

## THE ESTABLISHMENT AND DEVELOPMENT OF A MARINE EPIFAUNAL COMMUNITY<sup>1</sup>

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**Abstract.** Because of the nature of their substratum, the sessile invertebrate species of the marine epifaunal community living on rocks occur in discrete patterns of distribution. The rocks are finite patches or habitat islands with a limited space for colonization and growth. Such a system is ideal for studying the parameters affecting the distribution of species within a community. Also, because of the small size and immobility of the adults, the system is also ideal for studying the pattern of change in species composition and diversity within a community. This study used multiple series of manipulated experimental plates, which both duplicated natural rock surfaces and could be compared with samples of the rocks, to investigate the developmental and distributional processes of this community.

Five major factors were found to be important to both the development of the community and its distribution on the rocks: (1) the selectivity of the metamorphosing larvae as to site of attachment; (2) the seasonal fluctuation in larval abundances; (3) the biological interactions within and between species; (4) the size of rock substrata; and (5) the physical disturbance of the substrata (rock turnover). Initially, the developmental process can be uncoupled from the effects of substrate size and disturbance. Predation is relatively unimportant as a biological interaction within this community, but the species can be ranked according to their ability to compete for the available space on a substratum. This ranking implies a type of successional sequence in the development of the community: however, the sequence is greatly affected by historical components. The colonization of a substratum is directly dependent upon the abundance of settling larvae, which in turn is a function of seasonality and selectivity. The eventual competitive outcome and development of the community will depend upon which species have immigrated onto the substratum and is thus dependent upon history. The process is, therefore, open ended: colonization will be highly variable and change seasonally and, although one species may eventually dominate the substratum, it may be one of nine different species depending upon the individual history of that area.

The frequency with which a substratum is disturbed (with the resultant extinction of its fauna) is a function of wave force and is inversely proportional to both the size of the substratum and the depth at which it occurs. Disturbance will determine when a substratum is initially exposed for colonization and how long it will have for development. In the shallow subtidal (mean low water to -2.5 m), the frequent disturbance of small rocks will cause them to support less than their equilibrium number of species and their fauna will reflect immediate larval abundances. Large rocks will remain stable for long periods of time and will usually be dominated by a single species. Intermediate-sized rocks (1 to 10 dm<sup>3</sup>) will remain stable long enough to develop an equilibrium number of species but will be disturbed before dominance occurs. They will thus have the highest diversity because of their "optimal" frequency of disturbance. In deeper water (10 m) smaller rocks will be more stable. More rocks will develop dominance and the smaller size of a rock at the optimum frequency will mean that substrata at this frequency will have a lower equilibrium number of species and thus a lower diversity. The increased stability with depth will mean a lower overall diversity for the community. Lastly, the increased disturbance and lower pool size for rocks in the intertidal will also cause diversity to be lower in this area.

There appears, therefore, to be an optimal frequency of disturbance at which diversity is maximized. An increase or decrease in this level causes a reduction in diversity because of a decrease in the number of species present or an increase in dominance. This optimum will vary with the physical environment and the type of community.

*Key words:* community composition; competition; disturbance; diversity; dominance; island size; marine epifaunal; rocky subtidal; seasonality; succession; Massachusetts.

### INTRODUCTION

The parameters controlling the composition of communities and the development and maintenance

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of this composition have been investigated both theoretically and empirically by many authors. Within the marine environment, a great deal of this research has been conducted on the epifaunal community associated with such hard substrata as rocks and shells. This intensity of study is mainly the result of four factors: (1) the habitat is often located near the

shore and is easily accessible; (2) the habitat occurs as discrete, easily defined units (rocks); (3) the fauna is composed mostly of sessile invertebrates whose distributions and interactions can be observed and manipulated with relative ease; and (4) the rock substrata themselves can be duplicated by artificial surfaces which can then be experimentally manipulated.

The studies of epifaunal communities on rocks have been both descriptive and experimental. These studies have demonstrated that a variety of factors contribute to the species diversity, composition, and structure of the community. Scheer (1945) has depicted the development of the epifaunal community through time as a successional sequence, while others, such as Shelford (1930) and Kawahara (1965), have emphasized the importance of seasonal and annual changes in the physical environment in causing changes in the species composition. Paine (1966) demonstrated the role of predation in increasing species diversity and Sutherland (1974) has shown the effect of predation on species composition. Riedl (1964) and Rützler (1965) have shown that the physical disturbance of the rock substrata has an effect on the species diversity and composition. Since a large component of the epifauna consists of attached, sessile species, the distribution of individuals on the rocks is most often accomplished by a motile larval stage. The selectivity of site of attachment by these larvae at the time of metamorphosis has also been shown to be important to species distributions (Ryland 1959*a, b*, 1960, 1962; Ryland and Stebbing 1971; Crisp and Barnes 1954; Crisp and Stubbing 1957; Knight-Jones and Crisp 1953; Knight-Jones 1951*a, b*, 1953*a, b*; McDougall 1943; and many others). Other work has shown that differences in species diversity and composition can result from the combined effects of more than one factor. Dayton (1971), in an elegant study, found that physical (log damage) and biological (predation) disturbances combined to increase the diversity of a rocky intertidal community. Connell (1961*a, b*) also found that the vertical zonation of barnacle species was caused by the interaction of physical (desiccation) and biological (competition and predation) factors.

Although these and many other studies (Connell 1972 and Schoener 1974 for more extensive reviews) suggest that a variety of different parameters have an effect on the species composition and diversity of this community and its change through time, these results are not necessarily contradictory. The parameters will vary in relative importance depending upon the community being studied.

The majority of epifaunal species are sessile filter feeders, permanently attached to a substratum. The

limiting resource is the two-dimensional surface of this substratum to which they attach. This resource (space) is both finite and distributed in discrete patches (rocks). Any factor affecting a species recruitment onto a rock or its utilization of the available space should potentially effect the distribution of that species.

Five parameters which should have a major effect on the species of the epifaunal community are indicated by previous studies. These are: (1) the selectivity of the larvae at the time of settlement; (2) the biological interactions between the species; (3) the size and distribution of rocks or patches; (4) the seasonality of the environment; and (5) the magnitude and frequency of physical disturbance. Each of these factors will vary in its effect, both within an individual locality and between localities. The present study was designed to measure experimentally the effects of each of these parameters within a single locality. If the assumption that these parameters are ones of major "importance" in controlling the species diversity and composition of this community is correct, it should be possible to incorporate them into an accurate empirical model for the spatial and temporal distribution of this community. Since the magnitude of the effect of each factor should also vary predictably between locations a more general model is also possible. Such a model will be developed in a later section.

#### STUDY AREA

The study area was located in Sheep Pen Harbor, Nonamesset Island (41°31'N, 70°40'41"W); ≈ 1 km south of the Marine Biological Laboratory in Woods Hole, Massachusetts (Fig. 1). The area is a natural rock shore with two main patches of rocks. The patches are separated by ≈ 25 m, with the interlying area being sand and eelgrass. The northern cluster of rocks covers an area of ≈ 5300 m<sup>2</sup> and the southern an area of 6500 m<sup>2</sup>. An infrequently-used dock also lies between the two rock areas and served as a platform from which experimental substrata were suspended. At one time, the patches were probably connected then subsequently divided by the dredging associated with the original construction of the dock.

The rocks ranged in size from coarse gravel to boulders in excess of a cubic metre. All of these were well-rounded, coarsely crystalline granite and are part of the glacial outwash of ≈ 10,000 yr ago. Their distribution with depth was from the intertidal zone to a depth of 3 m.

The physical parameters of the environment, which have an effect on which species can successfully become established in the study area, exhibited random daily, cyclical daily, and seasonal patterns of

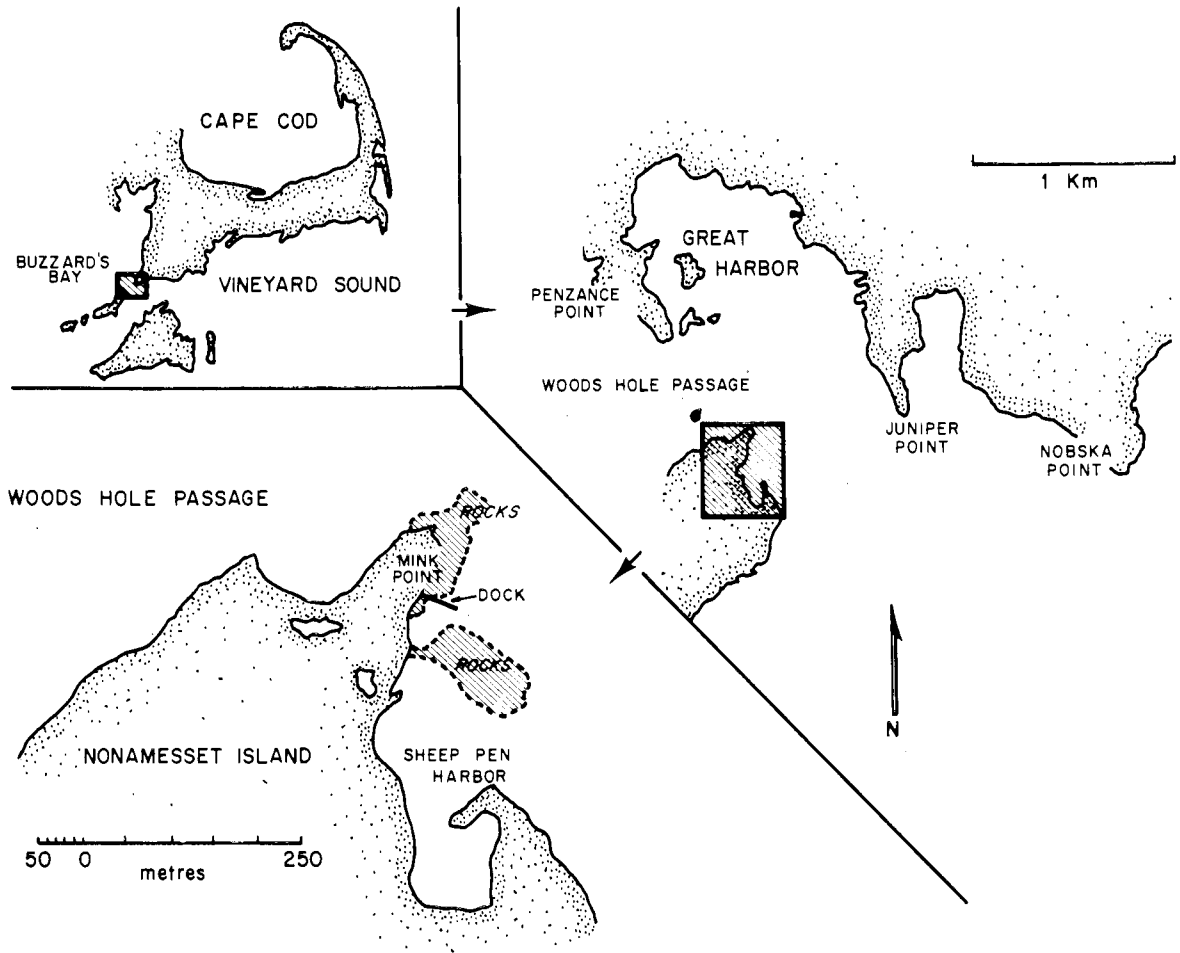


FIG. 1. Map of the Woods Hole region of Cape Cod, Massachusetts with a detailed map of the study area on Nonamesset Island.

fluctuation. The majority of the study was concerned with community changes in the subtidal areas (mean low water to  $-2.5$  m) and at any point in time the range of many of the physical parameters remained fairly constant over this area.

Salinity remained stable throughout the year, fluctuating randomly between 30 and 32 ‰, with no significant variation with depth. Turbidity varied directly as a function of wave action and also showed no significant variation with depth. Neither of these factors was found to affect measurably the distribution of the species within the study area.

The water temperature exhibited a marked seasonal fluctuation, rising to a maximum of  $\approx 23^{\circ}\text{C}$  in August and falling to a minimum of  $\approx -1^{\circ}\text{C}$  in January. For many of the epifaunal species, cycles of reproduction and growth are associated with this seasonal variation. Also temperature, in conjunction with wind and diurnal exposure to air, contributes to the desiccation and freezing which restrict the num-

ber of species found in the intertidal zone to only those true intertidal forms.

Current velocity is an important factor within the study area. The temporal stability of a rock substratum (the frequency at which it is overturned or disturbed) will depend on these velocities. The study area lies south of the Woods Hole Passage in which very strong tidal currents are generated (average max velocities are 185 cm/s). However, the area is somewhat sheltered by Mink Point (Fig. 1) and in open water to the east of the area average maximum velocities are reduced to 57 cm/s (ebb) and 77 cm/s (flow). In general, velocities of this magnitude will only disturb rocks  $< 1$  cm in diameter (Hjulström 1939, Fig. 1). The major current velocities in the area are thus those generated by wave action. For the most part these are highly variable and dependent upon the weather (wind velocity and direction). Also the velocity at any time will decrease with depth.

## METHODS

The study was conducted for a period of 27 mo; from June 1972 to August 1974. It consisted of both observation of the naturally occurring rocks and the experimental manipulation of artificial surfaces. Slate was used for the construction of these experimental surfaces. Although it differs from the granitic rocks in grain size, it closely approximates their surface texture and could be cut into an exact size. A similar cutting of the granite would have changed its surface texture, which was felt to be an important characteristic to the settling of larvae.

