Intra- and interregional comparisons of numbers of species on marine hard substrate islands

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ABSTRACT. Intra- and interregional comparisons of the number of species ($\hat{S}$) on hard substrate islands were made, and factors affecting $\hat{S}$ were examined. Contrary to previously published data, we found substantial variation in $\hat{S}$ with no clear geographic pattern. In fact within one region the range in $\hat{S}$ was as great as found among regions.

Regression analyses suggested that immigration rate, realized pool size (i.e. the total number of species observed locally), and island size all had significant positive effects on $\hat{S}$. Other factors such as latitude, temperature, salinity and regional pool size had no significant effect on $\hat{S}$. Analysis of the data nested by habitat, ocean and latitude gave the same results. This suggests that local factors affecting the ability of a species to reach an island, i.e. distance from a source of immigrants and species dispersal abilities, have a greater effect on $\hat{S}$ than regional factors that might determine the total number of potential colonizing species.

Given the apparent importance of local factors in determining the number of species on hard substrate islands, we question the relevance of interregional comparisons in assessing factors which may influence the distribution and abundance of species.

Introduction

The well-known MacArthur–Wilson model of island biogeography (MacArthur & Wilson, 1963, 1967) states that there is an equilibrium in the number of species on an island, that this equilibrium is dynamic, and that it is determined by the rates of immigration and extinction of species. It is further understood that immigration and extinction depend on other factors, including island size, the distance an island is from its sources of immigrants, and the size of the pool of species available to immigrate. Most studies have concentrated on these secondary factors, particularly island size and distance, in attempts to explain species distributions on islands (reviewed in Gilbert, 1980). A few studies have investigated the actual dynamics of the model. These have been either attempts to estimate immigration or extinction rates from historical data (e.g. Brown, 1971; Diamond, 1969, 1971, 1973; Gilpin & Diamond, 1976; Heatwole & Levins, 1973; Jones & Diamond, 1976; Strong, 1974; Strong, McCoy & Rey, 1977) or experimental studies of the colonization of small natural (e.g. Brown & Kodric-Brown, 1977; Crowell, 1973; Rey, 1981; Simberloff, 1969, 1976a, b; Simberloff & Wilson, 1969) or artificial islands (e.g. Cairns *et al.*, 1969; Dean, 1977, 1981; Henebry & Cairns, 1980a, b; Jack-

son, 1977; Molles, 1978; Osman, 1977, 1978, 1982; Schoener, 1974a; Schoener, Long & De Palma, 1978; Schoener & Schoener, 1981; Wallace, 1975).

Artificial substrates have been used most extensively as model islands in freshwater and marine systems. The substrates used have varied from artificial sponges (Schoener, 1974a) to flat asbestos-cement or tile plates (e.g. Osman, 1977; Schoener & Schoener, 1981). Artificial substrates are particularly useful in examining hypotheses concerning the equilibrium model because, unlike most natural systems, artificial ones can be easily manipulated and replicated. They can be used to measure directly the effects of specific factors on the immigration and extinction of species, which in turn determine patterns of species distribution and abundances.

An initial analysis of the colonization of artificial substrates by marine invertebrates indicated that a predicted equilibrium was not approached (Schoener, 1974b). However, later studies (Dean, 1977; Osman, 1978; Schoener *et al.*, 1978) concluded that equilibria were reached, but generally after periods of greater than a year. Further, it was determined that, in seasonal environments, immigration rates fluctuated seasonally resulting in colonization curves whose shape varied as a function of the time that the substrates were initially submerged (Schoener, 1974b; Dean, 1977; Osman, 1978). Substrates initially exposed in the winter when few colonists were available underwent long periods of little or no colonization followed by a rapid period of colonization in the spring and summer. On the other hand, substrates exposed in the spring would be colonized rapidly, often reaching equilibria in as little as 6 months (Osman, 1978). Because of continuing seasonal changes in immigration, the resulting equilibrium number of species also oscillated. However, these eventual oscillations were the same for all substrate islands at a site regardless of the season in which the colonization process was initiated (Dean, 1977; Osman, 1978).

The characteristics of experimental substrates that enable these local colonization processes to be thoroughly investigated are also important to the examination of the geographic variation in these same processes. Although an extensive literature exists which describes and discusses geographic patterns in diversity, there has been little effort to examine these patterns in terms of immigration/extinction dynamics. Most studies have concentrated on intraregional patterns (e.g. island archipelagos) involving a single pool of species. Thus, at present there is little empirical information regarding interregional or global variation in immigration or extinction rates, whether they co-vary, or whether there is any systematic change in these rates with other regional characteristics such as pool size.

Diamond (1971) made a cursory comparison of apparent turnover rates between single tropical and temperate islands. He suggested that extinction rates were similar, but that a smaller percentage of the pool (but a larger absolute number of species) immigrated on to the tropical island. He attributed this to tropical birds being more sedentary than temperate ones but did not test this idea. Schoener *et al.* (1978) made the only comparison of geographic variation in colonization. Based on the data of Thorson (1950), they suggested that immigration rates should be higher in tropical than in temperate or sub-arctic climates. With no empirical data to predict any differences in extinction rates, they assumed (as Diamond, 1971, suggested) that extinction rates were the same. They therefore hypothesized that the equilibrium number of species ($\hat{S}$) on substrates at tropical latitudes should be higher than found on identical substrate islands in temperate regions. However, when they tested this hypothesis they found that the apparent $\hat{S}$ was similar in all regions. Since the size of the pool of species (P) varied between regions, they also found no relationship between $\hat{S}$ and P. Schoener *et al.* (1978) suggested that in tropical regions with a large P, colonization curves rose to some maximum and then declined to a $\hat{S}$ similar to other regions. From this, they inferred that larger pool sizes in the tropics may result from a greater number of habitats rather than greater within-habitat diversity. Species colonizing the 'wrong' habitat would explain the initially high rate of colonization and their loss would explain the decline to the common $\hat{S}$. They also suggested that lack of concordance with the MacArthur–Wilson model may have resulted from biological activities (i.e. intense competition and predation) having a greater effect in tropical communities.

