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THE INFLUENCE OF SEASONALITY AND STABILITY ON THE SPECIES EQUILIBRIUM[1]

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Abstract. The species equilibrium theory has proven to be a useful framework in which to analyze the distribution and abundance of species, especially for islands and habitats distributed as islands. In this study, the distribution of marine epifaunal invertebrates on rocks has been interpreted using this model. The relationship between area and the number of species present is sustained within this community. However, the increase in the number of species with increasing area appears to result from increasing immigration rather than decreasing extinction, as predicted by the model.

Two factors have a major effect on the species equilibrium: seasonality and substrate stability. The seasonality of the climate causes the immigration rate to change seasonally. Colonization curves are dependent on the time of initial immersion of the substrate and vary in shape. However, with time, all converge. A simple model which allows immigration to fluctuate seasonally is developed. It predicts both the initial difference in the slope of the colonization curves and their eventual convergence. This same model also predicts that the colonization curve will cycle between a summer high and a winter low. The duration of the study was only long enough to test weakly this last prediction.

The physical and temporal stability of a rock "island" is also a function of its size. Smaller rocks are disturbed more frequently than larger ones. This leads to an undersaturation in species on small rocks, causing an increase in the rate of change in the number of species with increasing area. Other changes in the slope of the area–species curve were found to be caused by changes in other environmental parameters.

The species equilibrium theory is a fairly robust model in that changes in many parameters have a predictable affect on immigration and extinction which, in turn, determine species diversity. Although the utility of such an all-encompassing model may be questioned, its predictive framework makes it a very attractive tool for examining the diversity of communities.

Key words: Colonization; diversity; island biogeography; island size; marine epifauna; Massachusetts; rocky subtidal; seasonality; species equilibrium theory; stability.

INTRODUCTION

Many authors have tested the ability of the species equilibrium model (MacArthur and Wilson 1963, 1967) to account for patterns of species diversity on islands. They have examined its applicability to various taxa both on oceanic islands and for various types of habitats which are insular in nature. These include birds (Diamond 1973) and ants (Wilson and Taylor 1967) on oceanic islands, arthropods on mangrove islands (Simberloff and Wilson 1969), arthropods in caves (Culver 1970), mammals on mountains (Brown 1971), freshwater protozoans (Cairns et al. 1969), marine invertebrates (Schoener 1974*a*, *b*) and many others (reviewed by Simberloff 1974). Although a few studies (Brown 1971, Johnson 1972) have found some exceptions, the majority of research has shown that the distribution of insular species can be predicted by the equilibrium model.

The marine epifaunal community, comprised mostly of sessile invertebrates that attach to such hard substrates as rocks and shells, can be treated as insular. The substrates are discrete patches of environment, isolated from one another by water and intervening sediment. Although the planktonic larvae can survive in the water, the attached adults are totally restricted to the substrate. Access to the substrate is gained only by larval colonization (immigration) and the loss of a species is the result of the death of all individuals (extinction or local extinction). Additionally, the substrate or "island" can be simulated by an artificial surface and thus, the community can be experimentally manipulated in order to test any predictions made from a model. Panels of various substances have often been used to study the epifaunal or "fouling" community. Schoener (1974*a*) has reviewed many of these studies to test whether, in the colonization of these panels, an equilibrium was reached. She found that, in many studies, the number of species on a given surface was still rising at the completion of the study. She suggested that this was due to both the 2-dimensional nature of the panels and a very large pool of colonizing species which would act to reduce the effects of extinction.

Nevertheless, the utility of such a model is not its prediction of some equilibrium number of species ($\hat{S}$). In a sense, the equilibrium model is tautological; the number species present (S) must be equal to the number gained (immigration) minus the number lost (extinction). If immigration decreases as S increases and extinction increases as S increases, then at some $S = \hat{S}$, they will balance one another, and S might be expected to oscillate in the neighborhood of $\hat{S}$. The

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dynamic processes of immigration and extinction do not cease and species composition can continue to change. Actually, $\hat{S}$ itself does not have to be treated as a stable or static value. Over some longer period of time, the extinction rate and/or immigration rate with S species present may change. For example, Wilson (1969) hypothesized that, after an initial period of colonization, S may equilibrate at some value resulting from random extinction and immigration. Later, extinction may increase as a result of species interaction (i.e., competition for resources) and S may decline to a new $\hat{S}$. Likewise, a change in immigration rate with seasonal changes in larval production (see below) might result in an increase or decrease in S. What I hope to demonstrate below is that species equilibrium theory provides a method to predict and interpret complex dynamic patterns. Only after one has determined how much of a particular pattern can be attributed to simple changes in the probability of any species being lost or gained can one determine the effect of a particular species being lost or gained (i.e., through predation, competition, inhibition of larval settlement by species already present, etc.). I will begin with the simplest conditions (at times making oversimplified assumptions) and then by making simple modifications (or relaxing assumptions), test the ability of an immigration–extinction model to account for spatial and temporal patterns of species diversity (S).

This study was begun in June 1972. Artificial substrates (slate plates) and naturally occurring rocks were used both to test the predictions that could be made about the distribution of a marine epifaunal community using species equilibrium theory (reported here) and to determine the influence of a number of factors on changes in species composition within this community (Osman 1977). With the exception of 2 common predators, the flatworm, *Stylochus ellipticus*, and the oyster drill, *Urosalpinx cinerea*, only sessile or attached species were included in the analysis. This was done for both practical and theoretical considerations. Because as many as 50 substrates or islands were collected at any 1 time, it was impossible to keep each of these isolated in the laboratory. By only including those sessile species, the possibility of contamination could be avoided. This still left a pool of ≈140 species or taxa for the general region which I could identify with reasonable certainty. Approximately 90 of these were recorded at least once during the study (**Appendix I**).

Given this consideration, several features should be noted that separate this system from those of oceanic islands. First, immigration is almost exclusively a reproductive process. Because the species being studied are sessile as adults, the majority of them (at least 90%) must immigrate as larvae. Even for those species capable of some motility (i.e., 3 species of anthozoans, *Metridium senile*, *Diadumeme leucolena*, and *Haliplanella lucias;* the limpet, *Crepidula fornicata;* the mussels, *Modiolus modiolus* and *Mytilus edulis*) immigration onto experimental substrates occurred as larvae or juveniles. These immigrating larvae metamorphose and eventually become capable of sexual reproduction (also vegetative reproduction in many cases). Because of their immobility, these sessile species have evolved various reproductive mechanisms such as self-fertilization, hermaphrodism, external fertilization, and water transport of gametes which would allow them to reproduce with individuals not necessarily in close proximity with them. In the sense that it is capable of reproduction, each immigrating larva can be considered a propagule.

Second, because immigration is so closely related to reproduction and reproduction is usually seasonal (WHOI 1952), there should be a seasonal effect on immigration rate.

Third, because the majority of the species disperse as planktonic larvae, water cannot be thought of as a physiological barrier to dispersal as it is for birds on oceanic islands. Many bird species cannot survive in the intervening water, but larvae obviously can. However, distance is still an important limit to larval dispersal and water and sediment are effective barriers for adult dispersal. Thus, rocks may still be thought of as islands.

Fourth, source areas of the immigrants are difficult if not impossible to define. Larvae are released into the water from individuals on many different substrates, at various distances and directions from the substrate under study. How far and in what direction these larvae travel upon release should depend on how long they remain in the plankton before settling, and the speed and direction of the currents. As a first approximation, a rock island may be thought of as surrounded by its source area, just as a terrestrial island in a lake would be surrounded by its land source. Additionally, if a larva must remain in the plankton for any length of time to complete its development, it will have already traveled some distance before it is capable of settlement. Thus, even if the source area were known, the distance between it and a rock being colonized may not be an accurate measure of the realized distance. This inability to attach immediately would also seem to imply that a substrate in an area where currents would carry a released larva away from that substrate would rarely be colonized by larvae produced by individuals already attached to that substrate. For these reasons, the effects of distance cannot be tested for the epifaunal community. However, by choosing a single study site and assuming that all substrates within that site are effectively equidistant from a source, the equilibrium model can still be tested.

Fifth, the physical or temporal stability of the rock islands is proportional to their size. The rocks in the study area are all granitic in origin and their densities should be very similar. The force required to disturb

or to overturn a given rock should be a function of its size. These forces will either be generated by currents or wave action. The frequency of a force of a given magnitude should have an inverse relationship to the magnitude. Thus, we would predict that small rocks should be overturned more frequently and should be more disturbed or less stable than large ones. The overturning of a substrate will have a direct affect on extinction and the frequency of overturning (not to be confused with species turnover rate, X) can therefore be incorporated into the equilibrium theory.

Sixth, even within a limited study area, substrates may differ significantly in other environmental parameters. A good example of such differences might result from the comparison of an intertidal and subtidal substrate. Because an intertidal substrate is diurnally exposed to the air, the death of species not adapted to exposure would increase the rate of extinction and the reduced amount of time in the water would decrease the immigration rate of the water-borne larvae. Such predictions and their resultant predicted effect on species distribution are testable.

