CHAPTER 7

Geographical Distribution

Fouling varies greatly from place to place, both in the kinds of organisms and in the intensity of their growth. The differences are of two sorts: the broad, regional differences discussed in this chapter, and the variations observed on a more local scale within each large area. Different sorts of environmental factors are to be emphasized in interpreting regional and local distributions. On a regional scale, general geography, temperature, and currents are the factors of primary importance. Features such as salinity, pollution, and the detailed circumstances of exposure affect the fouling on a more local scale and are discussed in Chapter 8.

REGIONAL DIFFERENCES IN SHIP FOULING

Ships from different areas exhibit marked differences in fouling. Hentschel (5) examined the fouling on 48 ships docked at Hamburg, tabulating the species according to the general parts of the world to which the ships had voyaged. Ships from each region had a distinctive combination of forms. Individual species differed greatly in range of occurrence, some being limited to only one area, while others were common to several regions, such as the tropics at large. Genera and higher systematic units were usually more widely distributed than their constituent species.

Hentschel concluded that similar fouling was found on ships from the European and American North Atlantic. Except in the case of inactive ships, it was light, and frequently was composed largely of algae. Fouling of Mediterranean origin averaged more species per ship, and was in general more severe, though less so than that of the tropics. Hydroids and serpulid worms were found on about half of the ships from the Mediterranean. In the tropics, fouling was both varied and severe, but differed on different coasts. The Indian Ocean and tropical Pacific produced the most varied fouling. Tube worms were especially characteristic, however. In eastern Asia the variety of forms was less, and the barnacle fouling not as severe as in the tropics. The most unique feature of the fouling of ships from the Pacific coast of South America was the presence of the very large barnacle, Balanus pustulatus, which is endemic to that coast.

In addition to determining the average numbers of all species found per ship, Hentschel also measured the average number of barnacles present per unit area of ship bottom, and their maximum diameter. The data for the chief regions are given in Table 1. It appears, for example, that on ships from the West African tropics the barnacles are both numerous and large, whereas on ships from

<table>
<thead>
<tr>
<th>Region</th>
<th>No. Ships</th>
<th>Av. No. of All Species per Ship</th>
<th>Av. No. of Barnacles per 100 cm²</th>
<th>Av. Maximum Diameter of Barnacles, mm</th>
</tr>
</thead>
<tbody>
<tr>
<td>North Europe</td>
<td>9</td>
<td>2.0</td>
<td>46</td>
<td>—</td>
</tr>
<tr>
<td>Mediterranean</td>
<td>5</td>
<td>2.6</td>
<td>37</td>
<td>6</td>
</tr>
<tr>
<td>West Africa</td>
<td>6</td>
<td>4.5</td>
<td>53</td>
<td>21</td>
</tr>
<tr>
<td>Indo-Pacific</td>
<td>7</td>
<td>4.8</td>
<td>70</td>
<td>12</td>
</tr>
<tr>
<td>Tropics</td>
<td>3</td>
<td>3.7</td>
<td>18</td>
<td>11</td>
</tr>
<tr>
<td>East Asia</td>
<td>5</td>
<td>0.4</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>N. America Atlantic</td>
<td>3</td>
<td>3.7</td>
<td>22</td>
<td>7.4</td>
</tr>
<tr>
<td>S. America Atlantic</td>
<td>2</td>
<td>4.5</td>
<td>147</td>
<td>5</td>
</tr>
<tr>
<td>S. America Pacific</td>
<td>3</td>
<td>4.0</td>
<td>30</td>
<td>37.5</td>
</tr>
</tbody>
</table>

the West Indies they are few in number and of small size. The Atlantic coast of South America appears to have fouling with enormous numbers of quite small specimens.

The more general of Hentschel's conclusions agree with the results of studies of distribution of natural populations, and with similar evidence from other investigations of fouling. It is well established that separate regions support distinctive combinations of species. The higher average number of fouling species per ship on vessels from the tropics likewise agrees with the greater variety of forms found in tropical waters. The severity of fouling in much of the tropics is also widely recognized, and is usually interpreted as due to the long, often uninterrupted periods of breeding, and to the rapid growth which occurs in warm water.

