COMMUNITY INTERACTIONS ON MARINE ROCKY INTERTIDAL SHORES

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"The ultimate goal of an ecological survey should be to discover and measure the main dynamic relations between all organisms living on an area over some period of time" (Elton 31). This is a tall order but it describes the aim of many "community" ecologists pretty well. Most studies have not got past the first stage of identifying and describing the community, because of the very great difficulties of sampling and taxonomy (Fager 32). Even then, direct measurement of dynamic relations is difficult. Recourse is sometimes made to fitting available data, such as the abundances of the different species, to various mathematical distributions. If the data fit a particular model, the underlying assumptions of the model are then presumed to represent the mechanisms which produced the abundances.

However, where it is possible to measure directly the dynamic relations between organisms and their physical and biological environment, this is to be preferred to such indirect methods. Such direct measurement is difficult in most habitats, but it is possible in a few. The marine rocky intertidal is one of these. Because it is so accessible, it has been studied for a long time and the species are well known. Because many of the common species are sessile or slow moving and not hidden in the substrate, their abundance and other population characteristics can be estimated readily. Lastly, the populations are amenable to experimental manipulation in the field; their abundance and distribution can be altered in one place and left unchanged in another nearby. This last characteristic is particularly important. To measure dynamic relations between organisms one must either look for correlations between changes in the abundances and distributions of the coexisting organisms, or else make the changes experimentally. The last is usually better because replicate treatments and undisturbed controls can be set up at the same time (Connell 22).

Most ideas and models about how organisms live together, i.e. about "community structure," are based upon little, if any, direct evidence. For example, a common theme is that the "niche spaces" of species have been determined by the evolution of adaptations to reduce competition. If this were so, one would expect to see competition occurring where the ranges of two

similar species meet. But, aside from a few examples (some taken from the rocky intertidal), there is surprisingly little direct evidence that competition is important in determining the present distribution or abundance of species. Most community models are based either upon indirect evidence or mathematical constructs. In this review I will use evidence from direct measurements, particularly from field experiments, to evaluate the relative importance of physical and biological factors in determining the pattern of species composition in the marine rocky intertidal.

PATTERNS OF SPECIES DISTRIBUTIONS

VERTICAL ZONATION

Correlations between the increasing degree of exposure to air from low to high-tide levels and the pattern of distribution of organisms in narrow horizontal zones were recognized long ago (Audouin & Milne-Edwards 1). This "vertical zonation" has since been described in all parts of the world (see review by Southward 83).

Most hypotheses as to the causes of this zonation have emphasized the tide as the primary factor. Colman (16) found that the upper and lower limits of the common species of intertidal organisms on a British shore were most frequent at "critical" levels near the high and low neap-tide levels. A similar tabulation from Hewatt (48) and Doty (28, Figure 6) for western North America yields the same result. Doty (28) proposed certain additional tide levels as critical, since the maximum single exposure to air or submergence in water increases suddenly at particular levels. However, relatively few of the upper or lower limits of the species of algae given by Doty (28, Figure 6) or of animals given by Hewatt (48) actually occurred at these points of sudden change, so that the data seem not to support Doty's hypothesis. Colman (16) pointed out that the "critical" levels found by him represent the upper and lower limits of several species which are confined to the intertidal zone, and the upper limit of species extending up from the subtidal region. Judging from the species listed by Hewatt (48) and Doty (28), the same conclusion seems to apply.

Upper limits: the importance of physical factors.—Considering first the upper limit of a species' zone, it has often been noticed that it is raised in situations which are damper or cooler. For example, upper limits are often higher in the following situations: on north-facing rocks, in places where waves or spray keep the surface wet at higher levels, in high-tide pools, and in places where seawater drains slowly down the shore from a high pool (see review by Lewis 59). These observations suggest that upper limits must often be determined by increased desiccation, higher temperatures, or stronger solar radiation.

One of the first to test such a hypothesis was Baker (2, 3). She measured the rates of germination and of subsequent growth and mortality of four species of brown algae in jars under different lengths of exposure to air

and submergence in seawater. The species from the highest shore level showed no differences in all treatments, but the species from lower levels survived and grew better with longer submergence. Baker (3, p. 67) summarized her findings in the following prophetic passage: "On the whole it seems as though the greatest competition had been called into play in the lowest zones, the dry and uncongenial regions of the upper shore being left to the most tolerant forms, which, if left to themselves, are able to grow anywhere on the shore."

Field experiments indicate that the upper limits of some species of algae can be raised by running a stream of seawater down the rock surface. Moore (64) noticed that the upper limits of some algae colonizing a new seawall were higher where seawater seeped through cracks from a pool behind. Castenholz (13) found that attached diatoms extended higher in a stream draining a high-tide pool. Frank (37) dripped water from a large bottle set above the intertidal zone, and Dayton (26) built artificial tide pools arranged to drain slowly during low tide. In both cases, algae extended higher in the stream.

The upper limits of the common species of animals also seem to be determined by direct effects of the physical enviroonment. Hatton (41) transplanted rocks bearing barnacles to levels above their normal distribution. Young individuals quickly died but older ones survived longer. When a stream of seawater slowly draining from a basin which Hatton fixed above the intertidal zone was run over some of the transplanted young barnacles, they survived and grew. Foster (35) also has found that barnacles die if transplanted above their usual limit.

Strong sunlight may kill young animals at high shore levels; Hatton (41) found that young barnacles survived higher on north-facing surfaces than on south-facing ones. When protected from direct sun by shades attached to the rock, they survived well on the latter surfaces, even though the rock surface dried quickly.

