Marine Fouling and Its Prevention,
Contribution No. 580 from the Woods Hole Oceanographic Institute

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CHAPTER 6

Quantitative Aspects of Fouling

The severity of fouling in any given situation depends on the numbers of larvae of suitable organisms present in the water, the rate at which the attached organisms grow, and the bulk attained by the characteristic growths.

It frequently happens that such great numbers of larvae of one sort are present and ready to attach that a surface exposed in the water very rapidly picks up more larvae than can find room after growth has taken place. Under such circumstances a practically pure population of a single species may develop. Figure 1 illustrates the density with which barnacles may settle on a freshly exposed surface. The pure population of barnacles which develops as the result of such settlement is shown in Figure 2.

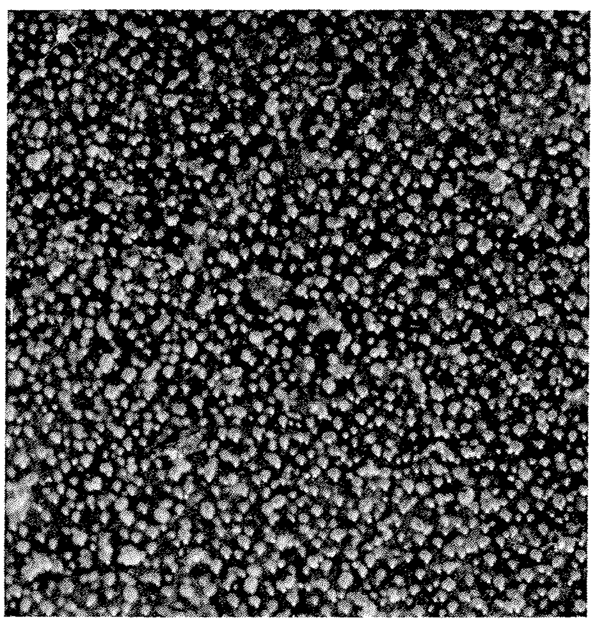

FIGURE 1. Photograph showing dense settlement of minute barnacles on a panel. Natural size. Photo by C. M. Weiss.

THE GROWTH OF COMMUNITIES

Except for the microscopic forms, few fouling organisms multiply by reproduction on the surface. After attachment has taken place, the increase in the bulk of the fouling depends on the rate of growth of the attached individuals. This differs naturally from species to species, and is controlled by the temperature of the water and by the availability of suitable food. However, a number of forms, such as the bryozoans and tunicates, develop branching colonies which spread rapidly over a surface on which a single individual has become established. (See Figure 3.) In addition, the bulk of the community may be increased by the continued addition of new individuals brought to it by currents as free swimming larvae. Figure 4 shows a test panel on which barnacles of varied size are growing as the result of successive attachments.

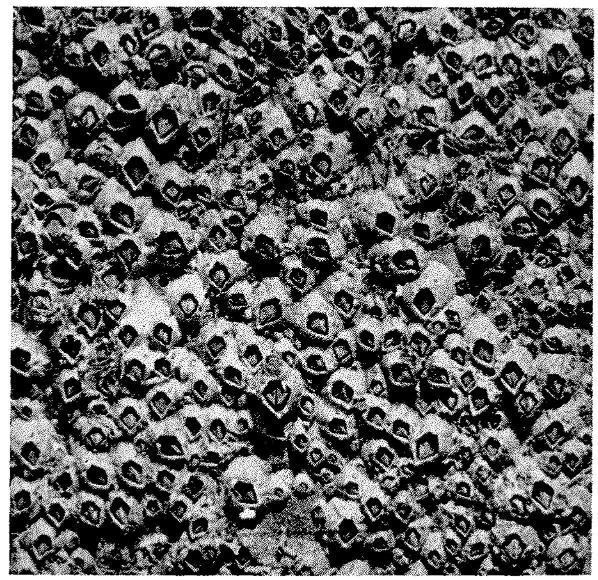

FIGURE 2. A population consisting exclusively of barnacles, resulting from exposure at time when barnacle larvae are most abundant. Natural size.

The growth rate of the individual organisms usually becomes slower as they increase in size, and most species tend to approach a fairly definite maximum size. This factor and crowding tend to limit the bulk of any type of fouling which can develop. The bulk of the community is not limited to a single layer of organisms, however, for frequently a later generation may attach to the individuals earlier established. Frequently small barnacles are found growing on the shells of larger predecessors. Mussel fouling very commonly develops in layers much thicker than the length of the larger individuals. (See Figure 5.)

The process of piling up of one layer of fouling on another has its natural limit since the animals in the deeper layers die from lack of nourishment or oxygen. Later their remnants may become de-

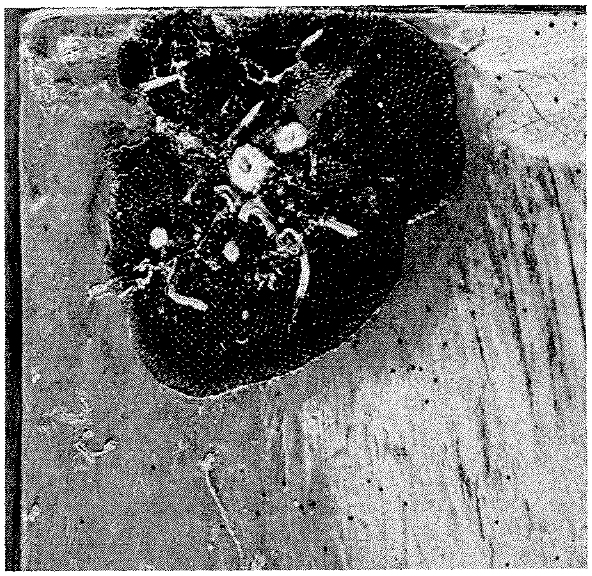

FIGURE 3. Photograph of a spreading colony of encrusting bryozoans. Natural size. The small dark spots on the panel are newly attached individuals. Photo by C. M. Weiss.

tached, and the entire mass falls away. However, some organisms, such as the corals, develop limey skeletons of such permanence that the encrustation may continue to grow in thickness indefinitely. In the competition between species for space, the forms which spread rapidly over those established earlier finally become dominant.

It is only in the case of two types of fouling, barnacles and mussels, that a quantitative account can be given of the development of the community. Growth curves for a number of other species are given by Paul (*16*), Coe and Allen (*2*), and Edmondson and Ingram (*4*).

FIGURE 4. Test panel after 4 weeks' exposure, showing barnacles of different sizes which develop as the result of successive infections. Natural size. Photo by C. M. Weiss.

The Barnacle Community

SETTLING OF CYPRIDS

Barnacles attach when the larvae are in a stage known as the cyprid. At Miami, where barnacles attach at all seasons of the year, C. M. Weiss has found, by counts of the number of cyprids settling on panels immersed daily, that the numbers available fluctuate greatly. (See Figure 6.) When the cyprids are abundant many more settle on the surface than survive.