Some of Hentschel's more specific conclusions are also supported by other investigations. The general similarity of North European and American Atlantic fouling can be recognized in Visscher's data on ship fouling (8). The latter, and other experience, also show that fouling is light or mod-
Figure 1. Examples of different types of fouling on buoys in American waters. 
A, Kelp and mussels, Newfoundland. B, Heavy mussel fouling off Delaware Bay. 
C, Mixed fouling, including barnacles, algae, and rock oysters, near Beaufort. 
D, Goose barnacles, with light growth of algae and amphipod tubes, Key West. 
E, Mussels and kelp outside San Francisco. F, Balanus tinctussulorum, a large tropical barnacle, Catalina Island, Southern California.
erge on ships in the North Atlantic, and that on the whole, algae and some of the smaller barnacles are the most characteristic forms.

Many of the more detailed observations recorded by Hentschel, however, are not reliable guides to the regional characteristics of fouling because of the small number of ships examined.

**REGIONAL DIFFERENCES IN FOULING ON BUOYS IN AMERICAN WATERS**

The fouling on buoys located from Newfoundland to the Gulf of Mexico, and from Southern California to Puget Sound, provides information about distribution on a near-continental scale, and is the only major source of such data for coastal seas. North of Cape Cod, Balanus balanoides and Balanus crenatus are the important barnacles, and kelp is often present in considerable amounts. Between Cape Cod and Cape Hatteras, B. improvisus and B. eburneus become the more important barnacles, although B. balanoides and B. crenatus are still found occasionally in much of this area.

South of Cape Hatteras, and in the Gulf of Mexico, the fouling is more diverse. Mytilus edulis is lacking. The barnacles B. amphitrite, B. improvisus, and B. eburneus, and several species of rock oysters, including Pteria colombus, are among the dominant forms. Algæ and hydroids, tunicates, and bryozoa are of occasional importance, and commonly present in lesser quantities. On the southeastern Florida coast, roughly from Cape Canaveral to Key West, and in the Bahamas, a distinct tropical element occurs, including, among the more conspicuous species, the large barnacle Balanus tintinnabulum and some of the coralline algæ. Tube worms, tunicates, and goose barnacles are also often found.

On the Pacific Coast of the United States, regions of distinctive fouling are less easily recognized, due in part to the fact that mussel fouling extends from Puget Sound to San Diego. Both Mytilus edulis and Mytilus californianus occur on the buoys, the latter particularly in the south. Other northern species ranging over most or all of the coast include kelps, and barnacles such as Balanus crenatus. A tropical element is also present, particularly south of San Francisco, and includes, especially, Balanus tintinnabulum.

Certain characteristics of the fouling appear to be common to nearly all areas. Thus, there is usually a band of green algæ at the water line, in which species of Enteromorpha, Ulva, and Cladophora are among the more widely distributed and conspicuous elements.

The fouling of navigation buoys shows that rather broad regions can be distinguished on the basis of consistent differences in the composition of the assemblages. The magnitude of the differences is indicated by the representative buoys shown in Figure 1. These differences depend chiefly on the presence or absence of a few conspicuous species, and the combinations in which these occur. The value of distinguishing areas by the combinations of dominant species, rather than by single forms, is shown by the simultaneous occurrence of both Mytilus edulis and Balanus tintinnabulum as important elements in the southern California fouling, whereas these forms occur in separate zones on the Atlantic seaboard.

A further illustration of this principle is given in Figure 2, which shows the approximate ranges
of several important species on the Atlantic coast. Individual forms drop out or enter the biota at different locations along the coast in such a way that there is nowhere a complete change in composition, and no region is characterized exclusively by all of the important species occurring in it. At least some of the forms important in each region spread into adjacent areas as well. The combination in each region, however, is distinctive. The distributions of the numerous less important species follow the same patterns.

In addition to the presence or absence of particular species, regions may be characterized by differences in the prevalence of various groups of organisms in the fouling. Some groups vary greatly in prevalence, although others are more constant in occurrence. Table 2 shows for six regions the percentage of samples of buoy fouling in which representatives of various groups have been found. Many of these groups differ considerably in prevalence from one region to another. Some, like the sponges, tube worms, nemerteans, and tunicates, occur in greater proportions of the samples from southerly regions. Other groups, such as the bryozoa and barnacles, vary without obvious relation to latitude, and a few, such as the amphipods and hydroids, are of very general common occurrence.

While broad, regional consistencies are recognizable in the fouling of buoys, there is, of course, local variation within each region. Some differences are due to the duration or season of exposure. The fouling of buoys in harbors and enclosed coastal waters is generally distinguishable from that of surrounding outer waters. Differences also are found related to distance from shore or from shoal water, and to depth in the water. Such in regional differences are discussed in Chapter 8.