With the results of their study appearing to contradict the predictions of the MacArthur–Wilson model, Schoener *et al.* (1978) rejected the model. They replaced it with several *ad hoc*

explanations for their results, these based on possible biological differences between species in the various regions. However, the model that they rejected incorporated several simplifying assumptions. Immigration and extinction rates were never measured but rather were assumed to be linear functions of the species present on the substrate islands. Extinction was assumed to be equal between all regions, and immigration curves were assumed to have equal slopes thus requiring that the immigration rate with S species present (I_s), and $\hat{S}$ be direct functions of the species pool. There are no *a priori* reasons why such restrictions should be expected. There is ample evidence from colonization studies (e.g. Osman, 1978, 1982; Osman & Whitlatch, 1978) that: (1) immigration and extinction rates vary within a region and both should be expected to vary between regions, (2) measured immigration and extinction curves are non-linear and/or have significantly different slopes, and thus, (3) I_s and $\hat{S}$ are not necessarily functions of P.

Although it is clear that the simplest form of the MacArthur–Wilson model cannot explain observed patterns, it still remains unclear whether the dynamics of immigration and extinction have any global pattern which might result in predictable patterns of colonization. In this communication we will examine the inter- and intraregional variation in several measurable parameters used in the MacArthur–Wilson model; $P, \hat{S}, I_s$. We will examine whether there is any systematic variation in these parameters and whether differences can be attributed to any measurable geographic variable.

Methods

We examined the geographic variation in colonization processes by comparing data in published reports supplemented with our own unpublished data. Studies were chosen in which (1) flat, hard substrate, fouling panels were utilized, (2) panels were submerged continuously for periods of 1 year or more and sampled frequently, and (3) at least some variables important in the island biogeographic model were estimated or could be estimated from the published data. Information is given in Appendix 1 regarding the location and duration of each study, the type of environment at each study site (ranges in salinity, temperature,

depth), sizes and types of substrates used, number of replicate surfaces, and whether destructive or non-destructive sampling techniques were used. Literature sources are also given and can be referred to for detailed descriptions of methods.

Estimates for each site of biological parameters important to the MacArthur–Wilson model are given in Table 1. These parameters are defined as they apply to communities on artificial substrates:

(1) *Equilibrium number of species ($\hat{S}$)*

Ideally, $\hat{S}$ is the number of species that an artificial substrate harbours when the colonization curve has reached its asymptote and the rates of immigration and extinction are equal. To estimate $\hat{S}$, values for S were measured on published colonization curves or taken from tables showing the number of species per panel. To be consistent in choosing the S values to be included, we assumed that 6 months was a minimum time for an equilibrium to develop and used estimates from all panels submerged more than 6 months. $\hat{S}$ was calculated for each panel size at a site as the mean for all S values included. Unfortunately, in most of the studies, individual panel islands were not followed and repeatedly sampled for the entire study. Instead, a large number of panels were started at the same time with some number removed and analysed each sampling period. Because of this destructive sampling, $\hat{S}$ could not be calculated for individual panels in these studies. Therefore, for consistency all panels were pooled by size at every site.

(2) *Initial immigration rate (I_0)*

This is the number of species which settled on previously unoccupied substrate during approximately 1 month of submergence or the Y-intercept of the immigration rate curve. In previous studies of fouling panels, I_0 has been shown to vary with size of the panel islands, its distance from a known source of immigrants, and with season (Osman, 1978, 1982). Because of this potential variability we have not only expressed this value as the mean, but have also indicated its maximum (I_{max}) at each site As indicated by Schoener (1974b), these estimates of I_0 and I_{max} have a bias toward underestimation since some

species that immigrated on to a substrate would have become extinct before the panels were observed.

(3) *Pool size (P)*

The number of potential colonist species in the system or pool size is defined in two ways. First, the actual pool (P) is the number of sessile species common to hard substrates in the study region. In general, this number was estimated from regional keys to invertebrate species with adjustments made for the ability to distinguish similar taxa using the particular sampling method. Second, we also refer to the realized pool (P_r). This is the total number of taxa observed at the same site at which the study was completed. This amounts to a counting of species in a species list obtained at each station. For studies in which more than one site was examined in a region, P_r, is expressed as the total for the region (all sites combined) and for each individual site.

These operational definitions are necessary to enable an objective comparison of studies employing somewhat different methodology and done in a diversity of environments. However, several potential problems arise in making such comparisons, regardless of attempts at objectivity.

The first problem is whether measured $\hat{S}$ values estimate true equilibria or just mean species abundances. Two conditions should exist if the $\hat{S}$'s are equilibrium values. The temporal change in S should be zero and, as Keough & Butler (1983) argue, the fluctuations in S must be 'sufficiently small.' They define an arbitrary constant, ω, such that 2ω is equal to the ratio between the band width of the region within which 95% of S values fall ($2(1.96\sigma)$) and the mean S. In most of the studies they reviewed. $0.1 \leqslant \omega \leqslant 0.3$ and they chose the median of $\omega = 0.2$ (corresponding to a coefficient of variation of 10.2) as a test criterion for an equilibrium in S. Both of these conditions were tested and the analyses are presented in the results below.

