DIVERSITY OF A NORTHERN ROCKY INTERTIDAL COMMUNITY: THE INFLUENCE OF BODY SIZE AND SUCCESSION

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Abstract. Hypotheses about diversity in succession in rocky intertidal communities in the Saint Lawrence estuary, Canada, were tested to evaluate whether results from the study of large organisms may be extrapolated to the entire community of macroinvertebrates. Varying the lower size limit of the organisms considered in the analyses (organisms >0.5, 1, 2, 4, and 8 mm) altered the observed trends in taxonomic richness and diversity (the latter calculated in terms of abundance, H'_{no}, and biomass, H'_{wt}). Diversity increased through succession when only the largest organisms were considered, but H'_{no} was maximal in midsuccession for the >2 and >4 mm size groupings and in late succession for the >1 and >0.5 mm size groupings, and H'_{wt} was greatest at the second stage of succession for all other size groupings. Richness increased through succession for all size groupings.

Whole-crevice manipulations (mimic crevices, modified to leave only the dominant structural taxa) were used to examine competing hypotheses about whether variation in richness and diversity through succession was a function of the structural heterogeneity provided by the dominant taxa (structural-heterogeneity hypothesis), or a function of the age of the communities per se (ecological-time hypothesis). The first is supported if the communities in mimic crevices resemble those in control crevices for each successional stage; the second is supported if mimic crevices resemble each other more than they do control crevices at the same successional stage. Within three months, control and mimic communities largely resembled each other in terms of H'_{no}, H'_{wt}, and richness, and the trends mirrored those observed four months earlier, thus supporting the structural-heterogeneity hypothesis. Nonparametric multivariate analyses that removed the manipulated species from the analyses also supported this conclusion. Results from 12 mo after the initiation of the experiment (following the winter, during which the communities within many of the crevices were greatly altered) further supported the structural-heterogeneity hypothesis.

Key words: body size; community structure; diversity; ecological time; Mytilus edulis; Mytilus trossulus; *richness; rocky intertidal; Saint Lawrence estuary; species engineering; structural heterogeneity; succession.*

INTRODUCTION

Animals display a wide range of body sizes, both intra- and interspecifically, with smaller animals being both more speciose and abundant (Elton 1927, Hutchinson 1959, Peters 1983). However recent studies on closely related groups, such as orders of insects (Siemann et al. 1996), fishes (Hall and Greenstreet 1996), and mammals (Marquet et al. 1995), have found that both species richness and abundance are greatest for intermediately sized organisms. This was also the case within diverse assemblages of intertidal organisms in central Chile (Marquet et al. 1995), but not in Panama (Navarrete and Menge 1997) where only species richness was maximal for intermediate size classes of organisms. Because of this, and because differently sized organisms perceive their environments at different spa-

tial scales, occupy different ecological niches, and may be sampled at different spatial scales (May 1978, Morse et al. 1985, Nee et al. 1991, Shorrocks et al. 1991), studies examining only the largest organisms may not accurately reflect what occurs in the community as a whole.

Examples of such studies form the basis of the "keystone predation" (Paine 1969, 1974), "diffuse predation" (Connell 1978, Menge and Lubchenco 1981), and "intermediate disturbance" (Connell 1978, Sousa 1979, 1984) hypotheses, all of which suggest that some disturbance agent keeps the abundance of the competitively dominant species in check, thereby increasing local diversity (Robles 1997). Different studies have variously supported and refuted these hypotheses. One possible explanation for conflicting results is the inconsistency in the size of the organisms considered in the different studies. For example, various size classifications have been used to define the community of macroorganisms associated with mussel beds (Table 1). Thus, any general conclusions drawn from the sum of these studies may be compromised by the diversity of methods used.

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TABLE 1.   Variation in sampling techniques used in 58 studies of the macrofauna associated with mussel communities.