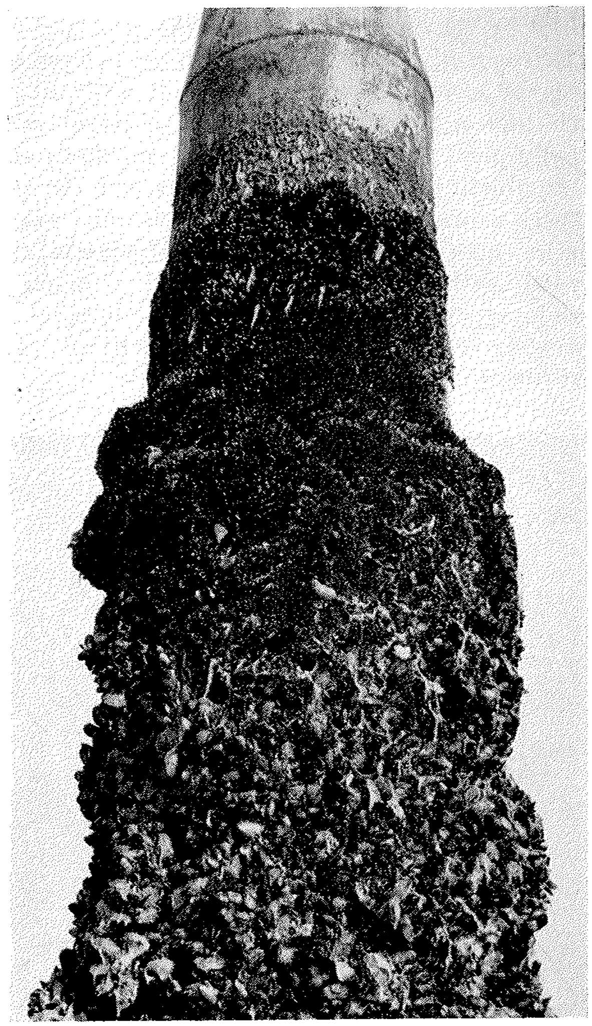

FIGURE 5. Navigation buoy fouled with mussels, showing a recent setting of small mussels growing over the larger mussels of greater age.

The number of barnacles which develop on the panels exposed for one month at Miami rarely exceeds 300 per square decimeter and usually does not exceed 100 per square decimeter. During their peak abundance as many cyprids may attach to a

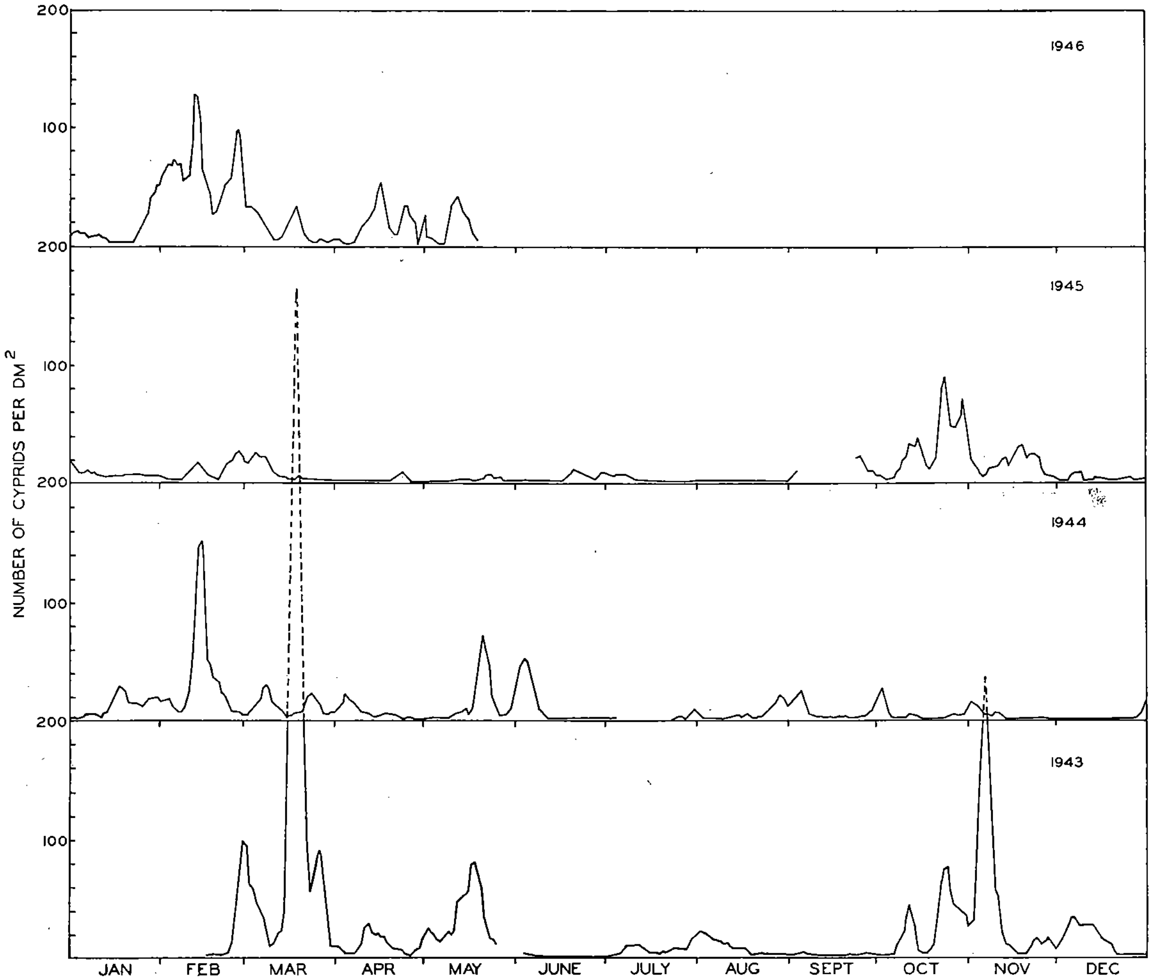

FIGURE 6. Number of cyprids attaching daily to a fresh glass test surface at Miami Beach, Florida. The numbers plotted are the average values for each three successive days. Observations by C. M. Weiss.

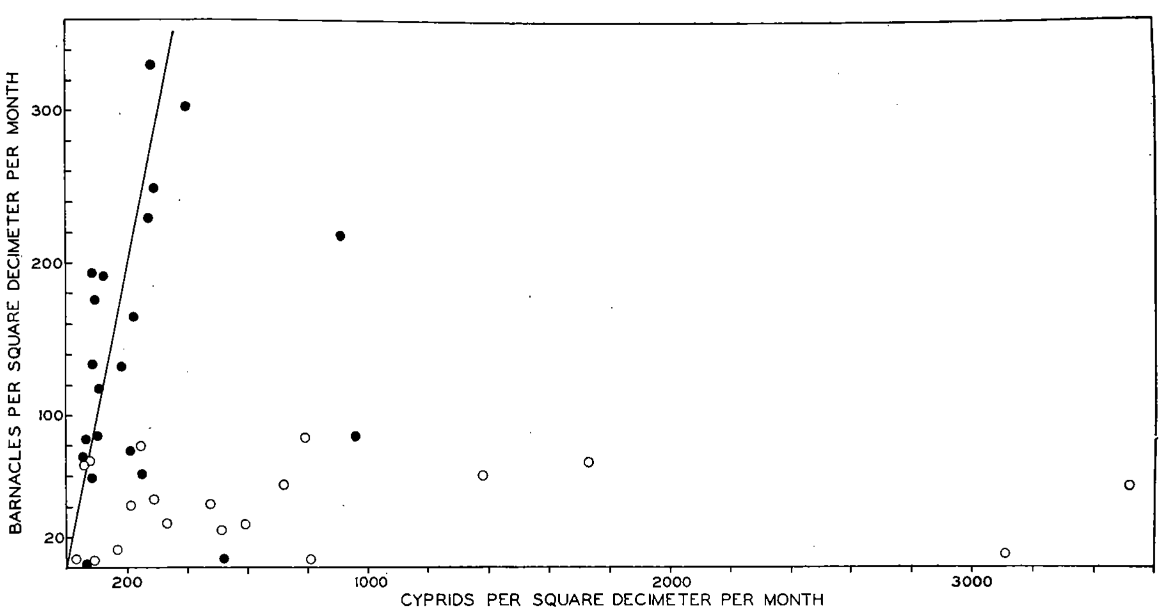

FIGURE 7. Comparison of the number of barnacles attaching in one month and the sum of the numbers of cyprids settling daily during the same period. Circles show observations made in 1943; dots, those made in 1945.

fresh panel in one day as develop into barnacles in the course of a month's exposure. During the two or three weeks of exposure when the cyprids which finally develop into barnacles are attaching, many more settle than survive. It is obvious that a limit to the survival of the cyprids is set by the area of the panel, which will not accommodate, per square decimeter, more than 100 to 300 barnacles of such size as can be reached in the course of a month's growth. Survival is thus limited by crowding. The survival of the cyprids which attach appears to be influenced also by other factors, which vary from year to year and from time to time. Thus, 1943 was a year characterized by exceptionally heavy settlings of cyprids at Miami; yet the number of barnacles attached to panels exposed each month was relatively small. In contrast, in 1945 the cyprid set was poor, while the number of barnacles developing on the panels was unusually great. (Compare Figure 6 of this chapter and Figure 3 of Chapter 5.)