Finally, the epifaunal community is essentially a system of 1 trophic level. The majority of the species are sessile invertebrates which feed on an external food source of suspended detritus, phytoplankton, and zooplankton. With the possible exception of predators whose presence or absence could change trophic structure or diversity (Paine 1966), the replacement of 1 species by any other should not affect trophic structure. Within this epifaunal community, predation seems to be relatively unimportant and does not disproportionally increase with increasing substrate size (Osman 1977). Therefore, it would seem that the arguments concerning the stability of trophic structure (Heatwole and Levins 1973, Simberloff 1976) with changing taxonomic structure are unimportant in considering this community.

From the above considerations, a number of questions can be asked which this study has attempted to answer:

1) Can the number of marine epifaunal species on rocks be represented as a dynamic equilibrium between immigration and extinction?
2) What is the affect of substrate size (independent of stability) on the rates of immigration and extinction?
3) How does a seasonally fluctuating immigration rate affect colonization patterns and does extinction also vary seasonally?
4) What interval of time is required for a virgin substrate to reach an equilibrium number of species?
5) How does size-dependent rock stability affect the species equilibrium and, in particular, the area-species relationship?
6) In what way might other measurable environmental parameters, such as exposure to air, freezing, or depth of occurrence, alter the species equilibrium and the area-species relationship?

Experimental Design

Assumptions

Three general assumptions were made in the design of the experiments. The first assumption was that all substrates (both the naturally occurring rocks and the experimental plates) were equidistant from any source of colonists. This assumption did not seem unreasonable, given the nature of the source area and dispersing larvae as previously stated. Within the study area, the maximum distance between substrates (including both rocks and plates) was 20 metres. The maximum distance between any 2 experimental plates was only 4 metres. Although some species can postpone metamorphosis for possibly a year or more (Sheltema 1971), the majority of shallow-water benthic species have a larval period of a few hours to several weeks with an average larval period of 3 wk (Thorson 1957, 1961, and *personal observation*). The average current velocity in the area is ≈57 cm/s. A larva drifting with this current and having a development time of only 1 h would travel a distance >2 kilometres. Therefore, it does not seem unreasonable to assume a dispersal distance for most larvae of at least 2 orders of magnitude greater than the maximum distance between substrates. If this is so, this first assumption is reasonable.

The second assumption was that both rocks and plates were equally suitable epifaunal substrates. The rocks in the study area were all well-rounded, granitic, glacial erratics. They were, therefore, very similar in both mineralogy and surface texture, the latter probably being the more important characteristic. Slate was chosen as the most manageable material for the construction of the artificial panels. It approximates the surface texture of the rocks, can be cut to an exact size, and more closely represents the natural rocks than other substances such as wood, glass, concrete, or asbestos used in previous studies. It was therefore assumed that microhabitat differences between substrates were not significant.

Finally, it was assumed that the disturbance to the fauna caused by collection and handling in both the field and in the laboratory was not significant. Because the species of the epifaunal community were attached to the surface of a hard substrate, their abundances could be recorded accurately without disturbing their spatial relationship. Substrates were collected and placed in open containers underwater with the aid of self-contained underwater breathing apparatus (SCUBA). They were quickly transported in seawater to the laboratory and placed in running seawater within 15 to 30 min. The source of water for the laboratory system was <1 kilometre from the study site and temperature differences between the laboratory water and

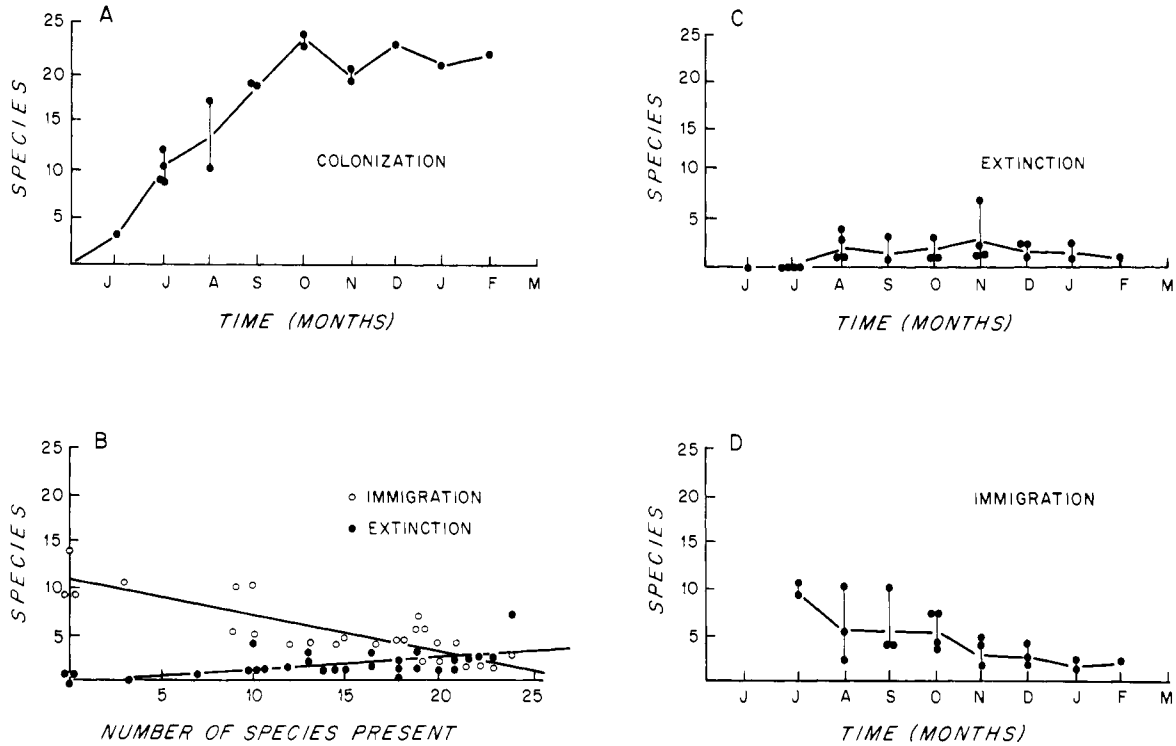

FIG. 1. Colonization, immigration, and extinction curves for large plates at −1.5 metres MLW, immersed in June. (A) Colonization curve plotted as the average number of species present per plate in each month after exposed. (B) Linearly regressed immigration and extinction curves, plotted as a function of the number of species present (open circles, immigration; closed circles, extinction). Average number of species per plate becoming extinct (C) or immigrating (D) for each month after exposure. Each point represents a measurement for an individual plate and the bars the range of values for each month.

that at the study site were never more than a few degrees at all times of the year.

Procedure

Data were collected between June 1972, and August 1974. The study site was located in Sheep Pen Harbor, Nonamesset Island (41°31′N, 70°40′4″W), ≈1 kilometre south of the Marine Biological Laboratory in Woods Hole, Massachusetts. The area was chosen because it was a natural rock shore, had an unused dock from which to suspend the artificial substrates, was relatively close to the laboratory, and was isolated (access was by boat only, thus discouraging human disturbance).

The experimental slate panels were square. Two sizes were used, 14.5 cm^2 and 103 cm^2. These were attached to the underside of wood boards which were suspended with ropes at 0.5-metre-depth intervals measured from mean low water (MLW) to 2.0 metres (≈0.25 metres above the bottom). Four replicates of each size at each of the 5 depths were used for all parts of each experiment.

Two sets of experiments were performed. In the first set, plates were emplaced for an interval of 1 mo, then removed and examined in the laboratory to determine the number of individuals of each species that had settled as larvae during that month. The plates were then scraped clean, washed in freshwater, dried for at least 1 day before being returned to the field. In the second set, plates were put in the water during June, July, August, September, and November 1972, and May and July 1973. During the first 6 mo of the study, all replicates were examined each month. After this time, the increasing number of substrates and the increasing abundance of the fauna made this impossible. Thereafter, at least 1 replicate of each size at each depth of each set was examined every month with all replicates being examined every 3 mo (obviously, plate losses and sampling errors occurred; see Osman [1977] for details).

Collections of rocks from at least 2 different depths were also made within the study area at less-frequent intervals. These were also examined in the laboratory to determine the number of species and individuals. The available surface area of each rock was approximated using a grid system. The sampled rocks ranged in surface area from 5 cm^2 to 400 cm^2. In the laboratory, all species were identified (a few groups, in particular, the polychaete family Spionidae, were lumped as 1 "species" when further identification would have resulted in removal or death) and the number of individuals and area covered by each species measured.

For the most part, this paper will consider only changes in species number; analyses of changes in composition, abundance, species interactions, etc. are included elsewhere (Osman 1975, 1977).

Terminology

To avoid a useless proliferation of jargon, I attempted to use the terminology of species equilibrium theory (MacArthur and Wilson 1967). To avoid confusion, I briefly explain my use of these terms. Immigration and extinction rates are measured in terms of species not individuals. Thus, the probability of mortality for an individual may be high, but if larval settlement is higher or population size is large, the probability of extinction for the species on a substrate may be low. Unless disproved, immigration and extinction will be considered functions of the number of species already present on a substrate. Thus, if either is hypothesized to change (i.e., a decrease in immigration in the winter), this change will still remain proportional (directly or inversely) to the number of species present and the whole curve will shift. Lastly, the equilibrium number of species ($\hat{S}$) is the number of species present at which immigration equals extinction and the curves intersect. It is obviously dependent on these curves and defines a value which the observed S is expected to approach. If either curve changes, $\hat{S}$ may change and S would approach a new value. Depending on the magnitude of (and time between) change, S may not reach a particular $\hat{S}$. Therefore, $\hat{S}$ may, at times, be a hypothetical value, but one that can be useful in interpreting patterns of S.