The experimental surfaces were square panels measuring 14.5 cm<sup>2</sup> and 103 cm<sup>2</sup>. These were attached to the underside of wood boards which were suspended with ropes from the dock at 0.5 m depth intervals. Four replicates of both sizes at each of the five depth intervals were used for all parts of every experiment. Two different experiments were conducted using the plates with > 200 plates of each size used throughout the study.

*Settling plates*

The settling plate experiment was conducted to estimate larval settlement rates and to detect selectivity of larvae as to the site of attachment. In this experiment, plates were initially exposed at the beginning of each month of the study. These plates were then removed at the end of the month and replaced by a clean set. The number of individuals of each species that had immigrated onto the surface were then counted. The plates were cleaned for reuse.

These data yielded information on both monthly (and seasonal) changes in the abundance of settling larvae and larval selectivity. By comparing the two sizes of plates at the same depth any selectivity for substrate size could be detected. Also by comparing the same size plate at different depths selectivity for depth could be determined.

*Colonization plates*

In this set of experiments, plates were placed in the water at the beginning of June, July, August, September, and November 1972. The series of small November plates were lost after  $\approx$  6 mo and are not included in the analyses. Also partial series of plates (two replicates of each size at each depth) were started in May and July 1973. Each of these was periodically examined in the laboratory and then replaced on its board in the field without disturbing the accumulated fauna. Initially, all plates were examined every month, but after 6 mo both the increased number of substrata and the increasing abundance of the fauna on each plate prohibited examination of all the plates. However, at least one

replicate was examined each month with all plates usually being examined every 3 mo. Both the number of individuals (or colonies) and the area covered (a more accurate predictor of abundances when comparing small solitary species with large colonies) were measured for each species on each plate. The total surface of each plate was examined carefully using a dissecting microscope, and the area covered was estimated by using a grid projected onto the specimen from a camera lucida. For stalked species, such as *Bugula turrita*, which have a small basal area of attachment but can present a broad crown of branches, the area covered by the crown was recorded. The few stoloniferous species, such as many members of the Campanularidae, in which individual zooids were widely spaced could not be accurately measured for area covered. They represented a small portion of the fauna (by area) and were included in analyses as 0.5 mm<sup>2</sup>.

The data were analyzed in several ways. The development of the community on an individual plate or group of replicates was followed. The effects of substrate size, depth, and time of initial exposure were also determined. Finally, the effect of disturbance was duplicated by assuming that a substratum initially exposed in one month and disturbed in a later month (with total extinction of its accumulated fauna) will develop a fauna similar to that of a substratum initially exposed in that second month.

Losses of plates should also be noted. These losses are important in that they determined how long an individual series of plates could be followed and they also account for the absence of potential data points in various analyses (i.e., Figs. 3, 4, and 5). Permanent losses of plates were usually due to physical damage. The shallowest series of plates (those at mean low water [MLW]) suffered the most from wave energy. The wood boards holding these substrata never survived for more than 6 mo, usually being pulled free or destroyed during storms. Because of the insufficient data for these plates, they are not included in the analyses. Also a substantial number of substrata were lost during the second spring (1974). Boring organisms had greatly damaged the wood boards and whole series of replicates were either lost or disturbed through scraping by loose boards. These losses were particularly prevalent among series exposed for the longest time period (June, July, and August plates). Absences of individual data points resulted from errors in sampling and the inability to sample at the planned time. These losses were most frequent during winter months when temperature limited diving time and diver efficiency, and weather restricted the number of times the study site could be visited. These losses

are mentioned only to explain why some data points are missing (samples were never arbitrarily excluded from analyses) and why at times it was necessary to pool certain data.

### Rocks

Throughout the study the rocks within the study area were also examined. Collections of rocks from at least two different depths were periodically made in the patch of rocks to the north of the dock. These were also examined in the laboratory and the number of individuals and area covered by each species was measured. Each rock was weighed, its volume measured, and its available surface area was approximated using a grid system. The sampled rocks ranged from 15 g to 3 kg in weight, 5 cm<sup>3</sup> to 1.5 dm<sup>3</sup> in volume, and 5 to 400 cm<sup>2</sup> in surface area.

All collections (both rocks and plates) were made underwater with the aid of diving equipment. Substrata were quickly transported to the laboratory in seawater and placed in running seawater within 15 to 30 min. In the laboratory, an individual substratum was placed in a large culture dish with fresh seawater for examination. If the examination time was long the seawater was changed frequently.

Because of the large number of substrata sampled each month, individual plates and rocks were not physically isolated in the laboratory. Since mobile species could therefore move between substrata and might also be lost during collection, only those sessile species attached to the substrata were included in the quantitative analyses. All organisms were identified to the species level, unless a proper identification could not be made without disturbing the animal. Thus individuals of groups such as the polychaete family, Spionidae (in which identification could not be made to the species level without removing the animal from its tube) were grouped as one "species." With this in mind it was estimated from the literature (Smith 1964; Pratt 1935; Osborn 1910; Sumner et al. 1913; and Fraser 1944) that 140 sessile species comprised the available species pool, of which 91 were recorded at least once during the study. All sessile species recorded on a plate were used in any calculations presented unless otherwise indicated. Species recorded as present but < 1 mm<sup>2</sup> were arbitrarily entered as 0.5 mm<sup>2</sup> in any calculations based on area.

## RESULTS

### Larval selectivity

The majority of epifaunal species depend upon a planktonic larvae for dispersal. These larvae generally remain in the plankton for a few hours to a few weeks, after which they metamorphose and attach to a substratum. Any selectivity as to site of at-

tachment which these larvae display will have a direct effect on the distribution of the adults.

A wide range of factors have been demonstrated to have an influence on the settlement and attachment of epifaunal larvae. Factors such as light (Thorson 1964), temperature (Ryland 1962), water currents (Crisp and Stubbings 1957), and the contour, texture or angle of the surface (Crisp and Barnes 1954; McDougall 1943) have been shown to be important. Also biological factors, such as the presence of a microbial film (ZoBell and Allen 1935), type of algae (Ryland 1959a, b), and the presence of the same species (Knight-Jones 1951b, 1953a, b; Knight-Jones and Crisp 1953; and Wisely 1960) affect larval settlement.

McDougall (1943) found that the selectivity of the larvae was often important in determining the vertical distribution of many species. Connell (1961a, b) also found that the depth range of settlement contributed, in part, to the intertidal zonation of barnacles. The depth at which a larva settles can result from a number of factors; light, currents, temperature, gravity, etc. Although depth is thus a crude and all encompassing parameter, it is nonetheless both an important and easily measured variable for a large number of species.

Figure 2 shows the depth distribution in average number of larvae attaching to large settling plates per month for 12 common species. Except for the species *Balanus balanoides* and *Lichenopora verrucaria*, these data were collected in the months of August and September, the time of peak settlement for most species. The peak settlement of *B. balanoides* and *Lichenopora* occurs in the spring and the data for these species were collected in March and April. Although the depth range is small and the abundances of different species are very variable (with *Spirorbis* and *Balanus amphirrite niveus* being the most abundant species at all depths), a number of patterns emerge. Several species (*Schizoporella biaperta*, *Cryptosula pallasiana*, *Crisia eburnea*, and *Didemnum candidum*) seem to increase in settling abundance with increasing depth, while others (*Spirorbis pagenstecheri*, *B. a. niveus*, *Schizoporella errata*, *Hydroides dianthus*, and *Scypha* sp.) have distributions which seem to peak at intermediate depths. Also, the species *B. balanoides* and *Lichenopora* appear to decrease in abundance with depth and *Sabellaria vulgaris* shows no pattern.

It should be noted that individuals of most species were recorded at all depths within the shallow depth range of the study area. However, the observed patterns in larval settlement will have a direct effect on the initial and cumulative abundance of each species at the different depths. In the extreme cases where larval production is low, the pres-

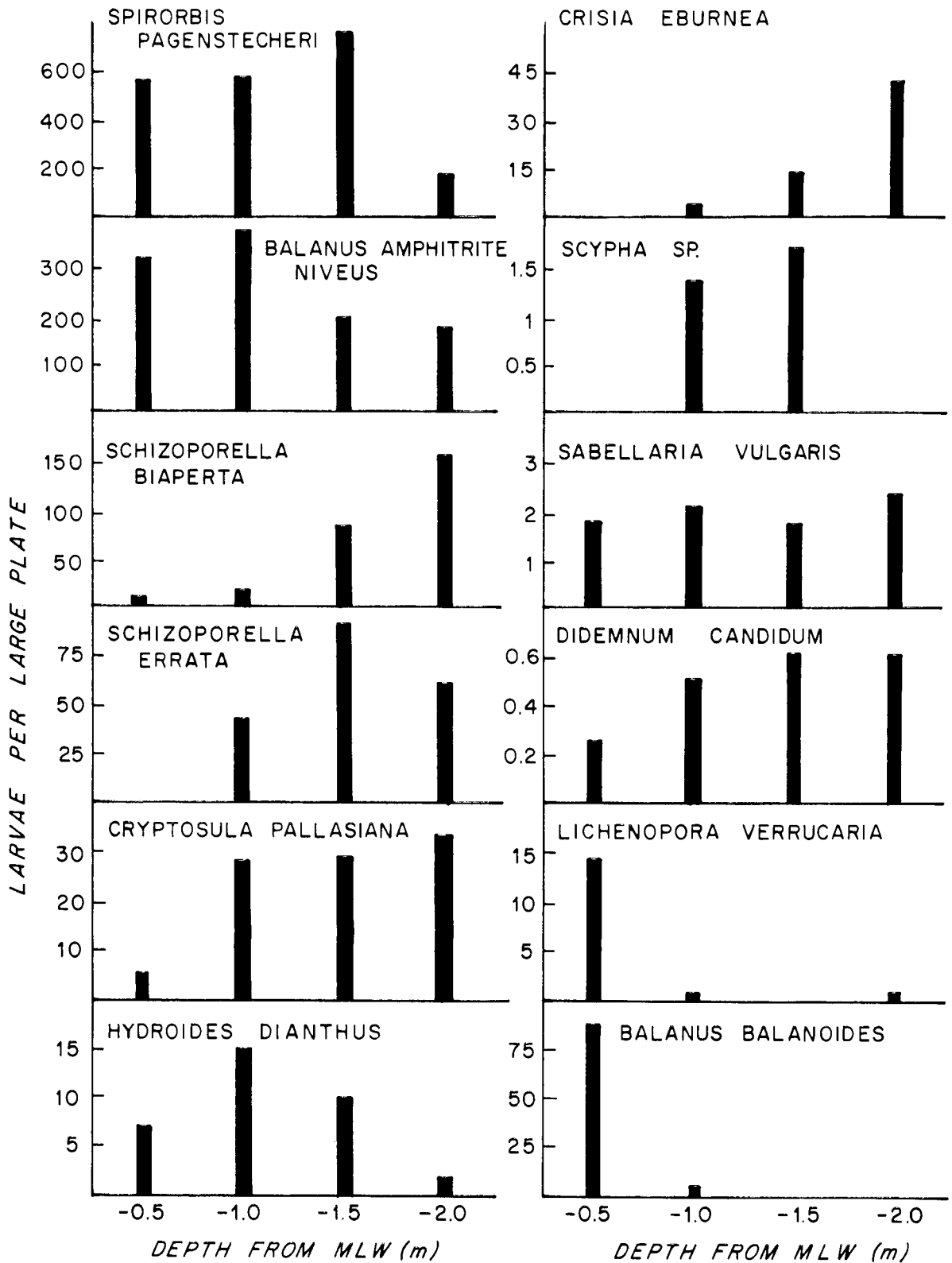


FIG. 2. Bar diagrams showing the depth distribution of settling larvae of 12 common species. The data show the average number of larvae attaching to a large settling plate per month at each depth. These plates were  $\approx 103 \text{ cm}^2$  in exposed surface area and were exposed for a period of 1 mo. These data were collected in the 2 mo of peak larval settlement for each species (see text for further description).

TABLE 1. Comparison of settlement on large and small plates

Species	Month	Mean no. of individuals settling per plate		Magnitude of difference	Probability that magnitude same as $7 \times$
		Large	Small		
<i>Spirorbis pagenstecheri</i>	Aug	736	92	8.04	$p > 0.5$
	Sept	744	158	4.72	$p > 0.05$
	Oct	711	183	3.88	$p > 0.05$
<i>Hydroides dianthus</i>	Aug	12	1	10.00	$p > 0.2$
<i>Balanus amphitrite niveus</i>	Aug	183	31	5.86	$p > 0.2$
	Sept	282	63	4.51	$p < 0.05$
	Oct	257	36	7.21	$p > 0.9$
<i>Schizoporella biapertura</i>	Aug	34	6	5.87	$p > 0.5$
<i>Schizoporella errata</i>	Aug	51	6	8.12	$p > 0.5$
<i>Cryptosula pallasiana</i>	Aug	31	4	7.69	$p > 0.5$
<i>Crisia eburnea</i>	Aug	6	1	5.00	$p > 0.2$
	Sept	9	1	7.00	$p > 0.9$

ence or absence of a species may result from selectivity. The abundance of a species will be an important parameter in its ability to utilize the available space of a substratum and will have a direct effect on the possible inter and intraspecific interactions that will occur. As will later be shown, these patterns in larval settlement will have consequences in the eventual development and structure of the epifaunal assemblage on an individual substratum.

The difference in larval settlement between substrata of different size was also investigated. As with depth, larvae were not expected to actively select substrata of a particular size. However, they may be responding to some other parameter, such as current velocity or turbulence, which would differ with substrate size. The large plates have a surface area  $7.11 \times$  that of the small plates. If larvae were nonselective with respect to the substrate size, the large plates should sample  $\approx 7 \times$  as many larvae per species. Table 1 compares the average number of individuals settling per month for large and small plates sampled at the same depth. For all the species shown, the large plates have a much larger number of individuals settling than the small. In only one case (*B. a. niveus* in September), was the number on the large plates significantly different than  $7 \times$  the number on the small, but this same species showed no significant difference at two other sampling times. It therefore appears that the larvae are settling without any selectivity as to substrate size, being sampled by the substratum in proportion to its available surface area.