These relations are brought out in more detail in Figure 7, in which the number of barnacles developing on test panels each month is plotted against the sum of the number of cyprids attaching each day to freshly exposed surfaces.[1] It may be seen that in 1943 the number of barnacles surviving never exceeded about 80 per square decimeter, although many more cyprids were attaching. Mortality in the early stages of development was high. In 1945, in contrast, numbers of barnacles developing were approximately equal to the numbers of cyprids attaching during most of the periods tested. During many periods much larger numbers of barnacles were found on the panels than at any period in 1943.

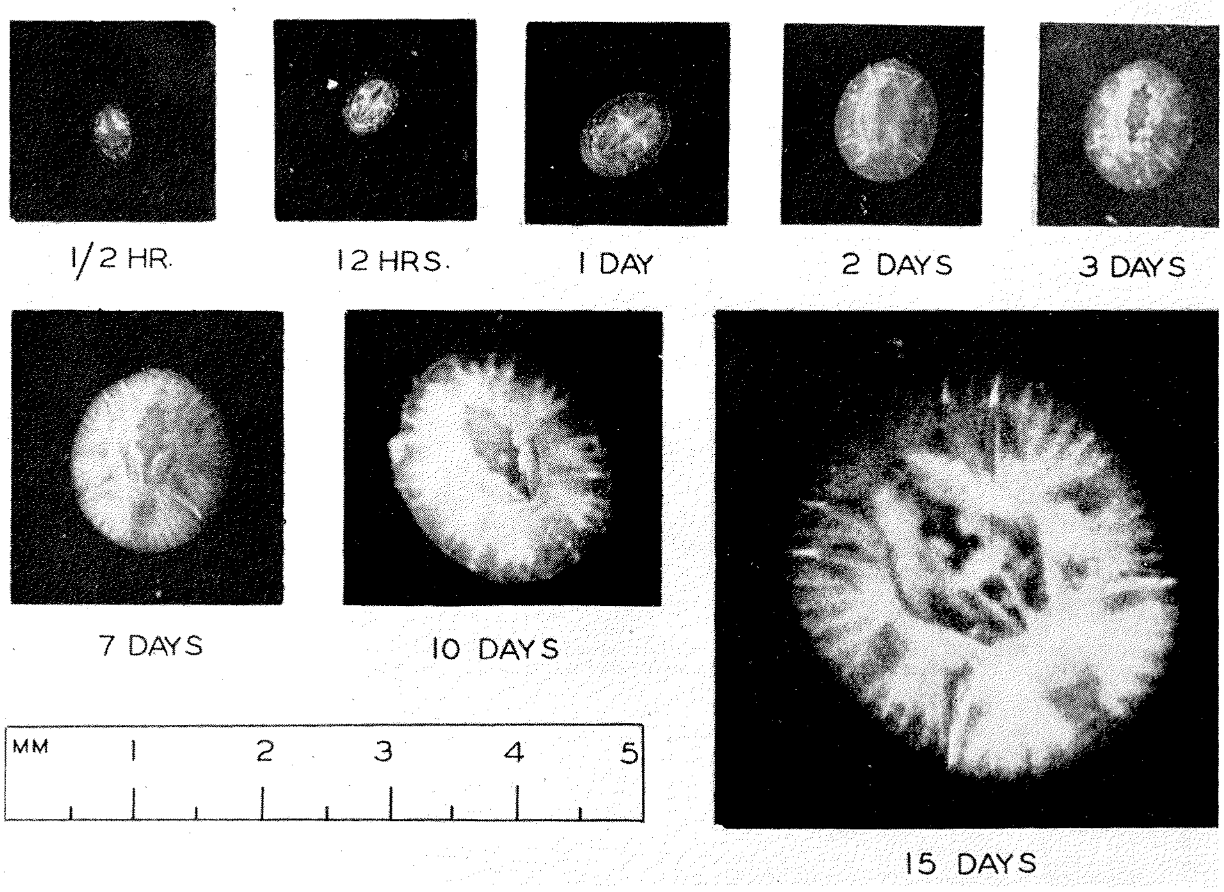

FIGURE 8. Enlarged photographs of a barnacle growing in the laboratory at Miami, showing increase in size from 30 minutes after metamorphosis to an age of 2 weeks. Photographs by C. M. Weiss.

The metamorphosis of the cyprid into the adult barnacle form is described in Chapter 9. The

[1] In estimating the number of cyprids attaching during the month, the numbers observed to attach each day during the first two or three weeks were added together. In summer the attachments during the last week, and in winter during the last two weeks, were not included because cyprids attaching during these weeks would not grow to be barnacles of the size counted.

process requires up to 24 hours after the cyprid settles on the surface. The growth of a young barnacle in the laboratory during the first two weeks is shown in Figure 8. At the end of that time its diameter was about 3.5 millimeters.

GROWTH OF BARNACLES

The growth of *Balanus balanoides* in its natural environment has been studied by Hatton (*11*) at St. Malo, France. Rectangular areas of rock, situated at different tidal levels, were cleaned off in the early spring before spatfall. The number of barnacles on these areas and their growth in size was followed during a period of three years.

To avoid the influence of crowding during growth, the initial population density was not allowed to exceed 100 barnacles per square decimeter. The growth curve for the barnacles situated at three different intertidal levels is shown in Figure 9. Growth was very rapid during the first month, after which it proceeded very much more slowly. A second period of accelerated growth occurred in the spring of the second year. The populations on areas at the higher tide levels showed the least growth during the first months, but subsequently grew to greater size than those at lower levels.

The effect of seasonal differences in temperature on the rate of growth of barnacles is brought out in Figure 10. This figure shows the maximum size of three species of barnacles found on test panels following one month's immersion at different seasons of the year. The sizes are plotted against the average temperature of the water during the month of exposure. *Balanus improvisus* and *Balanus amphitrite* grow more rapidly as the temperature increases to about 25° C, when they reach a diameter of about 10 mm. in one month. No increase in the size attained is apparent at higher temperatures. *Balanus eburneus*, in contrast, continues to increase in size through the full range of temperature which prevailed.

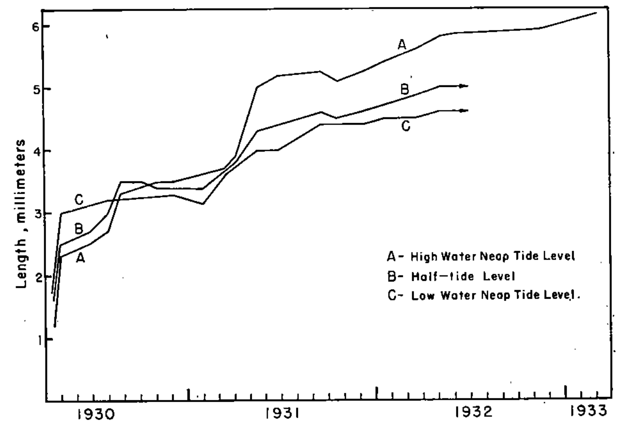

FIGURE 9. Growth curves of *Balanus balanoides* at three different tide levels at St. Malo, France. After Hatton (*11*).