Sampling method	No. studies using method
Lab (sieve mesh size)	
0.25 mm	2
0.5 mm	13
1.0 mm	4
2.0 mm	1
Not given	23
Field measurements	
Percent cover	12
Field counts	13

Notes: The methods are broken down into two large groups: samples processed in the lab and those where measurements were taken in the field. The total count does not equal the number of published studies included, as some studies use more than one method. Field studies commonly used two methods to describe community structure.

For example, Paine's classic studies on the effects of the "keystone predator," *Pisaster ochraceus,* considered only macroscopic species competing for primary space and did not consider smaller ones associated with the mussel beds (Paine 1966, 1991, Paine and Levin 1981). Although primary space may be monopolized by a dominant species, many or most displaced species may find refuge upon or within the structure provided by the dominant species (Dayton 1971, Lee and Ambrose 1989, Lohse 1993). The increase in physical substrate provided by these dominant species, variably known as "foundation species" (Dayton 1972), "keystone modifiers" (Mills et al. 1993), or physical ecosystem engineers (sensu Jones et al. 1997), over that of the actual substrate may be substantial. For example, the mussel *Mytilus californianus* provides ~30 times more hard substrate than the underlying rock substrate (Suchanek 1994), and barnacles may triple the surface area of the substrate they occupy (Osman and Whitlatch 1995). Moreover, the diversity of habitat types may also be increased by the presence of ecosystem engineers. For example, the interstices between dominant species such as mussels also provide habitat for organisms that would otherwise be unable to survive on a simple rock substrate (Suchanek 1985, Tsuchiya and Nishihira 1985, 1986, Witman 1985). Indeed, >300 species and a diversity rivaling that of any temperate ecosystem have been reported to be associated with the mussel beds studied by Paine (Suchanek 1994).

Similarly, in the same paper where Frontier (1985) suggests that succession ultimately decreases diversity, he later states for an algal community that ". . . *Fucus* can develop almost exclusively in belts parallel to the coast, and eliminates the rest of the community; all species can be seen, however, under the alga, but stunted and scarce" (Frontier 1985:276). Looking at the macroalgae and sessile invertebrates occupying primary space on boulders, Sousa (1979, 1984) found that diversity was maximal in communities maintained at intermediate stages of succession and declined thereafter. In contrast, the diversity of the small invertebrates associated with these algal communities plateaus at intermediate levels of succession (Dean and Connell 1987*a*). These examples suggest that diversity may not necessarily decrease with increasing dominance of a community by one or a small number of species. They do, however, indicate that the size of the organisms being considered may greatly influence the conclusions drawn from experiments.

The apparent structure of benthic communities is known to change markedly with the size of the mesh used to extract the fauna (Reish 1959, Schlater and Wooldridge 1996) and numerous authors have stressed the importance of using a range of size resolutions to study biodiversity (Peters 1983, Bell and Woodin 1984, Thompson et al. 1996, Hurlbert 1997). Despite this, little research has been directed at examining how studying different size ranges of organisms can influence patterns of diversity.

The goals of this study are therefore twofold: (1) To examine how the range of body sizes considered may influence one of the fundamental paradigms in ecology relating diversity to ecological processes in the intertidal zone. Specifically, we tested the hypothesis that the trend in diversity of macrofaunal communities through succession is a function of the size of the organisms considered. (2) To examine why diversity increases with succession, we tested two alternative hypotheses. The first is the ecological time hypothesis (Pianka 1988), which states that communities that have existed for longer periods have had a greater time for colonization to occur and thus more species have immigrated into those communities, increasing diversity. The second, the structural heterogeneity hypothesis, states that older communities are more structurally complex habitats and may provide a greater number of habitat types, thereby increasing diversity. This is similar to Pianka's (1988) spatial heterogeneity hypothesis, except that we explicitly include the element of time (age). These hypotheses were tested through a series of experiments done in a rocky intertidal community on the eastern coast of Canada.