A second problem is the absence of certain types of data, particularly estimates of a pool size (P) and extinction rate. With the exception of Osman (1978), P was not estimated in any of the studies. We were able to add these estimates of P for regions in which we have worked. However, without an intimate knowledge of

both the fauna of the remaining regions (life histories, habitat preferences, etc.) and their ability to be recognized using the particular methods, we could not estimate P for the remaining studies.

Extinction rate is a very difficult parameter to measure. It is estimated by regression using data collected by repeated (non-destructive) sampling of panel islands. Only two of the studies (Osman, 1978, 1982) have attempted to estimate extinction, thus making multiregional comparisons of this important parameter impossible.

A final problem concerns the differences in methodology between the various studies. In some studies species numbers were estimated by counting a discrete number of randomly placed or evenly placed points while in other studies panels were surveyed completely for species. Also, the taxa included or excluded, recognized or unrecognized in each study will affect comparison. In particular, the inclusion of motile species is likely to increase estimates of immigration and extinction (plus emigration) rates, because of transient species (Simberloff, 1976b). When possible, we have limited the data set to include only sedentary species, by editing source data which included motile forms such as isopods and nudibranchs. However, at one site, a positive correlation between numbers of motile and sedentary species was found (Dean, 1981), and the general conclusions reached here should also apply to motile species.

Results

The data compiled for various fouling communities are given in Table 1. Before analysing these data we examined the nature of the data with regard to equilibrium assumptions.

Assumptions

The equilibrium assumption that S did not change temporally was tested using linear regression. Regression coefficients for 75% of the ninety-seven means (Table 1) were not significant (t-test) and five of the remaining twenty-three significant regressions were from Woods Hole stations at which $\hat{S}$ itself had been shown to change seasonally (Osman, 1978). As another test, a regression was computed for each individual panel from the San Onofre and

TABLE 1. Estimates of equilibrium species number, immigration rate, and pool size for sites in different geographic regions. (a) Three panels pooled with two surfaces/panel counted. (b) Based on mean recruitment rates in Fig. 2 of Sutherland & Karlson (1977). (c) Four panels pooled. *Significant change in S over time.

Region/station	Size (cm²)	Depth	$\hat{S}$		I_0	I_{max}	P	P_r	
			n	$X\pm SE$				Total	Site
Pamlico River, N.C.	155	2.4						21	
Site 1			6	11±0.3	4.0	10			15
Site 2			6	4±0.3	2.8	4			7
Site 3			6	4±0.6	2.1	5			6
Site 4			6	1.5±0.4	2.0	4			5
Broadkill River, Del.	100	0.5	89	7.8±0.3	6.0	12	85	35	35
Woods Hole, Mass.							222	92	
Large panels	103								
Depth 1		0.5	14	*12.6±1.5	5.2	17			53
Depth 2		1.0	29	20.4±0.9	7.3	20			72
Depth 3		1.5	52	*23.2±0.6	8.2	19			68
Depth 4		2.0	31	*21.0±0.7	6.7	13			62
Small panels	15								
Depth 1		0.5	61	*9.3±0.6	3.2	9			52
Depth 2		1.0	65	13.1±0.4	4.1	12			72
Depth 3		1.5	52	14.8±0.4	4.6	15			68
Depth 4		2.0	39	*13.3±0.6	4.0	14			62
San Onofre, Calif.							649	327	
Inshore stations									
1600 North	103	8.1	87	*23.2±0.4	7.1	18			97
	15	8.1	33	12.9±0.5	4.5	10			97
	103	0.5	36	12.0±0.5	3.3	7			41
800 North	103	6.6	18	25.1±1.6	10.3	20			83
	15	6.6	15	12.6±0.9	4.9	8			83
400 North	103	6.6	18	23.1±1.2	8.6				72
	15	6.6	15	11.1±0.7	5.1	10			72
200 North	103	6.3	45	27.8±0.8	7.3	16			104
	15	6.3	33	13.3±0.7	5.0	8			104
100 North	103	7.2	21	25.6±0.8	10.6	20			80
	15	7.2	15	10.8±0.9	5.7	12			80
50 North	103	6.6	54	*32.0±0.7	9.9	22			110
	15	6.6	33	*16.5±0.6	4.6	9			110
	103	0.5	31	20.0±1.1	5.8	12			74
50 North – I	103	6.8	16	23.6±1.0	8.3	15			78
	15	6.8	11	14.1±0.9	5.3	8			78
	103	0.5	9	17.9±0.9	5.1	10			47
50 South – I	103	6.8	16	*25.7±1.4	9.0	13			84
	15	6.8	11	10.7±0.7	5.5	8			84
50 South	103	6.6	54	27.2±0.6	7.3	12			106
	15	6.6	33	13.2±0.7	4.3	8			106
	103	0.5	15	*14.3±1.8	7.4				106
100 South	103	6.9	27	*28.3±1.3	8.9	21			98
	15	6.9	15	13.9±0.7	5.5	14			98
800 South	103	8.4	27	22.8±0.7	6.9	16			83
	15	8.4	15	11.1±0.6	5.0	9			83
1600 South	103	9.0	87	18.8±0.4	5.2	15			94
	15	9.0	33	10.4±0.4	3.1	5			94
	103	0.5	36	*10.1±0.7	4.2	8			40
San Mateo Kelp Forest									
Inside	103	10.6	57	38.8±0.9	5.5	22			157
	15	10.6	36	18.0±0.8	3.2	6			157
Edge	103	12.7	52	27.4±0.6	4.7	13			115
	15	12.7	15	12.3±0.6	2.9	7			115
Outside	103	13.0	54	19.7±0.5	3.6	8			93
	15	13.0	15	10.1±0.3	2.2	5			93

