Marine Fouling and Its Prevention,
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CHAPTER 4

Temporal Sequences and Biotic Successions

Fouling communities may be understood only in terms of their development. The population present on a surface exposed in the sea changes with time as the result of a variety of influences. On a newly exposed surface, microscopic organisms appear first and multiply rapidly. Later the more rapidly developing macroorganisms may cover the surface only to be replaced by more slowy developing forms which crowd out the first comers. There is thus a *temporal sequence* in the development of the community.

There is reason to believe that the presence of a population of one type may facilitate the subsequent development of other species. Temporal sequences controlled by biological relations of this sort are called *biotic successions*. Finally, the sequence in which organisms appear in the fouling is influenced by the time of the year at which a structure is exposed, since different organisms reproduce at different seasons and attachment can take place only when their larvae are present in the water. The *seasonal sequences* which result differ greatly according to the geographic location.

TEMPORAL SEQUENCES

On a newly exposed surface the fouling process usually begins with the formation of a slime film which is produced by bacteria and diatoms. The bacteria attach and grow rapidly; their numbers on each square centimeter of surface may reach one hundred in a few minutes, several thousand in the first day, and several million in the first forty-eight hours. Algae and diatoms are uncommon during the first two or three days, but then may develop rapidly so that several thousand per square centimeter may be present within a week. Protozoa follow. They are generally uncommon during the first week and reach their maximum growth by the end of the second or third week. A typical example of the sequence of these forms on a freshly exposed plate is shown in Figure 1. Depending upon local conditions, each form may persist at a high population level, or may decline to a lower level.

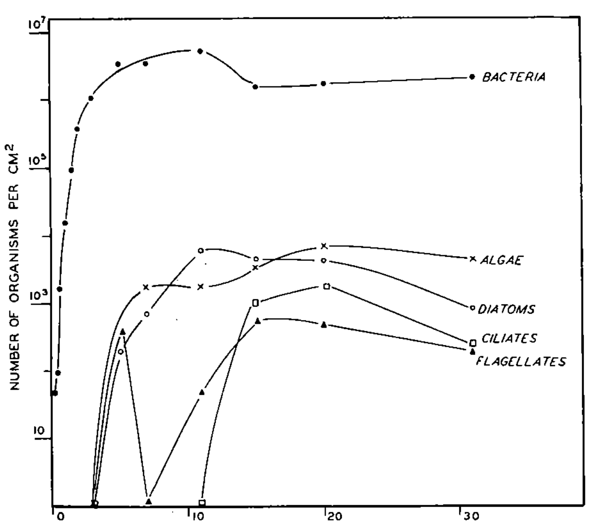

FIGURE 1. Temporal sequence of bacteria, algae, and protozoa in the slime film developing on a surface immersed in the sea.

A similar sequence may also be observed in the appearance of the larger forms which make up the bulk of fouling. The first to attach will be those species whose swimming larvae are present in the water at the time of immersion. They will vary in kind according to their seasonal breeding habits. Rapidly growing forms, which become noticeable first, may ultimately be crowded out by others which grow more slowly.

A temporal sequence of this sort is illustrated in Figure 2, which shows the history of a community of barnacles (*Balanus improvisus*) on a test panel at Miami. After four weeks' exposure the panel was covered uniformly with barnacles of various sizes. At the end of ten weeks a few tunicates appeared growing over the barnacles. At the sixteenth week the tunicates had increased in numbers and size. The barnacle shells were larger, but much fewer in number. Most of the shells were unoccupied, the animals having died and disintegrated. A few large solitary tunicates had also appeared. By the twenty-sixth week tunicates and bryozoa completely dominated the community and the barnacles were buried beneath them. Figure 3 shows in greater detail a community of barnacles which has been almost completely covered by a layer of colonial tunicates.