#### Biological interactions

The biological interactions which occur both within a species and between species may be very important to the developing species composition, structure, and the diversity of a community. Although the physical parameters of the environment

will often determine which species can occur in a particular area, their effect on the development of the community may be mediated through these interactions. Biological interactions can be grouped into two broad categories: predation and competition.

**Predation.** In numerous studies of shallow water marine communities, predation has been shown to be a controlling factor of both diversity and structure (Connell 1961a, b; Paine 1966; Dayton 1971, 1975; Porter 1972, 1974; and others). In general, these authors have demonstrated that predation on competitively dominant species creates open space and allows less competitive species to coexist within the community. This type of predation becomes a mechanism for increasing diversity.

Although several species of predators were observed on both the plates and rocks, most such species were either rare or occasionally seen and none appeared to have a major effect upon the community. Two species of asteroids, *Asterias forbesi* and *Henricia sanguinolenta* were seen infrequently in the study area and never observed feeding. They were never encountered on the plates, except for three larvae of *A. forbesi* ( $< 1$  mm in diameter), found at various times during the study. Nudibranchs (*Cratena aurantia*, *Eubrancheus pallidus*, and *Onchidoris* sp.) were occasionally associated with hydroid colonies (especially *Tubularia larynx*). These were also rare and their presence could not be correlated with any change in hydroid abundance.

The most abundant predators were the turbellarian, *Stylochus ellipticus*, the oyster drill, *Urosalpinx cinerea*, and several species of small fish. Both *Stylochus* and *Urosalpinx* prey on barnacles and were seen actively feeding on *B. a. niveus* on the experimental plates. The predation pressure exerted by these two species did not appear to differ

with substrate size. As with the settling larvae, the abundance of these species on the different size plates showed no significant difference from what would be predicted from differences in plate size ( $p > 0.5$ ). Although the abundance of *B. a. niveus* declined through the first winter of the study, observations indicated that predation was only one cause of the mortality. Less than 5% of the empty barnacle tests on plates (including many in which the opercular plates were found inside the test and unbored) had the characteristic hole made by *Urosalpinx*. Also, as many as 30% of the dead barnacles on a substratum still had all or most of their soft tissue intact. Presumably if predation were the cause, most of this tissue would have been ingested by either of these predators.

Even if it were assumed that *B. a. niveus* is predator limited, this predation has little effect on the diversity of the community. The barnacle is not a good competitor for space and is easily overgrown by encrusting species (see below). Predation on it does not make available "free space" which would otherwise be unattainable.

Predation or the evidence of predation on other species was very seldom observed during the study, either on the rocks or plates. Only twice were fish observed feeding on the surface of the plates, and there was little evidence that they or other predators were disturbing the epifauna to any great extent. Signs of cropping, such as tracks, trails, wounds or missing parts of individuals or colonies, were never observed on either plates or rocks.

Additionally, during a pilot study substrata were exposed in the same study area from June 1971 until May 1972. These substrata (glass slides) were enclosed in protective cages of galvanized screening with openings of 0.75 cm<sup>2</sup>. These cages successfully excluded large predators such as *Urosalpinx* and fish. The substrata were only slightly larger (19.35 cm<sup>2</sup>) than the small experimental plates and the two series can be compared. Comparisons of substrata from the same depth and exposed a similar period of time (although different years) showed no significant difference in the number of species present ( $t$ -test,  $p > .5$ ). After 1 yr, both series were also very variable in species composition. Several individual substrata did become dominated by a single species, including *Schizoporella errata*, *C. pallasiana*, *Molgula manhattensis*, and *Halichondria bowerbanki*. However, this dominance occurred both on the caged substrata and on the exposed experimental plates and does not seem to result from the enclosure of macroscopic predators. From the data, predation seems to be relatively unimportant in determining the diversity and composition of this epifaunal community.

### Competition

The invertebrates of the epifaunal community form an assemblage of species feeding at only one trophic level. They have developed a variety of mechanisms to feed on an external food source of zooplankton, phytoplankton, and detritus suspended in the water. Although this external food source undergoes seasonal (and probably daily) fluctuations, it is generally abundant. A much more limiting resource is habitat space. Rocky areas are both finite and discrete. Once an individual attaches to a rock surface it is restricted to that surface and its ability to survive will be dependent upon how well it can utilize the available surface area. The animals should therefore compete for this resource.

This competition is both active and passive and is usually a function of a species growth rate or growth form. Rapidly growing species actively overgrow slower growing ones, and this usually results in the death of the overgrown species. Other species, because of their arborescent, stoloniferous or linear growth form, can often avoid being overgrown, yet these species are incapable of overgrowing or outcompeting other species. They passively resist being outcompeted, and are able to persist in the community even though they are "competitively inferior."

*Intraspecific competition.* Species must not only compete with other species for available space, but also with other individuals (or colonies) of the same species. However, through a variety of mechanisms, intraspecific competition has been greatly reduced in the epifaunal community being studied. For example, a number of species distribute themselves with a minimum distance between individuals. These species, such as *Spirorbis* and many barnacles, tend to aggregate, but have a maximum size to which they can grow. The settling larvae attach near other individuals of the same species but at a distance great enough to allow for growth (Knight-Jones 1951; Knight-Jones and Crisp 1953; Wisely 1960; and Knight-Jones and Moyses 1961). This allows for maximum utilization of space while minimizing intraspecific competition.

Likewise, colonial species, which normally overgrow other species, have a variety of mechanisms which prevent overgrowth of a colony of the same species. Many species, when they encounter another colony of the same species stop growth in that direction (Knight-Jones and Moyses 1961 and *personal observation*). This can be seen particularly well in the ectoprocts, where the development of a colony is easily distinguished by the pattern of zooids. Species, such as *Schizoporella errata* and *Cryptosula pallasiana*, which were frequently observed overgrowing other species, were never observed to over-



TABLE 2. Competition between species pairs (measured as overgrowth). Percent contacts in which A overgrows B (no. contacts in parentheses if < 20). 1 = *Botryllus schlosseri*, 2 = *Halichondria bowerbanki*, 3 = *Schizoporella errata*, 4 = *Amaroucium constellatum*, 5 = *Didemnum candidum*, 6 = *Cryptosula pallasiana*, 7 = *Schizoporella biaperta*, 8 = *Balanus amphitrite niveus*, 9 = *Spirorbis pagenstecheri*

Species A	Species B								
	2	3	4	5	6	7	8	9	
1	60.0 (5)	66.67 (6)	75.00 (4)	100.00 (3)	100.00 (5)		100.00	100.00	
2		55.00	66.67 (3)	85.71 (7)	100.00 (4)		100.00	100.00	
3			50.00 (6)	68.29	73.17	95.15	100.00	100.00	
4				50.00 (8)	81.82 (11)		100.00	100.00	
5					75.61	95.00	100.00	100.00	
6						90.00	100.00	100.00	
7							100.00	100.00	
8								100.00	
9									

grow colonies of their own species. Growth stopped at the point of contact or reoriented in a direction parallel to the edge of contact. However, this cessation of growth in the direction of contact is not common to all ectoprocts. Colonies of *Schizoporella biaperta* continue to grow when they contact one another, but the growth is reoriented. The colonies grow away from the surface of the substratum using the underside of each other as attachment surface. Such growth often results in flower-petal type structures, and allows both colonies to increase in size without detriment to either. Lastly, sponges such as *Halichondria bowerbanki* and possibly some of the colonial tunicates exhibit apparent fusion of adjacent colonies. On the glass slides in the pilot study, positions of each individual or colony were mapped. In subsequent observations some individuals of *Halichondria bowerbanki* or colonies of *Didemnum candidum* were seen to merge and could not be distinguished visibly from above or below (when the glass slide was turned over and examined from the bottom).

*Interspecific competition.* Interspecific competition for the available space is easily observed in this community. Although the barnacles, *B. a. niveus* and *B. eburneus* are capable of undercutting other species and lifting them from the substrate and hydroids such as *Tubularia larynx* tend to trap sediment around their basal stolons, smothering intolerant species, the most prevalent means of competitive exclusion is overgrowth. In general, the ability to overgrow other species is dependent on growth rate. This ability is most developed in the fast-growing, encrusting species.

It is possible to rank many of the species in a linear sequence of dominance based upon their ability to overgrow or outcompete one another. Table 2 shows this ranking. It can be seen that species with solitary individuals of limited size (*B. a. niveus* and *Spirorbis*) are easily overgrown by the colonial

species. Also a hierarchy seems to exist within the colonial species. This would seem to imply that a substratum will eventually become monopolized by a single species or a small group of dominant species.

Total dominance of a substratum is seldom attained on shallow subtidal rocks. This is prevented not only by the physical disturbance of the substrata (discussed in a later section) but also by the ability of many of the epifaunal species to avoid being competitively eliminated. Tube building polychaetes, such as *Hydroides dianthus*, *Sabella microphthalma*, *Fabricia sabella*, *Nicolea venustula*, or *Sabellaria vulgaris*, extend their tubes linearly and are able to keep the open, feeding end of the tube ahead of an overgrowing species. In fact, the overgrowth of all but this portion of their tubes may offer them an additional layer of protection. Colonial species, including many hydroid species, the ectoproct, *Barentsia laxa*, the ectoprocts, *Bowerbankia gracilis*, *Bowerbankia imbricata*, and *Aetea* sp., and the tunicate *Perophora viridis*, grow by extending stolons from which single individuals are budded. These linear growing stolons are also able to remain ahead of an overgrowing colony and in a few cases grow back over the encrusting colony. Other species, including the sponge, *Scypha* sp., the ectoprocts, *Crisis eburnea* and *Bugula turrita*, the anemones, *Metridium senile* and *Diadumene leucolena*, the solitary tunicates, *Molgula manhattensis*, *Styela partita*, and *Ciona intestinalis*, and many hydroids, grow upright or away from the surface. They have a relatively small basal area of attachment with the remainder of the individual or colony held above the surface where competition for space occurs. Because of the ability of these species to avoid competitive elimination, the number of species on a substratum often remains unchanged, even when the majority of the surface becomes occupied by one species.

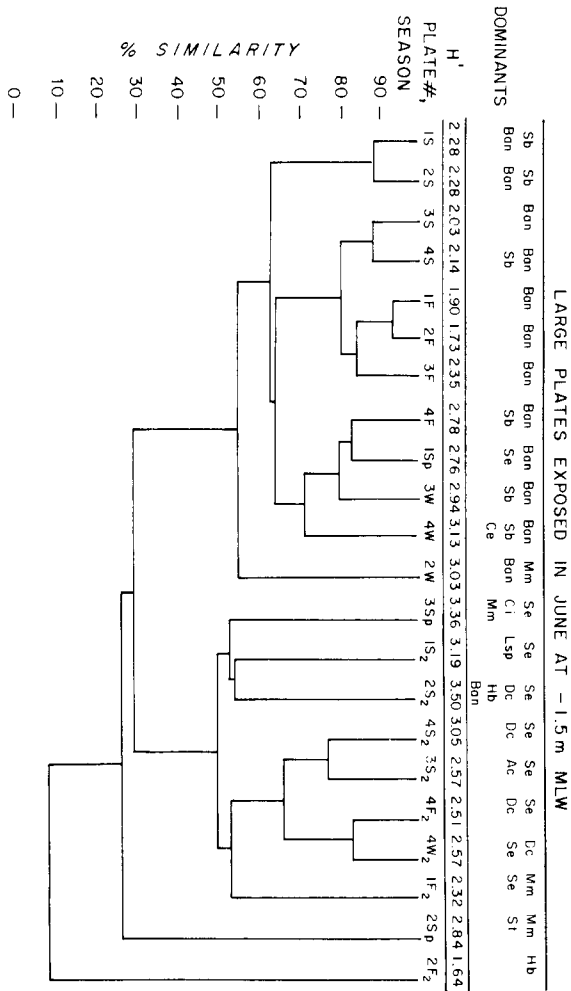


FIG. 3. Dendrogram for large plates at -1.5 m MLW initially exposed in June 1972. Plates are clustered by their similarity in species composition based on the percentage of the total area covered that was covered by each species. The level at which two plates or groups are linked indicates their similarity in composition (see text for more detail). The number indicates the replicate plate examined and the letter(s) the time of examination (S, summer; F, fall; W, winter; Sp, spring; S<sub>2</sub>, second summer; etc.). Also shown for each sample is the Shannon-Weaver diversity index value ( $H'$ ) and a list of the most common species (in order) which comprise at least 50% of the total area covered by the epifauna. Symbols used are Ban, *Balanus amphitrite niveus*; Se, *Schizoporella errata*; Sb, *S. biaperta*; Cp, *Cryptosula pallasiana*; Ce, *Crisia eburnea*; Ci, *Ciona intestinalis*; Mm, *Molgula manhattensis*; Lsp, *Leucosolenia* sp.; Dc, *Didemnum candidum*; Hb, *Halichondria bowerbanki*; Ac, *Amaroucium constellatum*; St, *Sarsia tubulosa*; Scy, *Scypha* sp.; Tl, *Tubilaria larynx*; Be, *Balanus eburneus*; Sp, *Stryla partita*.