TABLE 1 (*continued*)

Region/station	Size (cm²)	Depth	$\hat{S}$		I_0	I_{max}	P	P_r	
			n	$X \pm SE$				Total	Site
San Onofre Kelp Forest									
Inside	103	11.8	90	*28.8±0.7	5.7	17			140
	15	11.8	51	11.5±0.6	2.8	6			140
Outside	103	10.9	21	22.8±1.2	5.2	10			83
	15	10.9	15	10.3±0.6	4.1	10			83
Outside	103	10.6	21	23.6±0.8	5.2	11			74
	15	10.6	15	10.5±0.6	3.7	7			74
Edge	103	12.7	87	*25.0±0.7	4.4	11			130
	15	12.7	33	8.9±0.5	3.0	8			130
Edge	103	11.8	33	27.2±0.8	7.8	13			94
Edge	103	12.7			9.5	12			66
Barn Kelp Forest									
Outside	103	12.7	83	20.8±0.5	5.2	17			101
	15	12.7	33	10.7±0.5	3.0	6			101
Outside	103	12.4	41	*21.8±0.9	4.2	9			70
	15	12.4	15	11.3±0.7	3.1	8			70
Outside	103	11.7	41	*23.8±1.3	4.3	13			69
	15	11.7	15	*10.3±0.5	3.6	8			69
Inside	103	13.3	15	*39.9±0.9	10.8	19			147
Puget Sound, Wash.		1.6							
	6.4		8	5.7±0.3	2.5	3		60	60
	25.8		8	9.9±0.6	2.8	3		60	60
	103		8	*16.5±0.8	3.3	5		60	60
	413		8	*19.5±1.4	3.7	7		60	60
	1651		8	24.3±1.5	5	6		60	60
	6606		8	27.0±1.2	6	6		60	60
San Francisco Bay, Calif.	600[a]	0.8	4	18.5±0.5	12.5	19		36	36
Indian River, Fla.	225								
Ft Pierce Inlet		1.0		–	11.2	19		31	29
Link Port		1.0	48	8.7±0.2	8.7	13		31	21
Vero Beach		1.0		–	5.2	9		31	14
Beaufort, N.C.	232	0.3		9	4.5[b]	9[b]		36	21
Discovery Bay, Jamaica		39.4							
	4		12	2.2±0.3					
	15		12	2.5±0.3					
	58		12	4.7±0.5					
	232		12	8.4±0.9					
Ashdod, Israel	1600[c]	0.2	3	24.3±1.2	10			34	34
Red Sea, Israel	1600[c]	0.2	5	29.0±1.4	15	15		52	52
Thailand	466	16	13	8.3±0.7	9.4	13		47	47
Washington	466	14	5	4.2±0.3	1.0	1		17	17
Maine									
Islesboro	466	5	4	5.3±0.5	1	1		30	23
Searsport	466	7	4	4.0±0.4	1	1		30	14
Pt Clyde	466	5	4	5.0±0.9	1	1		30	27
Newfoundland	466	16	5	5.0±0.9	1	1		34	34
Alaska									
Woman's Bay	466	15	6	7.5±0.6	1	1		22	12
Middle Bay	466	15	6	7.0±0.3	1	1		22	11
Hawaii									
Site 2	466	15	4	10.7±1.1	2.5	5		76	56
Site 3	466	3	3	11.2±1.6	4.5	6		76	36
Site 2	225	15	2	12.0	2	3		76	56
Site 2	1365	15	1	21.0	3.3	5		76	56

TABLE 1 (*continued*)

Region/station	Size (cm²)	Depth	$\hat{S}$		I_0	I_{max}	P	P_r	
			n	$X\pm SE$				Total	Site
Site 2	1830	15	1	22.0	4	7		76	56
Site 2	225	30	2	7.5	2	3		76	45
Site 2	466	30	2	10.5	3.5	5		76	45
Site 2	915	30	1	17.0	2.2	5		76	45
Site 2	1365	30	1	19.0	2.7	5		76	45
Site 2	1830	30	1	16.0	2.2	5		76	45

Woods Hole studies for which we had sufficient data. Only 7% (6/85) of the panels from the Woods Hole and 17% (50/303) of the panels from San Onofre had regression coefficients which were significantly different from zero.

These analyses indicate that in most cases we had chosen data from the zero slope part of the colonization curve. However, there were both locations and panels for which S did change significantly over time and the frequency at which these exceptions occurred was greater than would be expected by chance. Some of the potential reasons for this are discussed below.

To test the second condition for equilibrium, that fluctuations in S were 'sufficiently small' we used the analysis developed by Keough & Butler (1983). We applied this test to all $\hat{S}$ values in Table 1 for which there were the necessary minimum number of observations ($n\geqslant6$). Only 12.1% of the means were found to have $\omega\leqslant0.2$ and 36.3% had $\omega\leqslant0.3$. Based on this analysis it would appear that in most locations measured S values fluctuated too much for their means to be considered equilibria even though no overall change in S occurred over time.