### Table 2. Per Cent of Samples of Buoy Fouling Containing Various Groups of Organisms

<table>
<thead>
<tr>
<th></th>
<th>Atlantic Coast</th>
<th>Pacific Coast</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>North of C. Hatteras</td>
<td>Carolina, Georgia, &amp; Gulf of Mexico</td>
</tr>
<tr>
<td>Sponges</td>
<td>7.5</td>
<td>29.4</td>
</tr>
<tr>
<td>Hydroids</td>
<td>86.3</td>
<td>87.0</td>
</tr>
<tr>
<td>Anemones</td>
<td>23.1</td>
<td>48.9</td>
</tr>
<tr>
<td>Tube worms</td>
<td>10.2</td>
<td>43.9</td>
</tr>
<tr>
<td>Nemerteans</td>
<td>0.5</td>
<td>14.1</td>
</tr>
<tr>
<td>Bryozoa</td>
<td>37.5</td>
<td>61.5</td>
</tr>
<tr>
<td>Nudibranchs</td>
<td>33.4</td>
<td>9.5</td>
</tr>
<tr>
<td>Muscles</td>
<td>87.0</td>
<td>21.0</td>
</tr>
<tr>
<td>Oysters</td>
<td>0.5</td>
<td>38.5</td>
</tr>
<tr>
<td>Acorn barnacles</td>
<td>65.6</td>
<td>93.9</td>
</tr>
<tr>
<td>Goose barnacles</td>
<td>7.4</td>
<td>3.8</td>
</tr>
<tr>
<td>Amphipods</td>
<td>88.0</td>
<td>93.5</td>
</tr>
<tr>
<td>Star fish</td>
<td>17.2</td>
<td>1.1</td>
</tr>
<tr>
<td>Tunicates</td>
<td>13.5</td>
<td>21.0</td>
</tr>
</tbody>
</table>

**BIOTIC PROVINCES**

The areas of reasonably consistent fouling observed on the buoys resemble the established biotic provinces of general coastal faunas and floras. Since these have been worked out in some detail, and in view of the facultative origin of fouling, it is of interest to consider briefly the value of such provinces as indices of the distribution of fouling.

Ekman (2) has provided the most comprehensive compilation of the data for marine animals. He concluded that the shallow waters of the world could be divided into fifteen major provinces having fundamentally distinctive faunas. These provinces, mapped in Figure 3, are as follows:

1. Indo-West Pacific Tropics.
3. Atlantic American Tropics.
7. European Boreal.
9. Arctic.
15. Antarctic.

In Ekman's view, a province is distinguished by possessing a large proportion of species which are unique to its area. His provinces are so circumscribed that each contains a nucleus of such endemics, usually amounting to better than 50 per cent of its entire fauna. The endemic forms of a province, however, do not necessarily extend
The Indo-West Pacific Tropics and others of the large provinces can be subdivided, accordingly, on the grounds of the more restricted distributions of smaller aggregations of the contained endemic species. Boundaries of the provinces are generally located at points where pronounced changes in the biota are found; i.e., where the ranges of a number of species begin or end. The margins of the provinces may overlap, giving a small area in which species characteristic of two adjacent provinces are found. Such an overlap exists between Cape Hatteras and Florida, Cape Hatteras marking the northern limit of many tropical forms, while many of the boreo-temperate species extend south as far as eastern Florida.

The use of biotic provinces such as Ekman's to predict fouling expectancy meets with several difficulties. One reason is that practical considerations place extremely unequal importance on individual fouling species. General biogeography, in contrast, tends to give equal weight to all forms, or to emphasize particular species for reasons having no relation to fouling, with the result that biogeographic provinces often are not applicable to practical problems. Thus, a number of species which commonly dominate fouling and determine its character, range over several Ekman provinces or have distributions not particularly well represented by any province or combination of provinces. Among these wider ranging forms are Balanus crenatus and Mytilus edulis, which are circumglobal in northern waters, and Balanus amphitrite, B. tintinnabulum, and Bugula neritina, circumglobal in the tropics and warmer waters. The distributions of these species often give a better indication of fouling conditions than can be afforded by provincial biogeography. The differences suggested by provincial boundaries, though biologically valid, may be realized only in the case of species of comparatively little practical consequence. The prevalence of Mytilus edulis and Balanus crenatus on fixed installations throughout northern waters provides a similarity that outweighs other differences for many practical purposes.