Discussion

The existence of equilibrium conditions

In its simplest form, the MacArthur–Wilson (1967) equilibrium theory states that the number of species present on an island or in an insular habitat results from a balance between the immigration of species onto the island and the extinction of species already present on it. It is also argued that the rate of immigration should decrease and the extinction rate increase as the number of species present on the island increases. If the immigration rate and extinction rate are plotted as functions of the number of species present, the 2 curves should intersect. This point of intersection, where extinction equals immigration, defines the equilibrium number of species ($\hat{S}$). If the number of species present on an island (S) is greater or less than $\hat{S}$, the difference between immigration and extinction will cause a return to $\hat{S}$. The theory also predicts that on a new or barren island, S will increase to $\hat{S}$ at a decreasing rate with time and then equilibrate at $\hat{S}$.

Colonization curves (species present *versus* time) were plotted for each group of plates. Plates started at the same time, at the same depth, and of the same sizes were grouped and the average number of species present plotted for each month. Figures 1 and 2 show 5 typical initial colonization curves for the experimental plates. They demonstrate the fairly rapid rise to $\hat{S}$ and then an initial oscillation around this value. Immigration and extinction rates and the resultant colonization curves can be influenced by other factors. To reduce the contribution of these factors, only the initial data are plotted in Figs. 1 and 2. Later sections will consider the complete curves and the factors contributing to their shape.

Immigration (number of new species observed/month) and extinction (number of previously recorded species lost/month) rates were also plotted, both as a function of the number of species present and of time, for plates grouped by size, depth, and time of initial immersion. Figure 1 illustrates the data for large plates, immersed in June, at a depth of 1.5 metres below MLW. Linear regressions of immigration and extinction *versus* species present, for all groups, had significant positive regression coefficients for extinction and significant negative regression coefficients for immigration (all $P < .01$, t-test, Sokal and Rohlf 1969:424). Although it appears that the criteria of the equilibrium model (decreasing immigration rate and increasing extinction rate) have been met, it should be noted that immigration and extinction are continuous functions, but the estimates are for discrete time intervals. Both Simberloff (1969) and Schoener (1974*a*) have shown that these estimates may be biased because of unrecorded immigrations and subsequent extinctions between sampling times. Simberloff has also suggested that much of the interperiod unrecorded immigration and extinction was due to obligate transients, which included as many as 75% of the species in his mangrove study. Less than 10% of the epifaunal species studied have the ability to emigrate after they attach to a plate, and transience is much reduced. Also, many of the species that immigrate and become extinct between observations can be counted because of the presence of hard parts which remain attached to the substrate. However, even if the estimates are biased, it still appears that immigration and extinction are respectively decreasing and increasing functions of the number of species present, and affect the colonization process and the number of species.

The effect of substrate size

The 2 major parameters which have been hypothesized to affect $\hat{S}$ are island area (or substrate size) and the distance from the source of immigrants. In its simplest form, the equilibrium theory states that the immigration rate should vary inversely with distance from the source and extinction rate should vary inversely with island size. Because the experimental plates were considered to be equidistant from the source, the major differences between plates of different size should be due to extinction rate. Smaller plates should have a higher extinction rate and thus a

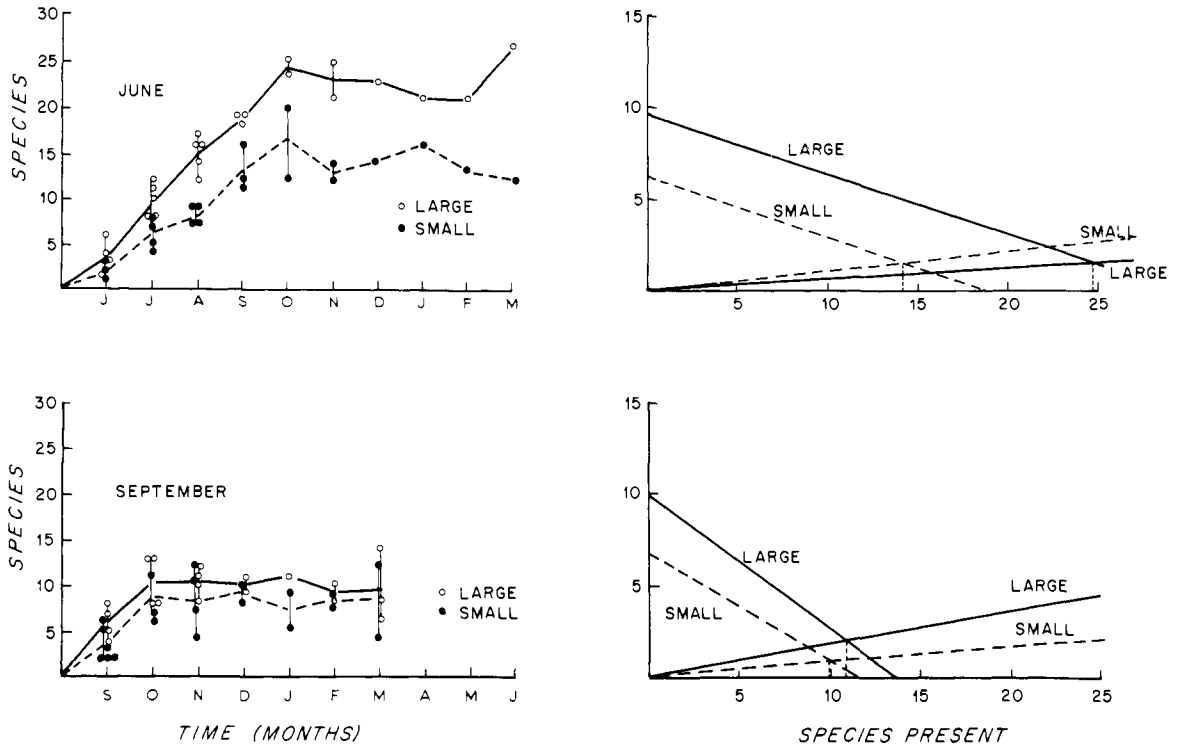

FIG. 2. Comparison of colonization, immigration, and extinction for large and small plates. Top—Plates immersed in June. Bottom—plates immersed in September. Points for plates at −1.0 and −1.5 metres MLW. Colonization curves were plotted in the same manner as in Fig. 1. Immigration and extinction curves were linearly regressed.

lower $\hat{S}$. Figure 2 shows the initial colonization curves for 2 groups of large and small plates with the smaller ones equilibrating at a lower S as predicted.

For each of the 4 colonization curves in Fig. 2, extinction and immigration were linearly regressed against the number of species present. Analysis of covariance (Dixon and Massey 1957) showed no significant difference in extinction between adjusted means ($P > .05$), within-group slopes ($P > .25$), and indicated that 1 regression line was sufficient for all points ($P > .05$). Analysis of covariance for immigration, however, showed highly significant differences between adjusted means ($P \ll .001$), within-group slopes ($P \ll .001$), and indicated that 1 regression line was not sufficient ($P \ll .001$). It therefore appears that the differences between substrates in $\hat{S}$ are due to differences in immigration rate with size rather than extinction rate.

Although this differs from the simplest equilibrium model, it is not totally inconsistent with the general equilibrium theory. From MacArthur and Wilson (1963: Eq. 6), it can be seen that island size will affect immigration. In most cases, however, the overriding effect of distance will act as a filter, causing a reduction or elimination of this effect on immigration. If the source of immigrants is represented by a point, then the number of immigrants that an island receives should be proportional to the angle subtended by the diameter of the island at a given distance. Since the difference in angles will decrease with increasing distance, the effect of island size on immigration will rapidly decrease with increased distance. Thus, for oceanic islands, where distances from the source are large, the effect of size may be insignificant. For the experimental plates, however, the distance from the source may be sufficiently small, relative to the dispersal capabilities of the organisms, such that size is the critical parameter affecting immigration.

MacArthur and Wilson (1963) hypothesize that extinction rate is a function of the mean population size of the species present and the annual mortality rate of the organisms. If the initial equilibria represented by Fig. 2 are considered to be noninteractive, the probability of mortality of an individual should be independent of the plate on which it has immigrated. Because epifaunal organisms produce planktonic larvae, which have an extremely low probability of settling on the substrate from which they were produced, the mean population size on a plate, measured in individuals, should be a function of the species-specific immigration rate (i.e., recruitment from without in individuals per species per unit time). This, in turn, is a function of the plate size (a larger plate will sample a larger number of individuals than a small plate in the same time period). If population size is measured as the amount of space occupied, which is probably a better measure because of the coloniality and subsequent vegetative growth exhibited by many of the species,

then it is also a function of the growth rates of the species.

Estimates of mean population size, both in individuals/species and area occupied/species averaged ≈4 × higher for the large plates than for the small. It would, therefore, appear that the annual mortality rate must be sufficiently low in relationship to population sizes or the number of settling individuals, such that no significant difference exists between plates. Even for species in which each individual has a high probability of mortality, the number of individuals settling often exceeds greatly the number that die, so that the probability of the species becoming extinct on a given plate is fairly low.