Several factors potentially contribute to either these large fluctuations in S or a significant temporal change in S. First, in seasonal environments, $\hat{S}$ itself can fluctuate in a predictable cycle resulting from seasonal changes in larval availability and thus immigration rates. Representing such sites (e.g. Woods Hole, Delaware), by a single mean results in the overall fluctuations in S being large. Also, the seasons in which panels are originally exposed and finally removed could lead to a disproportionate number of low (winter) or high (summer) values at the beginning or end of the analysed portion of a colonization curve. This could result in a significant regression of S versus time.

Second, means for most sites are based on measurements of several individual panel islands. If some substrates at a site reach slightly different $\hat{S}$'s or diverge from $\hat{S}$ (e.g. with disturbance) the variability associated with the overall mean may also be large. Of the forty-eight means for the San Onofre sites 4.2% had an $\omega\leqslant0.2$ and 36.3% had an $\omega\leqslant0.3$. Analysis of each of the 104 individual panels with six or more observations showed that 44% had an $\omega\leqslant0.2$ and 82% had an $\omega\leqslant0.3$. Thus for individual substrates fluctuations around $\hat{S}$ seemed to be 'sufficiently small' in a much larger percentage of cases.

Third, establishing only 6 months exposure as a criterion for $\hat{S}$ to be reached resulted in non-equilibrium values being included from sites at which $\hat{S}$ was approached more slowly. This could affect both temporal regressions and the size of fluctuations.

Finally, it still remains that not all significant slopes or large fluctuations in S can be accounted for in the context of an equilibrium model. For example, in the San Onofre study, strong competitive dominance on fifteen of the 400+ panels studied resulted in significant decreases in S from apparent $\hat{S}$'s. On each of the nine panels that were observed after these decreases, physical disturbance resulted in a loss or reduction of the dominant and a return to the original $\hat{S}$ (Osman, 1982, in preparation).

Even though large fluctuations can be seen to result from a variety of factors that do not necessarily support the rejection of an equilibrium model, the $\hat{S}$ values in Table 1 must be interpreted conservatively. They are the means for the zero-slope portions of the colonization curves for all panels of a particular size.

Relationships

In contrast to the results of Schoener *et al.* (1978), $\hat{S}$ (for equal sized panels) varies widely. For example, $\hat{S}$ for panels between 100 and

TABLE 2. Results of a stepwise multiple regression analysis with the equilibrium number of species $(\hat{S})$ as the dependent variable and immigration rate (I_0 and I_{max}), pool size (P and P_r), panel size, panel depth, temperature (minimum, maximum, range), and salinity (minimum, maximum, range) as the independent variables. NS=not significant. NE=not entered.

Variable	Regression coefficient	Partial correlation coefficient	Step entered	Increase in R^2	F to enter	p
Intercept	−8.043	–	–	–	–	–
I_{max}	0.736	0.615	1	0.555	62.31	<0.001
P_r	0.137	0.734	2	0.145	23.64	<0.0001
Panel size	0.097	0.682	3	0.139	41.71	<0.0001
P	−0.001	−0.069	NE		0.23	NS
I_0	0.018	0.006	NE		0.00	NS
Depth	−0.089	0.079	NE		0.30	NS
Temperature minimum	−0.106	−0.118	NE		0.60	NS
Temperature maximum	−0.065	−0.020	NE		0.02	NS
Temperature range	0.063	0.089	NE		0.37	NS
Salinity minimum	0.250	0.224	NE		2.50	NS
Salinity maximum	−1.372	−0.118	NE		0.66	NS
Salinity range	−0.293	−0.249	NE		3.11	NS
Latitude	−0.064	−0.124	NE		0.79	NS

Overall R^2=0.839, N=52, F=83.57, p<0.001.

TABLE 3. Results of a stepwise multiple regression analysis with the equilibrium number of species $(\hat{S})$ as the dependent variable and immigration rate (I_0), pool size (P_r), panel size, panel depth, temperature (maximum, minimum, range), and salinity (maximum, minimum, range) as the independent variables. NS=not significant. NE=not entered.

Variable	Regression coefficient	Partial correlation coefficient	Step entered	Increase in R^2	F to enter	p
Intercept	−0.753	–	–	–	–	–
I_0	1.548	0.613	1	0.395	54.18	<0.0001
P_r	0.130	0.631	2	0.198	39.97	<0.0001
Panel size	0.003	0.347	3	0.049	11.12	0.0013
Depth	0.057	0.072	NE	0.41	NS	
Temperature maximum	−0.016	0.013	NE	0.01	NS	
Temperature minimum	−0.071	−0.088	NE		0.62	NS
Temperature range	0.070	0.082	NE		0.55	NS
Salinity maximum	0.009	0.007	NE		0.00	NS
Salinity minimum	0.054	0.061	NE		0.30	NS
Salinity range	−0.158	−0.100	NE		0.81	NS
Latitude	0.001	0.007	NE		0.00	NS

Overall R^2=0.646, N=85, F=48.49, p<0.001.

155 cm^2 ranged from two to forty species per panel. Overall, estuarine localities such as the Palimico, Broadkill and Indian Rivers appeared to have both lower $\hat{S}$'s (2–11) and smaller species pools (P_r<35) than marine areas such as Woods Hole and San Onofre ($40>P_r<160$, $10<S<40$). However, given the wide variation within localities, such comparisons tell us little about what parameters influence $\hat{S}$.