The history of colonization of a substratum is also important in determining the outcome of competitive interactions. Newly settled or small individuals are particularly vulnerable to being overgrown. A

small colony of a dominant species will be easily overgrown by a colony or individual of a subdominant species which is larger in size. Also species such as *Spirorbis*, which are easily overgrown by most other species, have an extremely high reproductive rate and are continually recolonizing a substratum. They settle in newly created open areas or even on top of species which have previously overgrown older *Spirorbis*. Because of their continuous invasion, these species often escape extinction on a substratum.

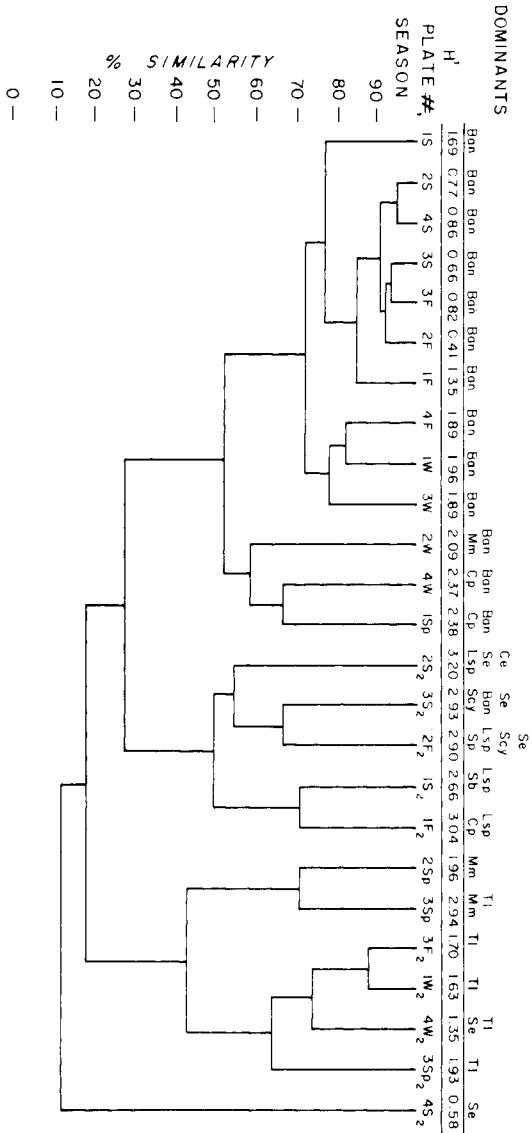
The sequential ordering of species with regards to competitive ability implies a unidirectional change in the species composition of the epifaunal community on a given substratum. However, the ability of many species to avoid competitive exclusion and the effects of a unique colonization history for each substratum allow for a great deal of variety in composition. This variety is greatly enhanced by the interacting effects of substrate size, seasonality, and especially physical disturbance.

*Substrate size*

Although a large part of the effect of substrate size is associated with the effects of differential disturbance (discussed in a later section), several differences in diversity and species composition result solely from size differences.

Since rocks exist as discrete units they are really habitat islands and the species equilibrium theory of MacArthur and Wilson (1963, 1967) is applicable. In a previous paper (Osman 1975, 1976), it was shown that experimental plates have an equilibrium number of species which is dependent upon the size of the plate. (These differences in number of species on large and small plates can also be seen in Fig. 6). The increase in species with increasing size was found both to be very close to the theoretical value predicted by Preston (1962) and to result from an increased immigration rate rather than a decrease in extinction that is predicted by the MacArthur-Wilson model. This is really a function of sample size; a larger substratum will "sample" a larger number of individuals and species of the settling larvae.

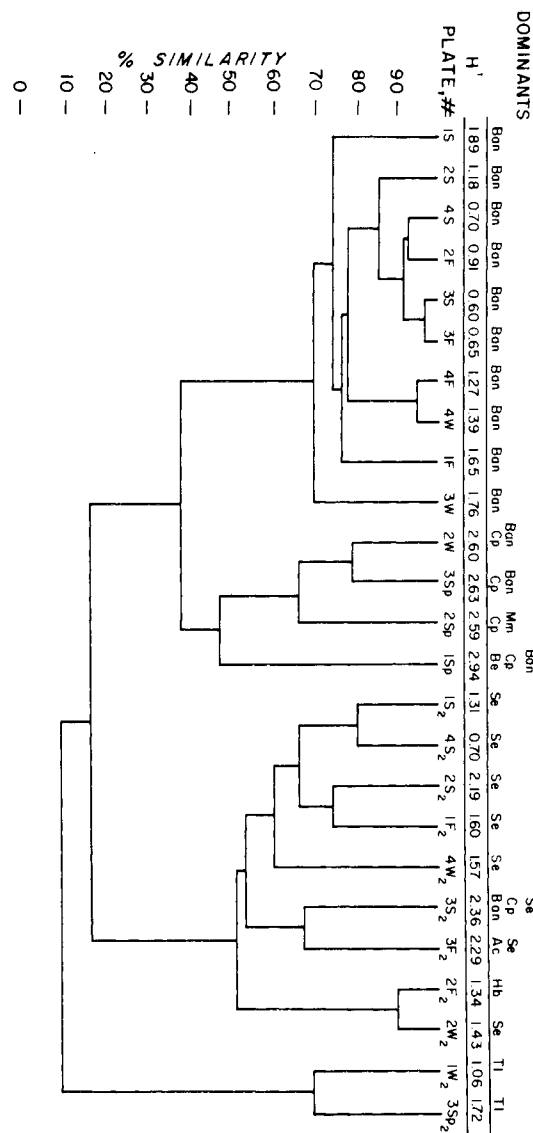
Substrate size also appears to affect the composition and structure of the epifaunal community. Figures 3, 4, and 5 are dendrograms which cluster substrata according to their similarity in composition. For each substratum or sample, the percentage of the total fauna based on surface area occupied was determined for each species. Each sample was then compared to all other samples using Sanders' (1960) index of affinity and a matrix was constructed. Samples having the greatest similarity were then clustered together. For the combination of two previously formed clusters or a single sample to a



SMALL PLATES EXPOSED IN JUNE AT -1.5 m MLW

FIG. 4. Similarity dendrogram for small plates (14.52 cm<sup>2</sup>) at -1.5 m MLW initially exposed in June 1972. Symbols are the same as in Fig. 3.

previously formed cluster the mean of all similarity values between all the members of the two clusters was used as the level (%) similarity. Samples were always clustered in order to produce a group with the highest possible similarity. If a group showed almost equal affinity with two other distinct groups (within 1%), the clustering that produced the least variance around the mean level of similarity was used. All three dendrograms are for plates initially exposed in June 1972. Each is a 1.5- to 2-yr time series of four replicate plates (indicated by numbers) with samples from each season. (As noted earlier, a few data points are missing because of



SMALL PLATES EXPOSED IN JUNE AT -1.0 m MLW

FIG. 5. Similarity dendrogram for small plates at -1.0 m MLW initially exposed in June 1972. Symbols the same as in Fig. 3.

sampling problems and the majority of the second spring [and second winter for one series] are missing and result from the loss of the plates. No points were arbitrarily excluded.) Figure 2 is for large plates at -2.0 m MLW, Fig. 3 is for small plates at the same depth, and Fig. 4 is for small plates at -1.5 m MLW. Additionally, the value of the Shannon-Weaver diversity index ( $H'$ ; Pielou 1969) and a list of the most abundant species (in area covered) which together comprise at least 50% of the total fauna on a plate are included for each sample.

In general, samples cluster by the time or season

TABLE 3. Time period over which species found reproducing (settling). Numbers indicate mean abundances of settling larvae in individuals/large plate. × indicates that at least one individual was recorded on a plate at that time

Species	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan
<i>Tubilaria larynx</i>	××××××××××××××××××									××		
<i>Balanus balanoides</i>	4	87	96	101	3							
<i>Nicolea venustula</i>	<1	<1	<1	7		1						
<i>Microporella ciliata</i>	××											
<i>Electra crustulenta</i>	××											
<i>Spirorbis pagenstecheri</i>		<1	<1	2	35	225	700	740	705	200	20	<1
<i>Obelia geniculata</i>	××××××××××××××××××											
<i>Lichenopora verrucaria</i>		14	2	<1								
<i>Balanus amphitrite niveus</i>			38	22	10	40	190	285	290	60	<1	<1
<i>Opercularella pumila</i>			××××××××××××××									
<i>Hippodiplosia pertusa</i>			×××××									
<i>Cuspidella</i> sp.			×××××						×××××			
<i>Cryptosula pallasiana</i>				2	1	26	28	5	3	2	<1	
<i>Mogula manhattensis</i>				1	6	5	<1	<1	<1			
<i>Cribilina punctata</i>			×××									
<i>Bowerbankia gracilis</i>					××××××××××××××××××							
<i>Hippothoa hyalina</i>					××××××××××××××××××							
<i>Crisia eburnea</i>					<1	4	1	1	<1			
<i>Bugula turrita</i>					3	5	3	4	<1			
<i>Schizoporella biaperta</i>					25	87	32	3	<1			
<i>Fabricia sabella</i>					××××××××××××××							
<i>Schizoporella errata</i>					50	80	52	10				
Spionidae					××		×××××					
<i>Perophora viridis</i>					××		×××××					
<i>Clytia johnstoni</i>	××					××××××××××××××××						
<i>Hydroides dianthus</i>						7	7	14	7			
<i>Stylochus ellipticus</i>						××××××××××××××						
<i>Ciona intestinalis</i>						1	0.5	<0.1	<0.1			
<i>Scypha</i> sp.						0.25	0.5	1.25	0.5			
<i>Halichondria bowerbanki</i>						××		×××××				
<i>Didemnum candidum</i>						<<1	0.5	0.4				
<i>Zanclaea gemmosa</i>						××××××××××						
<i>Aetea</i> sp.						××××××××××						
<i>Styela partita</i>						××××××××××						
<i>Leucosolenia</i> sp.						××		××				
<i>Sabella micropthalma</i>						×××××						
<i>Amaroucium constellatum</i>						××××××××						
<i>Callopora aurita</i>						××						
<i>Pedicellina cernua</i>						××						
<i>Clytia edwardsi</i>							××××××××××					
<i>Sabellaria vulgaris</i>							0.25	1.4	0.1			
<i>Balanus eburneus</i>							×××××					
<i>Ectopleura dumortieri</i>							××					
<i>Barentsia laxa</i>							××					
<i>Botryllus schlosseri</i>							××					
<i>Eudendrium tenue</i>								××		××		
<i>Bougainvillia superciliaris</i>								××				
<i>Bowerbankia imbricata</i>								××				
<i>Diadumene leucolena</i>								××				
<i>Alcyonidium polyoum</i>									××			
<i>Eudendrium ramosum</i>									××			
<i>Sarsia tubulosum</i>	××									×××××		
<i>Electra hastingiae</i>	××											××
<i>Spirorbis borealis</i>												××
Total species per month	8	6	10	13	18	30	32	33	21	10	5	4

they were taken. All three groups initially seem to develop in the same way. During the initial colonization phase of the first summer the barnacle, *B. a. niveus*, dominates. Through the winter and spring, other species begin sharing this dominance and in the second summer  $H'$  reaches a maximum with the largest number of species sharing the dominance. This more even distribution then begins to dissolve with a subsequent decrease in  $H'$ .

A comparison of the large substrata (Fig. 3) with the two groups of small substrata (Figs. 4 and 5) indicates two differences in the smaller substrata. In Fig. 4 there is a cluster of some samples from the first spring and the second fall, winter and spring dominated by *Tubularia larynx* and having a lower diversity. This species, like many other hydroids, grows seasonally. It grows at a maximum rate in the late fall and spring and remains dormant (with a loss of polyps) during the summer. The colonies seem to attain the same absolute size on both large and small substrata, however, the reduced available surface area of small substrata increases the probability of this species becoming dominant. Thus, decreased substrate size increases the probability of short-term seasonal dominance.

Some plates also seem to develop a long term dominance by an individual species. This species is usually one of the higher ranked competitors, and once this dominance develops, it usually persists. Figure 5 shows the development of this type of dominance on one series of small substrata. By the second summer, the majority of samples are dominated by *Schizoporella errata* and cluster together.

Dominance by a single species also occurs on large plates, but apparently at a slower rate. By the second summer, 90% of all small substrata were dominated by a single species while only 40% of the large plates showed such dominance. Again, a small substratum increases the probability of dominance, because a colony is able to occupy a major proportion of the available space at a much smaller size. It should be noted that such dominance does not necessitate a reduction in the number of species. Because of avoidance mechanisms, many species are able to escape competitive exclusion. However, they do become restricted in abundance.

#### Seasonality

The seasonality of the climate has a marked effect on the reproduction and growth of epifaunal species. Most species produce larvae during a limited time (Table 3). The peak abundances of larval production and settlement occur during the late summer and then both the number of species reproducing and the number of larvae produced per species de-

cline to a low in the late winter. It has been shown that this seasonality in reproduction and immigration (settlement of larvae) causes a cycle in the equilibrium number of species on a substratum (Osman 1975, 1976). It was predicted that no single equilibrium value existed. Seasonal changes in larval immigration caused the number of species to fluctuate between a high point at the end of the summer and a low point at the end of the winter. This can be seen in the June-July species curves in Fig. 6.

Colonization also appears to be dependent upon when a plate is originally immersed. In Fig. 6, the species curves for September and November differ greatly from the June-July curves. September and November substrata were first exposed as larval abundances were declining and initially did not accumulate as many species as those exposed during peak abundances. Only after the following summer did the number of species reach that found on the June-July plates.