Most studies of the causes of limits in vertical zonation in natural populations have been made on plants or sessile animals such as barnacles. The most complete study of a mobile animal is that of Frank (37) who marked about 9500 limpets (*Acmaea*) with individual numbers on a large isolated rock in Oregon. Over several years he made periodic censuses, noting positions and measuring growth. He found that the limpets moved upward in autumn and winter and, to a lesser extent, downward in spring. Mortality near the upper limit of distribution was high in the two summers which were drier and sunnier, when many of the limpets dried out and died. Mortality at high shore levels was also increased in two winters when severe frosts caused patches of the surface of the rock to exfoliate, carrying off the limpets. Thus, the upper limit was determined by increased mortality from direct effects of extremes in the physical environment.

Heavy wave action also raises the upper limit of intertidal organisms, presumably because the rocks are wetted by wave splash above the usual level

reached by high tide. Lewis (59) provides many convincing examples of this phenomenon. The species which live at higher shore levels are the ones whose upper boundaries are so raised. Presumably, they must be able to withstand fairly long periods of exposure to air during occasions of calm spells, and only the upper shore species can tolerate these. The upper limit of some "understory" algae has been found to be raised through the indirect effect of larger algae which keep the surface beneath them moist, shaded and, presumably, cooler (Hatton 41, Lodge 60, Dayton 26).

Lower limits: the importance of biological interactions.—The lower limits of intertidal species have sometimes been ascribed to the direct action of physical factors. For example, it has been found that certain intertidal algae, *Pelvetia canaliculata* and *Fucus spiralis* (Fischer 34), and snails, *Littorina saxatilis* (Herdman 46), will die if submerged continually. However, these species all have their lower limit above the mean tide level. Therefore, evidence of death from constant submergence cannot be used to explain why their lower limits were at levels submerged less than half the time.

Species which extend down to the low-tide line might be prevented from going further by intolerance to continual submergences. But those species which have been tested are able to live continually submerged at shallow depths, either in the laboratory or in the field—e.g. *Fucus evanescens* (Gail 38), the barnacles *Chthamalus stellatus* (Fischer 33, Barnes 4, Connell 18) and *Balanus balanoides* (Barnes & Powell 6), the mussel *Mytilus edulis* (Scheer 78), and the snail *Littorina littorea* (Hayes 45).

Decreased light intensity might set the lower limit of intertidal algae, but the evidence available renders this unlikely. Gail (38) shaded *Fucus evanescens* on the shore (tidal level unspecified); they survived without damage in one quarter of the light normally reaching them. With such a tolerance for low light intensity, it seems unlikely that they could not extend from the low shore level at which Gail found them to just below low water. As compared to low intertidal shore levels, the region just below, which is continually submerged, should receive at low tide about one quarter less light the amount of reduction in passing through the surface (Shelford & Gail 81).

Some intertidal algae are limited to very high shore levels; experimental transplanting to lower levels in the intertidal zone has not been done. However the experiment by Jones (50) of removing limpets and algae from the shore accomplished this unintentionally. One alga, *Fucus spiralis,* usually occurring only at very high shore levels, was found after 3 years growing luxuriantly and reproducing at the lowest intertidal level (Burrows & Lodge 11). At the present time, there is apparently no evidence that any intertidal species is prevented from extending to a lower level by intolerance to the physical conditions there. In fact, intertidal species may grow faster when kept continually submerged (Barnes & Powell 6).

The most likely reason why such intertidal species live in the physiologi-

cally less congenial region at high levels is that they are forced to do so by interactions with competitors or natural enemies. Several controlled field experiments have demonstrated this to be so. For example, I measured the survival of one species of barnacle, *Chthamalus stellatus,* at different shore levels, both with and without another barnacle, *Balanus balanoides,* and watched what happened when the two species grew after touching (Connell 18). *Balanus* grew faster and killed *Chthamalus* by undercutting, smothering, or lateral crushing. *Chthamalus* kept out of contact with *Balanus* survived well at all shore levels, even submerged in a tide pool. Thus the restriction of adult *Chthamalus* to very high shore levels at this location in Scotland was caused by competition for space with *Balanus.*

Intertidal algae often have abrupt lower limits adjoining another species just below. Although it has been suggested that competition determines these boundaries (Southward 83, Lewis 59), no field experiments have been done to test the hypothesis. Since algae are easily transplanted on pieces of rock (Hatton 41), such experiments are eminently feasible. Many studies have shown that growth is faster at lower shore levels, e.g. in algae (Hatton 41), barnacles (Moore 63, Hatton 41, Barnes & Powell 6, Connell 18, 21), limpets (Hatton 41), and mussels (Seed 80, Harger 40). Hatton (41) showed by experimental shading and by growing algae sparsely versus in clumps, that this increased growth was probably due to increased humidity. For the animals, longer feeding time is probably the reason. Since competitive exclusion is accomplished by shading, smothering, or crushing, faster growth at lower shore levels means that competition should be more severe there.

The other sort of interaction which has been shown by field experiments to determine the lower limit of an intertidal species is grazing or predation. I will give two examples of differing complexity. At San Juan Island, Washington, adult *Balanus glandula* occur only in a narrow vertical band near the upper edge of the intertidal zone. Young which settle lower down are all eaten within 12 to 15 months (Connell 21). They survive at lower levels if protected by cages or if in regions where predators are scarce, such as in quiet muddy bays. Their lower shore limit is set by the presence of predators; they never grow to a size at which they are safe from even small predators.

A more complex case is afforded by *Balanus cariosus* at the same place. Again in every year since 1959 all have usually been eaten within 12 to 15 months, except when protected in cages. After two years protection of the 1959 year group I found that when I put predators (*Thais lamellosa*) inside the cages they ignored these barnacles and fed only on younger ones. After 5 years protection I removed a cage and covered the area with a "roof" of wire mesh which allowed access to small predators and excluded large ones such as the starfish *Pisaster ochraceus.* Some of these *B. cariosus* were still surviving at the last census when they were 12 years old. Thus, if *B. cariosus* can survive for 2 years it is safe from smaller intertidal predators; Dayton (26) has confirmed this. However, they are never invulnerable below the

intertidal zone. When I transplanted very large *B. cariosus* in cages with *Thais* to very low levels where they were exposed by only the lowest tides every two weeks, the *Thais* ate them.

