Marine Fouling and Its Prevention,
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CHAPTER 8

Relations to Local Environments

Marked differences exist between the fouling in different parts of the same general region, such as the open coast and the harbors, or even in different parts of the same harbor. The local factors responsible occur in similar patterns in many different regions. They produce differences in fouling of two sorts: those which distinguish estuaries, harbors and other enclosed waters from the open coast, and those related to depth and distance from shore along the coast.

FOULING IN HARBORS, BAYS, AND OTHER ESTUARIES

The varied fauna and flora which may occur in different parts of the same estuary are illustrated by the fouling found on navigation buoys in San Francisco Bay. Near the Golden Gate, where the open sea is near at hand, the conspicuous elements in the fouling are mussels and kelp. Further within the Bay the kelp disappears, but heavy mussel fouling persists. At greater distances from the sea, mussels may persist but hydroids become more conspicuous, particularly on the underside of the buoys. In San Pablo Bay, the mussels occur only in patches on the deeper parts of the buoys and mooring chains, while hydroids and barnacles become dominant. At the confluence of the San Joaquin and Sacramento Rivers, fouling is limited to an algal scum.

These changes in the local character of fouling in San Francisco Bay are illustrated in Figure 1.

In a detailed study of fouling on buoys at Plymouth, England, Milne (*26*) also observed that a number of forms were found only on buoys in the Sound and outer waters, while others were limited to the estuary. Some, however, were common to parts of the Sound and estuary. The distribution of the individual species at Plymouth is illustrated in Figure 2. Similar observations have been made for the fouling of buoys in the Elbe (*19*) and of floating structures in the Liverpool area (*10*).

The variation in fouling at different places within an estuary must be due to differences in the characteristics of the water in different places. Three factors of the environment which singly or in combination may be responsible for many differences in the character of the fouling are the salinity of the water, pollution, and the prevalence of silt.

Salinity

An estuary receives sea water at the mouth, and fresh water at the head. Mixing of the two takes place in the intermediate reaches, establishing a gradient. The salt concentration of the coastal sea water varies with the region, but is usually between 3.0 and 3.5 per cent. At any one station in an estuary, salinity usually increases from the surface to the bottom. Where river discharge is great or mixing is poor, a sharply defined layer of nearly fresh water may occur at the surface.

Salinity is recognized as the most important factor controlling the occurrences of organisms in estuaries. Comparatively few species are able to tolerate the entire range of conditions available in such places. The organisms therefore exhibit restrictions in both horizontal and vertical distribution, correlated with the distribution of salinity.

Most of the common fouling forms are unable to withstand low salinities, and therefore do not appear in fouling on structures exposed well inside the estuaries of rivers or in similar places. The tolerances of different species vary, however, and a few marine forms are able to survive even in nearly fresh water. Thus, among the barnacles common in American waters, *Balanus tintinnabulum* and *B. amphitrite* never invade very brackish localities, though they are common on coastwise installations. Other species, such as *B. balanoides*, penetrate somewhat further. Finally, there are two species, *B. eburneus* and *B. improvisus*, also common along the coast, which are able to withstand extreme variations in salinity (*29*), often being found in water fresh enough to drink. The marine bryozoan *Bowerbankia gracilis*, has been taken in the headwaters of Chesapeake Bay (*28*), and in similar nearly fresh localities (*17*). Several other marine bryozoans also penetrate to extreme dilutions.

Ships which are habitually moored in fresh water between trips to sea enjoy some protection from fouling. The frequently suggested practice of taking seagoing vessels into fresh water to remove the fouling has little to recommend it, since this does not remove the adherent shells of such organisms as barnacles, and some species may not be killed by such treatment.

Some species of fouling are unable to survive in fully marine situations, and appear to be limited

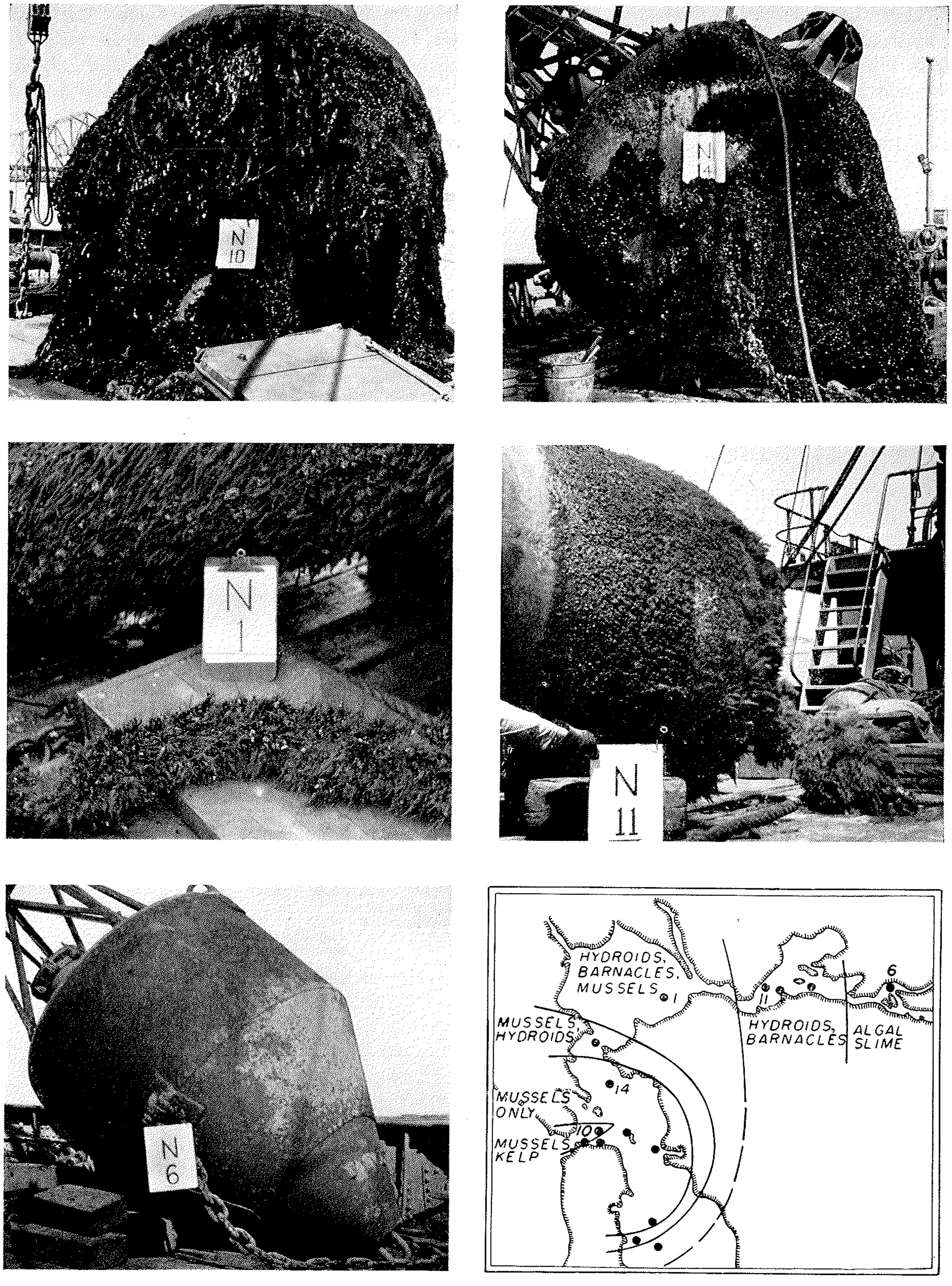

FIGURE 1. Fouling on representative buoys in San Francisco Bay, 1943. *N-10*, Mussels and kelp near Golden Gate. *N-14*, Mussels without kelp, further inside Bay. *N-1*, Heavy hydroid and barnacle fouling with few mussels, near Mare Island, San Pablo Bay. *N-11*, Lighter hydroid and barnacle fouling, Suisun Bay. *N-6*, Algal scum, Sacramento River. Map shows position and summarizes data for all buoys.

to brackish water. *Bimeria franciscana*, the dominant hydroid in fouling in San Francisco Bay, shown in Figure 1, is such a form. Other examples are the widely distributed hydroid, *Cordylophora lacustris*, the bryozoan *Victorella pavida*, common in Chesapeake Bay (*28*), the encrusting bryozoan with exposure at ports well up rivers. At Hamburg, Hentschel (*14*) recorded many fresh water forms on test panels, among them the sponge, *Spongilla*, the hydrozoan *Hydra*, bryozoans such as *Paludicella* and *Plumatella*, oligochaete worms, leeches and rotifers.