METHODS

Experimental system

Succession in the intertidal zone of the Saint Lawrence Estuary and northeastern Gulf occurs along a fairly slow but predictable path (Archambault and Bourget 1983), with mussel communities limited mostly to crevices and other irregularities in the substrate due to an intensive annual scouring by ice (Bergeron and Bourget 1986). Although algae (Ulothricale and Ulvale) generally recruit quickly, only to be replaced by Fucoids (*Fucus* spp.) (Archambault and Bourget 1983), *Fucus vesiculosus* (hereafter, *Fucus*) is typically the first and usually sole species of macroalgae that
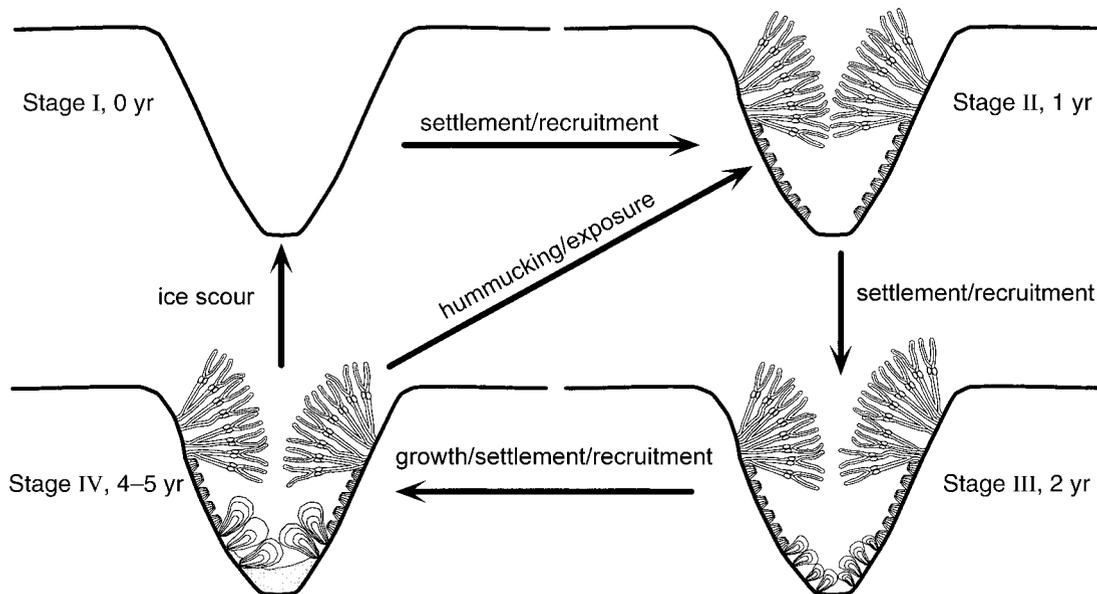
FIG. 1. General overview of the major processes influencing succession in intertidal crevice communities in the Saint Lawrence Estuary (after Bergeron and Bourget [1986]). Numbers adjacent to crevices indicate the successional stage of crevices in years. Arrows represent the major pathways occurring in the development of communities and give the main factors contributing to changes in them. Stage IV shows all zones: rock, *Fucus* spp., barnacles (*Semibalanus balanoides*), and mussels (*Mytilus edulis* and *M. trossulus*).

recruits to crevices within the study area (C. W. McKindsey, *personal observation*). Within crevices, barnacles (*Semibalanus balanoides*) are the first animal species to arrive in any number in the first year. These are followed in subsequent years by mussels (*Mytilus edulis* and *M. trossulus,* hereafter referred to as simply mussels or *Mytilus*) that increase in size and contribute to an underlying matrix of pseudofeces, sand, etc., which eventually destabilizes the community as mussels become less solidly attached to the rock substrate (Fig. 1).