In contrast to *B. glandula, B. cariosus* has no spatial refuge on the high shore above these predators and relies on large size as its refuge. How it manages to escape for the first 2 years remains to be demonstrated conclusively. Two instances of "natural escapes" have occurred, in different years at different levels, during my study since 1959. Both occurred only on small areas of shoreline and must have resulted from local reductions in predator activity. That quite widespread general weather extremes can affect local populations quite differently is shown by the following examples. Two periods of extremely cold weather occurred during the winter of 1968–69. At my study site on the east coast of San Juan Island the population of *Thais emarginata* was reduced to less than one quarter of what it had been before that winter. On the outer coast of Washington about 110 km away, Dayton (26) found the same species also greatly reduced over this winter at one site (Portage Head) but not at another site (Waadah Island) only 10 km away. In the following year, Dayton (26) found young *B. cariosus* covering most of the surface at his study site on the west coast of San Juan Island. But at the same time on my site only 7 km away along the same west coast, young *B. cariosus* were scarce.

While *B. cariosus* occasionally escape smaller predators, they apparently can be eaten at any size by *Pisaster ochraceus*. *Pisaster* moves up into the intertidal zone at high tide and quickly wrenches even very large *B. cariosus* off the rock and then retreats to the low shore to finish eating them. It seldom reaches the upper margin of the zone of *B. cariosus* so that the barnacle has a spatial refuge above this predator. Thus, the lower limit of *B. cariosus* is determined by occasional escapes from its smaller predators and the presence or absence of *Pisaster*.

Predation has been shown to determine the lower limit of other intertidal species. Paine (69) removed all starfish (*Pisaster ochraceus*) from a stretch of shore on the outer coast of Washington and found that *Balanus glandula* and *Mytilus californianus* survived lower on the shore, as compared to an adjacent control area. Luckens (61, 62) enclosed three species of barnacles in cages to protect them from predation at various shore levels in New Zealand. They survived at lower than normal levels only in these cages.

Although grazing by intertidal molluscs and, in pools, by sea urchins has a great effect on the recruitment and survival of algae, there is no direct evidence that it sets the lower limit of any intertidal species.

Variations in age structure.—With changes in severity of physical factors, populations exhibit variations in their age structures. Under very harsh conditions the population may be composed of a single "dominant year class." For example, the population of *Balanus balanoides* in Scotland at the uppermost

margin of its distribution consisted mainly of 3-year olds, with few older or younger individuals. Mortality due to desiccation is usually very heavy in young individuals at this level (Hatton 41, Connell 17), and evidently only in occasional favorable years do many survive. In California, the limpet *Acmaea scabra* at the upper edge of its shore distribution consisted mainly of 4-year olds (Sutherland 87).

Under slightly less harsh physical conditions where predators are absent naturally, some young individuals may survive every year, producing mixed age distributions. This was the situation in populations of *Balanus glandula* in Washington (Connell 21) and in *Acmaea scabra* in California (Sutherland 87).

Under more benign conditions, prey are usually all eaten within a year. When *Balanus balanoides* in Scotland and *B. glandula* in Washington were protected in cages at lower shore levels for several years, mixed age distributions were produced (Connell 17, 21). A different situation occurs in those species which have evolved the trait of growing to such a large size as to be invulnerable to most predators. Since they are vulnerable when they are small, they must somehow escape being eaten until they have grown. Because this happens only occasionally, the population consists mainly of individuals of one or two older year classes. Thus under either very harsh or very benign physical conditions, populations may consist of "dominant year groups." Sometimes in intermediate conditions there are mixed age distributions, e.g. *Balanus glandula*.

The larger algae also have populations consisting only of older year groups. After Jones (50) had removed the limpets from the experimental strip, *Fucus* colonized the shore. Then young limpets settled thickly and by their grazing prevented further recruitment, so that the population of *Fucus* consisted of large older plants which evidently were invulnerable to these smaller limpets (Lodge 60).

Other examples of populations consisting mainly of large old individuals are the starfishes *Pisaster giganteus* and *P. ochraceus* (Landenberger 57, Dayton 26), the sea urchin *Strongylocentrotus purpuratus* (Ebert 29, Dayton 26), the mussel *Mytilus edulis* in quiet waters (Kitching et al 53), the snails *Shaskyus festivus* and *Ocenebra poulsoni* (Fotheringham 36), *lamellosa* (Connell 20), and the limpet *Lottia gigantea* (Stimson 85). These all occur at middle or low shore levels and are all large species, so that their age structures might be the result of occasional escapes from predation similar to that of *Balanus cariosus*. However, no direct evidence exists for these species. In the snail *Tegula funebralis* those on the upper shore are smaller than those at lower levels. Paine (70) suggested that they moved down as they got older; this represents an entirely different mechanism for producing older age distributions in more benign physical conditions. It does not happen in the other species listed, since they do not have smaller-sized individuals at higher shore levels.

HORIZONTAL DISTRIBUTION

Effects of variations in water movement.—As one moves along a shore from wave-beaten to sheltered sites, the appearance of the community changes drastically. In Britain, the shore is usually covered with mussels on exposed headlands, with barnacles in moderately wave-beaten sites and with brown seaweeds in quiet water (Lewis 59). In other parts of the world the particular pattern is different, but striking changes along this gradient are evident everywhere.

Some species are obviously excluded from turbulent shores by direct mechanical stress. Hatton (41) showed this experimentally by transplanting two species of algae from quiet water to a location with strong currents. Large individuals were quickly washed away unless they were placed in enclosures which reduced the water movements; smaller plants survived longer. This probably accounts for the stunting of algae in more wave-beaten sites. Two species of snails (Kitching & Ebling 55) and one species of mussel (Harger 39) which were transplanted from quiet to turbulent water were torn from the substrate, whereas ecotypes and related species native to the turbulent water survived when transplanted within it, as controls.

