CHAPTER XVIII

ENVIRONMENTAL FACTORS AFFECTING OYSTER POPULATIONS

	Page
Positive factors of environment	399
Character of bottom	399
Water movements	400
Salinity	404
Temperature	407
Food	408
Negative factors of environment	409
Sedimentation	410
Disease	415
Malpeque Bay disease	415
Dermocystidium marinum	415
Disease associated with *Haplosporidium*	417
Shell disease	417
Foot disease	418
Hexamita	419
Nematopsis	419
Trematodes and parasitic copepods	419
Commensals and competitors	420
Boring sponges	420
Boring clam	421
Mud worms	421
Oyster crab	425
Spirochaetes	426
Perforating algae	426
Fouling organisms	426
Predators	430
Carnivorous gastropods	430
Starfish	437
Flatworms	438
Crabs	439
Mud prawns and fish	439
Birds	439
Man	440
Pollution	441
Domestic sewage	442
Industrial waste	443
Radioactive waste	445
Combined effect of environmental factors	445
Bibliography	446

The various species of the family Ostreidae inhabit the coastal waters within the broad belt of the sea, limited by the latitudes 64° N. and 44° S. Some large aggregations cover many square miles of bottom of littoral and intertidal zones; they also thrive above the bottom attached to rocks and underwater structures, branches and trunks of fallen trees, and miscellaneous objects. These aggregations of live oysters and empty shells are called oyster bottoms, oyster beds, oyster banks, or oyster reefs. The expressions are not well defined either biologically or in the legal sense and are used interchangeably. Only those species of oysters which form large and dense populations are important to man as a source of food. Those living singly and widely dispersed are of no commercial value.

Descriptions of oyster bottoms found in the world literature combined with personal observations over the course of years in the United States, France, Italy, the West Indies, Cuba, Venezuela, Panama, Hawaii, and some of the South Pacific islands have convinced me that, regardless of the species of oysters present, certain major factors are common to all oyster bottoms.

It is a matter of historical interest that more than 80 years ago Möbius (1883) established the concept of a biocenosis or a social community using an oyster bank as an example. According to his definition every oyster bed is to a certain degree—

> . . . a community of living beings, a collection of species, and a massing of individuals, which find here everything necessary for their growth and continuance, such as suitable soil, sufficient food, the requisite percentage of salt, and a temperature favorable to their development. Each species which lives here is represented by the greatest number of individuals which can grow to maturity subject to the conditions which surround them, for among all species the number of individuals which arrive at maturity at each breeding period is much smaller than the number of germs produced at that time. The total number of mature individuals of all the species living together in any region is the sum of the survivors of all the germs which have been produced at all past breeding or brood periods; and this sum of matured germs represents a certain quantum of life which enters into a certain number of individuals, and which, as does all life, gains permanence by means of transmission.

Möbius further commented that a change in one factor of a biocenosis affects other factors of the environment and eventually changes the community character. Relative abundance of various species constituting a bottom community is affected by changes in estuarine environment and by man's activities which alter the environment. Patterns of currents, salinity gradients, and turbidity of water may be changed by dredging operations, construction of inshore installations, and other harbor and waterway improve-

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ments. Commercial dredging removes substantial portions of natural oyster grounds; planting of seed oysters for growing increases artificially the population densities. Inadvertent introduction of foreign species, competitors, and predators disturbs the established biological balance. Finally, excessive discharge of domestic sewage and trade wastes causes irreparable damage to productive oyster bottoms.

The productivity of a sea bottom may be measured by determining the sum of weights of all animals and plants in a unit of area. The value, called community biomass, is of considerable theoretical interest to the marine ecologist engaged in the study of oceanic productivity. It has, however, no practical application in determinations of the productive capabilities of a community dominated by a single species such as oyster, clam, or scallop. The species productivity of any bottom may be materially reduced by competitors, predators, and other conditions that may suppress the reproduction and growth of commercially utilizable organisms while not affecting or even sometimes encouraging the growth of noncommercial forms.