The sizes attained by barnacles under natural conditions are further illustrated by data from navigation buoys. Table 1 shows measurements of the maximum size of several species collected from buoys which had been set for known periods in different locations along the United States coast. How long the buoys had been exposed before the barnacles settled is unknown. It may be seen, however, that diameters of 15 mm. were attained in several cases after one month's exposure, though few buoys developed barnacles more than

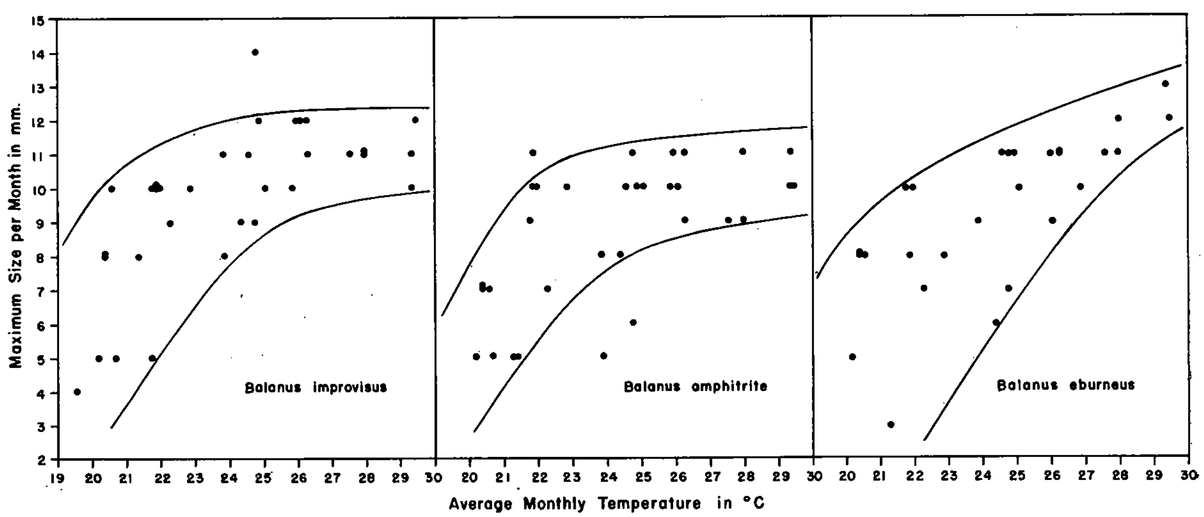

FIGURE 10. Maximum size attained by barnacles of three species on test panels immersed for one month; related to the temperature of the water during the period. Observations by C. M. Weiss at Miami Beach, Florida.

TABLE 1. Size Attained by Barnacles on Buoys and Test Panels. Size is Expressed as Greatest Diameter Measured in Millimeters. In the Case of Goose Barnacles it is the Length of the Body, Exclusive of the Stalk

Acorn Barnacles	*Greatest Diameter*	*Months Exposed*	*Period of Immersion*	*Locality*
B. amphitrite	17	11	Oct. '43–Sept. '44	Cape Lookout, N. C.
	15	1	July–Aug. '45	Miami Beach, Fla.*
	13	10	Oct. '42–Aug. '43	Fort Pierce, Fla.
	11	7	May–Dec. '43	San Diego, Cal.
	9	11	May '44–Apr. '45	Off Delaware Bay
	7	1	Jan.–Feb. '45	Miami Beach, Fla.*
B. balanoides	25	13	July '43–Aug. '44	Off Jonesport, Me.
	17	17	Feb. '43–July '44	Argentia, Newfoundland
B. crenatus	40	25	Nov. '41–Dec. '43	San Francisco, Cal.
	25	10	Oct. '41–Aug. '42	Off Baker Island, Me.
	21	38	Feb. '40–Apr. '43	Nantucket Sound, Mass.
	19	12	July '42–July '43	San Pablo Bay, Cal.
	19	10	Oct. '43–Aug. '44	Off Lapush, Wash.
B. glandula	18	9	Jan.–Oct. '43	Admiralty Inlet, Wash.
	10	7	Jan.–Aug. '43	San Francisco, Cal.
B. improvisus	23	18	May '42–Nov. '43	Norfolk, Va.
	16	11	May '44–Apr. '45	Off Delaware Bay
	15	1	July–Aug. '45	Miami Beach, Fla.*
	14	12	July '42–July '43	San Francisco, Cal.
	12	12	July '42–July '43	San Pablo, Cal.
	8	1	Jan.–Feb. '45	Miami Beach, Fla.*
B. tintinnabulum	44	10	Oct. '42–Aug. '43	Balboa, Panama
	40	16	Apr. '42–Aug. '43	Caribbean Entrance, Panama Canal
	40	25	Nov. '41–Dec. '43	San Francisco, Cal.
	36	7	Jan.–Aug. '43	Port Everglades, Fla.
B. eburneus	21	11	Oct. '43–Sept. '44	Cape Lookout, N. C.
	19	27	May '41–Aug. '43	Houston Ship Canal, Tex.
	17	19	June '43–Jan. '45	Woods Hole, Mass.
	16	8	Feb.–Oct. '43	Nawiliwili Reef, Hawaii
	15	1	July–Aug. '45	Miami Beach, Fla.*
	8	1	Jan.–Feb. '45	Miami Beach, Fla.*
Chelonibia sp.	40	5	Feb.–July '43	Matagorda Island, Texas
Tetraclita sp.	24	16	Apr. '42–Aug. '43	Caribbean Entrance, Panama Canal
	21	17	Mar. '42–Aug. '43	Lake Worth, Fla.
	16	18	Feb. '42–Aug. '43	Port Everglades, Fla.
	15	8	Apr.–Dec. '43	Los Angeles, Cal.
	14	8	Jan.–Sept. '43	Walker Cay, Bahamas
	13	18	Feb. '42–Aug. '43	Port Everglades, Fla.
Goose Barnacles				
Lepas sp.	50	12	Sept. '43–Sept. '44	Off San Francisco
	43	8	Oct. '43–June '44	Off Chesapeake Bay
	39	10	June '43–Apr. '44	Off Nantucket
	34	13	Aug. '42–Sept. '43	Bahamas
	33	13	Nov. '42–Dec. '43	Block Island, R. I.
	30	15	May '43–Aug. '44	Cape Lookout, N. C.
	30	5	July–Dec. '43	Off Santa Barbara, Cal.
	30	19	Jan. '42–Aug. '43	Key West, Fla.
	26	16	Apr. '42–Aug. '43	Caribbean Entrance, Panama Canal
	25	3	June–Sept. '43	Off Cape Flattery, Wash.
	21	10	Oct. '42–Aug. '43	Balboa, Panama
Conchoderma sp.	35	6	Feb.–Aug. '43	Key West, Fla.
	25	13	Nov. '42–Dec. '43	Block Island, R. I.
Mitella sp.	30	17	Feb. '42–July '43	Bonito Channel, San Francisco
	22	10	Oct. '42–July '43	Golden Gate, San Francisco
	14	8	Apr.–Dec. '43	Los Angeles, Cal.

* Data from test panels; data from all other localities are from buoys.

20 mm. in diameter during the first year. *Balanus tintinnabulum* and *Chelonibia* are larger species which reach about 40 mm. in diameter in the first six to twelve months. For the most part, the barnacles found on buoys exposed for longer periods are not larger than those on buoys exposed for one year.

THE BULK OF BARNACLE FOULING

The bulk of barnacle fouling is indicated by the weight of the material growing on a unit area of surface. Such measurements have been made from the growth on navigation buoys and are recorded in Table 2. As much as 5 or 6 pounds of barnacles may collect on a square foot of surface in less than a year. The heaviest collections are for the most part those for which the larger species, *Balanus tintinnabulum* and *Balanus crenatus*, are responsible.

LONGEVITY AND MORTALITY

According to Runnström's observations in Norway, *Balanus balanoides* ordinarily reaches an age of two years, but exceptional individuals may live to be three years old (*19*). At the Isle of Man, Moore found that these barnacles when living at the lower intertidal levels die in their third year, but at higher levels they may survive longer and may live for five or six years, or longer (*14*). The mortality rate of *Balanus balanoides*, based on a small number of observations on animals about four months old and older, was found by Moore to vary between 35 per hundred per year at midtide level and 3 per hundred per year at high water neap tide level. Similar values are given for the mortality rate of *Chthamalus stellatus* in which also the mortality varies with the tide level (*15*).