In some cases, unfavorable physical conditions may prevent species from turbulent water from invading quieter conditions. Round et al (75) transplanted rocks bearing hydroids and associated amphipod crustaceans from a seawater rapids to the quiet water of Lough Ine in southern Ireland. Both organisms quickly accumulated a covering of silt and began to die in the first week. Later on, the hydroids began to be covered by attached diatoms. However, the early onset of mortality indicates that the main cause was choking by silt.

Some species such as barnacles and mussels in Britain occur in both wave-beaten and sheltered places, but are usually commoner in the former. Moore (63) and Hatton (41) found that the density of settlement and the growth of two species of barnacles and one limpet were less in quieter water. This is usually attributed to the lower rate of supply of larvae and planktonic food by currents in quiet waters than in turbulent ones.

Studies of the relationship between sessile adult populations and their planktonic larvae are few. Some intertidal algae have large spores which evidently are not carried far. Burrows and Lodge (10) found that heavy recruitment adjacent to a newly established bed of algae was mainly in the downstream direction of the local tidal currents. Bousfield (9) and Sandison & Hill (77) were able to relate the recruitment of barnacles and other sessile species to currents carrying them from established adult populations.

Some differences in abundance between turbulent and quiet places may be due to biological interactions. Hatton (41) and Lewis (59) have suggested that the large algae in shelter might prevent planktonic larvae from reaching the surface, or rub them off soon after attachment. Dayton (26)

tested these ideas in Washington by removing *Fucus distichus* from patches in dense beds. On a wave-beaten site there was no difference in density of settling barnacles with or without *Fucus* and in a quiet site more barnacles settled or survived beneath the *Fucus,* so that the hypotheses were rejected. This is a rather small species of *Fucus,* and the much larger species which occur in shelter in Europe might have a greater competitive effect.

There is some evidence that grazing or predation may account for some of the differences between turbulent and quiet areas. Kitching et al (53) and Muntz et al (65) noted that, as in various places in Britain, mussels (*Mytilus edulis*) were common in either very sheltered or very wave-beaten areas, but not in intermediate sites, at Lough Ine, Ireland. Mussels transplanted to intermediate sites were killed, usually more rapidly at lower shore levels; they survived only when protected in cages. Crabs ate the mussels at high tide; large mussels could be eaten only by very large crabs. In very quiet water there were no large crabs and the mussels living there were also large, with some smaller ones mingled in. Thus, mussels escape predation either by reaching a large size in quiet water or by living in wave-beaten places where crabs are scarce. Lewis (59, Figure 7) showed that in Britain the predatory snail *Thais lapillus* also is absent from the two extremes of shelter and wave exposure, so that it, as well as crabs, may be instrumental in excluding mussels from intermediate sites. *Mytilus edulis* has been shown in laboratory experiments to be preferred over several other prey species by several intertidal predators (Landenberger 58, Murdoch 66), so that it is not surprising that it is quickly eliminated where predators are common. As described earlier, I found large adult *Balanus glandula* at lower shore levels only in very quiet bays where predatory snails and starfish were rare. Ebling et al (30) and Kitching et al (54) found that the predatory snail *Thais lapillus* was itself eaten by crabs, and where crabs were common in quiet waters *Thais* had a very thick, heavy shell. Thin-shelled *Thais* from the nearby wave-beaten shore were quickly eaten by crabs when they were transplanted to quiet water, whereas the thick-shelled forms were not eaten.

Estuaries.—The other obvious large-scale pattern is the change seen as one moves into estuaries. Although this is usually ascribed to direct effects of variations in salinity, it is by no means as simple as this. In estuaries wave action is reduced, turbidity often increased, and biological interactions changed. For example, Sandison & Hill (77) found that the distributions of four common intertidal invertebrates which live on hard surfaces in estuaries in Nigeria were greatly changed in the annual floods. In a nearby area unaffected by the floods the distributions were unchanged. The barnacle extended further into the low salinity lagoons and was higher in vertical zonation on mangrove roots; the tubeworms extended the least distance from the sea and were at the bottom of the vertical zonation; the oyster was intermediate in both situations. In laboratory experiments the barnacle was killed at both very low salinities and those of normal sea water (Sandison 76), so that its

relative position and the variations over different seasons could be explained by changes in salinity. However, the effects of turbidity or of biological interactions remain alternative possibilities.

SMALL-SCALE PATCHINESS

Besides these large patterns of vertical zonation and horizontal changes associated with variations in wave action and salinity, every shore shows variation on quite a small scale. Some of these are due to the direct action of the physical environment, others to the indirect or direct activities of organisms.

The irregular and broken nature of some rocky shores presents a great variation in the slope and orientation of the surface. South-facing steep slopes at higher north latitudes receive more direct insolation than north-facing ones. Hatton (41) found greater densities of settlement and greater growth rates on north-facing than on south-facing slopes at upper shore levels in two species of barnacles, one limpet, and two algae. By shading the south-facing slope with a slate, he found that *Fucus vesiculosus* and *Balanus balanoides* survived and grew better.

Vertical surfaces receive less insolation and this, together with the fact that they drain more quikcly, make them damper than horizontal ones. Haven (43) found that the limpet *Acmaea digitalis* at very high shore levels lived almost entirely on steep rocks, whereas *Acmaea scabra* lived on all slopes but was more common on horizontal ones. If *A. digitalis* was transplanted to a horizontal surface, it quickly moved into crevices, whereas *A. scabra* stayed out in the open. When large algae sheltering both species at low tide were removed, the same thing happened. *A. scabra* has a "home" spot to which it returns after grazing expeditions; its shell fits the surface irregularities exactly. In contrast, few *A. digitalis* have a home, and Haven (43) confirmed Frank's (37) finding that they will move higher on the shore in cool wet weather or when wave action increases and down again in warmer or drier weather. Probably as a result of this greater mobility, they grow faster than *A. scabra* and maintain a higher biomass per unit area, though with greater fluctuations. These two species live in the same habitat, viewed on a large scale. On a smaller scale they have partitioned it between them so that, by different behavioral responses, they live in different microhabitats.