Thus, the development of communities within crevices to their most advanced stage takes at least four to five years, and Bergeron and Bourget (1986) state that crevices in the study site (Capucins, Québec, on the south shore of the St. Lawrence estuary [49°03′ N, 66°51′ W], described in Bergeron and Bourget [1986]) may be classified as being at one of four distinct successional stages (Fig. 1). These four stages (I–IV, for year classes 0, 1, 2, and 4–5, respectively) are (I) bare crevice; (II) crevices with *Fucus* and barnacles; (III) crevices with *Fucus,* barnacles, and small mussels; and (IV) crevices with *Fucus,* barnacles, large mussels, and an underlying matrix of sand, pseudofaeces, etc. Each of these species (or closely related ones) has been shown to play engineering roles in other systems (Bertness and Leonard 1997).

General concept of experiment

We tested the hypothesis that the pattern of diversity observed through succession is a function of the size of the organisms considered by comparing crevices at different stages of succession for different size groupings of organisms. Testing whether changes in diversity are a function of the age or structural heterogeneity of the communities is less straightforward as the two factors are confounded. To overcome this obstacle, we created crevices containing only those engineering species that provide the primary structure found in crevices at successional stages I–IV (Fig. 1, Table 2); that is, mussels, barnacles and *Fucus* (''mimic crevices''). Communities within these mimic crevices were then compared to others within a series of natural, unmanipulated (''control'') crevices at the same stage of succession at subsequent sampling dates. If diversity is similar among all manipulated crevices, then the ecological time hypothesis is supported. However, if the diversity in mimic crevices more closely resembles that of the corresponding controls, then the structural heterogeneity hypothesis is supported.

Crevice selection.—All study crevices were in the midintertidal zone. To ensure that all organisms within a quadrat could be sampled, only crevices with smooth walls and formed from a single rocky outcrop were considered. Variance among crevices was minimized by considering only those 0.75–1.50 m in length, with walls 0.20–0.50 m high and a total opening of 70–110°, such that each wall was 0–60° to the vertical and had long axes ≤10° to the horizontal. Using these criteria, a total of 27, 25, 25, and 122 crevices at successional stages I–IV, respectively, were selected for study in May 1995.

TABLE 2. Criteria used for classifying crevices as being at one of four possible successional stages.

Succes- sional stage	Engineering species		
	Fucus	*S. balanoides*	*Mytilus* spp.
I	If present, only germ- lings or holdfasts fol- lowing ice abrasion	Not present	If present, few in number, not forming a continuous band
II	Present	Present	If present, few in number, not forming a continuous band
III	Present	Present	Present, small (<2 cm length), forming a continuous band
IV	Present	Present	Present, large (>2 cm length), forming a continuous band, overlying a well-developed matrix

Note: Crevices were classified as being at the stage where all criteria were met.

Creation of mimic crevices.—Potential differences among mimic crevices at different successional stages, due to their initial successional stage, were minimized by using only stage-IV crevices to create mimics. Stage-I mimics were created by removing all species present by scraping with a spatula and wire brush, followed by burning with a propane torch. This last step was to limit the recruitment of barnacles, which were settling at the time the crevices were created and are known to be attracted by adult barnacle extracts (e.g., Miron et al. (1996) and references therein). Stage-II mimics were created by removing all mussels in the bottom of crevices by scraping and by removing all organisms associated with both barnacles and *Fucus* with fine tweezers followed by repeated rinsing with water and a high-pressure spray from a hand-pumped compressed air sprayer. For stage-III and -IV mimics, crevices were treated as for stage-II mimics, but supplemented with live mussels. Mussels placed in stage-III mimics passed through a 6.3-mm screen, but were retained on a 4.0-mm screen; those used for stage-IV mimics were retained by a 6.3-mm screen. We standardized the quantity of mussels among mimics of the same stage by multiplying crevice length by the mean mass of mussels observed in five replicate crevices taken for each successional stage (7.5 and 12.5 g of mussels/cm for stage-III and -IV mimics, respectively). Mussels were held in place with 0.5-cm weld wire secured by screws in anchors for a period of five to seven days to allow them to attach to the crevice substrate. A cursory examination of the crevices one week after removal of the weld wire indicated that most mussels remained in the mimic crevices.