FIGURE 2. Distribution of fouling organisms on buoys at Plymouth, England. Salinity decreases from outer waters to Neal Point. After Milne (*26*).

Membranipora lacroixii, and some of the oysters, such as *Ostrea virginica*.

In fresh water, heavy slime films develop, and algae and bryozoa are the commonest macroscopic forms. O'Connell (*27*) has reviewed the slimes in water circuits, while Collart (*6*) has described their occurrence on vessels in the Great Lakes. Occasionally fresh water species are recorded from the fouling of seagoing ships, usually in connection

The extent to which marine species penetrate estuaries depends not only on the actual salinity at various points, but also on the degree to which the salinity varies with the tide. In Randers Fjord, a tributary of the Baltic where there is little tidal variation in salinity, a greater number of species extend into lower salinities than in more variable English estuaries (*1*). Similar differences in distribution related to tidal variations of salinity are observed when the occurrence of several bryozoans in Chesapeake Bay and in an estuary tributary to Long Island Sound is compared (*17*).

In estuaries there are usually marked changes in salinity resulting from seasonal differences in precipitation and fresh water run-off. Variation is also occasioned by wet and dry years. These variations in salinity give rise to sequences of expansion and contraction of the areas occupied by the organisms. The mean annual salinity at a point is therefore a poor guide to fouling expectancy in most estuaries. It is probable, in fact, that the distribution of species in an estuary as related to salinity is fully as complex, on a local scale, as the general distribution of organisms in relation to temperature. Examples of seasonal invasions have been described for the teredo in San Francisco Bay (*15*), and cases involving fouling were found by Milne in his investigations at Plymouth (*26*).

Salinity, like temperature, affects the growth of marine species in addition to limiting distribution. Commonly the rate of growth of marine forms is slower in brackish water than in sea water, and the ultimate size attained may also be less (*4*). Table 1 shows the maximum sizes attained by several molluscs in waters of different salinity in the Baltic area. Each species was progressively smaller as the sea water became more dilute. In the salinity gradient of the Kiel Canal, *Mytilus edulis* was found to reach sexual maturity at about the same age throughout, but specimens in the high salinity at the North Sea end were nearly twice as large as those in the low salinities near Kiel Bight.

Molluscs and other shelled forms tend to have thinner shells where the salinity is low (*21, 22, 30*). Some encrusting bryozoa are less calcareous, and less well attached to the substrate, in brackish waters (*3, 31*).

All species are not influenced by salinity in similar ways. Brine shrimps of the genus *Artemia* are larger at low concentrations than at higher ones (*2*). Federighi has claimed a similar size-salinity relationship in the snail *Urosalpinx cinerea* (*8*). In contrast to Borg's observation that an encrusting membraniporoid bryozoan in the Baltic has smaller zooids at lower salinities (*3*), a closely related American species has been demonstrated to develop larger individuals under such conditions, both in nature and under laboratory conditions (*16*).

Pollution

Pollution may be defined as any addition to natural waters resulting from human activity. It may include anything from domestic sewage to complex industrial wastes, or simple substances such as sawdust, oil well brines, and petroleum by-products. Pollution, in short, is diverse in character, and has no single effect. A pollutant may be harmful either directly through toxic effects, or indirectly as through depletion of oxygen. Some contaminants may be beneficial to living things by enriching the nutrient supply. The net effect on fouling in any given instance may be a balance between two or more such actions.

In habors and estuaries, pollution is most apparent near the outfalls of sewers and the points

TABLE 1. Maximum Size in Millimeters for Six Species of Molluscs Collected at Locations of Differing Salinity in the Baltic Area

Salinity	*Location*				
	North Sea 33°/₀₀	*Kiel Bight* 15°/₀₀	*Baltic Sea* 12°/₀₀	*Gulf of Finland* 7°/₀₀	*Gulf of Bothnia* 5–6°/₀₀
Mytilus edulis		110	50	27	21
Mya arenaria		100		55*	36.5
Cardium edule		44		22	18
Tellina baltica		28		17	15–19
Littorina littorea	32	27			
Buccinum undatum	120	58			

* Size of 70 mm. rarely reached in this locality.

of discharge of industrial wastes. Strong gradients of pollution commonly occur near such points of contamination, and depend on the general character of the local tidal circulation. As the harbor mouth is approached, the general state of pollution decreases as the proportions of clean water from the open sea increase. The upper reaches of an estuary may be polluted more or less than the harbor area, depending on whether the river itself is severely contaminated or not.

Some evidence suggests that domestic sewage can materially accelerate growth, providing other circumstances are suitable. Organic detritus is believed to constitute an important food supply for sedentary forms (*9*), so that the pollutants may have direct value as well as acting possibly through more complex food chains. It is familiar that oysters and other shellfish frequently flourish under conditions of extreme pollution.

Reports of adverse effects of pollution on fouling are not uncommon. Oil and grease pollution suppressed fouling of test panels at stations in the Hampton Roads area of Chesapeake Bay (*35*). Fouling of water mains of a ship based on Honolulu Harbor was reduced when the mooring area was shifted into water polluted by a pineapple cannery discharge.

Conclusive evidence of direct harmful effects of pollutants, however, is hard to obtain, although in some instances laboratory experiments have seemed to support this contention, as in the case of sulfite pollution of the York River estuary (*12*). entirely disappeared. These observations are summarized in Table 2.

Much the same results were obtained in a study of pollution of the Mersey estuary at Liverpool (*32*). The domestic sewage discharge alone was estimated at 35 million gallons daily, and contaminants from all sources were equivalent to 100

TABLE 2. Conditions Near Mouth of Channel Street Sewer, San Francisco, after Miller, Ramage, and Lazier (*25*)

Position	*Salinity*		*Oxygen*		H_2S		*pH*	
	Low water	*High water*	*Low water*	*High water*	*Low water*	*High water*	*Low water*	*High water*
	‰	‰	cc/liter	cc/liter	cc/liter	cc/liter		
200 yds. inside outfall	25.77	30.39	(1.60)	2.61	12.09	0.08	7.09	7.42
100 yds. inside outfall								
Surface	30.23	30.68	3.75	3.69	0.08	1.10	7.50	7.48
Bottom	30.73	31.29	4.38	6.17	0.08	0.08	7.50	7.67
100 yds. outside outfall								
Surface	30.53	30.53	6.14	5.69	0.10	0.10	7.61	7.77
Bottom	30.61	31.78	6.07	6.35	0.10	0.10	7.74	7.75

Usually it is necessary to prove deleterious effects of very extreme dilutions, which is not easily done, although the oyster and mussel fishery literature contains many supposed cases. Better evidence appears to be available for pollution of fresh water and streams.