Just as on oceanic islands, area does have an effect on $\hat{S}$. However, on islands it is the change in extinction rate with area that causes a change in $\hat{S}$. For the epifauna colonizing plates, the change in $\hat{S}$ with area seems to be mostly a function of changing immigration rates. Population sizes on the small plates may still be sufficiently large such that extinction shows no measurable increase over that observed on the large.

Seasonality

At present, little experimental data exist which would test the effect of a seasonal environment on the species equilibrium. Although Simberloff and Wilson (1969) hypothesized that a seasonal climate should have an effect on the colonization rate of islands and the shape of the colonization curve, they were unable to demonstrate such an effect in their mangrove study. Schoener (1974*b*) was also unable to show any seasonal effect in the colonization of plastic sponges. However, both of these studies were conducted in subtropical environments, in which one would not expect a high degree of seasonality. Schoener (1974*a*), in her review of epifaunal colonization, was able to demonstrate some seasonal effects on colonization rates, although as she indicated, the data were not always conclusive.

The site of the present study was in an area of typically temperate seasonal climate. Other investigations (i.e., WHOI 1952) have shown that there is a great deal of seasonal variation in reproduction and settlement of epifaunal species in this and other temperate areas. Figure 3 also illustrates the high degree of seasonality found in the study area. It shows the average number of individuals settling on each large settlement plate (clean plates placed in the field for 1 mo) for each month of the year. Although, for most species, the majority of larval settlement (and thus immigration) occurs in the late summer and early autumn, newly settled larvae have been recorded in all months of the year. This seasonal change in immigration is reflected in the colonization curves in Fig. 2. The experimental plates started in September, when the larval abundance begins to decline, initially accumulated a much lower number of species than the June plates, which

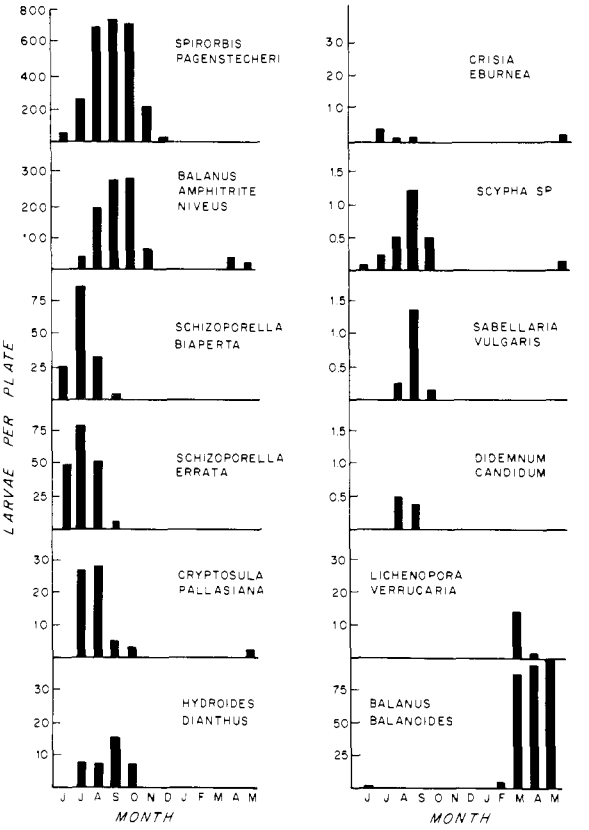

FIG. 3. Monthly settlement data for 12 common species. Height of bars represents the average number of larvae settling per large plate in each month.

were exposed during the period of maximum larval abundance.

To test initially the combined effects of seasonal changes and species present on both immigration and extinction, multiple correlation and regression analyses (Li 1967) were performed. Extinction and immigration for large plates initially exposed in June, July, August, September, and November were regressed to the number of species present and season. The average number of species settling on large settlement plates (those exposed for only 1 mo) each month were used as estimates of season. (These estimates were highly correlated with temperature, $r = .97$, and ranged from a high of 15 species settling/plate in August to a low of 1 in January. These estimates were preferred over temperature in order to avoid the possible effects of settlement lagging behind temperature, which were obviously very small). It should also be noted that these estimates (or temperatures) lump periods of change (spring and fall). The results of these analyses are shown in Table 1. Plates for June, July, and August were all from the same depth (−1.5 metres). September and November plates were from depths of −1.5 metres and −2.0 metres. These 2 depths were pooled to keep sample sizes for each

TABLE 1. Multiple correlation and regression of immigration/extinction on species present and season (species settling)[a]

Parameters	Month begun					Total	Unaveraged
	Jun	Jul	Aug	Sep	Nov		
			Immigration				
Time observed (mo)	20	19	18	18	16	21	21
Plates (n)	4	4	4	8	8	28	28
Observations (n)	35	28	19	31	31	144	60
a	7.14	6.43	9.28	2.77	−.24	1.91	1.70
Species present (n)							
b_1	−.24***	−.25***	−.37***	−.20***	−.13***	−.12***	−.16***
r	−.83***	−.81***	−.89***	−.52***	−.41***	−.34***	−.39***
r^2	.70	.65	.80	.27	.17	.12	.15
Species settling (n)							
b_2	.12	.20*	.18	.41***	.57***	.42***	.59***
r	.58***	.67***	.61**	.61***	.81***	.66***	.77***
r^2	.33	.45	.37	.38	.66	.44	.59
R	.85***	.85***	.91***	.85***	.88***	.76***	.80***
R^2	.73	.73	.83	.72	.78	.58	.64
P (all b = 0)	<.001	<.001	<.001	<.001	<.001	<.001	<.001
			Extinction				
Time observed (mo)	20	19	18	18	16	21	21
Plates (n)	4	4	4	8	8	28	28
Observations (n)	35	28	19	31	31	144	60
a	.20	.11	−1.10	.33	−.14	−.02	.11
Species present (n)							
b_1	.07*	.06	.13***	.09***	.08***	.08***	.14***
r	.46*	.42*	.74***	.64***	.96***	.67***	.77***
r^2	.21	.17	.55	.41	.92	.45	.59
Species settling (n)							
b_2	.01	.02	.06	−.01	.04*	.02	−.02
r	.20	.17	.20	−.01	.82***	.16	−.02
r^2	.04	.03	.04	.0001	.68	.03	.0005
R	.46*	.42*	.77***	.64***	.97***	.67***	.77***
R^2	.21	.18	.60	.41	.94	.45	.59
P (all b = 0)	>.10	<.10	<.01	<.01	<.001	<.001	<.001

[a] The regression equation used: Immigration or extinction = $a + b_1$ (No. spp. present) + b_2 (No. spp. settling). All observations for large plates at −1.5 metres MLW (and −2.0 metres for Sep and Nov) were used in the analyses. Unaveraged is based on only those observations exactly 1 mo apart.

* $P < .05$. ** $P < .01$. *** $P < .001$.

group approximately the same. (Losses of plates and shorter observation times reduced the number of observations for these 2 groups. Osman [1977] has shown that observations for these 2 depths were very similar and could be pooled.) The analyses for all groups combined are also shown. Because an individual plate was not always observed every month, it was necessary to average immigration and extinction over the period between observations. The last column shows the results of analyses using only unaveraged data in which only 1 mo elapsed between observations. The averaging of data does not appear to have greatly affected the analyses.

Several trends are indicated by these analyses. First, extinction shows a significant positive correlation with species present and, except for the November group, shows no relationship to season. Extinction appears to increase with an increase in the number of species present on a plate but shows no variation with season. Second, immigration seems to vary both positively with season and negatively with the number of species present. For plates initially exposed during peak larval settlement (June, July, and August), the relationship with species present seems most important while for groups initially exposed when larval settlement was declining (September and November) and for the total (averaged and unaveraged), season seems most important. This can also be seen in Fig. 2. The initial colonization curves for June plates can be accounted for by changes in immigration and extinction as the number of species present changes, but the September curves are very different and can only be explained by a seasonal change in immigration.

Model.—It is relatively easy to construct a graphical model for the possible effects of season on immigration and extinction and then to use this to predict the possible effects on the observed colonization curve. Assuming, as the data (Figs. 2, 3, Table 1) strongly indicate, that the immigration rate for the epifauna decreases in the winter, then any seasonal change in S will depend on how the extinction rate changes with respect to the change in immigration rate.