Descriptions of oyster bottoms usually provide information regarding their location, type of bottom, depth and salinity of water, the principal species associated with oysters, and the abundance or absence of predators. This type of description is found in the papers of Dean (1892) on South Carolina grounds; Moore on the condition and extent of oyster grounds in Texas (1907), Louisiana (1899), Mississippi Sound (1913), James River, Virginia (1910), Delaware Bay (1911); Pearse and Wharton (1938) on oysters of Apalachicola Bay; Frey (1946) on oyster bars in the Potomac River; Hagmeier and Kändler (1927) on oyster banks in North Freisland shoals, Germany; Joubin on the coast of France (1906, 1908), and many others.

Because of the great diversity in the kind and number of species forming an oyster community only a few generalizations can be drawn from descriptive data: 1) in common with other bottom communities, oyster grounds of the warm southern waters support a greater variety of species than do the colder waters of the northern latitudes, and 2) the variety of plant and animal species is less in waters of low salinity than in adjacent areas of higher salt concentrations.

The inferences are in accord with observations made by European ecologists and summarized by Hedgpeth (1953). In the Elbe estuary the weight of all invertebrates per square meter of bottom decreases from 6,068 g. in the area of full oceanic salinity to only 37 g. in brackish water. A similar decrease in the weight of community biomass is found along the northern coast of Germany, although the difference is much smaller ranging from 304 g. per square meter of sea bottom to 16 g. in the inshore areas. The decrease in the biomass cannot be attributed to a single factor of the environment since other conditions such as rate of water movements, sedimentation, and food content are associated with the salinity changes.

There are many well-documented cases of destruction of productive oyster bottoms by human activities. Möbius (1883) cites formerly rich oyster beds of Cancale, Rochefort, Marennes, and Oléron on the West Coast of Europe in which the oyster populations were replaced by cockles and mussels. The newcomers were present in small numbers while the oysters flourished but greatly increased in abundance when the removal of oysters left more space for them to settle.

Many well-documented examples may be cited of the destruction of oyster bottoms by sand and mud stirred up by dredging operations in nearby areas. One incidence of this nature occurred in 1935 to 1938 near the Buzzards Bay entrance to the Cape Cod canal, Mass., where valuable oyster grounds were buried under 8 to 12 inches of material that was disturbed by dredging and then settled on the oyster grounds. Three to four years later the area was repopulated by quahogs and continues to remain highly productive, although the species composition has been completely changed.

Discounting minor local variations, the basic requirements of the oyster are identical regardless of the location of the oyster bottoms. The suitability of a bottom area for the development of a productive oyster community can, therefore, be evaluated if the effects of different environmental factors are estimated.

Principal factors favorable for the propagation, growth, and general welfare of an oyster community are character of bottom, water movements, salinity of water, temperature, and food. The unfavorable or destructive factors that tend to inhibit the growth and productivity of a com-

munity are sedimentation, pollution, competition, disease, and predation. The interaction of these five positive and five negative factors acting simultaneously on a community determines its utilizable productivity.

POSITIVE FACTORS OF ENVIRONMENT

CHARACTER OF BOTTOM

Oysters may grow equally well on a hard, rocky bottom or on semihard mud firm enough to support their weight. Shifting sand and soft mud are the only types of bottoms which are totally unsuitable for oyster communities. With the exception of these extreme conditions oysters adapt themselves to a great variety of bottoms. They thrive well on shore rocks and underwater structures which are left exposed at low tide. The controlling factor in this situation is the climate, since no oyster can survive several hours exposure to below freezing temperature, and, therefore, none are found growing near the surface in the latitudes where in winter they may be killed at low tide, or frozen in the ice and carried away by tidal currents. The degree of softness and instability of the bottom can be quantitatively measured by penetrometers, and by determining the amount of bottom material transported by currents of different velocities. The depth of sinking into a mud layer of a probe of known dimensions under constant weight can be used as a measure of the relative softness of sediment. The determination must be made in situ because the removal of a sample and handling in the laboratory changes the consistency of mud. A penetrometer to evaluate certain physical properties of marine sediments in situ has been designed by Miller (1961). The instrument is a conical probe which is driven at low, constant speed into the bottom; resistance to penetration as the probe sinks into the bottom is recorded graphically. An instrument answering these specifications and constructed at the University of Rhode Island has been used in research at the Narragansett Marine Laboratory at Kingston, R.I., and has proved reliable in providing information about compactness, degree of plasticity, allowable bearing loads, and other properties of sediments. No reliable method has yet been developed for measuring the resistance of sediment to water current in the sea.