BIOTIC SUCCESSION

Among terrestrial plant communities it is well established that one type of vegetation may modify the soil or in other ways prepare a situation favorable for a succeeding community of plants. Thus in the eastern United States denuded rock

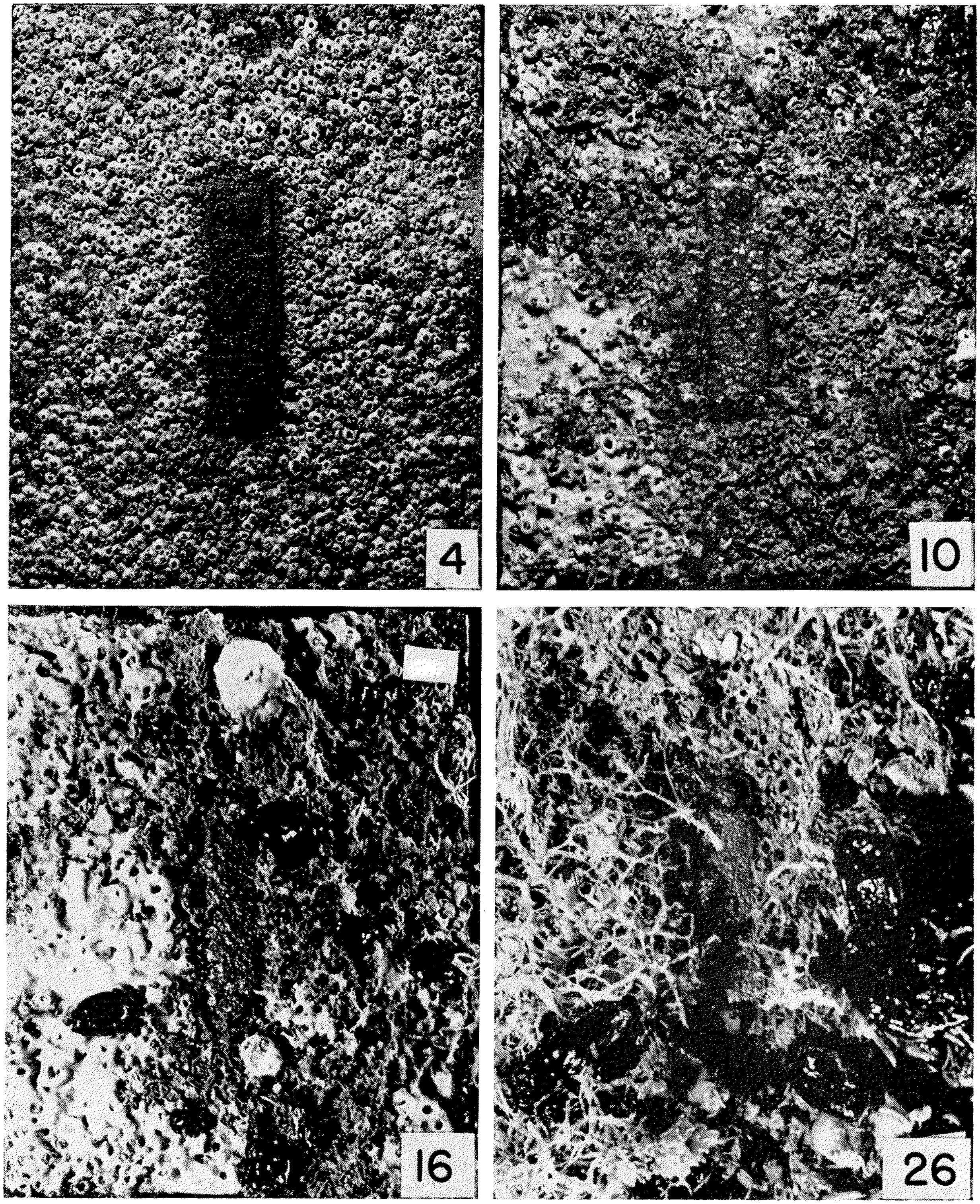

FIGURE 2. History of a community of barnacles, showing its replacement by tunicates and bryozoans in the course of one half year. Numbers indicate the duration of exposure in weeks. Photos by C. M. Weiss at Miami Beach, Florida.

may first be populated with lichens, followed in turn by grasses, pines, an oak-hickory forest, and finally by a climax community in the form of a maple-beach-hemlock forest. The climax is a final stage so stable that no further change is to be expected. The climax community developed in a given place will be the same, regardless of the particular temporal sequences which may precede it.