The effects on $\hat{S}$ of pool size (P and P_r), immigration rate (I_0 and I_{max}), island size (panel area), latitude, and several environmental varia-

bles (panel depth; temperature minimum, maximum, and range; salinity minimum, maximum, and range) were examined using stepwise multiple linear regression. Of these variables only I_{max}, P_r, and panel size had significant positive effects, together explaining 83% of the variability in $\hat{S}$ (Table 2). The remaining varia-bles showed no significant effect on $\hat{S}$. The change in the coefficient of multiple determina-tion (R^2) with the stepwise addition of the signifi-cant independent variables indicated that I_{max} alone accounted for 55% of the variation in $\hat{S}$,

TABLE 4. Nested analysis of variance of the equilibrium number of species ($\hat{S}$) with data nested by latitude within ocean within environment. *Mean square for ocean used as error term. **Mean square for latitude used as error term.

Source	df	SS	F	p
Environment	2	18.68	1.24*	0.5367
Ocean (within environment)	1	7.56	8.51**	0.2102
Latitude (within ocean)	1	0.89	0.09	0.7694
I_0 (within latitude)	5	430.68	8.42	0.0001
P_r (within latitude)	6	827.77	13.49	0.0001
Panel size (within latitude)	5	1114.45	21.80	0.0001
Error	57	582.92		

the addition of P_r explained another 14%, and the addition of panel size another 14%. This analysis included only those three regions in which all the parameters had been measured: Woods Hole, Delaware and San Onofre. To include more of the regions the infrequently measured P and the less frequently estimated I_{max}, were excluded and the analysis redone.

In the second analysis (Table 3), I_0, P_r and panel size, together explained 64% of the variance in $\hat{S}$. The remaining variables made no significant contribution. The change in R^2 with the stepwise addition of the three significant variables indicated that I_0 alone explained 39% of the variation in $\hat{S}$, while the addition of P_r and then panel size explained an additional 20% and 5% of the variation, respectively. Thus, in both analyses, immigration rate (I_0 or I_{max}) explained the greatest percentage of the variation in $\hat{S}$, I and I_{max} were highly correlated with each other ($r=0.83$, $p<0.01$) and were essentially equivalent estimates of immigration.

If the only variables having a significant effect on $\hat{S}$ are immigration rate, local pool size, and panel size, then it follows that the value of the intercept should be 0; i.e. when I_0, P_r, and panel size are 0, $\hat{S}$ must also be 0. Using an analysis model without an intercept results in I_0 explaining 83% of the variation in $\hat{S}$, P, an additional 7%, and panel size, an additional 2%.

Although the regression analyses indicate the importance of immigration, P_r, and panel size in accounting for the variation in $\hat{S}$, there is still the possibility that more general biogeographic patterns may be obscured by this method of analysis. In particular the imbalance in regional representation of the studies included and the number of sites within studies may have biased our results. Therefore, as an additional test for broad biogeographic patterns we grouped studies by environment (marine, estuarine or

harbour), ocean (Atlantic, Pacific, Indian, Mediterranean Sea), and latitudinal zone (10° bands). We then used a nested ANOVA with I_0, P_r, and panel size nested within latitude, nested within ocean, nested within environment. The results of this analysis are given in Table 4. Individual tests of the hypotheses that $\hat{S}$ is affected by environment ($F_{2,1}=1.24$, $p=0.54$), ocean ($F_{1,1}=8.51$, $p=0.21$), or latitude ($F_{1,5}=0.01$, $p=0.92$) show that none of these variables has any significant effect. The overall effect of I_0 ($F_{5,57}=8.42$, $p=0.0001$), P_r ($F_{6,57}=13.49$, $p=0.0001$) and panel size ($F_{5,57}=21.80$, $p=0.0001$) remain highly significant.

Discussion

Our overall objective has been to examine the relationship between regional and local patterns of diversity. The choice of the island biogeographic model as the framework in which to make these comparisons also resulted in an examination of the appropriateness of the model and the ability of the data to meet the model's assumptions.

There are several reasons why we continue to believe this model is appropriate. First, it recognizes that species number and composition are both dynamic. Species composition is seen as changing continually as species immigrate and go extinct. Species numbers are predicted to increase as a habitat or island is colonized and then reach an assymptote as immigration and extinction rates become equal. This pattern is observed in most colonization studies. It is important to note that the model can also accommodate changes in species number resulting from environmental changes (e.g. seasonal fluctuations). Second, most parameters of the model are measurable on both a local and regio-

nal scale. As can be seen in Table 1, estimates of $\hat{S}$, pool size and immigration rate were available from a large number of studies. Only estimates of extinction were generally unavailable. Third, even though the model recognizes the dynamics of colonization, it is simple conceptually and testable with available data. Finally, the model establishes a baseline for comparisons, $\hat{S}$. Such a baseline not only allows interregional comparisons to be made, but also helps identify the effects of non-equilibrium processes. For example, at one San Onofre site dominance by a rare species on a few substrates was found to cause decreases in S well below an established $\hat{S}$ (Osman, 1982, unpublished data). When a physical disturbance resulted in the loss of the dominant, S on those substrates affected returned to $\hat{S}$. Diversity on panels not colonized by the dominant remained at the measured $\hat{S}$.

Two major conditions for equilibria: (1) no significant change in S over time, and (2) sufficiently small fluctuations in S around $\hat{S}$, were tested. These analyses assumed that the local environment did not change sufficiently during the studies to cause changes in $\hat{S}$ itself. Clearly, in some cases (e.g. seasonal localities) this assumption was false.