A soft muddy bottom may be artificially improved by planting oyster or clam shells to attain the desired firmness. Other materials, such as gravel and slag from blast iron furnaces, have been tried experimentally but are less satisfactory, primarily because of the greater weight and higher cost. At present the reinforcement of oyster bottoms by shells remains the principal practical method used on a large scale for the improvement of oyster bottoms or for the establishment of new ones.

Soft muddy bottoms may be gradually converted by the oysters themselves into oyster banks or reefs because of an innate ability of larvae to choose a substratum upon which to settle. This ability is probably common to most species of bottom invertebrates having free-swimming larvae (Verwey, 1949). The process begins with the attachment of several larvae to a single shell or other hard object lying on the surface of the mud. Other larvae attach to those that have already settled, and soon a cluster of oysters is formed on the surface of the mud (fig. 365).

Dead oyster shells dropping from clusters provide additional surfaces, and the reef begins to grow horizontally and vertically. The process is typical for the tidal flats of South Carolina and Georgia where successive phases can be easily observed. Oysters grown on mud have long, slender shells.

The suitability of bottom to an oyster community may be expressed by an arbitrary scale from 0 to 10, according to the relative softness and stability. Bottom conditions fully unsuitable for the formation of any oyster community may be designated as zero. The zero value of any positive factor denotes conditions under which the community cannot exist, regardless of the values of all other factors of the environment. The zero value of bottom factor refers either to extremely soft mud not capable of supporting the weight of an empty shell or to shifting sand; both conditions are unsuitable for oysters. Marginal conditions are indicated by 1, and optimum conditions by 10. The highest value of bottom factor may be assigned to firm and stable bottoms such as rocks and hard or sticky mud. The value of 1 is assigned to the soft muddy bottoms of the South Atlantic States and Texas.

FIGURE 365.—Initial stage in the formation of an oyster bank on very soft mud of a tidal flat. Photographed at low tide near Brunswick, Ga.

WATER MOVEMENTS

Free exchange of water is essential for the growth, fattening, and reproduction of oysters. An ideal condition is represented by a steady, nonturbulent flow of water over an oyster bed, strong enough to carry away the liquid and gaseous metabolites and feces and to provide oxygen and food. Furthermore, an oyster bed can expand only if the larvae are carried by the currents and at the time of setting are brought in contact with clean, hard surfaces. Estuaries seem particularly suitable for the expansion of oyster communities and for the annual rehabilitation of oyster populations reduced by harvesting because some larvae, carried back and forth by the oscillating movements of tidal waters, eventually settle beyond the place of their origin.

In large embayments, such as Long Island Sound, the difference between the surface and bottom salinities is small, about 1‰ or 2‰. In tidal rivers and true estuaries the differences between the salinities of the lower strata and those at the surface are considerable. Salinity stratification, as will be shown later, complicates the pattern of circulation.

The great variety of conditions found in the bodies of water within the tidal zone makes it difficult to define the term "estuary" in a few precise words. A Latin dictionary (Andrews, 1907) defines the word "Aestuarium" or "Aestus" as a part of the seacoast overflowed at flood tide but at ebb tide left covered with mud and slime. Some authors extend the concept of an estuary to include such large bodies of water as the Mediterranean Sea and the Gulf of Mexico, while others restrict the use of the term to relatively small coastal indentures in which the hydrographic regime is influenced by the river discharge at the head and the intrusion of sea water at the mouth. Cameron and Pritchard (1963) define an estuary as "a semienclosed coastal body of water having free connection with the open sea and within which the sea water is measurably diluted with fresh water deriving from land drainage." The essential features of a true estuary are the inflow of river water at the head and the periodical intrusion of sea water at its mouth. Stommel (1951) classifies estuaries by the predominant

causes of movement and mixing of water, which may be due either to tide, wind, or river flow. Rochford (1951) points out the significant differences between brackish water and estuarine environment. According to his ideas, brackish water refers to a dynamically stable environment of lakes, lagoons, etc., in which sea water, diluted by fresh water, is not necessarily influenced by tidal movements. On the other hand, the estuarine environment, influenced by tidal rise and fall, is dynamically unstable.