Figure 4 illustrates the 3 hypothetical relationships between extinction rate curves for given summer and

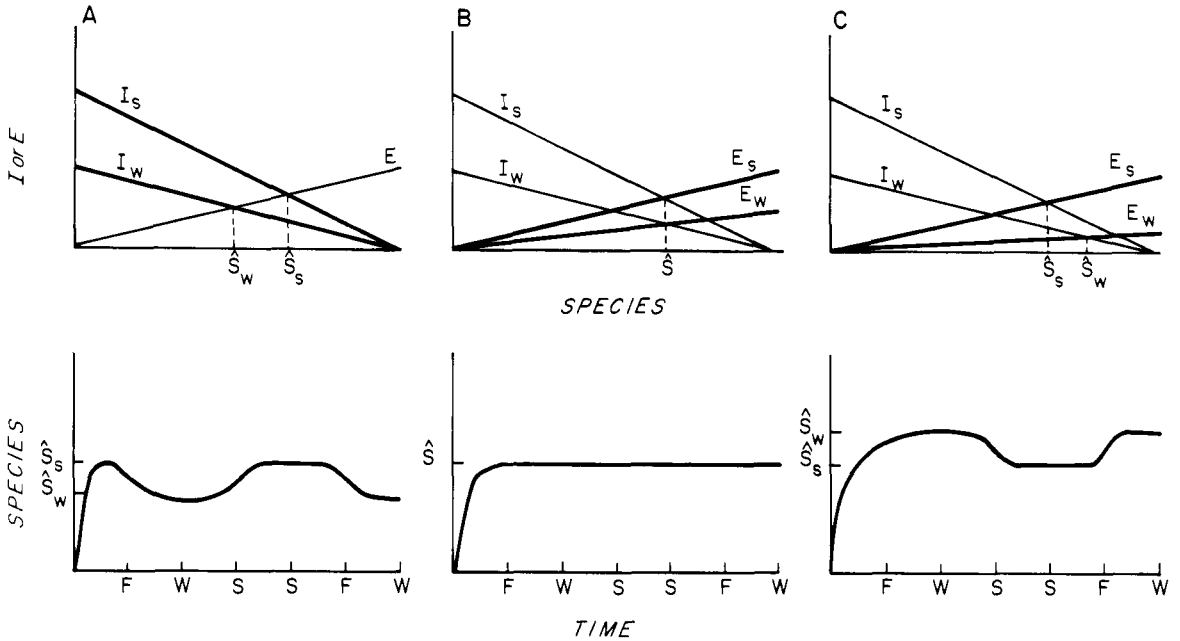

FIG. 4. General seasonal model with resulting colonization curves. Subscripts denote either summer (s) or winter (w). For pool size (P), it was assumed $P_s = P_w$. For immigration (I), $I_s = cI_w$ with $c > 1$.

(A) $I_s/I_w > E_s/E_w$.
(B) $I_s/I_w = E_s/E_w$.
(C) $I_s/I_w < E_s/E_w$.

winter immigration rate curves and the resultant colonization curves. If extinction rate shows proportionally less change with season (A) than immigration rate (all still showing their relationship to species present), then a lower $\hat{S}$ would be predicted for the winter than the summer. The resultant colonization curve would eventually be expected to show a cyclic change in the number of species with a high in the summer and a low in the winter. If the change in extinction rate is proportional to the change in immigration rate (B), both seasons would have the same $\hat{S}$. A more typical colonization curve would result. Last, if extinction rate exhibits a proportionally greater change (C), then $\hat{S}$ would be predicted to be greater in the winter than the summer. The number of species present would again be cyclic, but in this case, the colonization curve would peak in the winter. From Table 1, it appears that extinction rate does not change seasonally for epifauna and a colonization curve similar to that on the left would be indicated.

Again, it should be noted that $\hat{S}_S$ and $\hat{S}_W$ are not "true" equilibria in the sense that the number of species is expected to permanently equilibrate at these values. They are predicted values which the observed S would be expected to approach either from a higher S value (summer to winter) or from a lower S value (winter to summer). If there is not sufficient time for these to be reached, then S might be expected to oscillate between 2 intermediate values. However, it is the predicted cycle, not the actual values of S, that is most interesting.

Empirical model.—It is unrealistic to assume that immigration and extinction rates change instantaneously with the change of season. Although not ideal, a more testable model would be one in which we had estimates of these rates for short time periods (i.e., for each month). From these estimates, it would be easy to predict the shape of the colonization curve for a substrate begun at any time of the year.

To construct immigration curves for each month of the year, a minimum of 3 estimates for each curve are needed; the x- and y-intercepts and the general shape of the curves (linear, exponential, etc.). Because the immigration rate is 0 at the pool size, P, the x-intercept is P, which has already been estimated as 140 species. Settlement plates (those substrates exposed clean each month for only that month) were again used to estimate immigration with 0 species present, or the y-intercept. These values ranged from 15 for the month of August to 1 for January.

The most difficult parameter to estimate is the general shape of the curves. MacArthur and Wilson (1967) have shown that if the immigration curve is linear, the number of species on 2 similar islands will be equal to $2 - (\hat{S}/P)$ times the number on a single island. Additionally, Simberloff (1972) has suggested that, if competition is important, $2 - (\hat{S}/P)$ will approach 2. However, if the immigration curve is a sharply bending

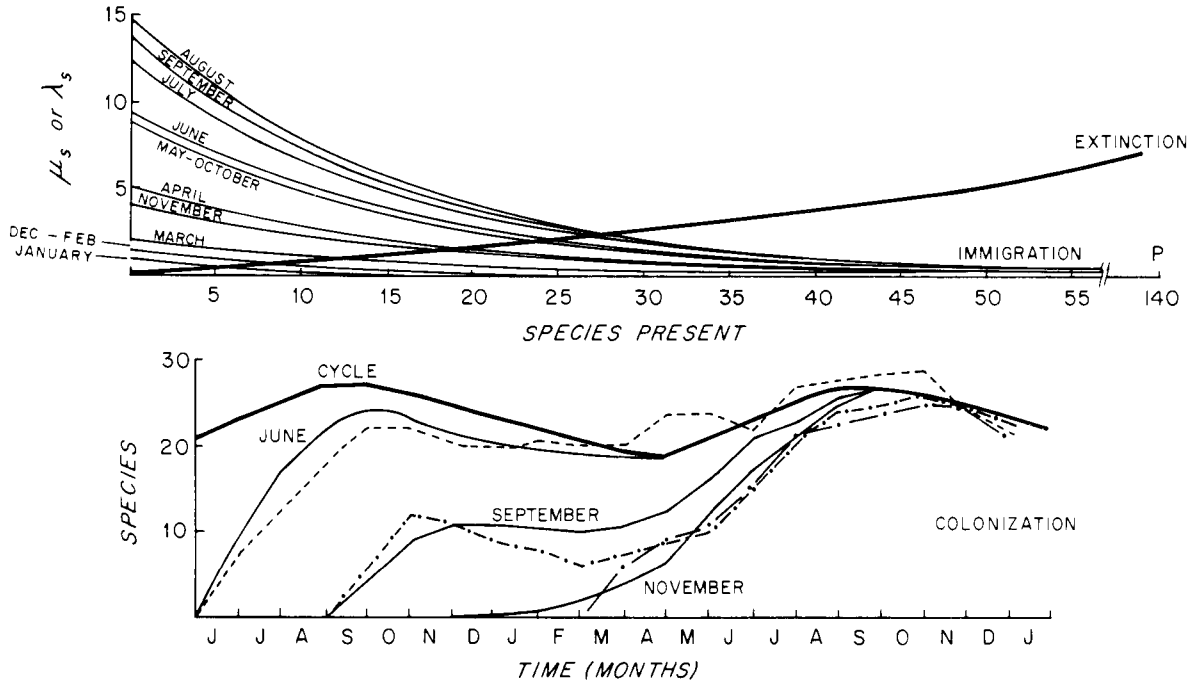

FIG. 5. Empirical seasonal model. Extinction rate curve is assumed constant for all months. Separate colonization curves for plates initially exposed in June, September, and November were derived from these immigration and extinction curves by starting with the immigration curve for the initial month and allowing these immigration curves to change successively after the elapsation of each month. Solid lines represent expected curves, broken lines are actual observed curves. All expected colonization curves converge with and continue in the cycle curve. **See text for additional explanation.**

exponential, the number of species on 2 islands will be equal to the number on 1. Calculations of the total number of species on various combinations of 2 plates out of groups of similar plates yielded values approximately halfway between these 2 extremes. It was therefore assumed that the general shape of the immigration curves was a shallow exponential of the form,

$$I = me^{-nS} - k, \qquad (1)$$

where m and n are fitted constants and k is a constant that allows I to equal 0 at P or

$$k = me^{-nP}.$$

The value, k, is dependent on the values, m and n. However, it is assumed that all immigration curves intersect at P, independent of k, such that k is a constant for all curves (allowing k to vary as much as 2 orders of magnitude between curves resulted in no significant change in their shape). Such shallow exponential curves "recognize" the differences in abundance of larvae produced by different species (Fig. 3) and thus differences in the probability of a given species settling. Of the 140 possible species that could immigrate, only 90 were observed during the study. Of these 90, as many as 30 species settled infrequently (observed between 1 and 10× during the study). Almost equally good results were obtained by excluding low-probability species from the pool and linearly regressing immigration to a pool size of 40–60 species. Using the y-intercept for the August curve (0, 15), and the highest average monthly S observed on August plates and turnover rate, X (predicted extinction rate with 28 species present), as a second point (28, 2.5), an exponential function was fitted yielding a k value of 0.0019. The immigration curves for the remaining 11 mo were regressed using their x- and y-intercepts with the y values adjusted for k (Fig. 5).

Because extinction rate seemed to be dependent only on species present and showed no seasonal variation (Table 1), a single extinction curve was regressed using data for all plates at a depth of −1.5 metres.