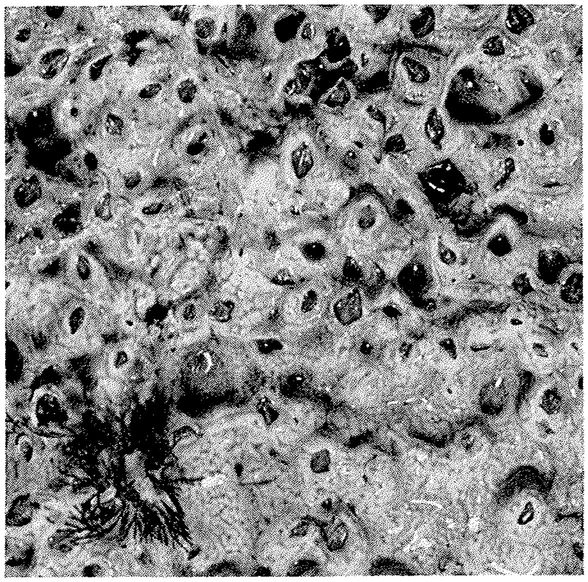

FIGURE 3. A population of barnacles which has been almost completely covered by colonial tunicates. Natural size. Photo by C. M. Weiss at Miami Beach, Florida.

Efforts to establish similar successional relations between the animal communities of the sea bottom have been repeatedly attempted (*4*, *7*, *18*). In the sea, in contrast to the land, the character of the bottom is not greatly modified by the activities of organisms, and the conditions which determine the kind of community present change little with time. Consequently it is doubtful whether the pattern of communities found on the sea bottom is the product of biotic succession. However, in the development of a new community on a bare surface there is evidence that a rapid type of succession takes place. This succession culminates in a community which may be regarded as a climax which is characteristic of the particular substratum and locality.

Brooks (*2*) stated in 1880 that the surface should be rough and clean to permit the attachment of young oysters. Later investigators have found that the presence of the slime film influences subsequent attachment of larger fouling forms. Some have claimed that its presence is essential. If true, this would be a real case of biotic succession. There has been much discussion but little critical investigation of this matter.

Some experiments by Phelps (*15*) indicate that the presence of a slime film on a submerged surface may favor the attachment of barnacles. In these experiments one panel was exposed continuously so that slime and a barnacle population developed on it. Each day a fresh, duplicate panel was also exposed. The numbers of cyprids attaching each day to the continuously exposed panels are compared, in Table 1, to the daily attachments to the fresh panels. During the first three days greater numbers of barnacles appeared on the fresh panels than on the panel which had been permitted to accumulate slime. After this time the attachments to the slimed panels increased until, in one experiment, these panels accumulated about twenty times as many new barnacles each day as the fresh panels. After about the tenth to fifteenth day the population of barnacles on the continuously exposed panel declined. Although cyprids were observed on the panel after this time, the loss of metamorphosed barnacles was greater than the new attachments.

These experiments indicate that the presence of a slime film on a glass panel favors attachment of barnacle larvae. The fact that Phelps observed attachments on freshly exposed panels shows that

TABLE 1. Comparison of Attachment of Barnacles to Slimed and Fresh Glass Panels (*15*)

Exposure Days	*Slimed Panels*: *Total Attachments No./cm²*	*Slimed Panels*: *Additional Attachments No./cm²/24 hrs.**	*Fresh Panels Daily Attachments No./cm²/24 hrs.*	*Ratio Daily Attachments Slimed/Fresh*
2	0.16		0.18	
3	0.18	0.02	0.28	0.07
4	0.66	0.48	0.24	2.0
5	1.01	0.35	0.09	3.90
6	3.36	2.35	0.11	21.4
8	9.55	(3.10)	0.13	23.9
9	8.61	—	0.32	—
10	10.38	1.77	0.28	6.33
15	7.28	—	0.12	—
19	6.02	—	0.27	—
2	0.20		0.22	
3	0.21	0.01	0.18	0.06
4	0.63	0.42	0.24	1.75
5	0.92	0.29	0.31	0.94
6	2.08	1.16	0.36	3.23
8	3.02	(0.47)	0.09	5.23
9	3.84	0.82	0.25	3.29
10	4.41	0.57	0.43	1.33
15	7.57	(0.63)	0.42	1.50
19	6.00	—	0.36	—

* Values in parentheses have been reduced from a longer exposure to a 24-hour basis.