The rapidity with which pollutants can be diluted on discharge into marine waters has been illustrated on a small scale on an open sewer in San Francisco Bay (*25*). In the sewer, 200 yards from the outfall, hydrogen sulfide was high and the pH was 7.09–7.42 at low tide; marine organisms were absent. Some species, however, were found for a short distance in from the outfall. In the bay, about 100 yards from the outfall the pH was 7.61–7.77, only slightly less than the general bay water values, and the other chemical evidence of pollution, such as hydrogen sulfide content, had almost

tons of organic carbon per day. This sizeable figure, nevertheless, was insignificant compared to the volume of water exchanged on every tide; water analyses indicated that contaminants were speedily dissipated. Even so, differences in the fouling of buoys in the Tamar and Mersey estuaries are attributed by Milne (*26*) to the greater pollution of the Mersey. He observed more species to be present in the relatively pure water of the Tamar than had been recorded from the Mersey. Some of the species common to both regions were also more abundant and penetrated into water of lower salinity in the Tamar.

Many contaminants are subject to oxidation. While this reduces the pollution, it renders the water unsuited to many forms of life. The condition in the river Tees illustrates the depletion of the oxygen in the water of an estuary by local pollution

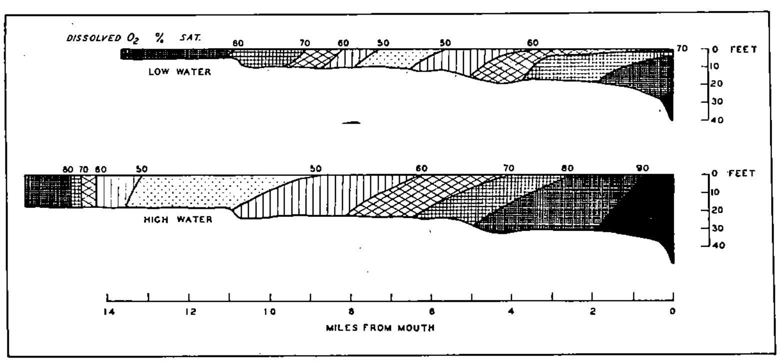

FIGURE 3. Depletion of oxygen by pollution in central and upper reaches of estuary of the River Tees, England. After Alexander, Southgate, and Bassindale (*1*).

and the movement of the depleted water with the tide (Figure 3). The river water is fully saturated with oxygen. The upper estuary receives extensive pollution and the oxygen concentration falls to 50 per cent saturation. Sea water saturated with oxygen enters the estuary along the bottom, and mixes with the surface water in such a way that the effects of pollution are most apparent in the upper layers, and have largely disappeared by the time the mouth of the estuary is reached.

Observations on occasion have suggested that low oxygen and low salinity together tend to reinforce each other as critical factors. It is thought that lower values of either alone can be tolerated than in combination, possibly because at low salinities organisms must do more work in osmoregulation. Such relationships have been reported for several types of organisms, and supporting physiological evidence has been advanced. Krogh (*20*), however, who has reviewed the data critically, states that no conclusive case has been demonstrated.

Silt and other Suspended Matter

Silt and other suspended matter is usually found in enclosed coastal waters such as harbors and bays. The settling-out of suspended matter may smother sessile organisms, or may produce substrates unsuited for the attachment of many forms. This phenomenon has been noted when test panels are exposed in a horizontal position (*5*, *11*). On the other hand, careful studies of the effects of silt on oysters, incidental to dredging operations in which considerable silt was stirred up, failed to show any significant effect on the oysters (*23*). This held true even for oysters in special cages hung under the dredges, where exposure to turbid water was maximum.

The fouling on buoys in the western Gulf of Mexico is characteristically heavily impregnated and compacted with silt. The fouling itself is generally light or moderate in bulk by comparison with that on buoys along the Carolina coast where the fauna is similar. Whether this is due to the silt, however, is not known.

Silt has been thought to interfere with the food assimilation of animals which filter water through sieves or ciliary mechanisms. The available evidence, however, does not support the idea that the distribution of animals in silty regions is limited by such effects. The numbers of species of organisms having such feeding mechanisms, and of organisms having other types, are about the same at various points in the turbidity gradients of the Tamar, Tees, and Tays estuaries (*1*, *26*).

The presence of silt reduces the penetration of light, and may thus restrict the vertical distribution of algae. Milne found that on buoys in the upper Tamar estuary where silt concentration was highest, the zones of algal growth near the sea surface were narrowed and restricted. Measurements of the intensity of light below the sea surface supported the interpretation that the depth to which the algae grew was controlled by the effect of silt concentration on the penetration of light.

FOULING IN RELATION TO DISTANCE FROM SHORE

A change in both the kind and intensity of fouling is found in passing from coastal to oceanic situations. While many species occur in coastwise waters, floatsam picked up at sea tends to be fouled, if at all, chiefly by goose barnacles. Although these are sometimes present in considerable numbers, they do not generally constitute severe fouling as judged by inshore standards. Larvae of the greater number of potential fouling species do not reach floating objects far from shore.

The change in the character of fouling on going offshore is illustrated by three representative buoys of a series extending seaward from the entrance of Chesapeake Bay for about 65 miles, or nearly to the edge of the continental shelf. On a buoy 20 miles from shore, in 70 feet of water, shown in Figure 4, a heavy accumulation of mussels was found. This is characteristic of inshore waters north of Cape Hatteras. The mussels also extended down the mooring chain in a uniform mat, nearly to the bottom. On a second buoy, 30 miles from shore, where the depth was 90 feet, the fouling was patchy, and continuous mussel fouling on the chain extended only to about 30 feet. (See Figure 5.) Below this the fouling consisted mostly of patches of sponges and hydroids, and was much less severe than the fouling of the buoy nearer shore. On a buoy 60 miles from shore, in 186 feet of water, the mussel fouling gave way almost entirely to goose barnacles and algae (Figure 6). The very few mussels present constituted only an insignificant element in the fouling. Aside from one or two links lightly overgrown by a sponge, the chain of this buoy was without fouling. Similar fouling was found on all buoys of this series more than 50 miles from shore.

Similar observations have been made in other series of buoys extending well offshore from Delaware Bay and Block Island. The common goose barnacle on these offshore buoys was *Lepas anatifera*. Sometimes they were accompanied by algae and hydroids, and in the case of the buoys off