The apparent distinctions between fouling of various types of structures, furthermore, make it necessary to consider the geographical aspects of fouling separately for each sort of problem. Very
different appraisals of the severity of fouling on the Atlantic coast are obtained depending on whether buoys or ships are being considered. For shallow buoys, Cape Hatteras is the important division point. The region to the north has the massive mussel fouling of considerable consequence; to the south, fouling is dominated by other forms whose bulk and weight are generally much smaller. For ships, on the other hand, fouling is light over most of the Atlantic coast, and on the more northerly part of the Atlantic coast has the more severe fouling.

Similar distinctions related to type of structure probably explain some of the seeming contradictions about fouling in other areas. It has been reported, for example, that ship fouling in Alaskan waters is negligible (3), although some barnacles have been collected from vessels after cruising in the region (4).

Even these few observations are sufficient to indicate that nothing in the nature of an over-all fouling map of the world is to be anticipated, and to show that biotic provinces based on all marine organisms have only very moderate applicability to considerations of the distribution of fouling for practical purposes.

**ANALYTICAL BIOGEOGRAPHY**

Analytical biogeography attempts to explain geographical distribution in terms of environment factors which may aid or limit the dispersal of individual species. Currents, physical geography, and temperature are the factors of special concern.
for interpreting the distributions of shallow water forms from which fouling is chiefly drawn.

Currents affect distribution in two ways: by transporting larvae and otherwise aiding the dispersal of species, and by transporting water masses of particular temperatures or other properties, thus fixing the conditions for life in the regions to which the currents flow. Specific boundaries cor-

zonal patterns of distribution result. The general distinction between "polar" and "tropical" biotas is thoroughly familiar, and reflects these zonal patterns.

A number of attempts have been made to utilize environmental conditions in subdividing the world into regions comparable to the faunistic provinces of Ekman and similar workers. The provinces may

related with currents are probably to be interpreted most often on the latter grounds, insofar as sessile fouling forms are concerned.

The most significant feature of physical geography for the broader aspects of distribution is the discontinuity of shallow waters, particularly between the continental tropical coasts, which tend to maintain the segregation of differently evolved biotas in various parts of the world. On a more local scale, of course, other features such as the amount and type of land drainage, and the geological character of the shore, are also important in determining the biotas.

Temperature is important because few organisms can tolerate the full range which exists between the equator and the poles. North-south

be defined in these cases in terms of their homogeneity as physical environments suitable for life. In usual practice there is some recognition of the biological data as a guide to the significant criteria chosen to separate provinces.

A simple example of the procedure has been given by Ortmann (7), who relied almost entirely on temperature. He divided the coastal waters of the world as shown in Figure 4. The basic distinction is drawn between the warm water tropics, and the two cold water zones toward the poles. Each of these three zones is then subdivided, the tropics being divided chiefly by continental coasts, and the polar zones being divided primarily into sub-zones of more and less extreme coldness. No absolute temperature values served as criteria for

FIGURE 5. Map for sorting data on ship fouling. In each area fouling of different composition, intensity, or season of growth might be expected. Numbering of the areas is arbitrary, and is not intended to indicate relative severity of fouling. From U. S. Navy Docks Report Manual (7).
the distinctions, but, in general, the boundaries between the tropics and cold water areas were located at points where winter temperatures first begin to drop to significantly lower values than found in the tropics. At these points the limits of the stenothermal warm water species are usually found. The limits of the major zones are actually set by the great circulatory system of the oceans.

Comparing Ortmann’s map with Ekman’s (Figure 3), it will be seen that they have many points of similarity, the subdivisions of the three major zones of Ortmann corresponding roughly to the provinces of Ekman. The greatest difference is in the southern hemisphere, where Ekman’s treatment is more nearly balanced in detail in comparison with the northern hemisphere.

The chart illustrated in Figure 5 is an application of the principle underlying Ortmann’s provinces. It was designed to provide a basis for sorting docking reports for statistical analysis. The various areas are intended to represent regions where somewhat similar fouling conditions are to be expected. Certain practical considerations, such as the presence or absence of ports used by naval vessels, also entered into its construction. The numbers assigned to the various areas are not intended to indicate the relative severity of fouling.