Experimental procedure

Six samples of each type of control crevice were taken in May 1995, and then six of each type of control and mimic crevices in both September 1995 and May 1996. Following the May 1995 sampling, all remaining crevices at stages I, II, and III and 24 crevices at stage IV were selected as controls for sampling on subse-

quent sample dates. The remaining stage-IV crevices were manipulated to create 22, 22, 24, and 24 type I, II, III, and IV mimics, respectively, in early June.

Sampling and sorting protocol.—A number of studies (e.g., Schwinghamer 1981, Warwick 1984, Gee and Warwick 1994*a*) have identified breaks in size distributions of benthic organisms in the 0.5–1-mm range, separating meiofauna from macrofauna. We thus use 0.5 mm as the lower cut-off for macrofauna in this study.

Flexible sampling quadrats 15 × 35 cm were used throughout. This quadrat size was chosen since, when placed flat along both sides of the crevices, it included the upper limit of algae on both sides of the crevices and ensured that a substantial amount of each substrate (i.e., mussels, barnacles, *Fucus,* and rock) was included in the total sample. Each sample was taken from a randomly determined location in the middle third of the crevices. Sampling was done such that each substrate and its associated fauna were kept separate. For example, all those species on the alga itself or that were directly reliant on its structure for maintaining their position (e.g., mussels that had settled around the stipe) were collected separately from those associated with the other substrates. This allowed for separate analyses of the organisms associated with the rock, *Fucus,* barnacle, and mussel zones as well as the ''total'' crevice communities (all zones combined). All samples were fixed in 4% formalin in seawater and stored in 70% ethanol until processed. Samples were passed though a series of five sieves with mesh sizes of 0.5, 1, 2, 4 and 8 mm and indices of community structure calculated for five size groupings of organisms (for organisms >0.5 mm, >1 mm, >2 mm, >4 mm, and >8 mm). Size ranges with successfully smaller minima included all those organisms that would have been trapped on that screen alone, had the larger screens not otherwise been in place. The organisms collected on each screen were identified to the lowest specific level possible, counted, and blotted masses measured to the nearest 0.0001 g (Mettler AE200 balance; Mettler, Co-

lumbus, Ohio). Although sieve size is not an absolute measure of body size, Edgar (1990) and Gee and Warwick (1994a) have shown the results obtained by such methods yield good approximations of actual body size measurements.

The adequacy of the sampling method was evaluated by constructing species accumulation curves (Colwell and Coddington 1994) using all of the samples taken on the three sampling periods for each successional stage–size class–substrate combination. The curves were based on 50 random permutations of the order by which samples were included in the calculations. Typically, the number of samples at which the curves reached asymptotes was greatest for the total crevice communities and least for the barnacle zone. For the total crevice community, the asymptote was typically near four to six samples (lower for the largest size groupings and to a maximum of seven samples for the two size groupings that included the smallest size groupings of organisms for stage-IV crevices). Similar curves constructed to examine changes in Shannon–Weiner diversity found asymptotes typically near three to four samples and never more than five. Thus, our use of six samples should be adequate to describe the communities examined in this study.

Statistical analysis

Two of the most commonly used indices of species diversity (Lande 1996), species richness (S) and Shannon-Weiner diversity (H', calculated using natural logs; Magurran 1988), were calculated as indices of community structure. Following the suggestions of Tokeshi (1993), Shannon-Weiner diversity was calculated both in terms of abundance (H'_{no}) and biomass (H'_{wt}). Although *Fucus* contributes significantly to the physical structure of the crevices studied, the number of individual algae present in each sample could not be determined, thus making indices based on abundances impossible to calculate. For continuity among data sets, only the animal fraction of the sample was included in the calculation of H'_{no}, H'_{wt}, and S.