Another direct effect of the physical environment which produces local patchiness is the damage caused by wave-borne objects smashing against the rocks. Barnacles on raised parts of the surface are often rubbed off. They choose to settle in grooves and depressions (Crisp & Barnes 25); when these are filled, later arrivals must settle on exposed surfaces and they are then killed during storms, as I found with *Balanus balanoides* in Scotland (Connell, 17). Dayton (26) measured the effects of damage from floating logs by installing nails in the rock at different places. Where the nails were quickly lost, indicating heavy log battering, the sessile organisms were restricted to protected areas such as crevices.

Another effect of wave action during storms is to cause mobile species, such as snails, to move into dense local aggregations (Lewis 59, Connell 17, Frank 37). Deep crevices in the rock provide shelter and also trap detritus, which can be eaten by many animals. A specialized "crevice fauna" exists there. Kensler & Crisp (51) provided artificial crevices which were colonized by these species.

An indirect effect of the presence of large organisms is to provide shelter for smaller ones beneath them. Many small animals live beneath mussels, which reduce water movements and trap detritus in a fashion similar to that of deep crevices. Large algae have sheltering beneath them smaller species which die back to their holdfasts if the canopy species are removed (Dayton 26). Hatton (41) removed large *Fucus vesiculosus* and found that young *Fucus* plants did not become established as quickly in the open as under the larger individuals. I found that *Thais emarginata* and *Thais canaliculata* required crevices as shelter and were present on smooth vertical surfaces only where large barnacles, *Balanus cariosus,* provided shelter (Connell 23). Dayton (26) found that large *B. cariosus* provided shelter against desiccation for the anemone *Anthopleura.*

Other more direct effects of biological interactions also produce local patchiness. Some occur between members of the same species. For example some colonial anemones spread over the surface by vegetative reproduction, forming clones. Adjacent clones of different genetic constitution remain distinct, the individuals along the border repelling those of adjacent clones, so that a space is left between (Childress 14). This has been called a "reproductive" pattern by Hutchinson (49). Hutchinson has termed another category the *social pattern;* in it aggregations are formed by signaling between individuals of the same species. For example, when larvae of certain sessile animals are ready to attach to the substrate, they exhibit great discrimination in their choice of site for attachment. Knight-Jones (56) and his co-workers have shown that larvae of barnacles, tubeworms, and oysters tend to attach more readily after they have touched previously attached individuals of their own species. This "gregarious" behavior should produce clumped distribution patterns. Social behavior leading to a spaced-out pattern has been demonstrated in settling barnacles (Crisp 24) and in tube-building amphipods in a laboratory aquarium (Connell 19).

Intraspecific competition for space also may result in whole populations being lost from a local area. When growing in dense concentrations, barnacles (Barnes & Powell 5) and mussels (personal observation) will grow in thick clumps which are insecurely attached. During storms these may be stripped off whole areas of shore, leaving only bases or byssal threads behind.

Interspecific competition also produces small-scale patchiness. Stimson (86) found that a species of large limpet, *Lottia gigantea,* held territories from which it excluded, by direct shoving, other species of grazers, as well as potential competitors for space, such as mussels and anemones. When a *Lot-*

tia was removed, other grazers quickly invaded its territory; when a *Lottia* was placed in a new place on the open rock surface, it shoved other grazers off an area the size of its original territory. The local pattern of distribution of several species was thus affected by this interspecific competition. Another example is given by Dayton (26): the colonial intertidal anemone *Anthopleura elegantissima* is evidently limited in its spread by the presence of the large barnacle, *Balanus cariosus*. When *Balanus* were removed, *Anthopleura* spread into the vacated space.

Local patchiness of algae may be determined by interspecific competition, although the evidence for this is not conclusive. When Dayton (26) removed a large alga, *Lessoniopsis littoralis*, whose canopy occupied over half of the surface in wave-beaten localities, other large algae, as well as some smaller species, increased markedly. Another large "canopy" species, *Hedophyllum sessile,* is abundant in calmer areas. When it was removed, many smaller species of algae, called the "obligate understory" by Dayton (26) died back, while others, the "fugitive" or "opportunistic" species, appeared. Since a large grazing chiton, *Katherina tunicata* also disappeared in great part when *Hedophyllum* was removed, it is not certain whether these opportunistic species had been kept at low numbers by competition with *Hedophyllum* or by grazing. When *Lessoniopsis* was removed, no data were given on changes in the numbers of grazers. Without such data it is impossible to determine whether the increase in the abundance of the other algal species was due to a decrease in competition or to a reduction in grazing.

Grazing is certainly capable of keeping all algae on a shore in check. Jones (50) removed all limpets and larger algae from a wide strip down the intertidal zone on the Isle of Man. Opportunistic species of algae quickly colonized the entire strip, followed by larger algae. This experiment was repeated with the same result on a nearby shore by Southward (82). On both cleared strips young limpets settled densely and survived well under the canopy and ate the young plants there, so that there was no further recruitment of algae (Lodge 60). As the older algae died they were not replaced, and finally the community consisted of large limpets and few algae (Southward 84). Castenholz (12) studied the seasonal appearance of attached diatoms on intertidal rocks in Oregon. He excluded grazing snails (*Littorina scutulata*) and small limpets (*Acmaea* sp.) with cages or enclosed known numbers of them. Grazers could remove all diatoms in summer but not in winter, when presumably they were less active.