TABLE 2. Quantity of Barnacle Fouling on Navigation Buoys

Region	*Species*	*Exposure Months*	*Fresh Weight pounds/sq. ft.*
Gulf of Maine	*B. balanoides*	4	1.8
	B. balanoides	4	1.4
	B. balanoides	7	2.0
	B. balanoides	12	1.2
	B. balanoides	14	4.5
	B. balanoides & crenatus	10.5	0.7
	B. balanoides & crenatus	10.5	2.9
	B. balanoides & crenatus	14	3.8
	B. balanoides & crenatus	14	5.0
Seattle	*B. crenatus*	10	3.9*
	B. crenatus	10	4.5*
	B. crenatus	11	3.2
California	*B. tintinnabulum*	8	6.2
Florida	*B. tintinnabulum*	10	5.0
	B. tintinnabulum, amphitrite & others	17	4.0
	B. tintinnabulum, amphitrite & others	17	5.5
	B. improvisus, amphitrite & eburneus	4	2.0

* Barnacle fraction only from mixed fouling.

The survival of *Balanus balanoides* at different tide levels has also been studied in detail at St. Malo, France, by Hatton (*11*). As shown in Figure 11, at the two higher levels heavy mortality occurred during the first winter. After that the barnacles at the high tide level continued to live with few losses through the third winter; those at half-tide level died off during the second year. The population at low tide level, which was almost continuously submerged, died off steadily after the first summer and became extinct at the end of the second year. By inspection of the curves in Figure 11 it may be seen that in general the mortality is greatest at the time when the number of barnacles per unit surface is largest.

Hatton's observations have been submitted to

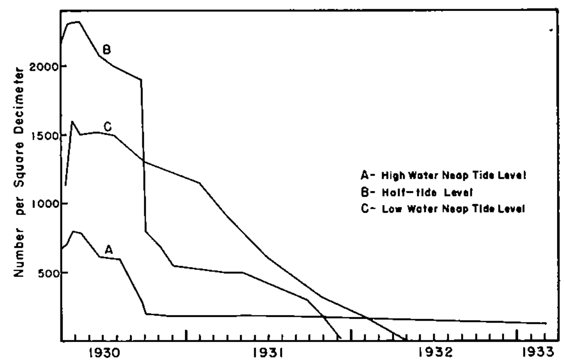

FIGURE 11. Survival of barnacles at different tide levels at St. Malo, France. After Hatton (*11*).

an elaborate statistical analysis by Deevey (*3*). Life tables have been prepared showing the mortality rate and expectation of further life of the barnacles at different ages and in the various situations where they grew. Hatton concludes that the population density has an effect on the survival of the barnacles, which have a shorter expectation of further life as crowding increases. This relation becomes less definite at advanced ages.

Observations on the longevity of other species of barnacles which live continuously submerged do not appear to have been made.

The life of the barnacle population is frequently terminated by natural causes other than crowding or old age. In northern waters, winter ice may be very destructive by grinding off the barnacles. Fish equipped with heavy teeth, such as the tautog, parrot fish, or sheepshead frequently feed on the barnacles growing on submerged rocks or on test panels. A more severe danger is overgrowth of the community by soft bodied organisms such as the tunicates, or by larger forms such as mussels, which eventually exterminate the barnacles. An example of such a temporal sequence is illustrated in Chapter 4, Figures 2 and 3.

THE IMPORTANCE OF BARNACLE FOULING

Barnacle fouling is important because the larvae settle in great numbers on newly exposed surfaces and grow so rapidly that the surfaces are covered completely in a short time. This type of fouling consequently is very evident on test panels which are examined at short intervals. On ships, barnacles are usually the first forms to appear in numbers if the protective paints are inadequate or become so. The firm attachment of barnacles to the surface also favors their persistence on ships in active use.

In situations where competing forms are absent or unable to attach and grow, as on active ships, the barnacle community may persist for several years, or permanently if replacement takes place. More commonly, however, the barnacle community is replaced by more massive forms such as mussels and tunicates. This often occurs on fixed installations such as buoys, and on ships which are laid up in harbor.

The Mussel Community

SPAWNING AND SETTLING

The larvae of mussels undergo a complete metamorphosis into the adult form before attach-

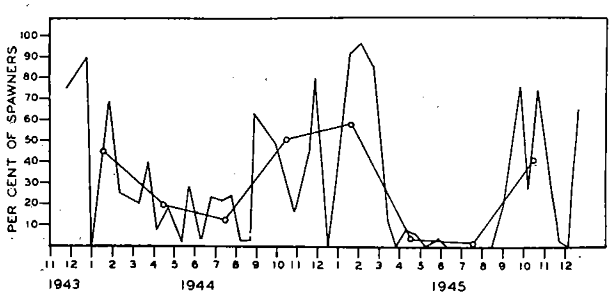

FIGURE 12. Season of spawning of mussels, *Mytilus californianus*, at La Jolla California. The smoothed curve was charted by averaging the percentages for three-month periods. From Young (*26*).

ment takes place. The larvae assume a form which, while still capable of swimming freely through the water, is protected by a completely formed bivalve shell. Like the adult, it attaches by secreting a byssus composed of tough threads with which it holds fast to the surface on which it settles.

The periods of spawning of *Mytilus californianus* at La Jolla, California, have been studied by Young (*26*). The numbers of mussels in condition to spawn at any time vary greatly from week to week, but show a distinct seasonal trend, as shown in Figure 12. Young's observations at several nearby locations, however, show great differences in the numbers spawning at any time and in the character of the yearly trend. Young reviews the observations of others on the season of spawning, which are in poor agreement, but states that in his observation there is a maximum spawning period between October and March, with infrequent spawning during all parts of the remainder of the year.

The settling of *M. californianus* follows spawning by periods of one to three months. There is consequently ample opportunity for the larvae to be carried great distances to infect new areas. The mussels range in size from 1 to 10 mm. in length at the time of settling. On the Atlantic Coast at Woods Hole, where the seasonal variation in temperature is more extreme, the larvae of *Mytilus edulis* are present early in June, and breeding continues on into September (*5, 7*).

GROWTH OF MUSSELS

The rate of growth of *Mytilus californianus* is shown in Figure 13. In contrast to the barnacle, *B. balanoides*, growth continues with only slight abatement during the second and third year. Growth curves for *Mytilus edulis diegensis* indicate that this form grows more rapidly than *M. californianus* during the first year, but at a much slower rate in later years (*1, 8*).

The growth of mussels is more rapid during the summer. This probably is due not only to the direct effects of temperature on growth but also to variations in the amount of food available at different seasons. Figure 14 shows the growth rate of *Mytilus edulis* at different times of year, and the associated temperature of the water at Woods

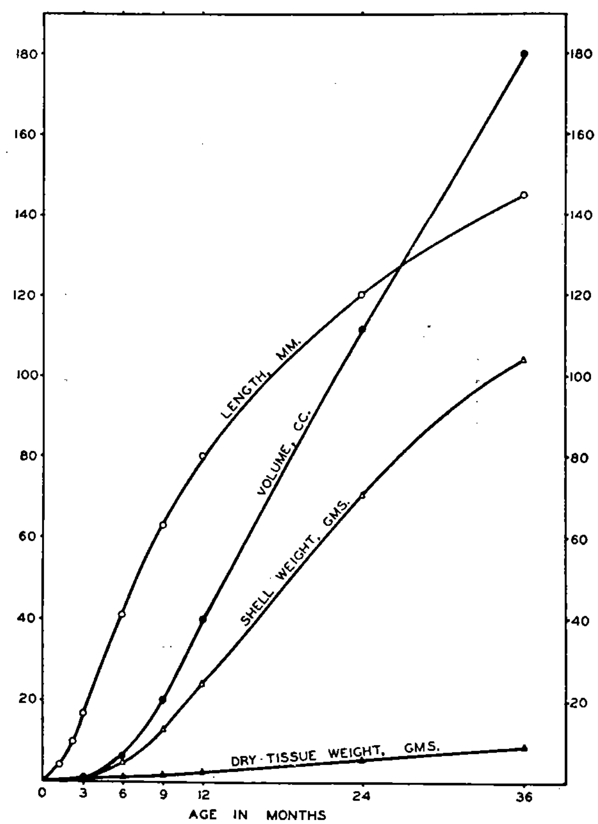

FIGURE 13. Average increase in length, volume, weight of shell, and of dry tissues during growth of *Mytilus californianus*. From Fox and Coe (*8*)

Hole where the observations were made. Figure 15 shows similar data for *M. californianus* growing at La Jolla, California (*17*). It may be noted that the seasonal variation in growth rate is much greater at Woods Hole, where the temperature fluctuates greatly in the course of the year. The growth curves do not follow the temperature cycle very exactly. This may indicate that some factor other than temperature, such as the nutrient supply, is influencing the growth rate.

