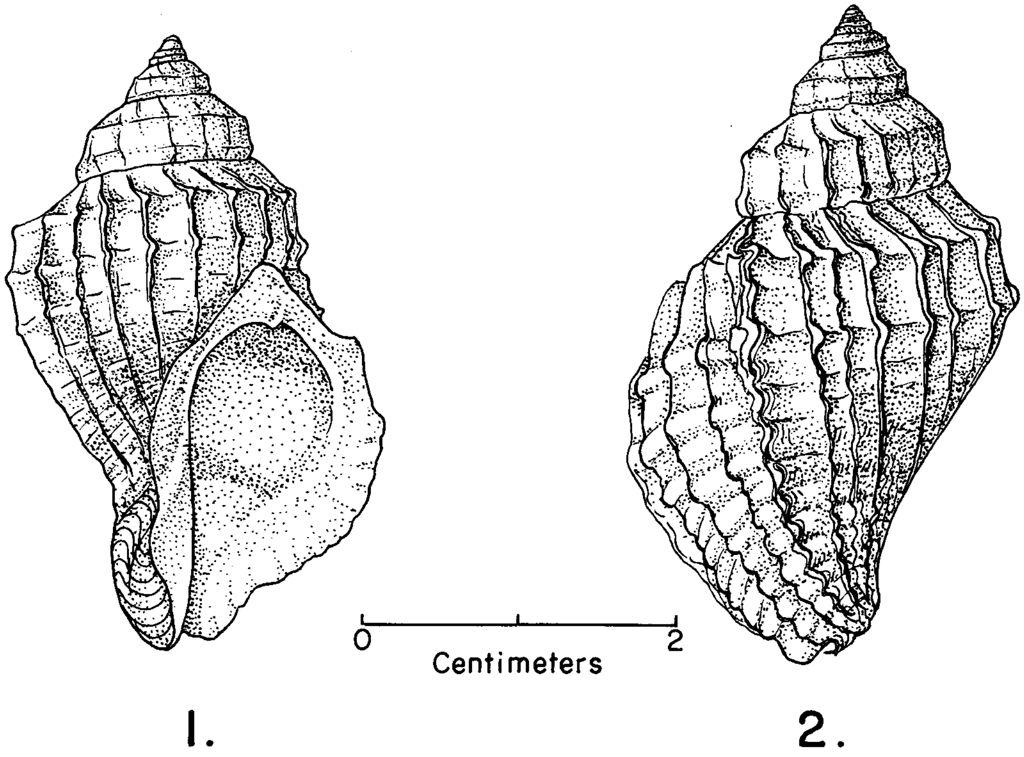

FIGURE 393.—*T. lamellosa* Gmelin, a native species of the Pacific coast of the United States. 1—apertural view; 2—abapertural view.

The Japanese species, *Ocenebra japonica*, is far more dangerous than the native snail. Mortalities due to devastation by this snail are estimated at 15.4 to 22.6 percent. The first specimens of *O. japonica* were introduced into the waters of Puget Sound with the planting of Japanese seed oysters, a practice which began in 1902 and 1903 and which reached considerable proportions by 1922 when from 1,500 to 4,000 boxes, each containing about 5,000 seed, were planted annually. In October 1928 while examining the oyster beds in Samish Bay, Wash., I found a number of *O. japonica* Dunker (Galtsoff, 1929, 1932), and warned oystermen and state officials of the possible damages that could result if the practice of bringing infested seed oysters from Japan was continued. The warning received no attention. In the late 1940's *Ocenebra* was well established in the waters of Puget Sound and became a serious menace to the native oysters. When given a choice of food, *Ocenebra* prefers *O. lurida* and Manila clams, *Venerupis japonica*, to *C. gigas* (Chew, 1960). It drills holes in the shell by combined chemical and mechanical action (Carriker, 1961a). The fertility of the species is high, the female laying an average of 25 egg cases, each containing about 1,500 eggs. The egg cases are often found in the inaccessible crevices of the concrete walls of dikes surrounding the Olympia oyster beds. Salinity of 18‰ adversely affects *Ocenebra*, and brackish water of less than 12‰ salinity is lethal.

Large conchs or whelks, *Busycon carica* Gmelin and *B. canaliculatum* Linné, are common in the shallow water of the Atlantic coast and occasionally attack oysters and open them by inserting the edge of the shell between the valves and forcing them apart (Colton, 1908). Carriker (1951) reinvestigated the problem and found that penetration of shells of oysters and clams is a purely mechanical process which consists of chipping by the edge of the conch's shell combined with rasping of the radula. The shell edge of an oyster destroyed by these conchs bears the marks of the attack (fig. 395). In the northern part of Cape Cod, *Busycon* seems to attack the oyster in preference to other mollusks, annelids, or dead fish, which they are known to consume. Local depredations on oysters observed in the Cape Cod area (Shaw, 1960, 1962) may be severe enough to warrant trapping of conchs during their reproductive