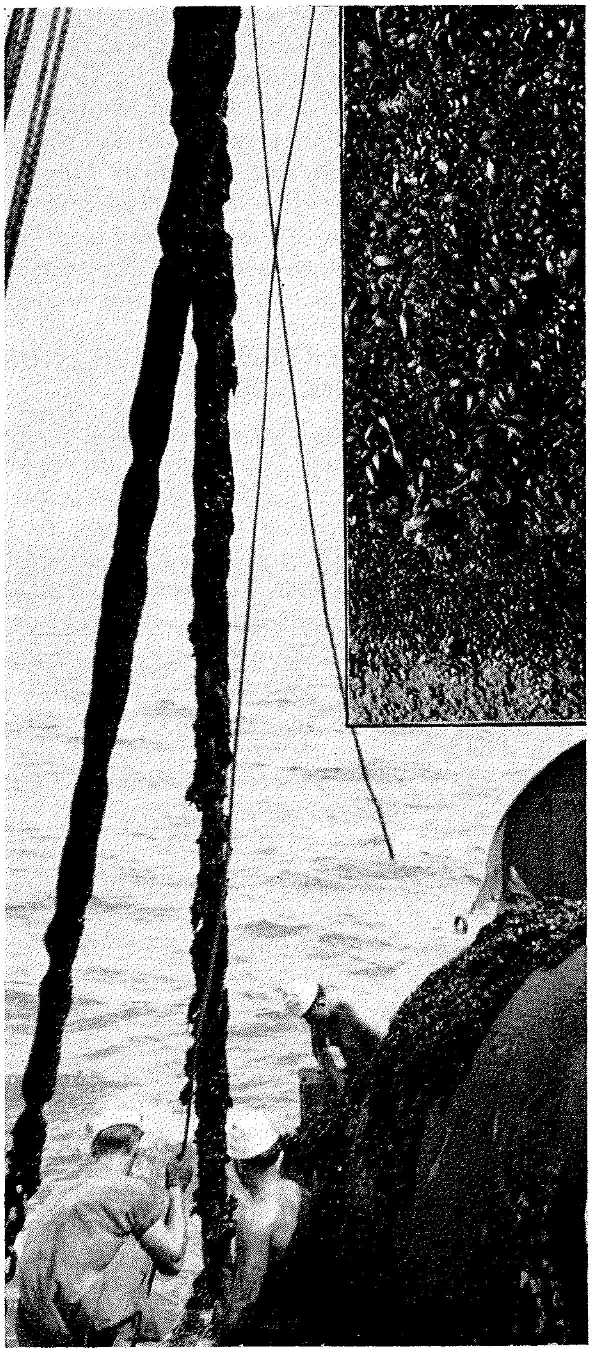

FIGURE 4. Buoy 20 miles from shore, off Chesapeake Bay. Heavy mussel fouling on both buoy and chain is typical of inshore buoys north of Cape Hatteras. Inset shows uniform coverage of side of the buoy. This buoy, and those in Figures 5 and 6, were all set for about one year, midsummer 1943 to midsummer 1944.

Block Island a few mussels occurred at distances of 25 to 44 miles from the nearest land.

The offshore limit of heavy mussel fouling appears to be set by the distance from shoal water rather than by the distance from shore (*18*). A number of buoys in the Gulf of Maine and near Cape Cod foul heavily with mussels, although at considerable distances from the nearest land. Among such are the buoy on Cashes Ledge, about 55 miles distant from land, and Nantucket Lightship station buoys, 40 miles offshore. Mussels have been reported even from the Cultivator Shoals buoy on Georges Bank, some 80 miles from land and the furthest offshore of all American buoys (*13*). All of these buoys, however, are fairly close to shoal waters. Since mussels live on the

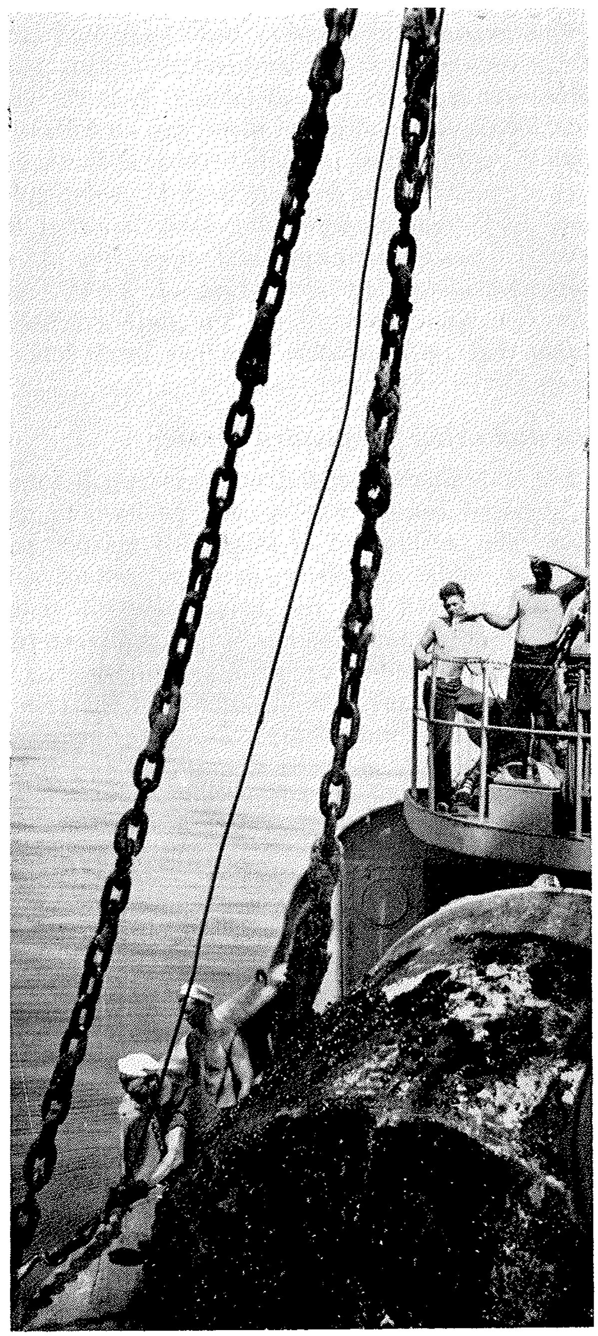

FIGURE 5. Buoy 30 miles from shore, off Chesapeake Bay. Patchy mussel fouling on buoy and uppermost parts of chain with spotty fouling of sponges, hydroid, and other forms. Chain at lower left was at depth of about 70 feet. Compare with Figures 4 and 6.

FIGURE 6. Buoy 60 miles from shore, off Chesapeake Bay. Fouling on buoy chiefly goose barnacles and algae, shown in detail in inset. Chain almost free of fouling. Compare with Figures 4 and 5.

bottom at depths to about 100 feet, it may be supposed that buoys near areas of less depth are generally exposed to severe mussel fouling. Accessibility to a natural source of infection, in other words, determines the offshore extent of coastal fouling. The set of local currents, in addition to proximity to shallow water, must be presumed to affect this accessibility. For *Mytilus edulis*, however, the off shore limit of intense fouling is probably roughly approximated by the 20-fathom contour.

Data are not available in sufficient quantity to establish such limits for other forms and in other other regions. On the northern Atlantic coast, hydroid fouling by species of *Tubularia* seems to be most common on the more inshore buoys, while the *Campanularian* forms tend to predominate on buoys farther out. In the San Francisco region, the extensive shoals and bar outside the Golden Gate appear to influence the fouling of the buoys in a fashion comparable to the effects produced by shoals on the New England coast. Characteristic inshore forms such as mussels occur on the outer buoys along with the oceanic goose barnacles.

Although marine bacteria are much less plentiful in oceanic waters than near shore (*33*), slime films may readily form on surfaces exposed at great distances from shore. Test panels towed behind a vessel in the open ocean, never less than 75 miles from shore, developed slimes comparable to those formed in adjacent coastal waters (*34*).

FOULING AND DEPTH

Conflicting opinions on the depth to which fouling extends are often encountered. Positive information shows that structures lying on the bottom, such as submarine cables, may foul at any depth. The mooring chains and anchors of buoys in coastal waters may foul at all depths. The character and quantity of the deeper fouling is frequently different from that at the surface.

Fouling on the mooring chains of buoys usually extends continuously from the surface to within at least 25 feet of the bottom. Data for the vertical extent of fouling on buoys set in 40 feet or more of water are given in Figure 7. These data apply to the chains only, and do not include anchors, whether fouled or not. In the extreme case observed, a buoy set in 462 feet of water, fouling extended along the chain to this exact depth. The deep fouling on an adjacent buoy is shown in Figure 8.