The derived monthly immigration curves and the extinction curve are shown in Fig. 5. Also graphed are the expected and observed colonization curves for plates initially immersed in the months of June, September, and November. Expected colonization curves were plotted by first algebraically manipulating the equations of MacArthur and Wilson (1967),

$$S = \hat{S}(1 - e^{-Gt}) \text{ and } G = (d\mu/dS) - (d\lambda/dS),$$

to yield

$$t_S = \sum_{S=0}^{S} \frac{-\ln[1 - x/(\hat{S} - S)]}{[(\mu_{S+x} - \mu_S) + (\lambda_{S+x} - \lambda_S)]/x}, \qquad (2)$$

where t is the time from the date exposed in months, S is the number of species present, μ_S and λ_S are the extinction and immigration rates for S species present, and x is the change (±) in S (see **Appendix II** for derivation of Eq. 2). Second, to plot the expected coloni-

TABLE 2. Comparison of the average number of species present in the fall 1972 and in the summer 1973 for plates initially exposed in different months

	Fall 1972[b]		Summer 1973[c]			
Month exposed[a]	Plates (n)	Species/plate	Plates (n)	Species/plate	F[d]	P
Jun	14	22.29 ± 1.86	12	25.25 ± 1.82	16.80	$\ll .001$
Jul	7	21.14 ± 1.21	6	26.17 ± 2.14	28.80	$\ll .001$
Aug	13	19.85 ± 1.99	9	24.50 ± 0.58	20.41	$\ll .001$
Sep	18	9.39 ± 2.30	5	24.20 ± 0.84	193.67	$\ll .001$
F[d]		138.49		1.53		
P		$\ll .001$		$>.20$		
Without Sep.						
F[d]		6.13				
P		$<.01$				

[a] Based on all large plates exposed at −1.5 and −2.0 metres MLW.
[b] Sep samples from Oct through Dec, other months Sep through Nov.
[c] Samples from Jul through Sep.
[d] Analysis of variance, Sokal and Rohlf (1969).

zation curve for a plate begun in June (for example), $\hat{S}_{June}$ and $\lambda_S = I_{S\ June}$ (Eq. 1) are used in Eq. 2 and the graph of the points (t, S) will be the beginning of the colonization curve. When t = 1, 1 mo has elapsed and the values, $\hat{S}_{July}$ and $\lambda_S = I_{S\ July}$, are substituted into the equation. By continuing this substitution after the passage of each month, the expected curve can be generated. To plot the colonization curve for plates begun in any other month, the calculations are begun using the $\hat{S}$ and λ_S for that month and are continued in the manner outlined above.

The predicted colonization curves in Fig. 5 show a broad range in shape, this shape dependent upon the month in which they were initially exposed. Curves begun in any of the other months can also be generated and their shapes vary between those illustrated. The observed colonization curves (dashed lines), plotted as monthly averages for each of the 3 groups of plates (see Osman [1977] for confidence limits and similar curves) are remarkably similar to the expected (solid lines). The seasonal model seems to account for the observed difference in the shape of the initial parts of the 3 colonization curves. This greatly varies depending on the month in which the plates were initially immersed. The model also predicts a seasonal cycle in S (as in Fig. 4) and both the expected and observed curves for plates started in different months converge with this cycle. In fact, the cycle curve results from continuing the model past the points of convergence. Both these initial differences and eventual similarity in S are shown in Table 2. Significant differences in S existed between the 4 groups in the fall, 1972 (also when the very different September plates were excluded from the analysis). Each fall value was also less than the average S for the same group in the summer, 1973. However, the mean numbers of species for each group in the summer, 1973, were not significantly different, and convergence in terms of S is indicated.

To test additionally this seasonal model, the data of Cirino (1958) were analyzed in a similar manner. In studying the development of the marine algal community at a site within 1 km of the present study, she exposed wood panels (76 × 6 cm) in all months and for various lengths of time. From her data, monthly immigration curves, an extinction curve, and resultant colonization curves were constructed in the same manner as outlined above (Fig. 6). Again, the shapes of colonization curves for different months vary initially but, as for the epifauna, these curves converge into a similar seasonal cyclic pattern. Also, for these much larger panels (and a different group of organisms), the cycle seems to continue for >1 yr. After convergence, the greater-than-expected values of S in the second winter also suggest that the extinction rate might be fluctuating seasonally (declining slightly in the winter and increasing slightly in the summer).

This model, predicting the cycle in S, is basically noninteractive. Competition between species might be expected to increase extinction, lowering and perhaps stabilizing S. Unfortunately, most large plates were lost during the winter of 1973–1974 and it could not be determined whether the cyclic pattern in S would have continued. The plates exposed during summer 1972 were very different in species composition than the September or November plates. Many (40% of the large, 90% of the small) were becoming dominated (in terms of area covered) by 1 or a few species (Osman 1977).

Certainly, over a longer time period, interactions between species could affect immigration or extinction. However, this relatively simple model does predict the pattern one might expect ignoring these interactions and thus supplies a basis from which to evaluate the importance of these interactions.

Time to equilibrium

MacArthur and Wilson (1967) have suggested that the time to 90% saturation, $t_{0.90}$, should be a good estimate of the time required for an island to reach equilibrium. They found that if the absolute values of the slopes of the extinction and immigration curves are equal,

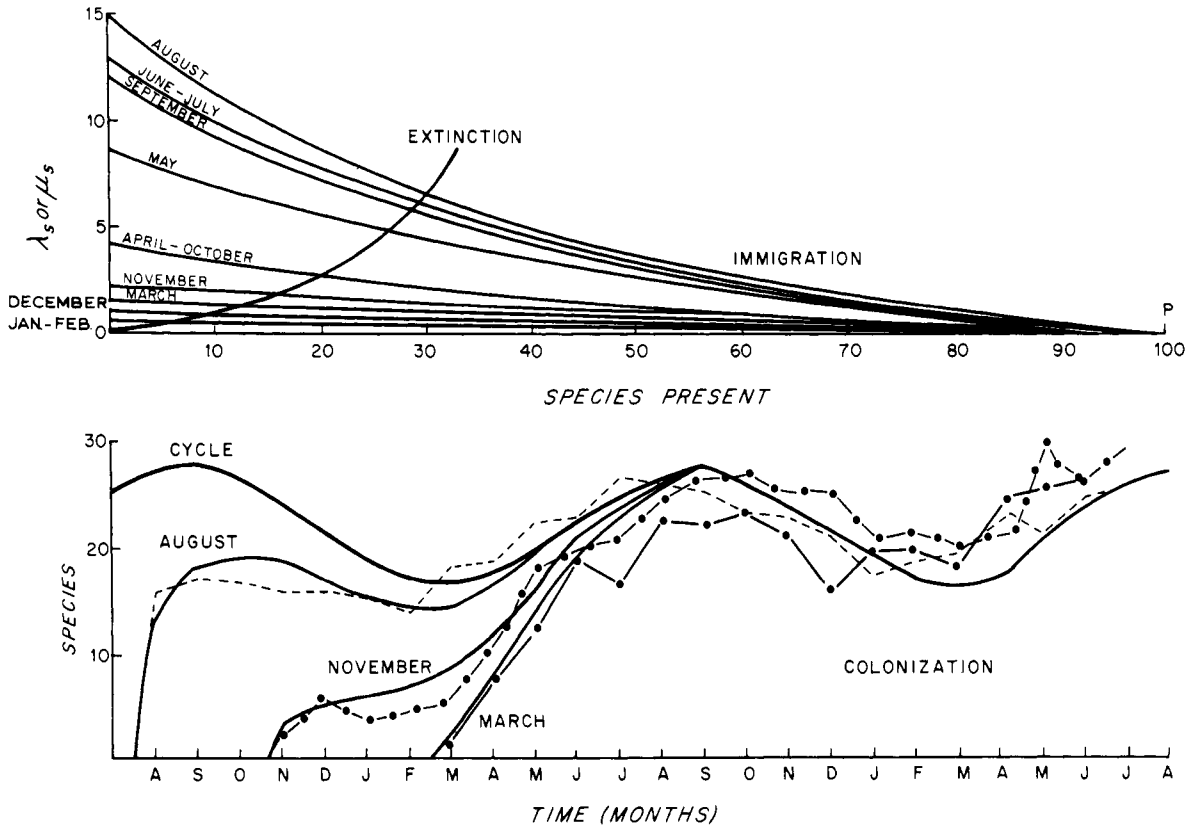

FIG. 6. Empirical seasonal model plotted from the data of Cirino (1958). Description the same as Fig. 5.

$$t_{0.90} = 1.15\hat{S}/X,$$

where X is the turnover rate at equilibrium. Obviously, since a seasonal environment seems to preclude any single $\hat{S}$ or X for epifauna, direct substitution is not possible.

Depending on how one views the expected cycle in S, it can either represent an example of nonequilibrium conditions, in that no $\hat{S}$ was ever reached (over the time studied), or the cycle itself can be a type of oscillatory equilibrium. Hedging this philosophical question, it is perhaps better to ask how long a given substrate might take to converge with this cycle. The time until convergence with this cycle does at least give an indication of the speed of the colonization process and its dependence on when a substrate is initially exposed. Table 3 lists the predicted convergence times for all months of the year and observed means for those months in which plates were actually started. As the table indicates, these values range between 6 and 13 mo. Obviously, convergence occurs more quickly during times of increasing larval abundance and it usually occurs only after exposure for 1 full summer. Thus, plates first exposed in the fall, winter or spring generally converge at the end of the following summer, while those exposed during a summer converge somewhat earlier (spring or early summer) the following year.

Rock stability

The data from the experimental plates have shown that the number of species present on a substrate is a function of the size of the substrate and the seasonality of the environment. For naturally occurring substrates (rocks, in this case), an additional parameter, the physical (or temporal) stability may be defined as the length of time that a rock remains in 1 position or the time until it is overturned. Because smaller rocks can be overturned or disturbed more frequently, stability will be proportional to the size of the substrate.