The effectiveness of mimic crevices at imitating the physical structure provided by the engineering species in control crevices was evaluated by two-way MANOVA (Stage × Exco; hereafter, "Stage" refers to the successional stage of crevices, with "Exco" as the variable indicating whether the crevices were control or experimental) were performed using the manipulated species and size groupings (i.e., *Mytilus, S. balanoides,* and *Fucus* ≥4 mm) as dependent variables. Separate MANOVAs were performed for the abundance and biomass data, the former not including *Fucus* in the analysis.

The experimental design necessitated the use of a statistical model that takes into account the covariance between the different size groupings for the analysis of H'_{no}, H'_{wt}, and S. A series of repeated-measures ANOVA models were thus used to analyze the data, with the different body size groupings being considered as the repeated variable. Although unusual, this procedure is appropriate because the same sample was measured repeatedly under a number of different conditions (varying size resolution), much as in a typical repeated-measures design. As the assumption of sphericity was rarely met, the significance of factors involving body size (Size) was evaluated using an Huynh-Feldt adjustment (Girden 1992, Green 1993). A simple one-way model was used to examine the spring 1995 data with Stage as the main factor, whereas a crossed model with Stage and Exco as main factors was used to examine the fall 1995 and spring 1996 data. Although size was usually significant, this effect was not interpreted, as it is not of interest for this particular experiment; rather, only differences between successional stages and how the patterns change with respect to the sieve mesh size used (i.e., interactions) are interpreted. If the within-subjects (Size) by between-subjects (Stage and Exco) main effects were significant, these were then examined further by computing all possible contrasts between mesh sizes by using the differences between the mesh sizes as the data analyzed (Girden 1992). Multiple comparisons for a given diversity index and community or zone were controlled for by sequential Bonferroni corrections (Rice 1989). Rather than restating the "within-" and "between-subjects" extensions for the different variables, the name of the variables will be subsequently used.

Separate analyses were done for the total crevice community and for each of the four zones sampled (mussel, barnacle, *Fucus,* and rock zones). This violates the assumption of independence of the data sets. However, short of sampling five times as many crevices, an impossibility due to the limited number of crevices in the study site, there was no way around this problem. There were often cells of the experimental design in which all the values were equivalent (e.g., all data points were equal to zero). As this lack of variance leads to insurmountable problems in ANOVA, entire levels of one or two variables were dropped from some analyses to maintain balanced designs. The lack of variance within cells represents real biological phenomena (e.g., there were no large mussels in crevices at stage I of succession in the spring of 1995 (C. W. McKindsey, *personal observation*), and we consider cells containing only "0" values to differ significantly from the others in the experimental design, although this was not tested statistically. The criteria used to drop cells are based on logic and the ecology of the systems and are detailed in the appropriate sections below. The data were commonly square-root or ln (x + 1) transformed (detailed in *Results*) to meet the assumptions of normality and homoscedasticity (confirmed by examination of residual plots).

Pearson correlations between the values of H'_{no}, H'_{wt}, and S for each of the four zones and those for the total crevice community were calculated for the spring 1995

data set. As these data are obviously not independent, we attach no significance to the correlations measured and simply use the values as descriptors.

Detecting differences in community structure may at times be problematic using parametric analyses (Clarke 1993). For example, since quantitative indices such as S and H' are based only on the number or proportional masses of species, communities with completely different structures may be judged to not differ. Furthermore, standard parametric multivariate analyses cannot be used to compare communities, as the assumption of multivariate normality are rarely met due to the predominance of zeros in data arrays. Thus artificial and control crevices were compared using nonmetric multidimensional scaling (MDS) based on Bray–Curtis similarities calculated on fourth-root transformed data (Field et al. 1982). Statistical differences between ordinal groupings were determined by two-way analyses of similarities (ANOSIM; Clarke 1993).