The analyses indicated that in most cases, S did not change significantly after an initial 6 months of substrate exposure. However, fluctuations in S around $\hat{S}$ were much greater than would be expected under equilibrium conditions and slopes were significantly different from zero in more cases than would be expected by chance. As we discussed above, this inability of the data to meet rigorously the assumptions of the model resulted from a variety of causes. Many of these can be attributed to *a priori* conditions established to compare fairly data collected using different methods. It is likely that (1) S was still increasing in some localities after 6 months, (2) seasonal fluctuations in $\hat{S}$ resulted in larger than expected fluctuations in S, and (3) pooling substrates at localities increased the chances of finding significant fluctuations. Analyses of individual substrates did result in assumptions being met in a much larger percentage of cases. Furthermore, the $\omega \leqslant 0.2$ condition proposed by Keough & Butler (1983) may be too restrictive, particularly for localities with low $\hat{S}$'s. For example, with $\hat{S} < 10$, fluctuations in S of more than ± 1 species will result in $\omega > 0.2$. In addition, of the fourteen studies they compared twelve had

$\omega < 0.32$, while only four had $\omega < 0.2$. Although less conservative $\omega < 0.3$ (coefficient of variation < 15) may be a more realistic test for sufficiently small fluctuations. Using this test criterion, 82% of individual substrates examined were found to have sufficiently small fluctuations. None the less, for pooled data, 63% of the cases still had fluctuations in S too large to be judged in equilibrium.

From this we must conclude that for most sites in Table 1, fluctuations in S were too large for the $\hat{S}$'s to represent equilibria. These values only represent the mean number of species on substrates at the site which were exposed for at least 6 months. Although S fluctuated significantly after this time, at most sites, no temporal trends were detected. In this sense the diversity on substrates (of each size) at a site could be represented by a single mean. This mean was also likely to be influenced by variables in the equilibrium model (immigration, extinction, pool size) as well as others. We have tried to keep our analyses simple and address only the question of which of all the variables measured were likely to affect this mean on various geographic scales.

Contrary to the results of Schoener *et al.* (1978), we found substantial variation of $\hat{S}$ for panel islands of similar size. From the simple regression analyses there appears to be no overall biogeographic pattern or trend to these differences, that might result from suggested (Schoener *et al.*, 1978) regional differences in the number of available habitats or the intensity of biological interactions. Latitude, environmental parameters that correlate with latitude (e.g. temperature), or parameters that characterize a region (e.g. salinity or regional diversity) were unimportant.

Our analyses indicated that $\hat{S}$ is correlated with (if not a function of) immigration rate, realized pool size, and panel size. The significance of P_r and I_0, and the lack of an effect of pool size (P) suggest that those factors affecting the abilities of species to reach an island, such as distance from the source of immigrants and dispersal ability of species within the pool, generally overshadow the importance of the actual number of species available. Thus, any supposed patterns in interregional variations in diversity (P) such as latitudinal gradients would seem to have little relevance to local diversity ($\hat{S}$).

Immigration rate is clearly the most important parameter controlling local diversity within these epifaunal communities. The implication is that these communities are very much controlled by the rate at which new species recruit on to substrates. Of course the measured immigration rate is itself controlled by a variety of processes, including rates of production of dispersal (larval) stages, capabilities of the species within each pool for dispersal, and distance of the substrate islands from sources of immigrants.

The effects of production rate is most obvious for seasonal environments. As the rate of larval production changes throughout the year, species immigration rates and the resulting $\hat{S}$ also change (Osman, 1978).

The importance of distance from a source of immigrants has been demonstrated by Osman (1982). In the San Onofre region, kelp forests occupy the major cobble bed and reef areas and identify the potential source areas of colonizing invertebrates. With increasing distance from these kelp forests, immigration rate (I_0 and I_{max}), P_r, and the resulting $\hat{S}$ all decreased. This pattern can be seen by comparing the measurements in Table 1 for stations inside, outside, and on the edge of kelp forests.

Dispersal ability of species within the pool also appears to be important, especially with respect to interregional comparisons. Fouling communities are comprised of a broad range of taxa and include species that have dispersal distances ranging from metres (Gerrodette, 1981) to thousands of kilometres (Scheltema, 1971). Although it has not been demonstrated experimentally, it is probable that the species pools in some regions have a proportionally larger number of species with relatively limited dispersal ability than the communities elsewhere. The San Onofre community, for example, has a proportionally larger number of poor dispersers (sponges and bryozoans with non-feeding larvae) than the Broadkill River community (Table 5). As a result of these differences in dispersal ability among regions, P_r represents a different proportion of P in different regions. I_0, and thus $\hat{S}$, would be affected similarly by dispersal ability.