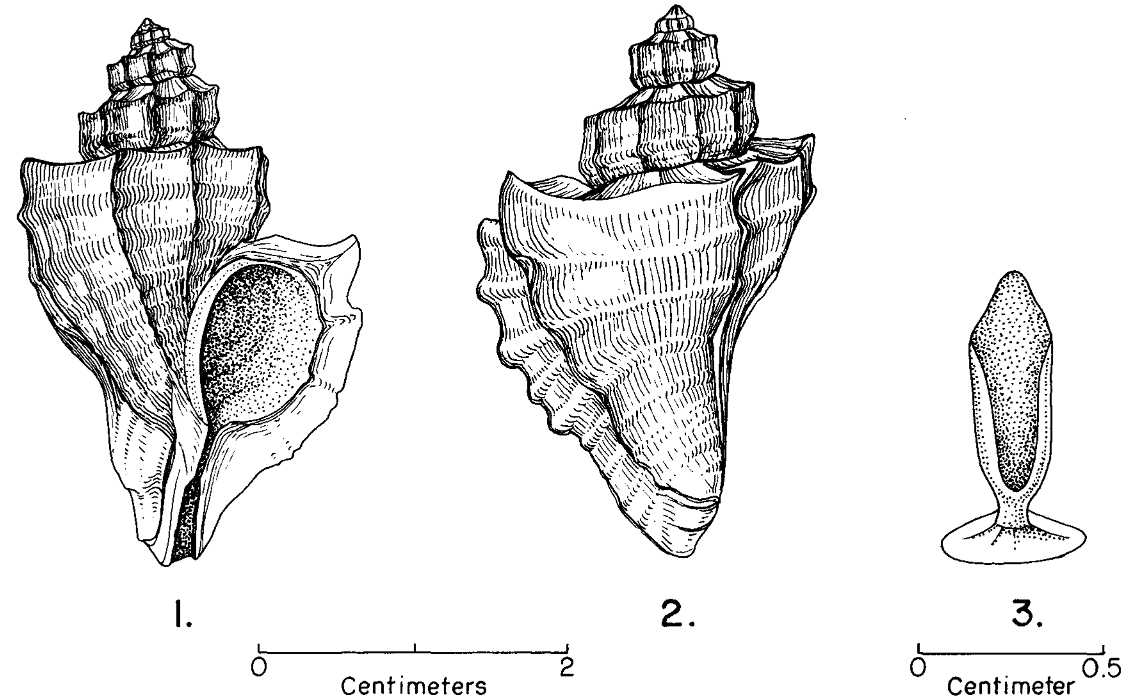

FIGURE 394.—*O.* (*Tritonalia*) *japonica* Dunker, Japanese species from oyster bottom of Puget Sound, Wash. 1—apertural view; 2—abapertural view; 3—egg case.

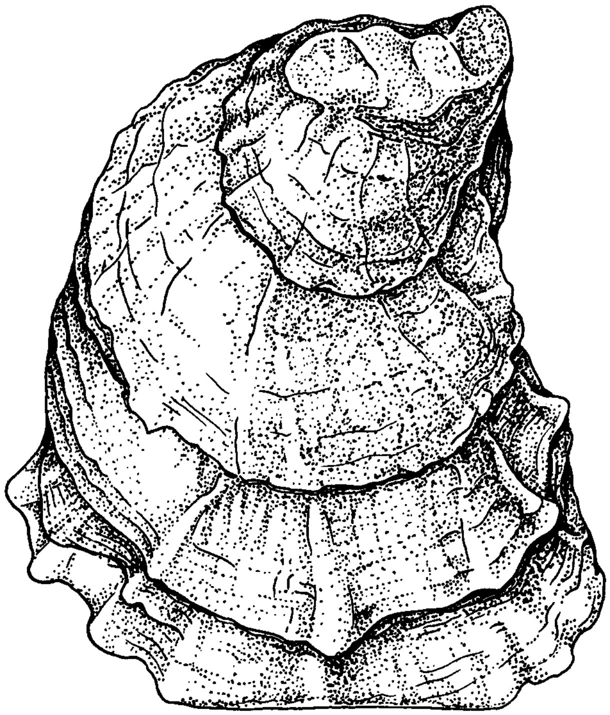

FIGURE 395.—Edge of the shell of an oyster killed by *Busycon* in Oyster River, Chatham, Mass. Straight line at the lower edge of the shell indicates the place of rasping by the conch's radula after the valves were chipped.

cycles. In Cape Cod estuaries, egg cases of conchs are a familiar sight on tidal flats at low water (fig. 396). Under experimental conditions the conchs were found to consume in summer about three adult oysters per week (Carriker, 1951).

Small parasitizing pyramilid snails of the genus *Odostomia* (*Menestho*) congregate in large numbers at the very edge of oyster shells. When the valves are open, the snails extend their pro-

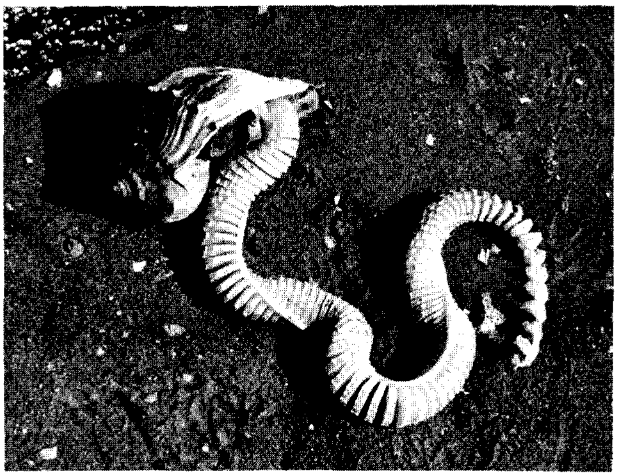

FIGURE 396.—*B. carica* depositing egg capsules at low Tide. Woods Hole.