Sea urchins (*Stronglyocentrotus purpuratus*) live in dense aggregations in tide pools on the Washington coastline. Paine & Vadas (71) and Dayton (26) removed them from some pools and found that there was a rapid growth of several species of algae. After keeping the urchins out of the pools for 3 years, Paine & Vadas (71) recorded 4 to 7 canopy species and 5 to 11 understory species; *Hedophyllum* was the commonest canopy species, covering 47 to 80% of the surface. Dayton (26) had 1 to 6 canopy species and 6

to 15 species of understory algae after 3 years without urchins, with no canopy species assuming dominance.

Predation on animals also creates local patchiness. The instance described above, when *Balanus cariosus* escaped predation until it reached an invulnerable size, happened on very small areas. Likewise, *B. cariosus* may escape predation by the large starfish *Pisaster ochraceus* in a very patchy manner. Along a 1 km stretch of continuous steep rocky shoreline on the east side of San Juan Island, Washington, I found only nine small patches of *B. cariosus,* none greater than 2 m in diameter. This shoreline supports a dense population of *Pisaster.* On the west side of the same island *Pisaster* is scarcer, occurring in dense herds on a few points. On one area I watched them increase and over a period of a few years eat all the *B. cariosus* off the lower two thirds of the intertidal zone. On the next headland, about 0.4 km away, *Pisaster* remained scarce and large *B. cariosus* continued to occupy the lower shore (Connell 20).

INTERACTIONS BETWEEN PHYSICAL AND BIOLOGICAL FACTORS

These observations and experiments have demonstrated that the local distribution of a single species is often limited by different sorts of environmental factors in different places. Physical factors tend to be limiting at upper shore levels or at extremes of wave action, turbidity, or low salinity. Biological interactions become limiting where physical ones are less harsh, as at lower shore levels and with moderate wave action or currents.

Several interactions between these factors have been shown to be of crucial importance. Without the refuge at high shore levels afforded by harsh physical conditions, *Chthamalus stellatus* would be completely excluded in competition with *Balanus balanoides.* The same refuge protects *Balanus glandula, B. cariosus,* and *Mytilus californianus* from being completely eaten by various predators. In locations with either heavy wave action or extremely quiet conditions, *Mytilus edulis* has a refuge from its predators in Britain. Weather extremes, such as cold snaps, may temporarily reduce populations of predators, allowing prey to escape long enough to reach an invulnerable size.

There are also important interactions between competition and predation. I have studied competition between the barnacles *Chthamalus* and *Balanus* both with and without predators. Where predators (*Thais lapillus*) were common at low shore levels in Scotland they reduced the intensity of competition, measured as the difference between the percentage mortality of *Chthamalus* with and without *Balanus* (Connell 18, Table 7). Where predators were less common (at upper shore levels) there was no reduction in the intensity of competition, and in fact it was greater outside the protective cages. This is evidently the only instance in which both predators and competitors have been manipulated in the same experiment. However, in another experiment in Washington I observed competition between *Chthamalus dalli* and two

TABLE 1. The effect of predation by snails on interspecific competition between barnacles

	Chthamalus stellatus in Scotland, 1954[a]				Chthamalus dalli in Washington, 1964[a]			
Presence of predators	absent (cages)		rare	common	absent (cages)		common	
Level on shore	upper	lower[b]	upper	lower[b]	upper	lower	upper	lower
Number of sites	2	3	2	3	3	6	2	6
Number of Chthamalus in June	153	152	98	118	493	593	232	468
Percentage mortality of Chthamalus by September, caused solely from crowding by Balanus	39	32	31	13	22	37	6	10

[a] In Scotland, Chthamalus stellatus was competing with Balanus balanoides, the predator being Thais lapillus (Connell 18). In Washington, C. dalli was competing with Balanus glandula and B. cariosus, the predators being T. emarginata and T. lamellosa.

[b] On pieces of rock from the upper shore, transplanted to the lower shore.

species of *Balanus*, both with and without predation in cages. Instead of removing *Balanus* as in Scotland,
Balanus by being smothered, undercut, or crushed. Again, this was done at both upper and lower shore levels, but in Washington *Thais* were common at both levels, in contrast to the situation in Scotland. Table 1 shows that predation greatly reduced the mortality which was caused by crowding of *Chthamalus* by *Balanus*. Because I had kept the same sort of records of individuals being crowded in Scotland, I have also included these, for the same period of the year, in Table 1. The results at both locations were the same: predators reduced the intensity of competition by thinning out the populations so that they were not competing as strongly for the limited resource, space.

Two other studies of this interaction have been made, both in Washington. After Paine (69) removed the starfish *Pisaster ochraceus, Balanus glandula* and then *Mytilus californianus* colonized the lower shore. No data were reported, but competition was inferred since *Mytilus* was gradually occupying more space. Dayton (26) excluded predators with cages, and in some instances one species of barnacle disappeared while another increased, so that it may be inferred that competition had intensified. In both these studies, there was no direct evidence that competition occurred. To demonstrate competition, the density of one or both of the competitors must be manipulated experimentally, or else increased mortality must be directly observed to be caused by interference of one competitor with another.

"DEVELOPMENT" OF THE COMMUNITY

In the past the ecological community has sometimes been compared to an organism, with a young "developmental" stage leading to some sort of "maturity." In a newly vacated area, a succession of species gradually leads to a climax community (Clements 15). In a recent statement of this concept by Odum (68), ecological succession is regarded as orderly and directional, and

therefore predictable, as a result of modifications of the physical environment by the community itself.

To achieve such a predictable order it is necessary to postulate that certain species must precede others. If this is to be a result of community control, the early species must necessarily modify the environment to make it suitable for the establishment of later species. This is the crucial test of the reality of this type of ecological succession.