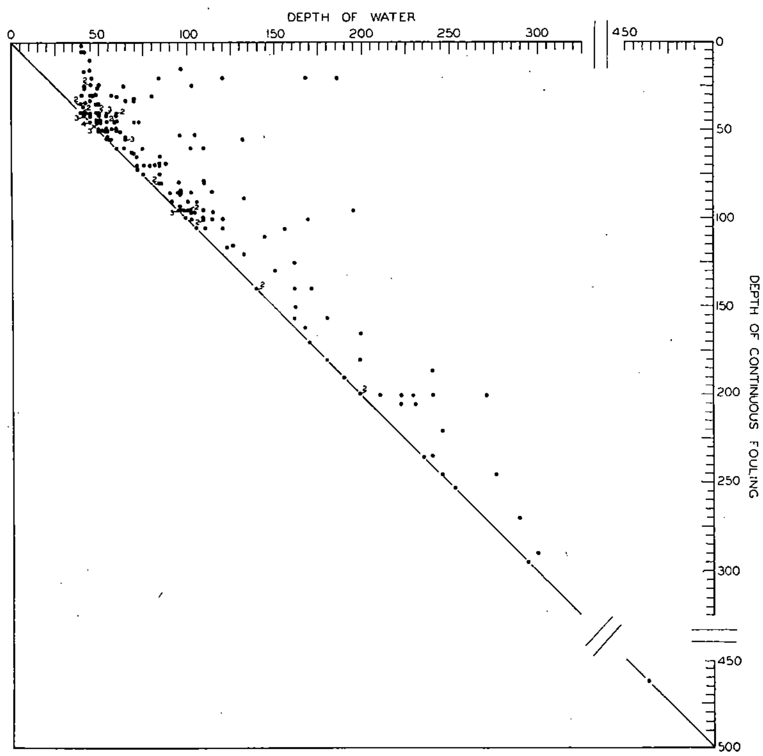

FIGURE 7. Depth, in feet, to which continuous fouling extended on mooring chains of buoys set in American coastal waters of various depths. Diagonal line, representing the bottom, is the limit to which fouling could have extended.

On buoy mooring chains, the termination of fouling at the lower limit is often sharp (Figure 9). When this occurs within 25 feet of the bottom, the chain beyond is usually abraded and scored, showing that these unfouled links have at times dragged on the bottom. Susceptibility to chafing thus appears to determine the lower limit of fouling. During storms and exceptionally low tides the links which are otherwise a few feet clear of the bottom may chafe, which explains the fact that fouling usually appears to terminate slightly above the bottom. This conclusion seems applicable to any form of gear suspended from a floating structure.

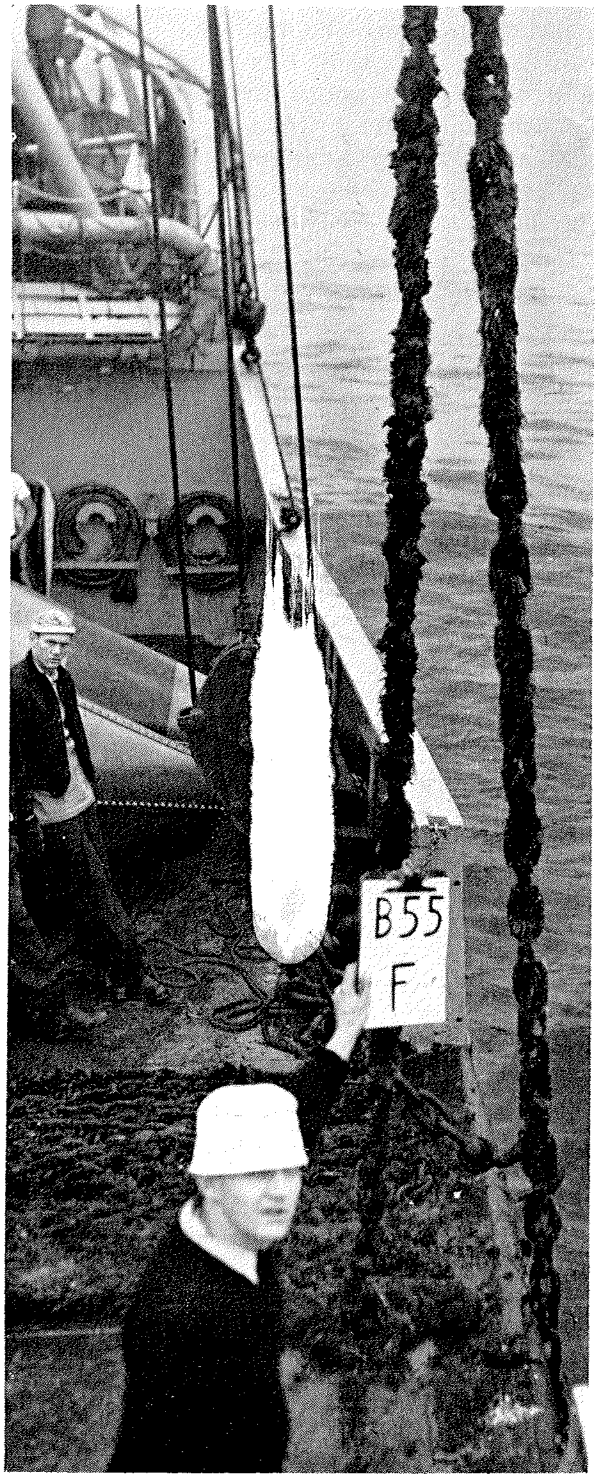

FIGURE 8. Mooring chain of a buoy set for 18 months in 300 feet of water on the Maine coast, showing portion of chain at 290 feet where fouling terminated. Chain has been lined back and forth on deck as brought aboard. Remnants of mussel fouling visible on upper portion (rear, on deck), with hydroids the dominant fouling on remainder of chain. Similar hydroid fouling extended to the bottom on a near-by buoy in 462 feet, the deepest-set buoy which has been examined.

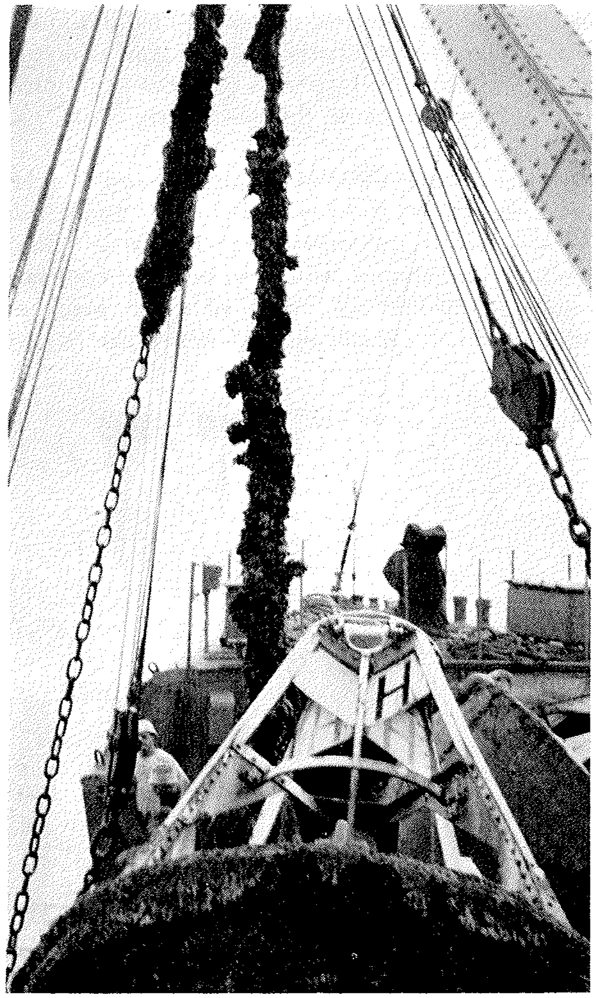

FIGURE 9. Heavy mussel fouling ending at depth of about 100 feet on the chain of a buoy set for two years in 100 feet of water off Narragansett Bay. Fouling usually ends abruptly, but the sharp termination is particularly apparent with mussel fouling on buoys in 100 feet or less water.