TABLE 2. Attachment of *Bugula* larvae to Slimed and Cleaned Non-toxic Surfaces (*11*)

Surface	*Age of Slime Weeks*	*Number Attached to*: *Slimed Surface*	*Number Attached to*: *Cleaned Surface*	*Ratio Slimed:Cleaned*
Paint A	4	72	19	3.8
Paint A	4	79	5	15.7
Paint A	10	95	48	2.0
Paint B	4	90	6	15.0
Paint B	10	56	6	9.3
Paint C	4	165	77	2.1
Paint C	4	55	12	4.6
Glass	6	45	4	11.2
Glass	6	65	23	2.8

the slime is not, however, *essential* for their attachment. This is further emphasized by the observations of Clarke (*3*), who obtained substantial numbers of cyprid larvae attaching to glass panels within an hour of exposure.

Miller and co-workers (*10, 11*) studied the attachment of larvae of *Bugula neritina* to nontoxic surfaces. They concluded that the presence of the slime film facilitated but was not essential for the attachment of this organism. In tests where both slimed and nonslimed surfaces were used, i.e., where the larvae had a choice of surface on which to settle, greater numbers of attachments occurred on the slimed surfaces. In some cases the numbers indicated a fifteenfold preference for the slimed panels. Examples from their data are given in Table 2. In other experiments in which no choice was given, and in which only one surface was presented for attachment, the larvae were found to attach in a shorter time to those surfaces which were covered with slime.

Whedon (*19, 20*) states that the presence of a slime film facilitates the attachment of Ciona larvae to glass panels, and that experiments with *Balanus tintinnabulum* gave similar results. The data on which these conclusions are based are not presented.

Scheer (*17*) has found that the numbers of erect bryozoans (mostly *Bugula neritina*) which settle on glass panels increase after the first weeks, when a slime film has had time to develop. Frequently no attachments occurred on a panel during the first two or three weeks of exposure, although many bryozoans settled on older panels during the same period. This evidence is shown in Table 3. These observations, made under natural conditions, indicate a greater influence of the slime film than was found in the laboratory by Miller. Scheer was able to show, furthermore, that the properties of the slime favorable for bryozoans can be attributed to an algal population consisting mainly of diatoms. Bacterial films were allowed to develop on panels in the laboratory, and the panels were then suspended in the sea. Although hydroids settled more abundantly on the surfaces coated with a bacterial slime than on clean surfaces, the attachment of bryozoans and ascidians was not increased. A diatom population developed on the panels after immersion in the sea, whereupon the surface appeared to become more suitable for the attachment of the bryozoans and ascidians.

TABLE 3. Number of New Settlements of Erect Bryozoans on Glass Plates during Successive Two-week Periods, 1944, at Newport Harbor, California (*17*)

Date Examined	*Date of Original Exposure*												
	Jan. 17	*Jan. 31*	*Feb. 14*	*Feb. 28*	*Mar. 12*	*Mar. 27*	*Apr. 27*	*May 9*	*June 8*	*July 6*	*Aug. 1*	*Sept. 11*	*Oct. 10*
Mar. 27	0	0	0	0	0								
Apr. 8	4	0	0	0	0	0							
Apr. 26	11	10	10	0	5	0							
May 9	20	29	28	35	48	3	0						
May 24	5	4	6	—	17	18	0	0					
June 7	11	18	7	22	14	17	5	10					
June 21	21	27	36	24	—	27	72	44	2				
July 6								40	5				
July 17									28	12			
July 31									33	3			
Aug. 14									28	11	1		
Aug. 28										13	4		
Sept. 11											9		
Sept. 25											19	1	
Oct. 10											18	0	
Oct. 23													1

Several other authors have found that a growth of diatoms facilitates the attachment of larger forms of algae (*1, 21, 22*). Coe and Allen (*5*) observed that fouling is heavier on previously fouled panels after scraping than on clean surfaces, and attributed this result to "a more favorable physical surface, resulting from the retention of microscopic organisms and minute particles remaining from the previous growth."