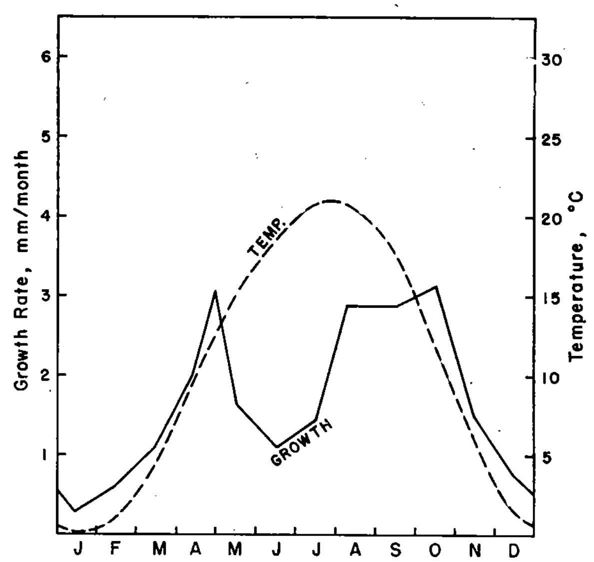

FIGURE 14. Growth rate of *Mytilus edulis* and sea water temperatures at Woods Hole, Massachusetts. Growth rates after Richards (*17*); temperatures after Sumner, Osburn and Cole (*21*).

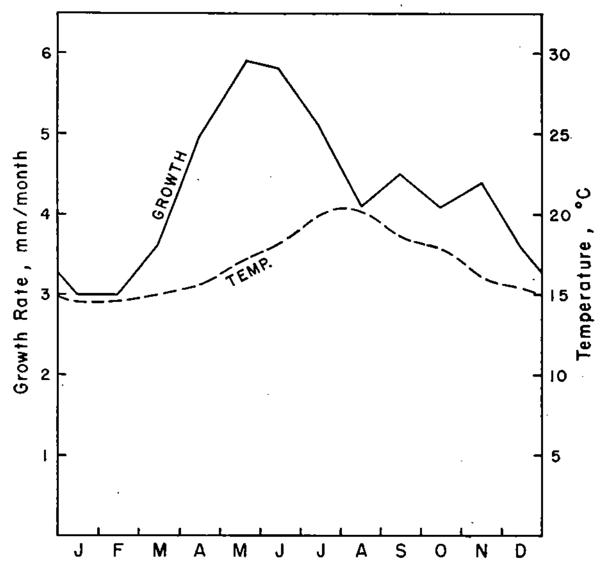

FIGURE 15. Growth rate of *Mytilus californianus* and sea water temperature at La Jolla, California. Growth rates after Richards (*17*); têmperatures from U. S. Coast and Geodetic Survey (*22*).

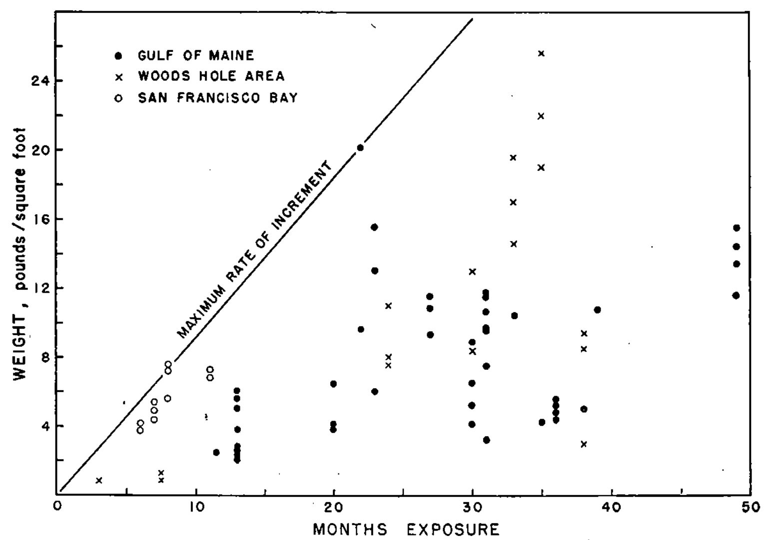

FIGURE 16. Weight of fouling dominated by mussels on navigation buoys related to time of exposure. After Hutchins and Deevey (*12*).

THE BULK OF MUSSEL FOULING

Observations on the *Mytilus* communities which grow on navigation buoys show how this type of fouling increases in bulk with time of exposure. Figure 16 shows the weight of fouling observed on a large number of buoys, plotted against the time during which the buoy had been set. The maximum rate of accumulation is 11 pounds per square foot per year, and the maximum weight recorded is nearly 26 pounds per square foot. There is much variation, and the average values are less than half of these maximum values (*12*).

The variation in the rate of fouling of buoys may be attributed to several causes, chief of which are the time of year at which the buoy was set and the temperature of the water throughout the period of exposure. On the Atlantic coast, buoys set during the winter do not begin to accumulate mussels until some time in spring when the water becomes sufficiently warm to favor attachment. Once established, the growth of the mussels is very much more rapid in the summer. The increase in

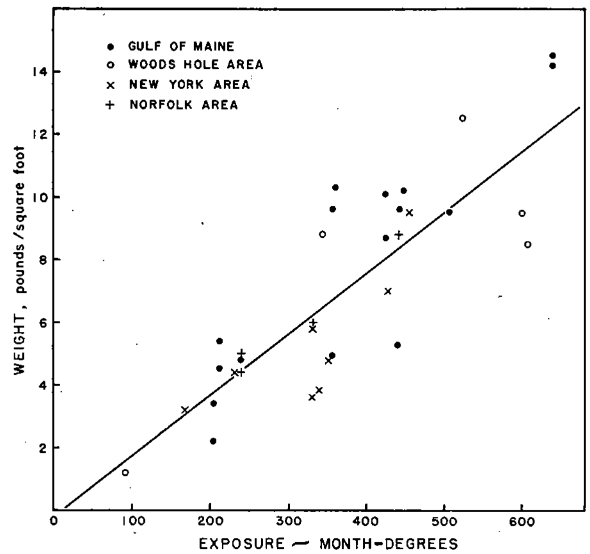

FIGURE 17. Weight of mussel fouling related to month-degrees of exposure. After Hutchins and Deevey (*12*).

fouling has been found to be related to the product of the duration of exposure and the average temperature in excess of 32° F during this period. This product is expressed as month-degrees and is symbolized by T_{32}. When the data from the East Coast buoys are plotted against the month-degrees of exposure, Figure 17 is obtained.

From these data an empirical equation has been developed from which the weight of fouling (in air), M_a, may be predicted from the seasonal temperature of the water as follows:

$$M_a = -0.18 + 0.019\ T_{32}$$

Figure 17 indicates that variations from the prediction of about 50 per cent are to be expected. A number of alternate equations, based on different assumed values for the minimal temperature at which growth will occur, were tried but did not significantly improve the correlation.