Both Riedl (1964) and Rützler (1965) demonstrated the effect of this size-dependent stability of rocks on the composition and diversity of their epifauna. In terms of the species equilibrium, the turnover of a rock will result in the extinction of most, if not all, of its epifauna. These animals cannot survive on surfaces in contact with the underlying sediments. With each turnover, however, the previously unexposed surface of a rock will be exposed and available for colonization. In a sense, turnover may be viewed as the destruction of 1 rock island and its fauna with instantaneous replacement by a barren island of approximately equal size.

The experimental plates, which were artificially stable (attached to boards), give an estimate of the number of species on a substrate of that size under "ideal"

TABLE 3. Time for convergence with predicted seasonal cycle

Month exposed	Observed time No. of months	Predicted time No. of months
Jan		9 (Sep)
Feb		8 (Sep)
Mar		7 (Sep)
Apr		6 (Sep)
May		12 (Apr)
Jun	9.7 ± 2.10	11 (Apr)
Jul	10.2 ± 1.92	10 (Apr)
Aug	10.2 ± 3.06	11 (Jun)
Sep	14.0 ± 1.26	13 (Sep)
Oct		12 (Sep)
Nov	13.6 ± 1.72	11 (Sep)
Dec		10 (Sep)

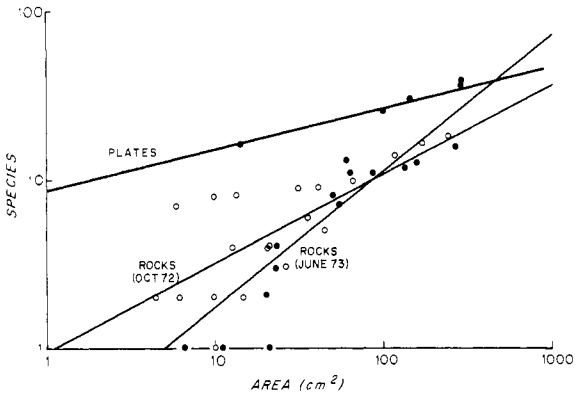

FIG. 7. Area–species curves for both plates and rock samples. Open circles indicate rocks collected in October 1972: closed circles indicate rocks collected in June 1973. Plate points (5 closed points on or above plate line) are means with the standard deviation less than ±2.0 for all points.

conditions (no disturbance). The area–species curve for the experimental plates, using the average S during the second summer, is shown in Fig. 7. Using averages from other seasons would yield lines parallel to this but of slightly lower absolute value. Since only 2 sizes of experimental plates were used, various numbers of similar-sized plates were pooled randomly to get estimates of S for larger substrates. As would be expected, such a pooling of islands results in values higher than the line for actual large substrates. This pooling of islands is identical to the addition of disjoint sets with similar individual-species distributions. Simberloff (1970: Appendix) demonstrated how such an addition will change the resultant distribution when the added distributions are inordinately overlapped or disjoint. He also suggested that with the increased importance of competition, the distributions on different islands will be more disjoint (Simberloff 1972). Thus, the pooling of substrates will result in an increasing overestimation of $\hat{S}$ for a substrate of the pooled size with the increasing importance of competition. For the experimental plates, this overestimation is fairly small and would seem to indicate that the distributions on different plates are not inordinately overlapped or disjoint and can be used to confirm the reliability of the curve.

Also shown in Fig. 7 are regressions to the area–species equation, $S = CA^z$, for 2 collections of rocks from the study locality; 1 set collected in October 1972, and the other in early June 1973. Although all rocks sampled had a lower S than would have been predicted from the plate curve, the change in the number of species with area was much greater ($z = 0.53$ and 0.81, respectively). This increase in slope is directly correlated with the instability of the smaller rocks. Rocks of sufficiently large size (data indicate those of ≈600 to 1,000 cm² exposed surface area or larger) will be disturbed so infrequently that they may be considered temporally stable. The number of species on them should therefore be approximated by the plate area–species curve. As the size of the rocks decreases, disturbance increases in frequency. Thus, as rock size decreases, a greater and greater percentage of the rocks per size class will be under-saturated in species. This will result in a depression of the lower end of the area–species curve relative to the upper end, therefore causing the observed increase in slope. Because most larger rocks are at or near equilibrium and smaller ones are in different stages of development, the deviation from the regression tends to increase with decreasing size.

This hypothesis is also supported by data for the epifauna on the shells of the living gastropods, *Littorina littorea*, *Bittium alternatum*, and *Mitrella lunata*. These animals, if overturned, have the ability to right themselves and they should, therefore, have a greater stability than rocks of similar size. Although these snails present a shell surface area much smaller than plates or rocks, values for these substrates were intermediate between those predicted from the plate and rock curves (Table 4).

The interaction of stability and seasonality also seems predictable. In months of high immigration, a disturbed substrate would be rapidly recolonized, whereas in months of low immigration, recolonization

TABLE 4. Comparison of number of species observed on snails with predicted values for rocks and plates of equal size

Size range (cm²)	Predicted no. for rocks[a]	Predicted no. for plates	Observed no. on snail
.01 to .05	.08 to .19	2.45 to 3.71	0.6 ± 0.55[b]
.5 to 1.0	.66 to .95	6.72 to 8.03	1.9 ± 0.87[c]
3.0 to 4.0	1.7 to 1.99	10.66 to 11.48	4.7 ± 0.52[c]

[a] Predicted from October 1972 area–species curve.
[b] *Bittium alternatum* and *Mitrella lunata*.
[c] *Littorina littorea*.

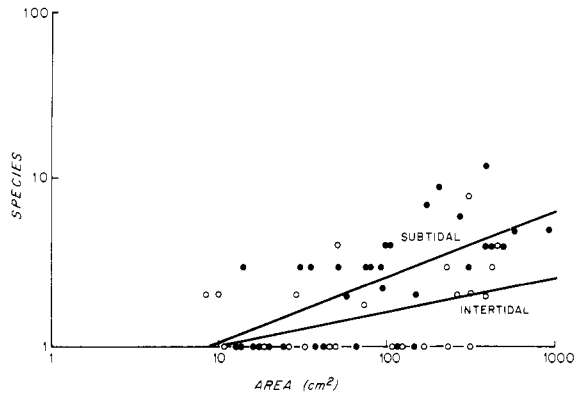

FIG. 8. Area–species curves for rocks collected at Nobska Point in July 1974. Open cirlces indicate intertidal samples: closed circles indicate subtidal samples.

should proceed at a much slower rate. This should result in an increased number of highly unsaturated smaller substrates during the latter times and a subsequent increase in the slope of the area–species curve and a reduction in the variation at the lower end of the curve. A comparison of the slopes for the June rock sample (0.81), collected during the early stages of immigration increase, and the October sample (0.53), collected just after peak immigration, tends to confirm this prediction. However, because of the small number of points, an analysis of covariance for these regressions showed no significant difference ($.05 < P < .1$).

Environmental differences

In the preceding sections, the effects on the species equilibrium of various parameters within the same general environment have been demonstrated. Rocks, just as islands, occur in very different environments and Diamond (1971) has shown that such differences can affect the equilibrium.

The depth at which a rock occurs often indicates the environmental conditions under which it exists. Earlier, it was noted that the forces which disturb rocks and cause their overturn were often wave generated. Because the effect of waves will decrease with increasing depth, the stability of rocks will increase with depth. Such an increase will mean that small rocks in deep water will approach the low frequency of overturn exhibited by large rocks in shallow water. Small rocks should, therefore, approach their equilibrium number of species in deep water and the area–species curve for deeper environments should more closely resemble the curve for experimental plates.

Unfortunately, no deepwater (>5 m) rock areas were located near the study site. Data from other localities in Vineyard Sound and Buzzards Bay indicate that the slope of the area–species curve is closer to that of the plates, but without experimental data for immigration and extinction rates, comparisons to the study area are difficult. The relationship may be fortuitous. Additionally, compositional changes on stable substrates, such as increased dominance of certain species (Osman 1977), suggest that experimental manipulation is required to adequately test this hypothesis.

Another environmental change associated with depth is seen in the differences between intertidal and shallow subtidal localities. Only a limited number of epifaunal species can survive the harsh conditions of exposure to air that are encountered in intertidal habitats. It could be argued that intertidal rocks will have a lower immigration and higher extinction rate of species. During times of exposure to air, immigration cannot occur, thus reducing that rate, and nonintertidal species will become extinct, thus increasing that rate. An intertidal rock will average 2 exposures per day, resulting in the fairly immediate death of nonintertidal species. Because of this "instantaneous" extinction, it seems better to exclude subtidal species from the intertidal pool. If this is assumed, the intertidal environment is characterized by a reduction in the species pool and also a possible reduction in the immigration rate.

MacArthur and Wilson (1967) have derived an equation for the relationship of species number to area:

$$d\hat{S}/dA = -[dE/dA][IP/(E + I)^2], \quad (3)$$
$$\text{where } E = E_P \text{ and } I = I_0.$$

This equation indicates that the change in $\hat{S}$ with area is proportional to the pool size. Data from the study area and 2 other localities confirm this relationship. Within the study area, the regression for an intertidal sample made in June, 1972 ($z = 0.46$) was significantly different from the June ($z = 0.81$) and October ($z = 0.53$) subtidal samples (analysis of covariance, $P < .001$). However, this comparison may lack validity, because the samples were taken at 3 separate times.