Growth also varies seasonally and, as has been shown in the previous section, the periodic seasonal "blooming" of species such as *Tubularia larynx* can lead to reoccurring patterns of dominance by these species. The majority of species, however, seem to grow at a maximum rate in the summer months and reach a minimum during the winter. Some species (in particular, the sponges) absorb tissue and decrease in size during the winter (Knight-Jones and Moyse 1961; *personal observation*) while others, such as *Bowerbanki gracilis*, survive in a dormant stage, with only newly budded, nonfeeding zooids. New growth was seldom observed on colonies, the surface area they occupied remaining constant or decreasing throughout the winter (through extinction of colonies). This general reduction in growth can be seen in Fig. 7, a graph of the mean percent of the total area covered per month by the epifauna. It should be noted that these estimates are minimum values, since the area covered by some species could not be accurately measured because of their growth (stoloniferous types) and recently dead individuals or dead portions of colonies were not included. However, the winter decrease is still obvious.

Because of this reduction in growth and reproduction during the winter, changes in the composition of an epifaunal assemblage occur more slowly. Few new species are added, while several are lost. The reduction in growth usually causes a similar reduction in the frequency and amount of overgrowth and thus a reduction in competition. The spring and summer are times of more rapid growth and thus of much greater change. However, those particular species surviving on a substratum through the winter will affect the compositional changes observed during the summer.

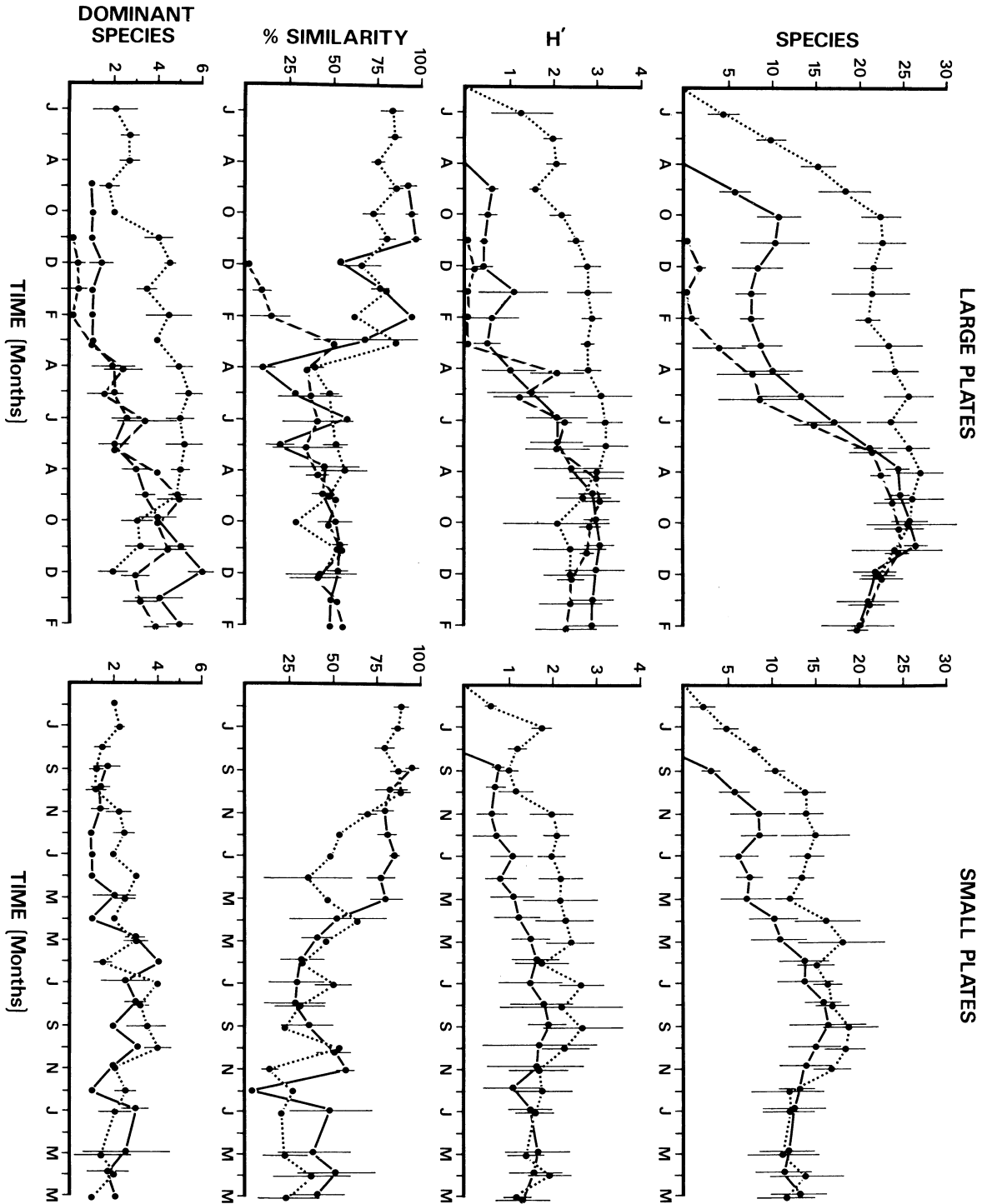


FIG. 6. Comparison of large plates exposed in June-July (pooled), September, and November and small plates exposed in June-July and September. June-July plates were from a depth of -1.5 m MLW. September and November plates were from depths of -1.5 and -2.0 MLW. Curves show the monthly means for each of four measurements and vertical bars indicate 95% confidence limits. Bars are absent on similarity curves where only two plates were compared (one data point), % similarity is the mean of all comparisons between plates sampled in each month. The number of dominant species was computed as the number of most abundant species (by area) necessary to cover 75% of the area covered by all species. Symbols are:  $\cdots$  June-July plates,  $\bullet$ — $\bullet$  September plates,  $\bullet$ — $\bullet$  November plates.

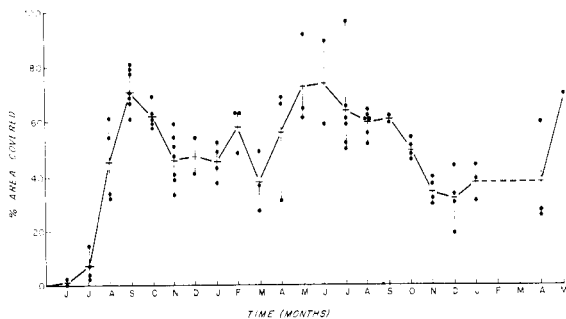


FIG. 7. Monthly means for the percentage of the surface area of a plate covered by epifauna. These data are from plates originally exposed in June and July 1972. The initial rise in % area covered (June through August 1972) is for the June 1972 plates and represents the initial colonization. Ranges are represented by bars.

*Physical disturbance*

Physical disturbance of the rock substrata is extremely important. The main source of disturbance is wave action of sufficient force to cause the turnover of a rock and the subsequent extinction of the fauna on it. Since the rocks in the study area are all granitic in composition with approximately the same density, their weight will be proportional to their size. The frequency of disturbance of the rocks will therefore be inversely proportional to their size. Also, since the effects of waves will decrease with water depth, the frequency of disturbance of a substrata of a given size should decrease with depth.

Riedl (1964, Fig. 7) estimated the frequency of disturbance for rocks from an exposed coast of the Mediterranean Sea and found such an inverse relationship between disturbance and size. Also a short-term (April-June 1974) experiment was conducted with the study area to test the relationship between size and turnover time. Rocks between 0.005 and 1.0 dm<sup>3</sup> were placed along transect lines at depths between 0.5 and 1.0 m below MLW. The number of rocks of each size class displaced from these lines after various time periods were recorded. Although the experiment was conducted for a limited time

period and during only one season, an inverse relationship is clearly indicated (Table 4).

A high degree of variability in turnover rate might be expected. Other than depth, factors such as the shape of a rock, the containing sediment, its position relative to other rocks, and seasonal variation in the size of waves might affect turnover. This variability was suggested by a second experiment conducted at the same time. Rocks between 0.005 and 0.01 dm<sup>3</sup> were positioned on the near shore and off shore sides of rocks at 1.0 dm<sup>3</sup>. There were five groups of five in each of the two positions. After 1 mo, all rocks on the offshore side had been displaced while at the near shore positions only 17 (4, 4, 4, 3, 2) had been disturbed. This difference was found to be significant (*t*-test, *p* < .01) and indicates one possible contributor to variability in turnover rate.

It is obvious from Table 4 that the majority of small rocks (< 0.5 dm<sup>3</sup>) will have been disturbed within a few months prior to observation. Also, the majority of newly exposed rocks will be from these smaller size classes. As rock size becomes larger, age (how long it has remained stable or undisturbed) also increases, with the majority of older substrata being larger rocks.

The age of a substratum will directly affect its faunal diversity and composition. From the data of the experimental plates, it appears that an equilibrium number of species (or equilibrium cycle) is attained only after 6 to 12 mo (Osman 1975). The species curves in Fig. 6 also demonstrate this. The curves for plates started in different months only begin to merge after being exposed for a complete summer. June-July plates reach this equilibrium cycle after ≈ 6 mo or when the cycle is declining to its winter low. September and November plates merge after ≈ 1 yr or at the high point at the end of the summer.

Since small rocks are disturbed more frequently than every 6 to 12 mo, they will usually be under-saturated in species. As the rock size increases, the equilibrium number should be approached because of the increased length of time for colonization to occur. This trend is confirmed by a comparison of

TABLE 4. Relative measurements for different size classes of rocks and the number of rocks in each class displaced from the transect line after different time intervals. <sup>a</sup>Weights computed assuming a density of 2.6 kg/dm<sup>3</sup> (an approximation of granite). <sup>b</sup>Percentage of total number of rocks of that size class used shown in parentheses

Volume (dm <sup>3</sup> )	Rocks (n)	Wt (kg) <sup>a</sup>	Mean available surface area (cm <sup>2</sup> )	Number displaced from line <sup>b</sup>		
				2 wk	1 mo	2 mo
< 0.005	53	< 0.01	2.6	42 (79.2)	53 (100)	53 (100)
0.005	47	0.01	5.0	34 (72.4)	46 (97.8)	47 (100)
0.01	25	0.03	8.1	16 (69)	23 (92)	25 (100)
0.05	10	0.13	23.2	3 (30)	5 (50)	9 (90)
0.1	10	0.26	40.1	2 (20)	4 (40)	7 (70)
0.5	10	1.30	123.4	0 (0)	0 (0)	1 (10)
1.0	10	2.60	197.2	0 (0)	0 (0)	0 (0)

TABLE 5. Comparison of number of species found on plates and rocks at different depths. Plates were exposed in July and August 1972. Samples taken July and August 1973. Rocks were collected at various times. Intertidal samples were collected in June 1972 and October 1972. Shallow samples were collected in June and October 1972 and June 1973. Deep samples were taken October 1971 and 1972, and June 1973. In the study area rock distributions did not extend to depths  $> 3$  m. This necessitated collecting these samples from other areas within 15 km of the study areas (Buzzards Bay and Vineyard Sound). Channels with strong tidal currents were avoided because these would not fit the depth-disturbance model

	Plates	Rocks		
		Intertidal (0 to -0.3 m MLW)	Shallow (-1 to -2 m MLW)	Deep (-10.0 m MLW)
<b>Small</b>				
Size (cm <sup>2</sup> )	14.52	24.95 ± 10.24	21.80 ± 12.20	21.04 ± 13.25
Samples	12	11	22	23
# Species	15.48 ± 3.01	2.46 ± 2.14	4.37 ± 2.61	2.76 ± 1.65
<b>Large</b>				
Size (cm <sup>2</sup> )	103	223.3 ± 47.6	217.6 ± 48.2	221.4 ± 59.5
Samples	12	6	8	5
# Species	25.29 ± 2.63	5.67 ± 2.59	13.5 ± 3.38	7.4 ± 2.08

experimental plates and rock samples. The experimental plates, which were attached to boards and thus undisturbed, estimate the effect of area on the number of species present in the absence of disturbance. A comparison of the effect of area on the number of species on plates and rocks (Table 5; also Osman 1975, Fig. 7) clearly shows the reduction in number of species on the rocks.

Although not directly measured, the majority of rocks which remain stable for 6 to 12 mo are probably between 5 and 10 dm<sup>3</sup>. Since this is the time required to reach the equilibrium number of species, rocks of this size or larger should have their normal equilibrium number of species. In general, small rocks in the shallow subtidal will be depressed below their equilibrium number of species (predicted from the plates) while large rocks will remain stable for a sufficient time to reach equilibrium.

Disturbance will also have an effect on the species composition of a substratum. Very small substrata, with their high frequency of turnover, will continually be in the early stages of colonization. Their fauna will be dominated by those species settling in the highest abundances at the time of the year sampled. In samples collected during the summer, rocks  $< 0.1$  dm<sup>3</sup> were almost exclusively dominated by the species, *Balanus amphitrite niveus* and *Spirorbis nagenstecheri*, which settle in very high abundances at this time.

On larger, or less disturbed substrata, the time of last disturbance will also greatly affect species composition. This can be seen by a comparison of experimental plates initially exposed at different times. These plates should duplicate the effect of a disturbance on a rock at the time of exposure. Figure 6 compares large plates exposed in June and July (pooled), September, and November and also small plates exposed in June–July, and September.

The June–July plates were from a depth of -1.5 m MLW and the September and November plates were from -1.5 m and -2.0 m MLW. (It was necessary to pool these two depths in order to provide a sufficiently large sample. These two depths were fairly similar in the various measurements made [Fig. 8] and in most cases the larger sample size reduced confidence intervals.) The graphs in Fig. 6 compare the plates in terms of number of species,  $H'$ , % similarity of plates sampled in the same month, and dominance (number of most common species occupying 75% of the total area covered).