From the foregoing equation it is possible to estimate from hydrographic data the expected

TABLE 3. Estimated Yearly Accumulation of Mussel Fouling

Location	*Mean Yearly Temperature °F*	*Month-degrees per Year*	*Estimated Fouling lbs./sq.ft./yr.*
Mount Desert Rock	44.7	152	2.72
Boston Lightship	48.3	196	3.55
Fire Island Lightship	52.9	251	4.61
Winter Quarter Lightship	57.5	306	5.65

rate of accumulation of mussel fouling at different places along the coast. Such estimates are given in Table 3, which shows that very substantial differences are to be expected because of the characteristic temperatures of the water in different localities.

A secondary cause for variation in the rate of increase in *Mytilus* fouling appears to be the strength of the tidal currents in which the buoys are set. A limited number of buoys examined by Hutchins and Deevey were fouled very much more heavily than those entered in Figure 17. These were located in positions where mean tidal currents stronger than one knot occur. The rate of increase in the fouling on these buoys and on a number of others which fouled at normal rates is entered in Table 4, together with the mean tidal

TABLE 4. Relation of Rate of Increase of Mussel Fouling to Velocity of Tidal Currents in the Woods Hole Region. Calculations Based on Data of Hutchins and Deevey (*12*)

Name of Buoy	*Mean Current Knots*	*Rate of Increase**
Chatham Lighted Whistle #6	1.02	0.055
Bearse Shoal Lighted Gong #6	1.34	0.047
Old Man Ledge #3	—†	0.044
Pollack Rip Lighted Whistle PR	1.23	0.033
Quicks Hole Bell #1	1.62	0.032
Nantucket Bar Bell	1.02	0.027
Naushon Lighted Bell #20	1.48	0.026
Fifteen Foot Shoal #9	0.95	0.024
Buzzards Bay Lighted Bell #7	0.28	0.019
Gong beside following entry	0.29	0.016
Buzzards Bay Traffic Lighted Buoy #6	0.29	0.014
Block Island Sound Approach Lighted Bell V	0.41	0.013
All Atlantic Coast Buoys—average	—	0.019

* Rate of increase in pounds per square foot per month-degree.
† Tidal current exceptionally strong in this area. No current data available.

current characterizing their location. The table indicates that the rate of fouling is correlated with the strength of the tidal current. Presumably this is because the rapid flow of water improves the nutrient condition to which the mussels are exposed.

Unlike most fouling organisms, mussels are able to move about after they have become attached to a surface. As a result, those which settle on spots which are crowded can move into more favorable positions. New generations of mussels frequently attach to the shells of the larger individuals which have become established earlier. (See Figure 5.) If there is room they tend to occupy the spaces between the larger mussels; if not, they build up an outer layer of shells attached to those growing beneath. Thus the layer of fouling may become much thicker than the length of the largest mussels. Mussel fouling on navigation buoys usually forms a layer about 2 inches thick, but in the cases of the most heavily fouled buoys the thickness is frequently as great as 6 inches, and occasionally as great as one foot.

There is a statistical relation between the weight of the mussel fouling and the thickness. Roughly speaking, the thickness in inches is given by one-third the weight in air in pounds. It may be estimated from Table 3 that the annual increment in thickness of mussel fouling on the Atlantic coast will vary from about one inch at Mt. Desert Rock to two inches at Winter Quarter Lightship.

LONGEVITY AND MORTALITY

While individual mussels and the communities which they form have been shown to grow continuously in bulk for two or three years, little is known of the later life of such communities. Field states that ordinarily the time required for *Mytilus edulis* to attain a length of 3 inches is five to seven years (*6*), but data on the longevity of mussels is lacking. Natural mussel beds are subject to many dangers. Frequently they are covered by shifting sand, or damaged by ice and by freezing. Small mussels are a favorite food of the sea ducks (Scooters and Eiders), which may collect in great numbers to feed on a freshly established bed. Larger mussels are destroyed by starfish, oyster drills, and other gastropods.

Scheer considered mussels to be the climax community in the fouling of floats at Newport Harbor (*20*). The relatively large size and motile powers of the mussel protect it somewhat from overgrowth by competing species, though it is notably absent from situations where large masses of tunicates, sponges, and anemones occupy the surface. Smaller varieties of fouling, such as barnacles and tube worms, may settle and grow on the mussel shells without doing obvious harm, and large numbers of free living invertebrates find shelter between the mussels.

THE IMPORTANCE OF MUSSEL FOULING

Compared to the barnacle community, mussel fouling develops very much more slowly and represents a more permanent stage in the biotic succession. Mussel fouling is relatively unimportant on ships, since it usually does not have an opportunity to develop unless the ship is laid up for some months in port. Within its natural range, however, it is the characteristic fouling of fixed installations; that is, of those structures such as buoys, mines, nets, and sea water conduits which remain submerged long enough to permit this climax community to develop.

WHAT DETERMINES THE LOCAL INTENSITY OF FOULING?

Ship operators have long recognized certain places as "clean ports" or "foul ports," depending on the severity of fouling. What can one say about the biological factors on which this separation is based?

In many cases fouling is light because the port is situated in the estuary of a fresh-water river, or because the water is so heavily polluted that fouling cannot grow. Both these conditions exist, for example, at the Philadelphia Navy Yard. The effects of such local factors as salinity, pollution, and distance from shore will be discussed in Chapter 8.

High water temperature increases the rate at which fouling develops. This is one of the reasons why severe fouling is frequently associated with tropical ports, where even a short sojourn may result in a heavy growth. In the tropics, fouling occurs at any season, while in temperate latitudes the period during which growth is apt to start is relatively short, being limited to the period of high temperatures. Massive fouling can develop in such regions, however, if given time for undisturbed growth. Such seasonal variations in the spawning habits of the fouling organisms have been considered in the preceding chapter.

In addition to these general regional factors to which the intensity of fouling may be ascribed, there exist differences between nearby areas which are more difficult to explain. Thus, in southern Florida fouling of test panels is much more severe at Miami than at Key West. This difference may be due to the great quantity of marl suspended in the water at Key West. At Miami, furthermore, equally great differences exist in the fouling of test panels at various positions within Biscayne Bay. Thus fouling has been found repeatedly to be many times more heavy at Miami Beach than at Tahiti Beach, located on the mainland side of the Bay and several miles south of the city of Miami. Figure 18 shows simultaneous records of fouling on test panels at these two sites for a period of over a year. There is no significant difference in the species collected at these two positions, though there is some difference in the relative importance of different species. Barnacles dominate at Miami Beach, while the tube worm, *Hydroides parvus*, is predominant at Tahiti Beach in the spring and fall. The barnacle set at Tahiti Beach is occasionally very large, but the barnacles grow slowly and suffer a high mortality so that few develop beyond the 3 mm. size (*23*).

A survey of fouling on test panels exposed more generally throughout the Biscayne Bay area indicates that conditions of light fouling, similar to that observed at Tahiti Beach, is characteristic of the southern part of the Bay, which is in relatively free communication with the open sea. The northern part of the Bay, on which Miami Beach is located, is somewhat cut off from the sea by a series of causeways and islands. The water is somewhat polluted, is turbid with suspended detritus, and is moved by strong tidal currents. These factors suggest that the nutrient conditions are better in the northern part of the Bay. In addition this part is heavily bulkheaded, which supports a large population to keep up the supply of larvae for new attachment.