THE DISTRIBUTION OF INDIVIDUAL SPECIES AS RELATED TO TEMPERATURE

Studies of the distribution of species in relation to temperature indicate that boundaries are correlated generally with either summer or winter temperatures, i.e., with seasonal extremes. Toward the poles, organisms may be winter-killed by cold, or may be unable to reproduce because temperatures do not rise high enough in summer. Either relationship can prevent further poleward dis-

![Figure 6](image-url)
GEOGRAPHICAL DISTRIBUTION

pends on the particular combination of seasonal conditions producing the northern and southern limits, as follows:

<table>
<thead>
<tr>
<th>Type of Distribution Limit</th>
<th>Northern Limit</th>
<th>Southern Limit</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Too cold in winter</td>
<td>Too warm in summer</td>
<td></td>
</tr>
<tr>
<td>2. Too cold in summer</td>
<td>Too warm in winter</td>
<td></td>
</tr>
<tr>
<td>3. Too cold in summer</td>
<td>Too warm in summer</td>
<td></td>
</tr>
<tr>
<td>4. Too cold in winter</td>
<td>Too warm in winter</td>
<td></td>
</tr>
</tbody>
</table>

Distinctive geographical distributions result from the four types, and in this fact lies the great importance of recognizing more than one kind of seasonal extremes defining its northern and southern limits: No portion of the European coast, on the other hand, has temperatures corresponding in all details with those between Newfoundland and Cape Hatteras.

Essentially similar results are reached in comparing any two coasts, since the temperature conditions on one are almost never duplicated exactly on the other. In general, however, the distinctive geographical features of distribution introduced by correlation with seasonal temperatures are most

Figure 7. Representative records showing the distribution of the barnacle Balanus balanoides. The southern boundary is closely approximated by the isotherm of the monthly mean of 45°F at the time of minimum temperatures in winter. After Hutchins (6).
apparent in temperate latitudes, where the differences in annual temperature conditions are most pronounced.

The distributions of *Balanus balanoides* and *Mytilus edulis* exemplify the type of differences suggested by the maps in Figure 6. The southern boundaries are of special interest. *Balanus balanoides*, Figure 7, extends nearly to Cape Hatteras, and to the English Channel in the Atlantic. The southern limit appears to be set by a winter temperature approximated by the monthly mean of 45°F. Farther south, the water is apparently always too warm to permit reproduction, an interpretation supported by the fact that near the southern limits of the distribution of the species, the larvae are liberated and attach during the winter months. *Mytilus edulis*, on the other hand, appears to be limited by the inability of the adults to survive where the monthly mean summer temperature exceeds 80°F (Figure 8). Although it is checked near Cape Hatteras, the species extends well into African waters in the eastern Atlantic. Despite their very similar distributions on the American Atlantic coast, the two species have distinctive distributions elsewhere, due apparently to the fact that winter temperature conditions are critical for the barnacle, while summer temperatures set the boundary for the mussel.

Relationships of this sort probably explain the
GEOGRAPHICAL DISTRIBUTION

joint occurrence in southern California of fouling forms which are segregated as northern or southern on the Atlantic coast. Figure 9 presents the interpretation in terms of two of the chief species involved, *Mytilus edulis* and *Balanus tintinnabulum*. As already pointed out, the southern boundary of the mussel appears to be set by inability of the individuals to survive where the monthly mean temperatures in summer exceed 80°F. The species thus cannot extend further south than about Beaufort, North Carolina, on the Atlantic coast. On the Pacific coast, however, upwelling of cool bottom waters along the coast keeps summer surface water temperatures low enough for the species to penetrate well down the shore of Lower California.

The barnacle, in contrast, seems to have a northern limit set by winter temperatures approximated by the monthly mean of 55°F. The isotherm for this value, shown in the figure, closely defines the extent of the species which extends as far north as San Francisco on the Pacific coast but is confined to Florida and southerly waters on the Atlantic coast, except for its occurrence in an isolated warm spot at Cape Hatteras. The overlap of the two forms on the Pacific results from boundaries established by different seasonal extremes in the two species, coupled with the smaller annual range of temperature on the Pacific coast as compared with the Atlantic coast.

STATUS OF STUDIES OF DISTRIBUTION OF FOULING

It may be noted in conclusion that studies of the distribution of fouling are not sufficient to warrant broad generalizations about fouling expectancies in many parts of the world. Chiefly, geographical coverage is inadequate. The British Isles-North Sea area, and the United States coasts, are the only places where adequate data on a regional scale exist. Elsewhere data are meager, and are apt to be limited to one or a few ports, which cannot be assumed to give a fair indication of provincial conditions. The latter point was illustrated during the war, when previous Hawaiian experience proved misleading regarding the character and severity of fouling in the tropical Pacific at large. The complications introduced by the peculiar fouling characteristics of different structures, and by other sources of variation in data, require that many more observational records become available before regional fouling potentials can be assessed with satisfactory accuracy. The evidence on hand must be taken as highly tentative for most regions at present.

REFERENCES