The persisting factors of a typical estuarine environment are seasonal salinity variations and circulation exchange between the river and sea water. The intruding salt water forms a wedge or prism with its base at the mouth and the tip at the upper part of the estuary. The position of the wedge along the bottom and its dimensions depend to a great extent on the flow of the river water.

Circulation and mixing of water is a highly complex problem adequately discussed in the papers of Rochford (1951), Ketchum (1951a, 1951b), Pritchard (1951, 1952a, 1952b), and in the textbook, The Sea, vol. II, edited by Hill (1963).

It is important for a biologist to understand that the type of circulation that prevails in a specific estuary depends on physical structure, i.e., size, depth, bottom configuration, etc., river flow, and vertical salinity gradients along the entire length from head to mouth. Circulation pattern and mixing have important biological implications in the study of the distribution and transport of sediments, pollutants, and plankton, including free-swimming larvae of sedentary invertebrates.

The volume of fresh water entering at the head of an estuary occupies the upper layer and exceeds the volume of the up-estuary flow in the lower and more saline layer by an amount sufficient to move the fresh water toward the sea (Pritchard, 1951). As one moves seaward, the volume of saline water contributed by the ocean increases while the river water, entered at the head of the estuary is being removed. The process of removal of river water, called flushing, continues throughout the estuary from its mouth to the so-called "inner end" which is defined by Ketchum (1951b) as "the section (of an estuary) above which the volume required to raise the level of the water from low to high water mark is equal to the volume contributed by the river during a tidal cycle." Consequently, there will be no net exchange of water through this section during a flood tide and the water above the section should be completely fresh.

The salinity at any location below the inner end varies with tide but returns to substantially the same level on successive tidal stages. Assuming that a net seaward transport of fresh water during any tidal cycle is equal to the volume introduced by the river in the same period of time, and that there is no net exchange of salt water through the cross section during the same tidal cycle, Ketchum (1951b, 1954) advanced a simplified theory which permits an easy calculation of the proportion of water removed by the ebb tide. This theory is based on the assumption that in each of the volume segments, limited by the average excursion of water on the flood tide, the water is completely mixed at high tide. Accepting this assumption, which is obviously a simplification of the actual conditions, the rate of exchange in a given segment (r_n) has the value $r_n=\frac{Pn}{Pn+Vn}$ in which Pn is the intertidal volume and Vn the low tide volume of the segment n. The average length of time required for the river water with a particle suspended in it to move through a segment of an estuary is called flushing time, which is defined as a ratio obtained by dividing the volume of river water, calculated from the salinity data, by river flow. The ratio is expressed in number of tides. In Raritan Bay, N.J., a survey made by the Woods Hole Oceanographic Institution indicates the flushing time for the entire estuary was 60 tides.

If a stable pollutant is discharged at a constant rate at the head of an estuary and is uniformly mixed as it is transported downstream, its proportion in the water can be calculated by using the formula of Hotelling which was applied in determining the concentration of pollutant over Olympia oyster beds (Hopkins, Galtsoff, and McMillin, 1931). According to this formula the proportion p of a contaminant in a basin is:

$$p=\frac{a}{a+b}\left[\frac{1^{-}(1-a+b)^{t}}{V}\right]$$

where a is the rate of discharge of contaminant in acre-feet per day, b the rate of influx of water into the basin in acre-feet per day, V the total

volume of the basin in acre feet, and t time in days since the pollution started.