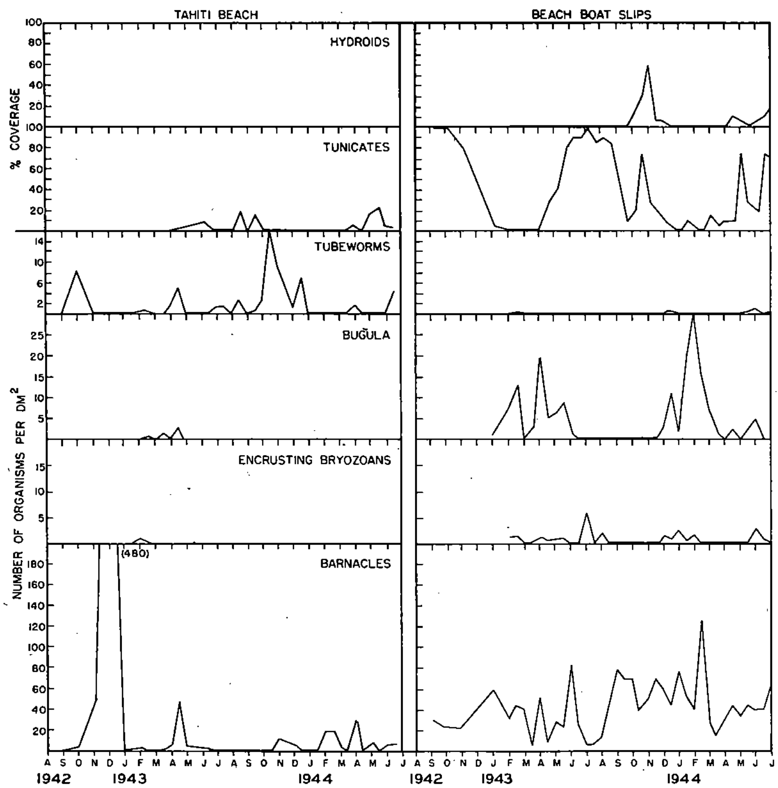

FIGURE 18. Comparison of fouling observed simultaneously at Beach Boat Slips, Miami Beach and Tahiti Beach.

THE NUTRITION OF FOULING ORGANISMS

Sedentary marine organisms obtain their food from the water which surrounds them. Plants absorb nutrients such as phosphates, nitrates, and carbonates which are in solution in the sea water, and convert them into organic matter with the aid of the energy of sunlight. The seaweeds do not, like land plants, obtain nourishment from the substratum. Their roots act simply as holdfasts. The organic matter produced by plants is the basic source of food for the animals. In producing this food the fixed seaweeds of the seashore are relatively unimportant, since they occupy a limited zone along the margin of the ocean. Of greater importance are the microscopic plants which live suspended in the waters near the surface.

The sessile animals which make up the bulk of fouling feed upon organic matter which is brought to them by currents. This may consist of living microscopic organisms, such as bacteria, diatoms, or protozoa, or of detritus which is composed of fragments of dead animals and plants. Different animals have different methods of collecting this material from the water. In general they are unable to select the kind of material ingested, and may take in many particles which prove to be indigestible.

The nutrition of the mussel has been carefully studied by Fox and Coe (*8*). They estimate that at La Jolla the living organisms present in the water filtered by the mussel are scarcely sufficient to account for the new organic matter synthesized in growth and in the production of eggs and sperm. They conclude that large quantities of organic matter present in the form of cell fragments, chloroplasts, starch granules, and the like, and perhaps of particles ranging in size down through substances of colloidal status or even those in true solution, must be drawn upon to supply the food which is required to meet the energy needs of the mussel. There is no evidence that mussels can extract dissolved organic matter directly from the sea water, and the lower limit of particulate size which can be concentrated and utilized by the mussel has not been established. The estimates indicate that a large fraction of the organic material present in the water filtered is not utilized, either because it is not passed through the gut, or because it proves to be indigestible.

A balance sheet for the exchange of nutrient material between sea water and a mussel during the second year of its life, selected from Fox and Coe's data, is presented in Table 5.

THE PRODUCTIVITY OF FOULING COMMUNITIES

A few simple principles control the nutritional relations of animals in the sea and help in understanding what limits the intensity of fouling. Animals require a certain quantity of energy, absorbed in the form of food, in order to keep alive and carry out their necessary activities. Growth requires additional sources of food to provide the materials needed for the formation of new tissue. As a rough rule we may say that only about 10 per cent of the food absorbed can be used for growth; the remainder is oxidized in meeting the needs of vital activity.

The food of animals is supplied by the plants. Animals cannot exist in greater numbers than can be fed by the plants being produced to supply their food. If the plant production is limited, the animal population may be kept at a low level for lack of necessary nourishment, and there may be little food available to provide for growth. If food is more plentiful, growth will lead to crowding, and this will limit the bulk of animal fouling which can develop. The relation between the actual standing crop of fouling which develops and the food supply may not be very close unless food is distinctly scarce.

A more exact relation is to be expected between the food supply and the rate of growth, or productivity, of the fouling. In general it may be expected that one-tenth of the food consumed will be used productively in the growth of the fouling community.

The rate of production of organic matter, which serves as the food source of marine animals, is controlled by the quantity of light falling on the sea's surface, by the hydrographic conditions which limit the rate at which the nutrient salts of sea water become available near the sea surface, and by the size of the standing crop of marine plants which absorb the light and nutrients, converting them into new organic matter. Estimates indicate that the pelagic plants produce from 0.1 to 2 kilograms of organic matter per year for each square meter of the sea's surface (*18*). Estimates of this character are not very exact, but they are supported by more direct observations on the rate of growth of algal communities in shallow water. Several algal associations show annual productivities of about 1 kilogram dry weight per year (*9*). The rock weed, *Fucus vesiculosus*, may grow at a rate of 5 kilograms per square meter per year and develop a standing crop of 10 kilograms per square meter. On buoys much heavier growths of kelp may occur. Thus, on a buoy set for one year off Boon Island, Maine, the growth of kelp and other algae weighed, fresh, 40 kilograms per square meter.

TABLE 5. Estimated Balance Sheet for Exchange of Organic Matter Between a Mussel and the Sea During the Second Year of Life. After Fox and Coe (*8*)

Sea water filtered		22,000 liters
Intake		
Organic matter present as		
Dinoflagellates	4.2 grams	
Diatoms	0.67 grams	
Bacteria	0.05 grams	
Detritus and in solution	105.0 grams	
Total	110.0 grams	(100%)
Utilization		
Formation of New Tissue	1.6	
Formation of Sex Products	2.7	
Oxidized	38.0	
Total Utilized	42.3	(38%)
Not Utilized		
Excreted as Faeces	26.0	
Not accounted for*	41.7	
Total Not Utilized	67.7	(62%)

* Presumably discharged in exhalent water.

It is interesting to compare the actual productivity of mussel communities with the estimated rate of food production by pelagic plants. If this amounts to 1 to 2 kilograms of organic matter per square meter of sea surface per year, and if 10 per cent is converted into animal matter by the mussels, then 100 to 200 grams of animal matter should be produced per year.

Uncultivated mussel beds in the British Isles are reported to produce about 1.09 kilograms of mussels per square meter per year, or about 40 grams of organic matter. Cultivated beds produce as much as 150 grams of organic matter (*6*). These figures are consequently quite in line with the productivity estimated from the plant production.

Mussel fouling on buoys, in conduits, and on ships frequently yields much higher figures for productivity, however. The average increase in weight of mussel fouling on buoys on the Maine coast is about 13 kilograms per square meter per year; off Virginia it is 28 kilograms. Mussels growing in the salt water intake tunnels of a powerhouse at Lynn, Massachusetts, have been observed to grow in weight to 64 kilograms per square meter in 21 weeks. On test blocks the accumulation of general mixed fouling over monthly periods had the following average values:

San Diego, California	25 kg/m²/year	(*25*)
Port Reyes, California	7.4 kg/m²/year	(*13*)
Norfolk, Virginia	13.2 kg/m²/year	(*24*)

Ships rarely are permitted to develop maximum crops of fouling. Lightships, however, provide noteworthy records as follows:

Elbe Lightships	40 kg/m² in 11 months
New York Lightships	23.5 kg/m² in 15 months
New York Lightships	21.6 kg/m² in 16 months

When such figures as those quoted above are translated into production of organic matter and compared with the food supply available per square meter of sea surface, it is evident that the communities growing on fouled structures avail themselves of much more organic matter than is produced, *on the average*, in the volume of water which they occupy. Two considerations may serve to explain this finding. In the first place the fouling communities consume large quantities of food brought to them from other parts of the sea where there is no great quantity of animals to consume the food matter locally produced. This is why currents favor the growth of fouling. In the second place fouling growth may occur in specialized localities where the production of organic matter by plants is much greater than average, or even where land and fresh water may contribute to the detritus utilized by the marine animals of the fouling community.

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