In general, the trends on the large and small plates are very similar with the small substrata having a lower number of species, lower  $H'$ , and greater dominance (fewer species contributing to the 75% cover). Also the species and  $H'$  curves are similar in shape for any group of plates.

First examining the June–July substrata, the species curves show an initial rapid rise (typical of colonization curves) and then become stable through the winter. The following spring and summer the number of species again increases only to decrease again in the second winter. This appears to be correspond to and demonstrate the seasonal fluctuation in number of species already discussed.  $H'$  follows a similar trend except for a small decrease during the first September. This corresponds to an increased dominance by *B. a. niveus* at this time and is also reflected in the dominance curve. As this dominance breaks down through the winter  $H'$  increases. With more species sharing the dominance, the similarity (based on area) between the plates decreases to below 50% during the winter and the spring. In general, the similarity remained below this level for the rest of the study. The number of species sharing the dominance seems to reach a high point during the second summer, but then decreases



TABLE 6. Comparison of plates exposed at two different times in 1972 and observed in the spring and fall 1973.  
\* *t*-test, Sokal and Rohlf 1969. \*\* Mann-Whitney *U*-test, Sokal and Rohlf 1969

	July–August	September–November	Probability of equal means
<i>Summer 1973</i>			
Number of plates	12	9	
Number of species	26.18 ± 1.83	22.91 ± 1.45	$p < .001^*$
<i>H'</i>	2.75 ± 0.53	2.37 ± 0.67	$p > .1^{**}$
Area covered (cm <sup>2</sup> )	59.36 ± 4.68	36.64 ± 15.16	$p < .001^*$
% plates dominated by:			
<i>S. errata</i>	83.33		
<i>D. candidum</i>	50.00	11.11	
<i>Leucosolenia</i> sp.	16.67		
<i>A. constellatum</i>	16.67		
<i>B. a. niveus</i>	16.67	44.44	
<i>B. schlosseri</i>	8.33		
<i>H. bowerbanki</i>	8.33		
<i>S. biaperta</i>	8.33		
<i>M. manhattensis</i>	8.33		
<i>B. balanoides</i>		66.67	
<i>C. pallasiana</i>		33.33	
<i>Scypha</i> sp.		11.11	
<i>Fall 1973</i>			
Number of plates	12	9	
Number of species	25.29 ± 2.63	24.44 ± 2.19	$p > .4^*$
<i>H'</i>	2.50 ± 0.48	3.05 ± 0.29	$p < .001^{**}$
Area covered (cm <sup>2</sup> )	38.87 ± 9.54	38.24 ± 10.55	$p > .2^*$
% total plates dominated by:			
<i>S. errata</i>	83.33	11.11	
<i>D. candidum</i>	66.67	33.33	
<i>H. bowerbanki</i>	16.67		
<i>Scypha</i> sp.	16.67	22.22	
<i>C. pallasiana</i>		55.56	
<i>Leucosolenia</i> sp.		44.44	
<i>B. a. niveus</i>		33.33	
<i>T. larynx</i>		11.11	

in the fall. From the small plates, it appears that dominance by a few species continued to the end of the study. Even though there is this increased dominance the similarity remained lower. Different plates were becoming dominated by different species. This dominance appears to be more well developed on the smaller substrata and seems to have prevented an increase in number of species during the second spring when larval recruitment was increasing.

The September and November plates developed in a much different manner. Because they were exposed as larval settlement was decreasing, fewer species were present on them during the first fall and winter. In fact many November plates remained bare until the spring. *B. a. niveus* was the dominant species on the September plates and remained so until the spring. This dominance is not only reflected in the *H'* and dominance curves but also in the similarity curves which indicate very high values until the spring for both large and small plates. With recruitment in the spring and summer, the number of species and *H'* rise, more species begin to share the dominance and this resulted in a drop in similarity. The November plates never develop the high similarity exhibited initially by the June–July and

September plates. They never develop the great dominance by *B. a. niveus* (although some became dominated by *B. balanoides* which settles in large numbers in the spring), with many other species already being present before *B. a. niveus* reached its peak in larval abundance.

Large September and November plates also seemed to maintain a high *H'* and a higher number of dominant species during the second winter, even though they had the same number of species as June–July plates. This is also evident in a similar comparison (Table 6).

This table compares the fauna that had developed after a similar period of exposure on two groups of plates at –1.5 m MLW; one group exposed during the peak of larval production (July and August 1972) and the other group exposed during the seasonal decline in settling larvae (September and November 1972). Differences in faunal composition were analyzed for the end of the following summer and for the following fall.

At the end of Summer 1973, the two groups showed no significant difference in diversity (*H'*), although the July–August group had a slightly (but significantly) greater number of species (Table 6).

The two main differences between the groups at this time were much greater abundances of species on the July–August plates, as indicated by the total area covered, and differences in the dominant species. A high percentage of the plates in both groups had one or two species dominating 50% or more of the area covered; however these species differed greatly between the groups. The July–August group was dominated mostly by colonial encrusting species of high competitive rank. The September–November group was dominated mostly by poor competitors such as the barnacles, *Balanus balanoides* and *Balanus amphitrite niveus*, and the ectoproct *Cryptosula pallasiana*. Both the low abundances and dominance by the barnacles and *Cryptosula* is related to the declining abundance of settling larvae in the fall. Many of the encrusting species did not colonize the September–November plates until the following summer and were thus small in size. These species were present on the July–August group at the end of the first summer and were thus able to grow to a much larger size during the second summer.

The difference in composition between these two groups was still observed in Fall 1973 even though there was no significant difference in the number of species present or in the total area covered. The dominance by encrusting species seems to have increased on the July–August group, while the dominance of the lower-ranked competitors on the September–November plates has declined causing a more even distribution of species. This is reflected in the significantly higher  $H'$  values for the September–November group.

Figure 6 demonstrates that even plates started at the same time tend to become increasingly different in composition through time. Along with Table 6, it also shows that major differences exist between plates started in different months, increasing variability. Since plates immersed at different times were assumed to duplicate disturbance, such differences in composition reflect the effects of physical disturbance on the resultant distribution of epifaunal species within an area and account for the high degree of variability. This variability increases when the interacting effects of depth are also considered. The frequency of disturbance or turnover for a given rock size decreases with increasing water depths because of the decline in wave generated current velocities. The increase in both stability and age of smaller substrata with depth might also be expected to cause their species composition to differ greatly with depth.

#### DISCUSSION

Each of the five factors discussed (selectivity of settling larvae, biological interactions, substrate size, seasonality, and physical disturbance) have both in-

dividual and combined effects on the development and distribution of the marine epifaunal community.

The major effects of each of these factors can be summarized as follows:

1) Larval selectivity. Although selectivity for specific environmental parameters was not demonstrated, larval distributions did vary with depth and size. Differences with size resulted from sampling differences with larger substrata sampling more larvae. For many species, the frequency of attachment also differed with depth. These differences in distribution will cause the probability of a species immigrating onto or attaching to substrata to possibly vary with depth and size.

2) Biological interactions. The most important interaction between species was competition for space. Species differed greatly in their ability to utilize the available space and could be ranked by their ability to overgrow each other. In general, fast growing encrusting species could out-compete most other species for this space. This often led to dominance by these species. This dominance, however, was often greatly affected by the other factors.

3) Substrate size. Size not only caused differences in the number of species present, but also caused differences in dominance. Smaller plates more frequently became dominated by a single species. Size can also be correlated with physical disturbance, with smaller substrata having a higher probability of being overturned.

4) Seasonality. Differences in larval recruitment changed seasonally. This caused a seasonal fluctuation in the number of species present on a plate. Plates immersed at different times of the year differed greatly in their rate of colonization and in their species composition.

5) Physical disturbance. The rate of rock turnover is greatly dependent on the size and depth of the substratum. The frequency of turnover will affect the number of species a substratum might be expected to have and its time of last disturbance will determine the time period over which colonization and species interactions have occurred.

The combination of so many variables will produce a system of great variety with many possible outcomes. However, the ability to measure independently each of the parameters and to compare experimental manipulations with field observations enables the construction of a generalized model for this community. This model is basically descriptive, but seems to account for the major trends in development and distribution observed in both this and other studies.

#### Development

The development of the community or assemblage of organisms on a substratum is really the individual

history of that substratum. This history depends on the sequence or history of colonization plus the subsequent biological interactions that take place. The colonization process itself rests on the abundance of larvae, which varies seasonally, and the selectivity of the larvae as to settling site. Finally, physical disturbance, which is dependent upon the size of the substratum and its depth of occurrence, determines when the substratum is initially available for colonization and the time interval over which development can proceed.

Although it might lead to a possible oversimplification and is certainly artificial, the development process can be uncoupled from the effects of physical disturbance. Disturbance can later be included and the modifications imposed by it on development considered. Three general types of compositional histories are possible for the epifaunal community: successional, seasonal, or random. Succession implies both a competitive hierarchy of species and an order of colonization, with the presence of one species or group of species necessary for the invasion by the next group. Seasonality implies a sequential but annually repeating change in composition. This pattern can result from a seasonal change in the competitive hierarchy or from species with life histories of short-term generation times and characterized by seasonal blooms. Finally, a random pattern denies the existence of any trends or order within the system.

From the data it is obvious that definite trends do exist for the development of this community. The system is certainly not random, but more likely stochastic with knowable probability distributions. However it is neither totally seasonal nor totally successional.

It has been shown that both the abundances of settling larvae and the growth rate (reflected in the percent area covered) vary seasonally. Some species, such as *Tubilaria larynx*, do undergo repeated seasonal blooms which can cause an occurring pattern of similarity in composition (Fig. 4). However, this is not the general rule. From Fig. 3 it can be seen that, although plates tend to initially cluster by season, plates from the same season but different years do not seem to cluster together. The pattern in composition does not repeat itself from year to year.

The development of this community, however, does not fit the classical successional model. Although there does appear to be a dominance hierarchy, there does not seem to be a direct order of colonization and there is no single discrete end point or climax. The hierarchy implies a unidirectional flow in the compositional change, but the system is open-ended. Colonization is a direct function of larval abundances, which vary seasonally. Substrata

initially exposed at the same time may at first appear to progress through the same compositional changes. This is illustrated in Fig. 3. These plates, all exposed at the same time (June), cluster by the time they were examined and appear to be going through successional changes in composition. They are initially dominated by *Balanus amphitrite niveus* and *Spirorbis pagenstecheri*, species with abundant larvae during the summer. (The small size of *S. pagenstecheri* prevents it from becoming dominant in an index based on area covered. Often, however, thousands of individuals were present in early stages.) This dominance declines through the winter and spring and distributions become more even by the following summer. During and after the second summer encrusting species, especially *Schizoporella errata*, appear to be beginning to dominate the substrata. This sequence is not a "true" succession (if anything the plates become more variable and different with time). Epifaunal species are able to immigrate successfully onto a substratum regardless of which species are or are not already present. Early stages are not necessary for the occurrence of later species. They may be absent or replaced by another species or group of species. Plates begun in November were initially dominated by *Balanus balanoides*, which settles in abundance in the spring, and did not usually develop the strong *B. a. niveus-S. pagenstecheri* dominance of plates begun between June and September. Thus the early composition of the community is a function of larval abundance during the time of exposure.

Many substrata eventually became dominated by a single species with the dominance continuing to the end of the study (for some plates a time period of more than a year). However, different substrata became dominated by different species. The history of colonization appears to be the important factor in determining which species will dominate and what time period is necessary for this dominance to occur. This is illustrated by Fig. 8 which compares four sets of large plates immersed in June and July (pooled). Each set of plates was at a different depth (-0.5, -1.0, -1.5 and -2.0 m MLW) and the changes in number of species, diversity ( $H'$ ), % similarity, and dominance are compared over a period of 19 mo (after which these series were lost). The curves for the two deepest sets (-1.5 m and -2.0 MLW) were essentially the same for all four measurements and the -1.5-m plates have been discussed previously. However, the differences between these and the curves for the other two depths are striking.