TABLE 5. Estimated dispersal abilities of larvae of invertebrates found on fouling panels in California and Delaware

Group	Potential larval dispersal					
	California			Delaware		
	Long	Short	Unknown	Long	Short	Unknown
Protozoa	4					
Porifera		44				
Coelenterate				6	1	
Hydroidea	27	14				
Anthozoa	9	3				
Sipuncula	3					
Annelida	40	13		10		
Arthropoda						
Cirripedia	6			2		
Mollusca				7		
Gastropoda	7	2				
Bivalvia	22					
Polyplacophora	3					
Entoprocta		5				
Ectoprocta	8	86		1	2	
Phoronida	1					
Brachiopoda		1				
Chordata						
Urochordata	14	13		1		
Total	144	181	2	27	3	5
Per cent	44	55	1	77	9	14

Finally, the size of the island panels had a significant effect on $\hat{S}$. This supports the predictions of the equilibrium model and the findings of most studies, including several panel studies in which size was considered (Jackson, 1977; Osman, 1978, 1982; Schoener & Schoener, 1981). However, the contribution of island size to the variation in $\hat{S}$ was relatively small. This lack of a strong island-size effect on $\hat{S}$ is a result of making interregional comparisons in which the stronger effects of differences in I_0 and P_r outweigh size effects. For example, a large panel in a region with a low I_0 and P_r will have a lower $\hat{S}$ than a small panel in a region with both a high I_0 and P_r.

Extinction is the one major parameter that could not be compared in this study. Local extinction rate should certainly be affected by panel size and should itself affect $\hat{S}$. Extinction rate has been shown to vary between sites within regions (Osman, 1982). Unlike the other factors considered, extinction rate is in part a function of the biological interactions occurring on each panel island. Although some variation in $\hat{S}$ within a site can be accounted for by the increased extinction rate when particular dominant competitors are present (e.g. see Osman, 1982), $\hat{S}$'s on most replicate panels at a site are similar regardless of which species are present.

Conclusions

Based on existing data for the colonization of artificial substrates, it is unlikely that interregional or biogeographic comparisons of the colonization process will result in any new ordering of the processes controlling the global distributions of species. Large differences in $\hat{S}$ were found within some regions and no consistent pattern could be found between latitudes, habitats or oceans. Even though it may be possible to explain differences in $\hat{S}$ in terms of the dynamics of immigration, and extinction, we cannot distinguish the relative importance of local, intraregional and interregional factors. Immigrational and extinction rates will be affected by local environmental conditions such as currents or the presence of predators or competitors, geometric constraints such as distance to sources of larvae, regional conditions such as degree of seasonality or the taxa available, and the specific biologies of the species present in

each pool such as the number and dispersal abilities of propagules. To separate and control any of these is presently impossible and a test of the effects of particular factors on interregional differences is also impossible. Within a region, or at least part of a region, factors affecting the colonization process can be investigated with a good chance of experimentally determining how immigration and extinction are affected by each factor. Given that the variation that occurs within some regions is equal to that found between regions, we must conclude that interregional differences in colonization, I_0, $\hat{S}$, P or P_r cannot be shown to be important to species distributions, abundances or ecology.

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APPENDIX 1. Locations of panel studies, site characteristics, methodology used, and literature source(s) for the information analysed. (a) Three panels pooled with two 100 cm² surfaces/panel counted. (b) 4400 cm² panels pooled.

Location	Latitude	Temper-ature	Salinity	Panel Size (cm²)	Type	Sampling method	Rep. no.	Study duration	Source
Pamlico River, North Carolina	35° N	3–31	0–16	155	Asbestos–concrete	Destructive	1–2	1 year	Dean & Bellis, 1975; unpublished data
Broadkill River, Delaware	39° N	−2–28	10–33	100	Asbestos–concrete	Destructive	5	20 months	Dean, 1977; unpublished data
Woods Hole, Massachusetts	42° N	−2–25	30–33	15–103	Slate	Non-destructive	5	2 years	Osman, 1977, 1978; unpublished data
San Onofre, California	33° N	11–22	34	15–103	Asbestos–concrete	Non-destructive	3	3 years	Osman, 1982, Osman et al., 1981; unpublished data
Puget Sound, Washington	48° N	7–14	32	6–6006	Formica	Non-destructive	1–7	90 weeks	Schoener & Schoener, 1981
San Francisco Bay	38° N	9–20	18–30	600[a]	Acrylic	Destructive	3	18 months	Ehrler & Lyke, 1980; pers. comm.
Indian River, Florida	27° N		24–35	225	Asbestos–concrete	Destructive	5	1–2 years	Mook, 1976, 1980, 1981
Beaufort, North Carolina	35° N	5–28	18–36	232	Ceramic	Non-destructive	3	4+ years	Sutherland & Karlson, 1977
Discovery Bay, Jamaica	18° N	25–27	34–36	4–3716		Non-destructive	6	1+ years	Jackson, 1977
Red Sea, Israel	30° N	20–27	39–41	1600[b]	Asbestos–polyethylene	Destructive	1	1 year	Goren, 1979
Ashdod, Israel	32° N	17–28	39	1600[b]	Asbestos–polyethylene	Destructive	1	1 year	Goren, 1980
Thailand	12° N	27–32	26–32	466	Asbestos–wood	Destructive	1	1 year	Schoener et al., 1978; DePalma, 1977
Washington	48° N	7–14	29–32	466	Asbestos–wood	Destructive	1	1 year	Schoener et al., 1978; DePalma, 1976
Maine	44° N	0–20	25–31	466	Asbestos–wood	Destructive	1	1 year	Schoener et al., 1978; DePalma, 1969
Newfoundland	47° N	−1–9	30–32	466	Asbestos–wood	Destructive	1	1 year	Schoener et al., 1978; DePalma, 1969
Alaska	57° N	3–11	20–34	466	Asbestos–wood	Destructive	1	1 year	Schoener et al., 1978; Long, 1972
Hawaii	21° N	22–28	34–35	255–1830	Asbestos–wood	Destructive	1	1 year	Schoener et al., 1978; Long 1969, 1970, 1974