The cases in which fouling terminated more than 25 feet above the bottom are probably due to a variety of causes. In some, the exposure times may have been unseasonable for the attachment and growth of deeper-living species. Other cases are certainly related to distance from shore, as in the series off Chesapeake Bay where the fouling on the buoys consisted of forms like *Lepas*, restricted chiefly to the uppermost waters. Because of this distance-from-shore effect, in considering the depths at which fouling may occur one must distinguish between exposures in oceanic situations, and exposures in deep channels in shallow water on the continental shelves. The latter are accessible to the many littoral species which produce the continuous fouling of mooring gear to great depths.

Differences in Composition Related to Depth

While fouling has been found at all depths in coastal waters, the composition is not the same throughout the vertical column. The individual species have characteristic depth ranges, which result in different combinations of forms at different depths. Some of these differences are quite conspicuous.

At the surface there is usually a band of green algae, species of *Enteromorpha*, *Ulva*, and *Cladophora* generally predominating. This zone seldom extends more than a foot or so below the surface, though occasional specimens of green algae are found at much greater depths. Below the band of green algae, red and brown algae predominate and may extend to depths of 100 feet or more. Kelps are among the more prominent of dominant brown algae. Light is important in limiting the vertical penetration of all algae. Other factors being equal, a given species will occur at greater depths in clear water than in turbid water.

Below the zone of green algae, the usual dominants are animals. The particular species present depend partly on the region, the season, and the duration of exposure. Other factors also seem to influence the vertical distribution, among them the distance from shore, as already described. Thus, the mussels extend less deeply on more offshore buoys.

On inshore buoys in the regions of mussel fouling, *Mytilus edulis* commonly extends to a depth of about 100 feet. *Mytilus californianus*, on the other hand, appears to be confined to somewhat nearer to the surface, not being numerous below 50 feet. *Balanus tintinnabulum* may be responsible for massive fouling to depths between 100 and 200 feet. Other species dominant near the surface extend down to various depths.

At depths below those occupied by these dominants of the upper waters, hydroids are generally the principal fouling. In some cases hydroid-dominated fouling has begun at or close to the surface, and extended continuously to the bottom. The chains of the buoys set in 462 feet and 300 feet of water, described on page 110 and in Figure 8, were fouled chiefly by hydroids, particularly the lower part. There are no data at present on the lower limits of such hydroid fouling.

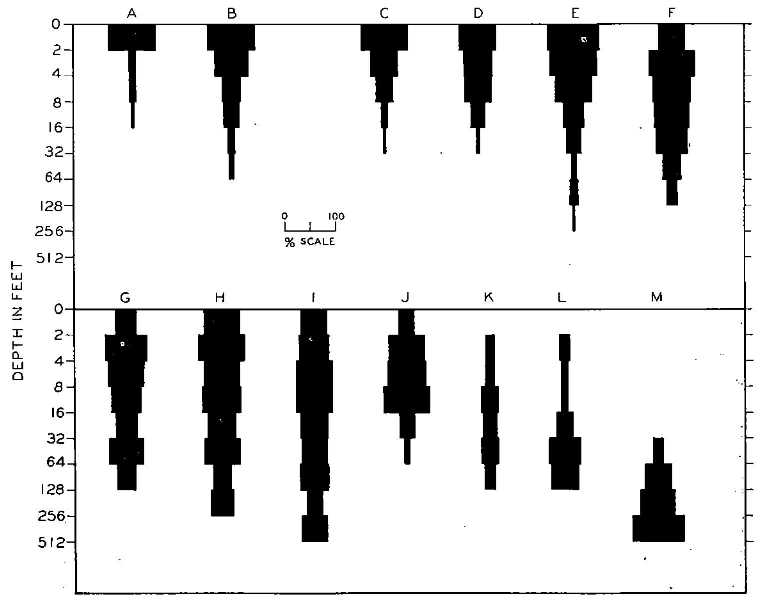

FIGURE 10. Vertical distributions of various species of barnacles on American buoys. The diagrams show for each depth zone the percentage of samples in which the species occurred. Calculations restricted to samples from the known geographical ranges of the individual species. A, *Lepas anatifera;* B, *L. anserifera;* C, *Balanus glandula;* D, *B. cariosus;* E, *B. balanoides;* F, *B. improvisus;* G, *B. amphitrite;* H, *B. tintinnabulum;* I, *B. crenatus* (East Coast only); J, *B. eburneus;* K, *B. balanus;* L, *B. nubilus;* M, *B. hameri.*

The variation in the depths at which different species of barnacles characteristically settle is illustrated by Figure 10. The diagrams show the frequency with which each species was found in samples of fouling on buoys at different depths. The 13 species of barnacles fall into characteristic groups, which range from those showing a preference for the surface water, to those which appear to avoid settling near the sea surface and concentrate at the greater depth. Intermediate types of distribution may show little selection of particular depths throughout the entire range, or may, in the case of *B. eburneus*, concentrate heavily at somewhat below-the-surface depths without extending into the deeper water.

The histograms shown in Figure 10 do not indicate the relative numerical abundance of the several species at the different depths. Thus, the deeper records for *B. balanoides* and *Lepas* all depend on rather rare, scattered specimens, in contrast to thick stands found in the upper few feet. Also, there are fewer samples at great depths. Nevertheless, in a general way the figure gives a fair picture of differences in the vertical distribution of these forms.

A conspicuous difference in fouling is often observed between the growth on the chain and that on the sinker or anchor of a buoy. Though not primarily related to depth, it is conveniently noted at this point. Some species common on buoys and chains, such as *Mytilus edulis*, were almost never found on the anchors, even in shallow water. Other forms such as the bryozoan, *Idmonea atlantica*, occurred on the sinkers but never on floating and pendant gear.

The data from submarine cables show that structures on the sea bottom foul at depths of more than 1,000 fathoms. Probably fouling may occur at all depths. Differences in the character of the fouling are related to the depth, for species which are never found in coastal waters, such as the barnacles *Scalpellum* and *Megalasma* grow on cables at the greater depths. The most marked change in the character of the fouling is to be expected at the limits of the continental shelves. Because of the apparent differences between the fouling on structures lying on the bottom and on gear suspended in the overlying waters, the data from deep cables can not be relied on to indicate the probable fouling of pendant gear at equivalent depths.

Intensity of Fouling at Various Depths

Observations on fouling by mussels and hydroids on buoys in the temperate waters of the American coasts have led to the following conclusions. Mussel fouling usually does not extend along buoy chains to depths much greater than 100 feet. Between the surface and this depth, however, there is no consistent tendency for the intensity of fouling to vary markedly with depth. On some buoys the weight of fouling may decrease with depth, but on others it may increase, remain uniform, or vary irregularly. (See Figure 11.) Hydroid fouling, like that by mussels, varies in distribution on individual buoys, but in general it tends to be about equally heavy at all depths.