In this formula it is assumed that the influx and efflux occur discontinuously once a day. By assuming that the influx of contaminated water and the efflux are continuous, Tuckerman (see: Galtsoff, Chipman, Engle, and Calderwood, 1947, p. 100) arrives at the following formula:

$$p=p\infty\,[1-(1-K)^t]$$

where $p\infty$ is the limit which the proportion of contaminated water approaches after a long time and $K=\frac{a+b}{V}$. Computations made by using the two formulas indicate the same value for the $p\infty=\frac{a}{a+b}$, but differ in the rate at which this limit is approached. For the small values of $K=\frac{a+b}{V}$ which are usually encountered in estuaries, the two rates are practically identical and the simpler Hotteling formula may be applicable.

In many estuaries the water is stratified. With relation to stratification and circulation patterns Pritchard (1955) distinguishes four types of estuaries—highly stratified (type A), moderately stratified (type B), and virtually homogeneous (types C or D). The reader interested in the dynamics and flushing in different types of estuaries should consult the original contributions of Pritchard (1952a, 1952b, 1955) and Pritchard and Kent (1953) in which the complex hydrodynamical problem is analyzed. It is sufficient for a student of oyster ecology to realize that vertical and horizontal distributions of oyster larvae will be different in each of the four principal types of estuaries.

A free-swimming organism such as bivalve larva cannot be considered in the same manner as a material dissolved in water or as an inanimate body passively transported by water movements. Larvae of bivalves, barnacles, and other invertebrates may have a tendency to swarm and, therefore, their distribution may not be uniform even in a homogeneous environment. Oyster larvae react to changes in the environment by periodically closing their valves and dropping to the bottom or by swimming actively upward or in a horizontal plane. Consequently, they may be carried upstream or downstream according to their position in the water column. Field observations in the estuaries of New Jersey and Chesapeake Bay (Carriker, 1951; Manning and Whaley, 1955; Nelson, 1952) in which the salinity of water increases from surface to bottom indicate that vertical distribution of larvae is not uniform. The late umbo larvae of *C. virginica* have a tendency to remain within the lower and more saline strata, and are probably stimulated to swim by the change in salinity at flood tide. A brood of larvae swimming within a given salinity layer will be passively moved in the direction of the current. Nelson observed that in Barnegat Bay, N.J., the brood of larvae of setting size was carried about 3 miles up the bay in a single evening spring tide. In Yaquina River, a small tidal stream along the ocean shore of Oregon, swimming larvae were transferred by tidal currents and set several miles above the natural beds (Fasten, 1931; Dimick, Egland, and Long, 1941). There are many other places where setting grounds are far above the spawning grounds. Since the seaward discharge of water in an estuary usually exceeds the landward movement, it was difficult to visualize a mechanism by which the larvae can be transported up an estuary and left there. The existence of such a mechanism became apparent, however, from the hydrographic studies by Pritchard (1951). He found that estuaries may be considered as being composed of two distinct layers: an upper layer in which the net movement is toward the mouth (positive movement), and the lower layer in which the net movement is toward the head of the estuary (negative movement). There is a boundary between the two layers which may be called "the level of no net motion" (fig. 366). Since the net movement seaward does not result in a net displacement of the lines of constant salinity in the upper layer, there must be a progressive transfer of the deeper, higher salinity water of the lower layer upward, across the boundary level, to be included in the seaward transfer. The role of the strongest tidal currents is primarily that of providing energy for the mixing processes. Computations made by Pritchard show that superimposed on tidal oscillation there is a residual or nontidal seaward drift on the surface and a net landward drift along the bottom. He applied his theory to a study of the seed oyster area of the James River, Va., and found that below a depth of about 10 feet there is a net (or residual) upstream movement of water at an average speed of slightly more than one-tenth of a knot. This is the type of estuary