We can first examine the differences between the -1.0-m and the -1.5-m and -2.0-m samples. In terms of species,  $H'$ , and dominance the curves are

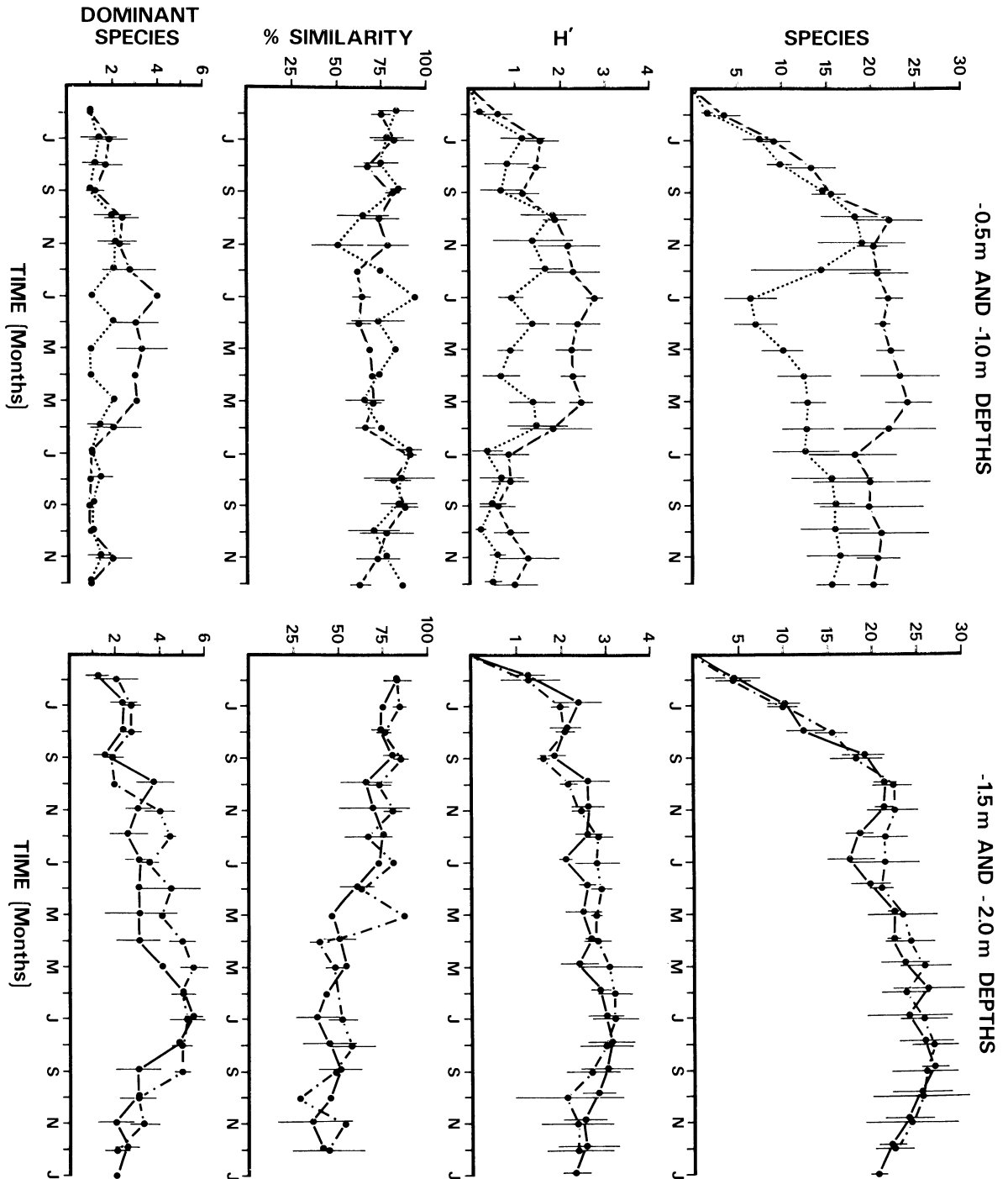


FIG. 8. Comparison of large plates exposed in June-July (pooled) at four different depths. Description of curves the same as in Fig. 6. Symbols are:  $\cdots$  -0.5 m,  $---$  -1.0 m,  $-\cdot-$  -1.5 m, and  $—\cdot$  -2.0 m.

similar for the first year or until the second summer. However, the -1.0-m plates do not drop as much in similarity during the spring as the deeper substrata do. The major differences for the -1.0-m plates are the sharp drops in the summer in number of species,  $H'$ , and number of dominating species and the continued

high (if not increasing) similarity. The -1.0-m plates appear to develop a great dominance by a single species causing a decline in the number of other species and a substantial decrease in  $H'$ . It would also appear that the same species is dominating all the plates from the high similarity in composition.

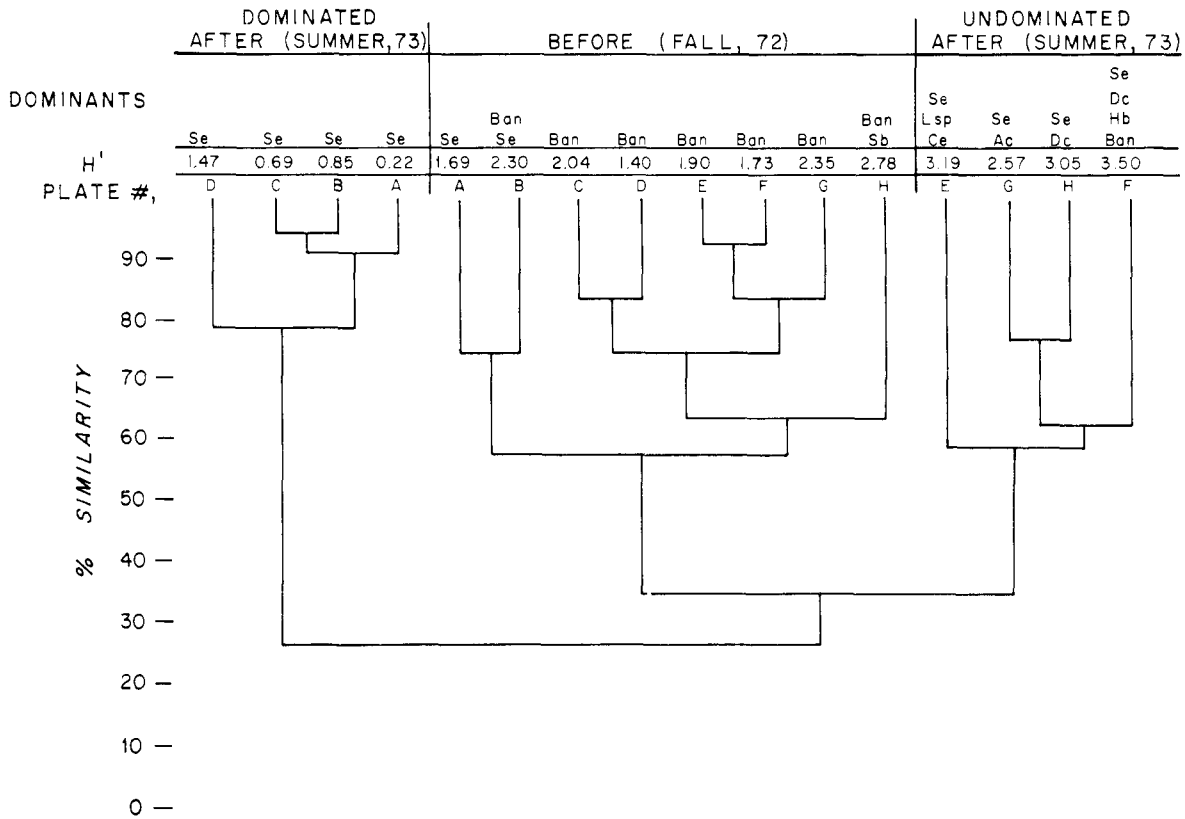


FIG. 9. Similarity dendrogram comparing two groups, of large plates at different depths (both groups originally exposed in June 1972) one group (plates A through D; -1.0 m) which became dominated by *S. errata* by Summer 1973 and the other group (-1.5 m) which did not become dominated (E through H). Observations for both before and after this dominance occurred are compared. The remaining symbols are the same as in Fig. 2.

These differences are more clearly shown in the similarity dendrogram in Fig. 9. This figure compares two subsets of -1.0-m and -1.5-m plates shown in Fig. 8, those plates exposed in June 1972. The dominated substrata are from -1.0 m MLW and the undominated from -1.5 m MLW. Samples from the fall of 1972 and the summer of 1973 are compared. After 1 yr the dominated group (-1.0 m MLW) had 60 to 95% of its area occupied by the ectoproct, *S. errata*. The other group (-1.5 m MLW) did not develop this dominance. Examined at a time previous to dominance (Fall 1972), the two groups were still fairly similar to one another. By the following summer, when dominance first occurred, the two groups were distinct from one another and from the fall samples. The dominance did not seem to derive from any major differences in abundances (in area covered) in the fall. However, when the species lists for the fall samples were compared, it was found that at least three of the other major encrusting species (*Didemnum candidum*, *Botryllus schlosseri*, *Amaroucium constellatum*, and *Halichondria bowerbanki*) occurred on the undominated group while

none occurred on the plates that became dominated by *S. errata*. There was also a difference in the number of fast growing, not easily overgrown species (*Ciona intestinalis*, *Molgula manhattensis*, *Styela partita*, *Scypha* sp., and *Leucosolenia* sp.) present in the fall; a mean of four on the undominated and two on the dominated plates. In the fall these species occupied very little area (often < 1 mm<sup>2</sup>/species), because they were very young colonies or newly settled larvae. They therefore had little effect on the similarity indices. However, with the accelerated growth in the spring, they began to occupy a large percentage of the available space. The presence of competing encrusting species and the greater presence of species able to avoid overgrowth on the deeper group of plates seems to have restricted the growth of *S. errata*. With the absence of these species on the shallow group, it was able to occupy the majority of the available space.

Thus, the history of colonization of an individual substratum is important in determining the resulting species composition. In the two groups of plates above, this history appears to be related to larval

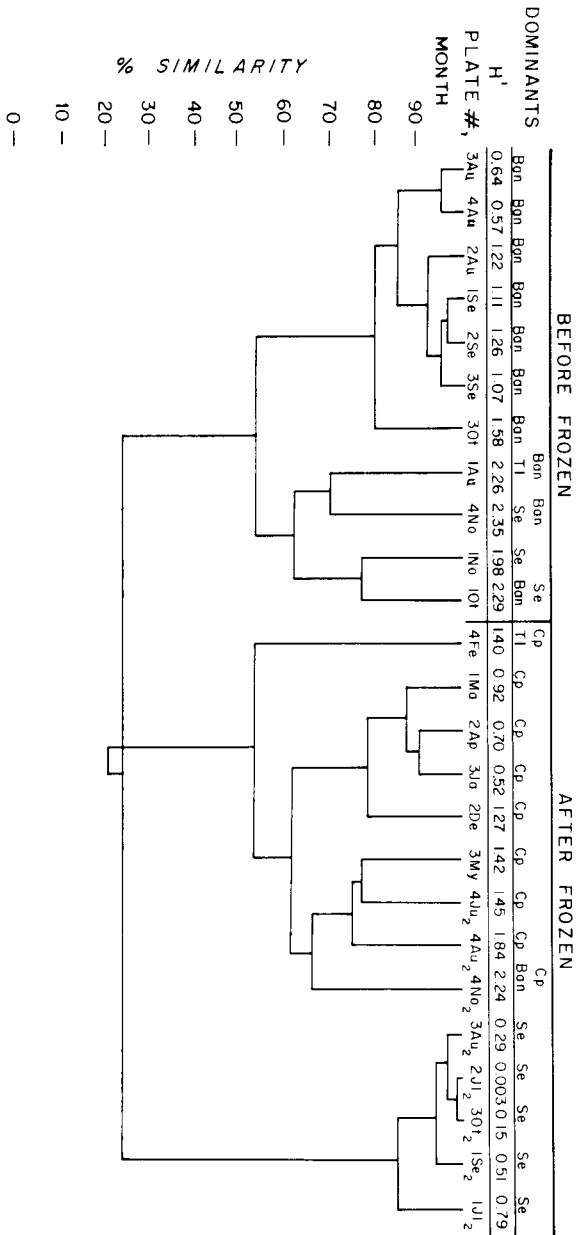


FIG. 10. Similarity dendrogram for large plates at -0.5 m MLW which were exposed to a single event of freezing in November 1972. All plates were initially exposed in June 1972. Plate number indicated replicate number and letter(s) indicate the month in which observations were made. All other symbols the same as in Fig. 2.

selectivity. On the settling plates, many species (especially encrusting) showed a greater abundance of attaching larvae at the deeper, -1.5-m depth (Fig. 5). A plate at this level would therefore have a higher probability of accumulating a larger number of competing species, and this difference seems to have resulted in differences in the composition

on the substrata. However, historical differences between substrata will obviously exist even at the same depth, and result in major compositional differences.

The -0.5-m plates (Fig. 8) demonstrate another way in which history affects composition. These substrata exhibit a sharp decline in numbers of species at the end of the fall, 1972. Also, diversity ( $H'$ ) and the number of dominants remained low while similarity remained high. Like the -1.0-m plates  $H'$  decreased even more the following summer even though the number of species increased (never, however reaching as many as found at other depths). Higher similarities and the low number of dominants (usually one species covering > 75% of the plate) indicate a dominance by the same species on all plates.

These differences appear to have resulted from a disturbance or more exactly a "selective" disturbance. In November 1972 a combination of offshore winds plus extremely low tides exposed these plates, which would normally be subtidal. Concurrently the area was subjected to temperatures below freezing. Subsequently the number of species present declined from a mean of 20 species/plate to a mean of 8 species/plate. In general, only the intertidal species were able to survive this freezing, and in this sense the disturbance was selective. Figure 10 represents the similarity dendrogram for the June sub-sample of these plates. It can be seen that after the freezing (and on one plate, continuing to the following November) these plates became dominated by *Cryptosula pallasiana*, a common low intertidal species. However, since the freezing was a single (presumably rare) event, the number of species on the plates began to increase in the following summer. In the summer these plates also become dominated by *S. errata*. Although a subtidal species, *S. errata* was able to survive up to 2 h at -11°C in laboratory tests. In these tests, only a few zooids of some of the colonies survived. On the plates, any surviving zooids would be able to frontal bud and in the absence of other high ranked competitors overgrow the *Cryptosula* and dominate the substrata. On true intertidal substrata, this final change in composition would probably not occur because of the high frequency (diurnal) of the selective disturbance.

The -0.5-m substrata demonstrate that even single, rare changes in history can have long term effects on composition. Since the history of any substratum can differ for many reasons, including physical disturbances such as rock turnover or freezing, and biological factors such as larval selectivity, and stochastic differences in colonization, a great deal of variability would be expected from substratum to substratum.

One trend that does seem clear is a tendency towards dominance by a single species. Even on plates where this single-species dominance had not developed by the end of the study, a decline in  $H'$  and number of dominant species was observed following the second summer on the larger exposed plates (Figs. 6 and 8). This decline began prior to the winter decrease in the number of species present, and resulted from a reduction in evenness or increase towards dominance. Other species besides *S. errata* became dominant on other plates (usually one of the other nine species listed above) and it thus appears that both which species becomes dominant and the time necessary for this to occur is dependent upon history.