Does this process happen during recolonization of rocky shores? In most instances studied there has been a definite sequence of species. The first colonists are usually colonial diatoms, certain fast-growing algae, or sessile animals such as barnacles or tubeworms. These may cover the whole surface in the first few weeks. Later on, larger sessile species such as fucoid algae or mussels become established. The larger algae sometimes do not appear until the second or third year after the rock surface is newly exposed; this has happened when very large new surfaces, such as sea walls, were built in the intertidal zone (Moore 64, Rees 74). This could be taken to indicate that prior occupation by the early species might be necessary, since the larger algae were producing spores during the first years on nearby shores. In contrast, where quite small areas of rock were cleared, the larger algae became established in the first months and covered much of the surface in the first year (Pyefinch 72, Northcraft 67). These later colonists tend to have larger or less motile spores (Northcraft, 67) so that they would not be carried as often to large areas of new surface as to small areas cleared in the midst of existing beds of these algae. Thus, the late arrival of large perennial algae cannot be taken as evidence that other early-arriving species were needed to prepare the surface.

More direct evidence has been summarized by Redfield & Deevey (73) based upon studies of colonization of continually submerged panels suspended from rafts. While these findings may not be directly applicable to intertidal communities, they sometimes include similar species and so may be helpful. Redfield & Deevey (73) cite an unpublished study of A. Phelps, who was testing the hypothesis that a film of "slime" (e.g. bacteria, diatoms, etc) facilitated attachment of barnacles. Glass panels were left in place in the sea to accumulate slime and barnacles, and the rates of settlement of the barnacles were compared to those on panels newly submerged daily. The rates on the panels left in place were higher than on the newly submerged ones after the first few days. However the same effect could have been produced by the "gregarious" settling behavior described earlier (Knight-Jones 56, Wisely 88). Since Phelps' slimed plates also had many barnacles on them, the higher rates of attachment could just as likely have been due to gregarious behavior as to the presence of bacteria and diatoms. Delay in the settlement of bryozoans and serpulids on submerged panels cited by Scheer (78) could also be interpreted as resulting either from facilitation by earlier settling species or of this same gregarious behavior.

However, one experiment performed by Scheer (78) provides direct evidence of increased settlement of one species due to previous colonization by another. Scheer suspended glass panels from floats in a harbor. Some of the panels were first coated with bacteria in the laboratory (by placing them in a solution of peptone in natural seawater), others were controls of various sorts, including being exposed in the sea, which coated them with diatoms. After all the panels were subsequently exposed together in the harbor for 3 or 4 days, many more hydroids were found to have attached to the plates which had first been coated with bacteria. Although bryozoans and ascidians were evidently not stimulated to attach by the bacterial film, more settled on the plates which had a coating of diatoms from being immersed in the sea.

These results seem definitely to show that bacteria facilitate the attachment of hydroids. Whether the coating by diatoms influenced the bryozoans and ascidians is more doubtful. The numbers attaching were very few, and the controls were not as strict as in the first case. Also, if a few bryozoans had attached and gone unnoticed during ther first immersion, they would have stimulated others of the same species to attach.

There is at least one other instance of the possibility of early colonists facilitating the establishment of other species. The mussel, *Mytilus,* seldom appears very early in the sequence of recolonization. It has been noticed many times (see review by Bayne 7) that larval *Mytilus* first attach preferentially to rough surfaces or filaments, such as are provided by byssal threads, algae, hydroids, etc. Therefore, these species may facilitate the establishment of *Mytilus.* However, they are evidently not essential; Seed (79) found that *Mytilus edulis* would settle on many sorts of surfaces, artificial or natural, providing that these were rough enough. Many settled in crevices in the shore rock.

In summary, the available evidence suggests that establishment of later colonists usually does not require modification of the physical habitat by earlier ones. The only unequivocal evidence for such facilitation is the short-term experiment by Scheer (78) with bacteria and hydroids on submerged glass panels.

As the early colonists disappear, later ones become established and spread. Several authors have suggested that the former are overgrown and smothered or shaded out by the latter (Hewatt 47, Kitching 52, Bokenham 8, Rees 74). However, this may not be so, since there is evidence that pioneers may disappear without being replaced. For example, every month during the first 6 months after clearance, Northcraft (67) mapped the position of each plant as it became established on cleared strips. On his area A, the green alga *Ulva lobata* covered the whole surface between the heights of —0.6 ft and +2.5 ft within 1 to 2 months. Then, in three of the four seasons in which he had cleared the strips, the *Ulva* began to disappear first along each side of the strip, with no other alga appearing on the exposed surface. The area covered

by *Ulva* continued to shrink for several months, depending upon the season, but the exposed area was only gradually filled by other algae. *Ulva* was clearly not being displaced by competition with other algae.

Although there were no records kept of animals on these strips, it is reasonable to assume that grazing gastropods invaded the area along the edge and gradually ate back the *Ulva*. This would explain the manner in which the *Ulva* disappeared from the sides. This also happened when Haven (42, 44) excluded grazing gastropods with fences on the same shore which Northcraft studied. Algae (particularly diatoms and *Porphyra*) quickly grew, and when the fences were removed the grazers invaded and ate off the algae.

In fact, the sequence of algal colonization after grazing animals are removed is very similar to that after all organisms are cleared or after new surfaces are exposed. When grazers alone are removed, the same early colonizing algae appear, and when the grazers return, these algae disappear.

Based upon this evidence, or lack of it, I feel that the process of recolonization of an intertidal rocky shore should not be described as analogous to the development of an organism. Those species which confer most of the structure of the mature community are large, long-lived, and relatively slow-growing, such as large perennial algae or large barnacles and mussels. They tend not to reproduce continuously so that they may not colonize newly vacated areas immediately. They also take a longer time to grow to maturity and to spread over the surface. During this time, space is not fully occupied and various "opportunistic" species take advantage of this space to settle and grow quickly to maturity. They produce many small motile spores or larvae and breed over a greater part of the year than do the mature species, so that they would be expected to be the first to settle (Rees 74, Northcraft 67). They are usually present in the mature community and should be considered as "opportunists," rather than as "fugitives" or "pioneers," terms which imply that they represent an intermediate stage in a hypothetical "development."