Usually mussels and hydroids occur together on buoys in temperate waters. When this occurs the total fouling decreases below about 100 feet because hydroids dominate below this depth, and are less bulky than the mussels. Growth may be somewhat slower at the greater depths because of the lower temperature of the water. Hydroid fouling apparently develops rapidly, nevertheless, reaching maximum dimensions in a month or so. Mussels, on the other hand, grow slowly so that the bulk of such fouling increases gradually over long periods. Such considerations explain in part the variable distribution of fouling with depth which is observed when buoys are examined.

Vertical Zonation Near the Sea Surface

In addition to the zonation which is related to considerable variations of depth, very conspicuous differences may be observed in the intensity and character of the growths which occur within small distances from the sea's surface. Small scale zonation of this sort is particularly noticeable in the case of fixed or floating installations in shallow water.

On floating installations, such as buoys or ships, the parts of the surfaces to which fouling may attach remain permanently at a relatively constant distance from the water line, and the distribution of fouling may be related directly to depth below the sea surface. The zonation of algae and of the various species of barnacles, previously discussed, are examples of this type of distribution. to fixed installations, such as wharf piles, the point to which fouling attaches varies in its relation to the sea surface with the rise and fall of the tide. The intensity and character of the fouling in this case is determined by the distance from the high and low water level, and striking zonation occurs particularly in the intertidal level.

The different distribution of a species of barnacle under these two kinds of exposure has been described by McDougall (*24*). His observations are summarized in Figure 12, which shows the numbers of *Balanus eburneus* which attached to test panels fixed at different depths on a floating and on a fixed pile. On the floating pile relatively few barnacles attached immediately below (within 6 inches of) the surface, but the numbers increased with depth and were greatest at the lowest level tested, which was at a depth of 6 feet. On the fixed pile a few barnacles attached as much as one foot above low water level where they were exposed to the air for about 2 hours each tide. Below the low tide level the numbers attaching were much greater than on the floating pile, and were maximal 3 feet below the low water mark, diminishing from there

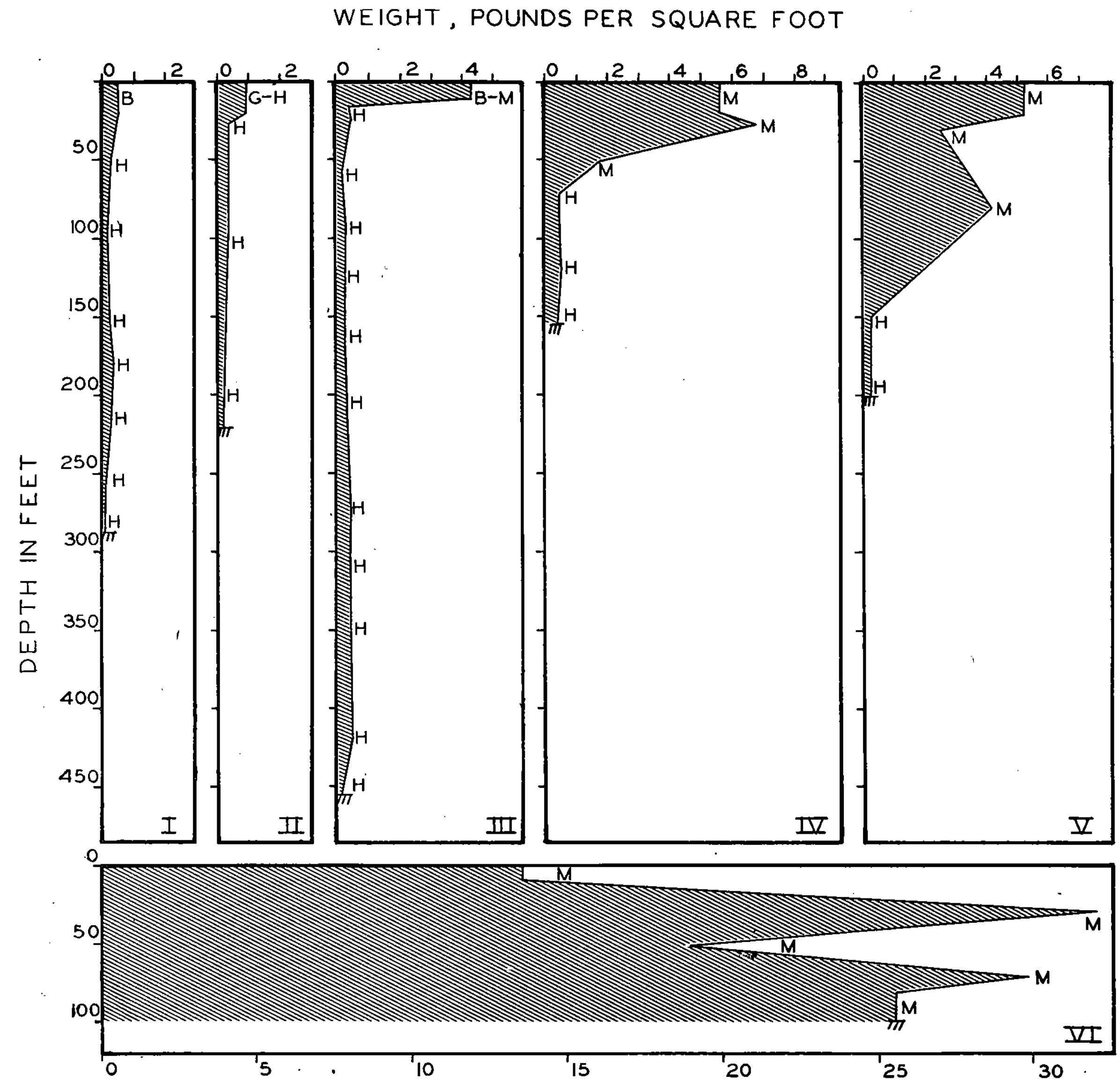

FIGURE 11. Intensity of fouling at various depths on selected buoys on which fouling extended to the bottom. Greatest differences in intensity as related to depth depend on changes in the species present. *I*, Barnacles and hydroids, Maine coast, June '43–October '44. *II*, Goose barnacles and hydroids, Block Island, November '42–December '43. *III*, Barnacles, mussels, and hydroids, Maine, March '44–October '44. *IV*, Mussels and hydroids, Maine, June '43–August '44. *V*, Mussels and hydroids, New York, August '42–November '43. *VI*, Mussels, Narragansett Bay, June '42–June '44 (this buoy is the one shown in Figure 9). *B*, barnacles; *G*, goose barnacles; *H*, hydroids; *M*, mussels.

downward. The reasons for this difference in distribution are not clear. McDougall suggested that the larvae were concentrated about 6 feet below the surface, and that attachment occurred chiefly at high tide when they would be at the depth of 3 feet below low water mark on the fixed pile. This agrees with other observations on barnacle attachment. The reason for the greater attachment to the fixed pile is not explained however. The precise results obtained doubtless depend on local conditions. It will be recalled that on navigation buoys this species of barnacle occurs with maximum frequency at depths of between 8 and 16 feet, as shown in Figure 10.

Vertical zonation in the intertidal zone has been widely studied. It is very conspicuous along rocky shores and on wharf pilings. Some forms, such as species of *Chthamalus* are largely or wholly restricted to the intertidal region. Others extend into it to greater or lesser degrees, depending on their abilities to withstand exposure to air, direct sunlight, and similar factors. The differences in vertical distribution of a variety of species in the intertidal zone on the coast of England are shown in Figure 13 (7). The breadth of such zones and their distance above low water level may be expected to vary with the range of the tide and other local factors, such as the exposure to wave action, since they are determined by the ability of the organisms to withstand drying during the periods of low water.