In many ways the historical effects on species composition described for this community agree with those found by Sutherland (1974). The composition seems to fluctuate with changes in seasonal colonization and differences in history can lead to dominance by different species. On some small substrata, reoccurring dominance by seasonally blooming species, such as *Tubularia larynx* occurs. Except for this seasonal dominance (which occurred only on the small substrata), those plates which showed a high degree of similarity in composition for long periods of time (6 mo to more than a year) were those that became dominated by a single species. These species were all encrusting species, including ectoprocts, colonial tunicates, and sponges. Although the study was comparatively short (depending on the series of plates 19 to 27 mo), this dominance continued to the end of the study unless related to some form of disturbance (i.e., the change from *Cryptosula* to *S. errata* dominance in the frozen -0.5-m plates). In general it appears that the species composition on a substratum continually changes until the composition (based on area) is fairly monospecific, at which time it appears stable. Unless some major disturbance (freezing, rock turnover, heavy predation, etc.) occurs, the composition will remain the same. Samples of rocks taken at depths of 5 to 10 m in Buzzards Bay and Vineyard Sound tend to qualitatively confirm this. These substrata were usually dominated by a single species covering > 90% of the available surface area. The size of many substrata was visibly increased by thick growths of such species as *Halichondria bowerbanki*, *Microcionia prolifera*, and *Schizoporella errata*. Presumably the dominance by these species had lasted a long time. Those substrata dominated by *S. errata* gave the best indication of long term dominance. *S. errata* has the ability to frontally bud new zooids which then, budding normally, overgrow older ones and give an old colony a layered structure. On experimental plates this frontal budding usually oc-

curred in the spring; however, it was impossible to determine whether it was a seasonal phenomena or a response to limited space. Nevertheless, this type of budding occurs at a much lower frequency than normal budding. Many of the deep rocks dominated by *S. errata* had multiple layers of this species and one substratum had at least 10 layers. This certainly indicates that dominance occurs for a long time, possibly as long as 10 yr. Additionally, individuals of species such as *Mytilus edulis*, *Balanus* spp., and *Hydroides dianthus* were found encased (and dead) between layers of *S. errata*. These species probably attached to dead parts of the colony but were easily overgrown. Small scale disturbances probably create some open space allowing other species to attach but the dominant by its size can apparently displace these new species, thus maintaining the monoculture.

Unlike Sutherland (1974), I feel that dominance by a single encrusting species is a stable endpoint and unless disturbed this composition will persist. Historical differences will allow different species to dominate, therefore allowing a group of stable endpoints. Between initial colonization and eventual dominance, change in composition occurs rapidly and is very variable. In this study there did not appear to be any intermediate long-lasting stable points (unless related to disturbance). Composition continued to fluctuate until dominance occurred and only then was any long-lasting similarity in composition observed.

This developmental model is idealized, since the development is also influenced by substrate size and physical disturbance. The size of the substrata will influence the development in two ways. First, in a previous section it was shown that the abundance of settling larvae was proportional to size. On an individual small substratum, this will cause a reduction in the number of rare species present. Since many of the dominant species settle in low abundance, fewer of these species should occur together on a small substratum, thus increasing the probability of dominance. Second, the reduced available area on a small substratum should also increase the frequency of dominance. With growth rate independent of area, a species could more frequently occupy the majority of the available area before the colonization of the substratum by competitors. This increased probability of dominance on smaller substrata is confirmed by the data from the experimental plates. In Fig. 6 both June-July and September small substrata show a decline in dominants after the second summer. This is unlike the large substrata in which the September and November plates still maintained a higher number of species sharing the dominance. Also the smaller plates show fewer species sharing

dominance than the large at most times during the year.

Physical disturbance also has a two-fold effect on development. The frequency at which a substratum is disturbed will determine the time interval over which the development will operate. Frequently disturbed substrata will be colonized for a short time and then will be disturbed, starting the process over again. Their composition should mimic larval abundances. Contrarily, substrata that remain stable for long periods of time (years) will have a high probability of being dominated by one of the high ranked competitors. The exact time a substratum is disturbed will influence the colonization history, which has been shown to effect the species composition. A substratum overturned in September may develop very differently than one disturbed in August.

#### Distribution

Although substrate size and physical disturbance have been shown to affect development, they are also of major importance in determining the distribution of species on rocks. The size and depth of a rock determine its frequency of disturbance, which in turn will determine the mean age of rocks of that size. By incorporating the observed changes in composition with time it is possible to make some general predictions concerning the distribution of species within this epifaunal community.

The greatest variability in distribution should be found in the shallow subtidal (0.5 to 2.5 m), where the majority of this study was conducted. Small substrata (< 0.1 dm<sup>3</sup>) have high turnover rates. From Table 4, it appears that the majority of substrata of this size would be overturned frequently or in a sense have an age of < 1 mo. These will be overturned before colonization can proceed very far. They will have a low number of species not only because their small size means a low equilibrium number but also because the high frequency of disturbance keeps them below this equilibrium. The species composition will be a reflection of larval abundances. These substrata are often dominated by species such as *S. pagenstecheri*, *B. a. niveus*, or *B. balanoides*, which have very high reproductive rates at various times of the year. These species seem ideally adapted for such highly disturbed substrata; their large numbers of larvae enable them to continually recolonize these rocks.

Large rocks (> 10 dm<sup>3</sup>) will probably remain stable for periods of time > 1 yr. Within this time the equilibrium number of species will certainly be reached. However, it has been shown that dominance by the highly ranked competitors may also begin to develop after this time interval. Thus, even though large substrata will have the highest equilibrium number

of species, their diversity ( $H'$ ) will be low because of the extremely uneven species distributions caused by dominance. Additionally, dominance may eventually lower species number and thus diversity even more. As rock size increases, the increased time of stability might be expected to increase the probability that a substratum will be dominated. This, in turn, should cause a decrease in the average diversity with increased size.

Rocks of intermediate age (6–12 mo) and of medium size (probably 1 to 10 dm<sup>3</sup> within the study area) should have the highest diversity. These rocks remain stable for a time sufficient to accumulate their equilibrium number of species, but should be disturbed before dominance can occur. In any area I would expect an optimum size corresponding with some frequency of disturbance at which diversity is maximized. (*Optimum* is used only to describe those levels at which diversity is maximized. It implies no value judgment as to the goodness of increased diversity by either the organisms or the author. In fact the author would be inclined to dispute such a value judgment. The organisms must speak for themselves.)

An optimum frequency of disturbance for highest diversity of  $\approx 1$  yr seems to be indicated for this community. Although this frequency might correspond to a substratum of 10 dm<sup>3</sup> in the shallow subtidal study area, in a different location this optimum size may change. On a more exposed coast the optimum size would increase because of the increase in intensity of wave action. Also, within the same area increasing depth will give rocks a greater stability. In deep rocks (–10 m MLW) the optimum frequency of disturbance will occur in smaller substrata. This shift would also lead to a greater number of substrata being dominated by a single species. In deep water samples from Vineyard Sound and Buzzards Bay, rocks as small as 0.25 dm<sup>3</sup> were dominated by one of the high ranked competitors. As previously discussed, rocks dominated by *S. errata* also indicated that this dominance was long term.

Not only would dominance (in terms of number of substrata) increase in deeper areas, but the absolute value of diversity would also be lowered at the optimum disturbance level. For example, substratum in deep water disturbed at the optimum frequency will be smaller in size than a rock in shallow water disturbed at the same frequency. It will therefore have a lower equilibrium number of species and thus a lower  $H'$ . An increase in the overall stability of an area therefore seems to lower the overall diversity of the community because the shift in the optimum to a smaller sized substratum both increases the number of substrata dominated and



lowers the number of species present at the optimum frequency.

The distributional pattern also changes for substrata in intertidal areas. It has been shown that the harshness of the intertidal environment causes a lowering of the available species pool which in turn causes a reduction of the change in number of species with area (Osman 1976). This can also be viewed as a process of selective disturbance. Unlike rock turnover which will cause the extinction of all the species present, the exposure, desiccation, and freezing encountered in the intertidal will differentially affect various species. In general, these parameters will only cause the death of subtidal species, while true intertidal species will survive.

The effects of such selective disturbance were illustrated previously for the -0.5 m plates (Figs. 8, 10). The single event of freezing restricted the composition to "true" intertidal species with *Cryptosula pallasiana* dominating. The dominance later shifted to *S. errata* but this second shift would not be expected on intertidal substrata where the disturbance would occur diurnally rather than once.

From the above, it can be concluded that not only are diversity and compositional variation maximized on a particular-sized substratum within the same area, but also that these parameters are maximized in a particular area. In this study it was found that the optimum level of disturbance occurred in the shallow subtidal, causing the highest diversities and highest variability to be found there. Similar results were obtained by Rützler (1965) in his study of the sponge fauna in the Helgoland Bight. In other regions with different physical conditions, the optimum frequency of disturbance may occur at a different depth or on rocks of a different size. In fact, an interesting prediction resulting from this model is that the highest diversities for an epifaunal community should occur on very large substrata in very exposed areas. Large substrata have a high equilibrium number of species and when the optimum frequency of disturbance coincides with large substrate size, maximum diversity should be attained on those substrata. Within different communities the optimum frequency may be higher or lower, depending on the life history parameters of the organisms. Selective disturbance can also have positive as well as negative effects, as illustrated by Paine (1966) and Horn (1974).

Finally, it should be noted that extremely large rocks ( $> 1000 \text{ dm}^3$  or  $1 \text{ m}^3$ ) may escape the predictions of this model. With such a substratum, environmental differences may be very different on different parts of it. In the shallow subtidal, a rock of this size may be partly intertidal and partly subtidal. Its extreme size will mean that extremities will

essentially be isolated from one another by distance and could have very different colonization histories. The large surface area of a rock of this size will be too great for any epifaunal species to have the ability to overgrow in a short time. Thus, although the rock will be extremely stable, the time for dominance to occur would be so great that localized disturbances will become important. This type of disturbance may still have a high frequency in relationship to the time necessary for dominance to occur. Parts of the rock or individual species may function as patches rather than the rock itself. Disturbances in the form of the log damage observed by Dayton (1971) or the predation observed by Paine (1966) should be more important. In this sense extremely large rocks with long-term stability (in terms of turnover) may have a much more diverse community than predicted by a simple turnover model. Nevertheless, this higher diversity seems to be associated with disturbance and such disturbance has an optimal frequency or magnitude at which diversity and compositional variation of the community are maximized. An increase or decrease in the level of disturbance should result in a lowering of these parameters.

#### CONCLUSIONS

Each of the five parameters investigated is certainly important in determining the diversity and species composition of sessile epifauna on rocks. However, physical disturbance is probably the most important. It greatly influences the history of an individual substratum or in a sense determines to what extent each of the other factors will influence diversity and composition.

The time of last disturbance determines when a substratum becomes available for colonization. Since larval abundances fluctuate seasonally, initial colonization will vary greatly depending on when such colonization begins. Plates immersed in June, September, and November differ greatly in their initial development and this also affected later composition. Rock turnover determines when a substratum's history begins and as in the plates, differences would be expected if the last disturbance occurred in June rather than September.

The frequency at which a substratum is disturbed is also important. Rocks turned over every few months do not remain stable for a sufficient time for them to accumulate their equilibrium number of species. They remain young in age and always in a state of initial colonization. Their species composition will reflect the seasonal changes in larval abundance. Substrata which remain stable for a longer time will accumulate their equilibrium number of species. However, if stability persists, dominance by a single species appears likely. The time

period for such dominance to occur and exactly which species will dominate will be greatly dependent on the history of colonization (which species are present) and development (when different species have immigrated and how long they have been growing). Nevertheless, with the development of dominance, diversity ( $H'$ ) will decline. A smaller decrease in the number of species is also expected.

In general, young and old substrata can be characterized by low diversity, the former because of a low number of species and the latter resulting from the overabundance of one (or a few) species. Substrata that remain stable long enough to accumulate an equilibrium number of species but are overturned before dominance occurs should have the highest diversity ( $H'$  and number of species). Given the nature of the mechanism of disturbance, turnover frequency can be expected to decrease with increasing substrata size and for any size class decrease with increasing depth. Deep substrata will be fairly stable and intertidal substrata highly disturbed, both leading to low diversity. At some intermediate depth, the maximum number of substrata will be of an age at which diversity is greatest. That is, if a certain time is required for an equilibrium number of species to be reached, but dominance begins to develop after another time interval, then substrata disturbed at a mean frequency between the time to equilibrium and the time until dominance will have the greatest diversity. This frequency at which maximum diversity can be expected is labelled the optimum frequency. For each size class, the depth at which an optimum frequency could be expected would be different (the smaller the substratum the deeper the depth of optimum frequency of disturbance). Nonetheless, with lower diversity at both extremes, an intermediate area should exist where diversity peaks. For small rocks ( $< 1.0 \text{ dm}^3$ ) the shallow subtidal appeared to be the depth at which diversity was greatest (Table 5). Given the wide range in rock sizes, the variability in species composition can also be expected to be greatest at this depth. Very small rocks will reflect recent colonization, large rocks will be dominated by various species, and intermediate rocks will show variability in composition depending on their history. In shallower water (intertidal), high disturbance will skew the age distribution of rocks toward the youth, causing most rocks to reflect recent colonization. In deep water more and more size classes will be relatively stable, causing dominance to be prevalent. Intermediate areas will be most variable, having a more even distribution of ages. Qualitatively, data for the study area (i.e., Table 5) seem to confirm that the shallow subtidal was an area of increased diversity and variability.

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