All parametric analyses were performed using the SAS system for Windows (SAS Institute 1996) and all nonparametric analyses were performed using PRIMER (Carr 1996). Species accumulation and diversity curves were constructed using R. K. Colwell's EstimateS (Version 5).[2]

RESULTS

The spring 1995 data set was used to test the hypothesis that the pattern of diversity of macrofauna seen in succession is a function of the size of the organisms considered, whereas the fall 1995 and spring 1996 data sets were used primarily to determine whether diversity is a function of the age or the structural heterogeneity of a community.

Influence of body size on succession: spring 1995 data

In terms of abundance, the dominant species observed were, in order, *Mytilus, Littorina saxatilis, L. obtusata,* oligochaetes, and the isopod *Jaera marina* (data not shown). In terms of biomass, the dominant species were *Fucus, Mytilus, S. balanoides, L. saxatilis,* and *L. obtusata*. The lower size limit of the organisms examined influenced the trend in diversity (by abundance H'_{no} and species richness, S) of total crevice communities through succession, but not always that of the four component zones. Only trends observed within the mussel zone and, to a lesser extent, the *Fucus* zone, consistently mirrored those of the total crevice community. Because of the paucity of organisms >8 mm, these cells were dropped from all analyses, as were cells for Stage = I for all except the total crevice community and rock zone. Similarly, Size > 4 mm was also dropped from all analyses for both the barnacle and rock zones. Stage = I was dropped from the anal-

yses of H'_{no} and H'_{wt} (diversity by biomass) for the rock zone.

Total crevice community.—The significant Size × Stage interaction for both H'_{no} and S supports the hypothesis of a reversal of trends in diversity as the smaller organisms are dropped from the calculation of the indices (Table 3). Few organisms except for *L. saxatilis* and *L. obtusata* were present in stage-I crevices and these were rarely >4 mm. Thus, H'_{no}, H'_{wt}, and S of stage-I crevices were consistently lower than that of crevices at more advanced stages. For crevices at stages II, III, and IV (Fig. 2a, c), H'_{no} and S increased with successional stage when all the sizes of organisms are included in the analyses. However, this trend reverses as the smaller organisms are dropped from the calculation of H'_{no}, whereas S stabilizes for organisms >2 mm. Although not compared with the other size classes statistically, the trend for Size > 8 mm was for all indices to increase with successional stage. This is similar to the trends observed for both H'_{no} and S for Size > 0.5 mm and Size > 1 mm, but differs from the trends observed for all size classes for H'_{wt}, which was greatest at stage-II succession and decreased thereafter (Fig. 2b).

Mussel zone.—Overall, the patterns seen for the mussel zone (Fig. 2) mirror those seen for the total crevice community. This is reflected by the usually high correlation between the mussel zone variables and those calculated for the total community (Table 4). However, the Size × Stage interaction was significant only for H'_{no} (Table 3). Despite the decreasing and increasing trends apparent visually for H'_{wt} and S, respectively, neither of these trends were statistically significant.

Barnacle zone.—As the community ages, more and larger organisms become associated with and dependent upon the presence of barnacles. This is reflected in the general trend for all indices calculated to increase with increasing successional stage (Fig. 2g–i). However, none of the diversity indices differed with respect to either the Stage × Size interaction or Stage (Table 3). As such, all indices were weakly correlated to those of the total crevice community (Table 4).

Fucus *zone.*—As with the mussel zone, the visual trends for H'_{no}, H'_{wt}, and S mirror those seen for the total crevice community for all size groupings (Fig. 2) and agree with the hypothesis of a change in the pattern of diversity through succession as the size of the organisms included in the analyses changes. However, Stage × Size interactions and Stage effects are never significant (Table 3), and correlations with the total crevice community for each of the indices measured are rarely as strong as those for the mussel zone (Table 4).