The vertical zonation on fixed test boards exposed at Miami is illustrated in Figure 14. Above the low tide level the fouling is limited to barnacles which extend upward in decreasing abundance for 6 to 8 inches or about to the one-third tide level. The barnacles decrease in abundance below the low tide level also. The fouling on the deeper parts of the boards is dominated by bryozoans and tunicates which, however, do not appear within 6 or 8 inches of the low tide level.

The important differences in the character of fouling within small distances from the sea surface, which depend also on whether the structure is fixed or floating, should be taken into account in comparing the results of test exposures. Failure of different observers to employ comparable conditions of exposure introduces many difficulties in attempts to compare the seasonal incidence and abundance of fouling in different places.

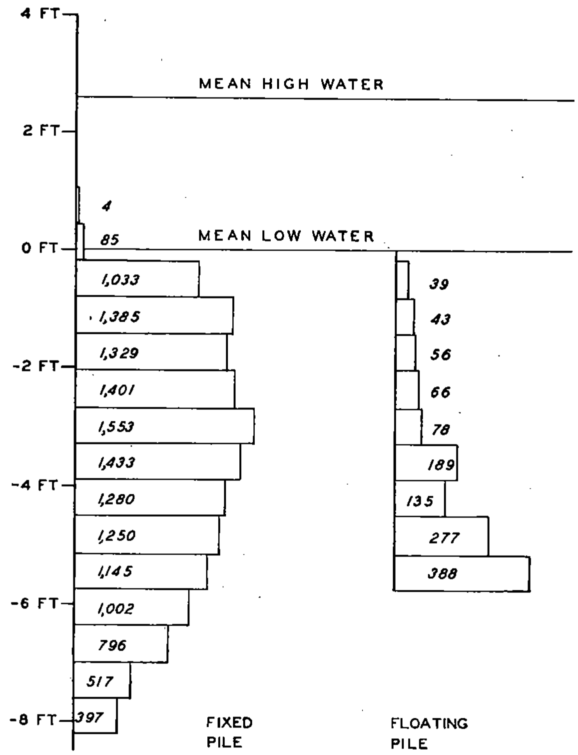

FIGURE 12. Numbers of barnacles (*Balanus eburneus*) attaching to 6 by 3 inch tiles mounted on a fixed pile and on a floating pile. At Beaufort, North Carolina. exposure 7 weeks. Floating pile exposed earlier in season than fixed pile. Horizontal scales in figure different for the two piles. After McDougall (*24*).

INTERRELATION OF FACTORS IN THE DEVELOPMENT OF FOULING COMMUNITIES

The many kinds of local differences observed in

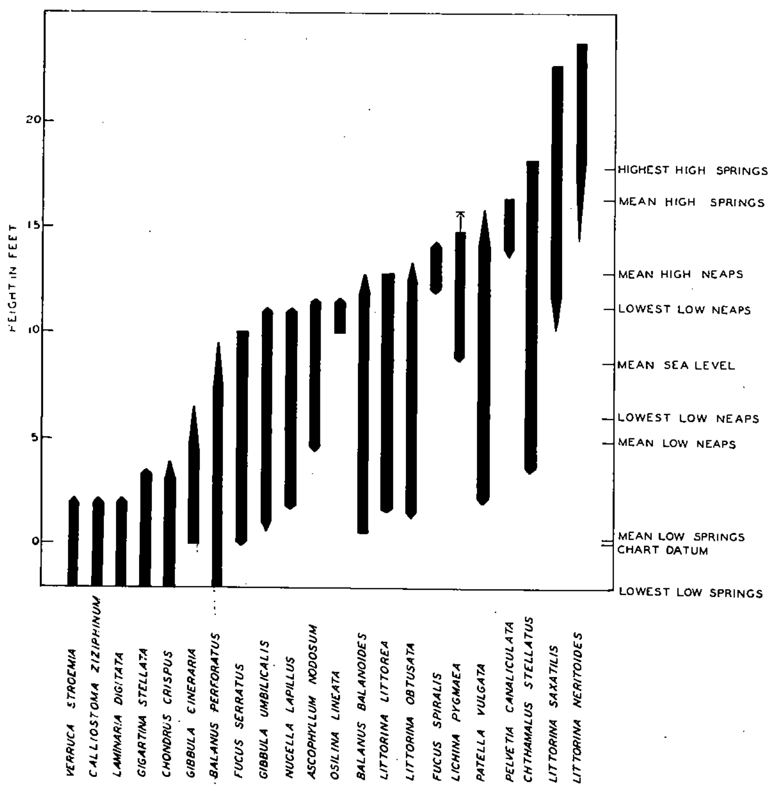

FIGURE 13. Vertical distributions of various organisms found between tides at Plymouth, England, illustrating differences in ability of species to withstand exposure to air. Redrawn from data of Colman (*7*).

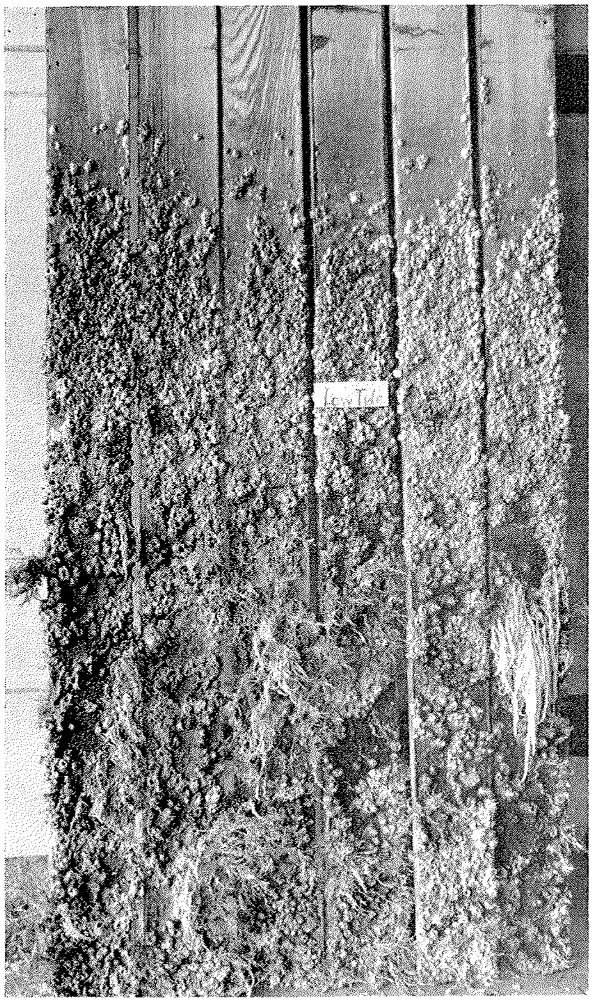

FIGURE 14. Vertical distribution of fouling on test boards exposed at Miami Beach, Florida. Card shows level of low tide, above which fouling was limited to barnacles.

fouling are so varied and so complex in their combined effects, that much more investigation is needed before a full understanding of them will be possible. It can be seen, however, that the development of a given fouling community on a particular exposure follows a selective process. Of all the fouling species in the world, only a small number indigenous to the region of exposure will have access to the unit. Further restrictions among these will be imposed by the season. The selection is still more narrowed by the innumerable local conditions such as the salinity, the composition, color, orientation, toxicity, and other characteristics of the exposed surface itself. The dominant species which first become established may finally impose biotic restrictions on the development of the few forms which have not been eliminated by the preceding conditions.

The variation in detail which is possible through the operation of local and biotic factors is enormous. Only a beginning has been made on its analysis. Fortunately, the complexity of the local variations is somewhat offset by their accessibility for study, and progress in understanding them therefore can be expected.

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