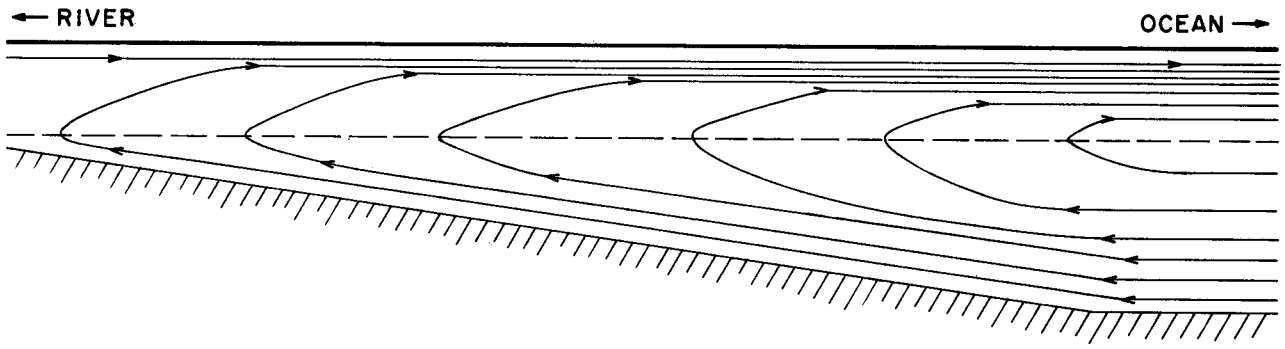

FIGURE 366.—Estuarine structure and net (i.e., nontidal or residual motion of water). Dotted line marks the boundary between the upper and lower net movement; the boundary is the level of "no net motion." From Pritchard, 1951, fig. 3.

in which larvae move from the spawning grounds at the mouth of the river up into the seed oyster bed area. Bousfield (1955) applied Pritchard's ideas to an analysis of distribution of barnacle larvae in the Miramichi estuary, New Brunswick, Canada. The retention of larval populations in this estuary was found to be due to a combination of two factors: changes in the average vertical distribution of successive larval stages, and the strength and direction of transport by residual drift at different depths. This theory of larval retention and the mechanism of transport is not applicable to bodies of water in which there is no salinity stratification or where the residual upriver drift is insignificant.

Least favorable in the life of an oyster community are occasional turbulent currents of high velocities which may dislodge and carry away young and even adult oysters not attached to the bottom. Oysters attached to rocks and other structures are not destroyed by strong currents, but their valves are injured by small pebbles and sand acting as an abrasive material. Live oysters with shells damaged by abrasion can be found in the Sheepscot and other tidal rivers along the coast of Maine.

Continuous renewal of sea water running over a bottom in a nonturbulent flow is the most desirable condition for a flourishing oyster community. On the basis of experimental studies discussed in chapter IX, p. 195, it may be assumed that under optimal conditions of temperature and salinity an average adult *C. virginica* transports water at the rate of 15 l. per hour. With 250 large oysters to a bushel and 1,000 bushels per acre, an oyster bed of that size would require 3.75 million liters of water per hour. My observations show that under the best of conditions oysters can take in water only from a distance not exceeding 2 inches from the shell. It is, therefore, necessary to know the rate of water exchange within the narrow layer adjacent to the oyster bottom. The situation may be different in the case of vertical mixing of water due to turbulent flow.

The amount of water available to an oyster population can be calculated if the number of individuals on the bottom and the rate of water movements are known. In the case of a turbulent flow, vertical mixing of water depends on the degree of turbulency. If the mixing extends to the height of 1 foot above the mud line, the total volume of water in which the oyster population lives in our example is 1 acre-foot or 325,851 gallons (1.25 million l.). It follows that the current velocity must be strong enough to renew the volume of the layer above three times (3.75÷1.25) every hour or 72 times in 24 hours. In cases of greater population density the current requirements are proportionally higher. Due allowance should be made, of course, for the presence of other water-filtering animals which compete with the oyster for food. It is clear, therefore, that great concentrations of water-filtering organisms are possible only where there is sufficient renewal of water. The oyster reef in the Altamaha Sound, Ga., (fig. 367) is a good example of this condition. Such concentrations of live oysters crowded over a limited space cannot exist in sluggish water and are found only in rapid tidal streams.

The water movement factor can be evaluated by determining whether the rate of renewal of water over the bottom is sufficient for the needs of the population and whether the pattern of circulation is such that a certain percentage of