Although most of the work on biotic succession has centered on the relation of the slime film to subsequent fouling, important interrelations between organisms are not confined to this single step. Some of the macroscopic forms may provide favorable conditions or otherwise influence the attachment of others.

According to Scheer, the development of communities on the bottom of floats at Newport Harbor, California, normally follows one of the sequences shown in Figure 4. These sequences were observed under natural conditions, and since most of the forms were found on some surfaces at all times of the year, Scheer concludes that the succession is nearly if not entirely independent of seasonal variations. Mussels were observed to settle only on surfaces bearing a bryozoan, Ciona, or Styela community. Together with Saxicava, sponges, and ascidians, the mussels appeared in measurable quantities only on plates exposed for

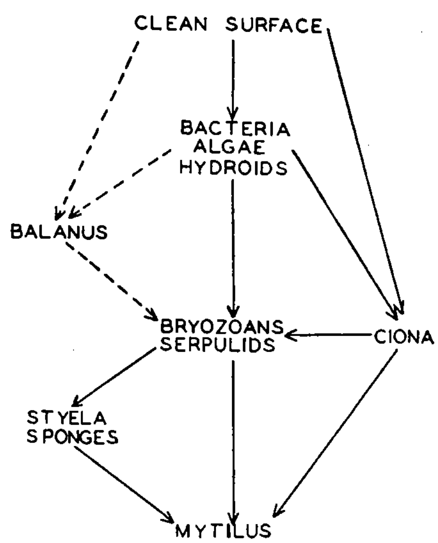

FIGURE 4. Sequences of dominant organisms on surfaces exposed in Newport Harbor, California. From Scheer (*17*).

twenty weeks or longer. Thus the presence of a bryozoan community seems to favor the attachment of mussel larvae. The growth of the mussels effectively covers the bryozoan community, which then perishes. Barnacles, on the other hand, appeared to settle irregularly without any relation to the duration of exposure, and thus their attachment did not seem to be favored by other communities, including the slime film. This conclusion contrasts with the observations of Phelps. Scheer considers that the Mytilus community represented a climax in the float-bottom associations of Newport Harbor.

Hewatt (7) removed the mussels (*M. californianus*) from an intertidal area in Monterey Bay, and found that the limpets and barnacles which normally lived at higher levels extended their range downward into the bare area. The species which depend on mussel beds for shelter were absent from the area for over a year. The mussels gradually returned, and with them their associated species, eliminating the barnacles and limpets. The reconstitution of the mussel community required more than two and one-half years. Compared to the rate of development of the plant climax on land, this is a very short period.

At St. Andrews, New Brunswick, in seasons favorable for the development of the Balanus-Mytilus association, surface conditions such as the accumulation of shells on the beaches permit the establishment of heavy sets of mussels. These spread rapidly and form a surface layer that kills the clams (*Mya arenaria*) and alters the physical and chemical conditions in the subsurface layers. Newcombe (*14*) concluded that this constitutes true succession in a marine community

According to Hatton (*6*), the sporelings of Fucus have a better chance of establishing themselves in the moist environment provided by a carpet of Enteromorpha than when they settle on bare rock exposed to the sun at low tide. The Fucus chokes out the Enteromorpha eventually, and is in turn choked out by Ascophyllum, the attachment of which is similarly facilitated by a mat of Fucus.

The growth of *Balanus balanoides* is inhibited in the immediate proximity of fucoids, such as Ascophyllum, by the mechanical action of the waves in rubbing the fronds over the surface of the rock (*8*). In this way fucoids can control the habitat to the extent of excluding the barnacles. On the other hand, Hatton (*6*) has shown that growing barnacles can eliminate young Fucus by "nipping their feet."

In conclusion, it appears that several authentic cases of biotic succession in sedentary communities have been described. It must be pointed out, however, that seasonal succession will dominate the picture in many cases, so that true biotic succession will be difficult to recognize. In this connection it may be significant that a high proportion of the evidence for biotic succession comes from the Pacific coast of North America (*5*, *7*, *17*, *21*), where seasonal phenomena are less pronounced than elsewhere in the temperate zone. Where seasonal variations are large, biotic succession may not be obvious (*9*, *12*, *13*, *16*).

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