Simultaneous intertidal and subtidal rock samples were taken at 2 other localities in July 1974: Nobska Point, 2 km from the study site; and Manomet Point, north of Cape Cod. At both localities, the intertidal area–species curves had lower slopes and were significantly different from the subtidal curves ($P < .01$). The data for Nobska Point are displayed in Fig. 8.

A similar lowering of the slope of the area–species curve was also observed on the −0.5-m experimental plates and resulted from a single event of mass extinction. At the beginning of the first winter of the study (November 1972), extremely low tides, offshore winds, and freezing temperatures occurred simultaneously. This resulted in the exposure to air of plates normally subtidal and the eventual freezing of their epifauna. For the most part, only intertidal species can tolerate the dessication and formation of ice crystals within tissues; both which result from freezing (Kanwisher 1955, 1959). Because of the subsequent mass extinction of nonintertidal species on plates at this

depth, the average number of species per plate declined from 14 to 6 for small plates and from 22 to 8 for large. Because of the greater reduction in the number of species on the large plates, the slope of the area–species curve also declined ($z = 0.16$). Such sudden environmental changes are probably infrequent and clearly unpredictable, but they do demonstrate the effect of environmental differences on the species equilibrium.

Conclusions

The species equilibrium theory is a fairly simple yet extremely robust model for interpreting diversity. It has 2 basic variables: immigration and extinction. Because changes in other parameters can often have a direct effect on either of these, the resultant effect on species diversity can be predictable and testable.

The 2 major parameters investigated in this study have been the seasonality of the environment and the physical stability of the substrate or rock islands. The seasonal climate was demonstrated to result in a seasonal change in the pattern of colonization. Plates exposed at different times accumulated species at very different rates. In terms of number of species, these plates with very different histories appeared to converge in S. The simple model which both predicted these initial differences and the eventual convergence also predicted a continued seasonal fluctuation in S. This pattern could only be weakly tested, and whether S would continue to fluctuate seasonally is unknown. Regardless, the point is that an array of complex patterns of colonization can be generated using a simple model which allows immigration to vary as a function of season and species present. The model predicts an increase in species in the summer and a decrease in the winter, regardless of species composition or potential interactions between species. In this sense, it supplies a base line which is necessary before such biological factors can be considered. It must be asked how much change should occur seasonally because of variability in larval production and settlement before an increase or decrease in diversity can be attributed to any species interaction.

Compounding the effects of seasonality is the natural instability of the rock islands themselves. Epifaunal species are necessarily adapted to the temporary existence of their substrate islands. Because rocks vary in their frequency of turnover, according to size, the area–species relationship is magnified. MacArthur and Wilson (1967) have correlated other changes in the area–species curve with the instability of small islands.

In addition, species composition may also be affected by differential stability. Small substrates, being overturned at a high rate, will have a species composition which reflects the reproductive capabilities of the species. Species producing an abundance of larvae at the time a sample is taken should also be found in abundance on small substrates. These species may also tend to be short lived. However, large substrates, which are less frequently disturbed, should develop a different fauna of "competitively superior," longer-lived species. Because a gradient exists between large and small rocks, differential stability should, therefore, greatly increase the variability in species number and composition found from rock to rock within this system. Other parameters, such as the environmental differences encountered by substrates in different localities, may also enhance the variability found.

In particular, species equilibrium theory appears to be a reliable model for predicting changes in the diversity of marine sessile invertebrates attached to rocks. However, it may be questioned whether this model, developed to explain biogeographic distributions of species on oceanic islands, can be used in such a limited sense. Rocks are not true islands, but more strictly discrete patches of the environment. The collection of individuals of a species on a rock is not a true population in that sexual reproduction contributes little to the immediate propagation of those individuals on that particular rock. They may be viewed as a subunit of a much larger population. In the same sense, the arrival of a larva to a rock may not be true immigration or colonization, but a change in distribution within a population. Likewise, extinction can be interpreted as just localized loss of individuals.

Certainly, these differences must be recognized, but they do not prevent the application of the model to this system, or the use of marine epifauna in testing the model. The attractiveness of species equilibrium theory lies in its ability to recognize the dynamic nature of ecological systems and to predict changes in diversity by the simple balancing of gains and losses. Recognizing that the theory is not strictly biogeographic allows it to be used and tested on many different levels from intrapopulation to biogeographic.

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Appendix I: Sessile species recorded during study.

Porifera
- *Halichondria bowerbanki*
- *Halichondria panicea*
- *Haliclona loosanoffi*
- *Leucosolenia* sp.
- *Microciona prolifera*
- *Scypha* sp.

Cnidaria
- Hydrozoa
  - *Bougainvillia superciliaris*
  - *Campanularia* sp.
  - *Clytia* sp.
  - *Cuspidella* sp.
  - *Ectopleura dumortieri*
  - *Eudendrium* sp.
  - *Hydractinia echinata*
  - *Obelia commissuralis*
  - *Obelia geniculata*
  - *Opercularella pumila*
  - *Pennaria tiarella*
  - *Sarsia tubulosa*
  - *Tubularia larynx*
  - *Zanclea costata*
  - *Zanclea gemmosa*
- Anthozoa
  - *Astrangia danae*
  - *Diadumene leucolena*
  - *Edwardsiella lineata*
  - *Haliplanella luciae*
  - *Metridium senile*

Annelida
- Polychaeta
  - *Fabricia sabella*
  - *Hydroides dianthus*
  - *Myxicola infundibulum*
  - *Nicolea venustula*
  - *Polycirrus eximus*
  - *Polycirrus phosphoreus*
  - *Potamilla neglecta*

Potamilla reniformis
Protula tubularia
Sabella microphthalma
Sabellaria vulgaris
Spionidae
Spirorbis borealis
Spirorbis pagenstecheri
Spirorbis violaceus

Arthropoda
Cirripedia
Balanus amphitrite niveus
Balanus balanoides
Balanus crenatus
Balanus eburneus

Mollusca
Bivalvia
Modiolus demissus
Modiolus modiolus
Mytilus edulis

Gastropoda
Crepidula fornicata

Entoprocta
Barentsia laxa
Barentsia major
Pedicellina cernua

Ectoprocta
Aetea sp.
Alcyonidium polyoum
Bowerbankia gracilis
Bowerbankia imbricata
Bugula turrita
Callopora aurita
Callopora lineata
Cellepora dichotoma
Cribilina punctata
Crisia eburnea
Cryptosula pallasiana
Ctenostome A
Electra crustulenta
Electra hastingsae
Electra pilosa
Hippodiplosia pertusa
Hippothoa hyalina
Lichenopora verrucaria
Membranipora tenuis
Microporella ciliata
Mucronella immersa
Mucronella ventricosa
Parasmittina nitida
Parasmittina trispinosa
Schizoporella biaperta
Schizoporella errata
Schizoporella A
Tegella armifera
Tegella unicornis
Triticella pedicellata

Chordata
Ascidiacea
Amaroucium constellatum
Botryllus schlosseri
Ciona intestinalis
Didemnum candidum
Mogula complanata
Mogula manhattensis
Perophora viridis
Styela partita

Appendix II.

MacArthur and Wilson (1967) derive the equation for the colonization curve as:

$$S = \hat{S}(1 - e^{-Gt}) \tag{A1}$$

with

$$G = d\mu/dS - d\lambda/dS. \tag{A2}$$

Solving the Eq. A1 for t_S, the time to accumulate S species, we have

$$t_S = -\ln(1 - S/\hat{S})/G, \tag{A3}$$

where $S/\hat{S}$ is the proportion of S reached in time, t_S, with 0 species initially present (S_0).

If S species are present with x = dS, the change in the number of species, then the proportion of the species that can be added ($\hat{S} - S$) in the next time interval ($t_{S-x} - t_S$) is

$$x/(\hat{S} - S).$$

Therefore, the time to add x species, with S species already present is

$$t_{S+x} - t_S = \{-\ln[1 - x/(\hat{S} - S)]\}/G.$$

When dS = x and S species are present

$$G = [(\mu_{S+x} - \mu_S) - (\lambda_{S+x} - \lambda_S)]/x.$$

The time interval to change from S to S + x species is

$$t_{S+x} - t_S = \frac{-\ln[1 - x/(\hat{S} - S)]}{[(\mu_{S+x} - \mu_S) - (\lambda_{S+x} - \lambda_S)]/x}$$

or

$$t_S = \sum_{S=0}^{S} \frac{-\ln[1 - x/(\hat{S} - S)]}{[(\mu_{S+x} - \mu_S) - (\lambda_{S+x} - \lambda_S)]/x}.$$

In the seasonal model, after the passage of each month, $\hat{S}$ and λ_s change because of a change to a new immigration curve. Also, if $S > \hat{S}$, x will become negative.

Intervals (x) were set at $-1 \leq x \leq 1$ (sign dependent on whether $S \lesseqgtr \hat{S}$). Usually $x = \pm 0.1$. However, as t approached its next integer value (1 mo added) smaller values of x were sometimes used in order to obtain an exact integer value for t. This was necessary so that the next $\hat{S}$ and λ_S could be substituted exactly at the beginning of each month.