Once the "dominant" species of the "mature" community grow enough in size and number to effectively modify the physical environment, many other species which can live only in these new conditions establish themselves. When Hewatt (47) cleared his test quadrat he found several very common species of amphipods, isopods, small crabs, and worms sheltering under the mussels. These did not return during the next year, when the colonizing mussels were few and small; apparently they require a covering of large mussels. When Dayton (26) removed large algae (*Hedophyllum*) from the shore, several species of smaller algae such as *Corallina* and others which grow only in the shade beneath, quickly died back. Like the animals under *Mytilus,* there is a group of "obligate understory" algae which thrive only in the shelter of the dominant larger plants.

Thus, while there is an orderly sequence of establishment of species colonizing newly vacated spaces, present evidence indicates that the order is a

result of differences in length of breeding seasons, motility of planktonic stages, rates of growth after settlement, and ultimate size reached by the species, rather than of successive modifications of the environment by the organisms themselves. The organisms comprising the community certainly do modify the environment in such a way that others are enabled to live there, but these modifications do not necessarily produce a predictable succession. I suspect that if all the early opportunistic species were removed as they arrived, the dominant species would still become established. Once the dominant species settled and grew, others would colonize the shelter provided or move in to feed on them. So far no one has done the crucial experiment of excluding the early colonists to see whether the species of the "mature" community can become established without them.

This is not to deny that the early colonists have certain characteristics which are very different from those of the "mature" community (Odum 68). My purpose is simply to point out the almost complete lack of evidence for any "internally controlled" development toward a "mature" community. A complex community such as a mussel bed, which confers protection from external perturbations, can evidently become established without the necessity of a predictable, orderly succession of "pioneers," and I suggest that field experimental studies of the process are long overdue.

The influence of grazers and predators on the process of recolonization also has not been studied. Rees (74) pointed out that grazers must be important, but other studies of algal recolonization have ignored them. Likewise, Hewatt's (47) study was limited to animals. Now that field experiments have indicated their importance, the role of interactions between plants and animals in the process of recolonization should be studied. In terrestrial plant studies, grazing animals have usually been regarded as "halting," "delaying," or "deflecting" succession from its "normal path." This concept has been applied to rocky shore communities by Paine (69) and Dayton (26), who regard grazing or predation as a "biological disturbance," evidently because it creates open spaces as do logs pounding on the shore. This is permissible if one is interested only in succession in plants or any other single trophic level. However, the community consists of a set of animals, plants, and microorganisms which, in living together, have evolved various adaptations to each other; and so grazers or predators cannot be regarded as causing "disturbance" or "delaying" the "normal" succession. Having evolved with the rest of the species in the community, they are an essential part of it at any stage in its history; and to regard their activities as disturbance relegates them to a special category for which there is little or no basis.

CONCLUSIONS

By comparison with many other communities, the rocky intertidal zone is relatively well studied. Yet most of the work has been restricted to temper-

ate latitudes in Europe and western North America, and to only a few of the commoner larger species. Many of the experiments should be regarded as only tentative and few have been sufficiently replicated.

However, there has been enough preliminary work to enable us to see the dynamic relations between some of the organisms in their proper context. This is unusual in discussions of communities, where examples from land birds, barnacles, and protozoans are sometimes jumbled together to provide backing for the theories being propounded. Some general patterns have emerged from the evidence presented in this review.

The vertical and horizontal limits of distribution of some common species have been shown to be determined by direct effects of the physical environment as it becomes harsher, for example toward the upper shore. Biological interactions set limits as physical conditions become less harsh. Within these limits there is much small-scale patchiness, caused directly by physical or biological stresses and their interactions. Long-lived sessile species of animals and plants may hold patches of surface, excluding others and modifying the environment in such a way that other smaller species are able to live there. Thus, the former truly "dominate" the areas they occupy. None of this is new to the general field of ecology. What is novel is that there exists direct evidence of both where and how the pattern is created in the marine intertidal region.

Two further conclusions of this review may be regarded by some ecologists as at least heterodox, if not new. The first regards "succession" in the marine intertidal. If the dominants are removed by some extreme event of either physical or biological origin, short-lived opportunistic species are usually the first to recolonize the vacated areas. However, it is possible for dominants to be the first colonists; there is no convincing evidence that the opportunists must necessarily prepare the way. The sequence of recolonization is apparently not "community controlled" (Odum 68); its orderliness is a consequence of differences in life history characteristics between opportunists and dominants. Community control comes after the dominant has become established, when other species are able to colonize the new environment.

The second point is that the dominant species seldom secures space (the essential resource) by a process of competition. In some situations, particularly where the physical environment is so harsh that natural enemies (grazers or predators) are relatively ineffective, interspecific competition determines which species secures the space. But under more benign physical conditions natural enemies are very effective, so that the only way a dominant can become established is by somehow attaining a size large enough to be safe from attack. This means that the natural enemies must be reduced, either by their own predators or by an unpredictable physical catastrophe which is not so extreme as to also kill the dominant species itself. Although this may seem unlikely, there is evidence that physical extremes do affect dif-

ferent species and even local populations of the same species to a different degree. In fact, such variability may be the most important thing to emphasize, as Den Boer (27) has pointed out: "After some time, I realized that heterogeneity and instability must not be considered as just a drawback of field data to be neglected ('averaged away' or 'seen through by intuition') or circumvented by retreating into the laboratory because they were mere deviations from the 'typical' or 'representative' case (or even 'noise'). On the contrary, heterogeneity and/or instability must be recognized as fundamental features of a natural situation."

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