Rock zone.—Although the Stage × Size interaction was significant for H'_{wt} (Table 3), no differences were apparent using contrasts (Fig. 2n). Likewise, differences indicated by the significant Stage effect for S (Table 3) were not identified by post hoc tests. All

TABLE 3.　Results of repeated-measures ANOVA on the effect of the lowest mesh size used (Size), and successional stage (Stage) on the diversity (calculated from species counts [H'_{no}] and biomass [H'_{wt}]) and richness (S) of crevice communities (total), as well as each of the four zones comprising them, in the spring of 1995.

Source of variation	Total			Mussel		
	MS	F	P	MS	F	P
Diversity (H'_{no})						
Stage	2.118	18.9	<0.0001	0.0741	0.2	>0.8
Error1	0.112	⋯	⋯	0.3431	⋯	⋯
Size	2.452	55.1	<0.0001	3.6071	84.3	<0.0001
Size × Stage	0.164	3.7	<0.01	0.1172	2.7	<0.05
Error2	0.044	⋯	⋯	0.0428	⋯	⋯
Diversity (H'_{wt})						
Stage	0.546	1.2	>0.3	0.9602	3.4	>0.05
Error1	0.456	⋯	⋯	0.2817	⋯	⋯
Size	0.557	52.5	<0.0001	0.2051	12.6	<0.005
Size × Stage	0.081	7.7	<0.0005	0.0137	0.8	>0.4
Error2	0.010	⋯	⋯	0.0163	⋯	⋯
Richness (S)						
Stage	166.3333	20.1	<0.0001	44.3472	2.3	>0.1
Error1	8.275	⋯	⋯	18.9167	⋯	⋯
Size	168.7778	70.7	<0.0001	190.0139	61.3	<0.0001
Size × Stage	12.5000	5.2	<0.001	4.2222	1.4	>0.2
Error2	2.386	⋯	⋯	3.0972	⋯	⋯

Notes: In order to have fully orthogonal models that obeyed the assumptions of ANOVA, it was necessary to exclude entire levels of some variables from the analyses. Probabilities given are those calculated using an Huynh-Feldt adjustment for nonsphericity. H'_{wt} and S data were square-root(x) and ln(x + 1)-transformed, respectively, for both the barnacle and *Fucus* zones prior to analysis. The degrees of freedom for Stage, Error1, Size, Size × Stage, and Error2 were 3, 20, 3, 9, and 60 for Total; 2, 15, 3, 6, and 45 for Mussel and *Fucus*; 2, 15, 2, 4, and 30 for Barnacle and Rock S; and 3, 20, 2, 6, and 40 for Rock H'_{no} and H'_{wt}.

indices measured were generally maximal at stage-II succession and decreased thereafter. As such, correlations with the total crevice community were never high (Table 4).

Influence of ecological time and structural heterogeneity: fall 1995 data

Two-way MANOVA on ln (x + 1)-transformed data showed that abundances of *Mytilus* and *S. balanoides* differed with the successional stage of the crevices, but not with respect to crevice type (control vs. mimic) (Stage, Wilk's W = 0.50, df = 4, 60, P = 0.0004; Exco, Wilk's W = 0.1164, df = 2, 30, P = 0.1164; Stage × Exco, Wilk's W = 0.88, df = 4, 60, P = 0.4079). Subsequent comparisons showed that only the abundance of mussels varied with Stage, as was expected (i.e., an increase in mussel abundance with successional stage). Experimental and control crevices also did not differ in terms of the biomass of the three engineering species and only predicted differences (i.e., a higher mass of mussels with increasing successional stage) between successional stages were evident (Stage, Wilk's W = 0.41, df = 6, 58, P = 0.0002; Exco, Wilk's W = 0.87, df = 3, 29, P = 0.2604; Stage × Exco, Wilk's W = 0.8189, df = 6, 58, P = 0.9957).

Overall, the patterns of diversity observed in the fall of 1995 agree rather well with those observed in the spring of that same year. Diversity was commonly a function of the interaction between the successional stage of the communities and the size of the organisms

examined. In contrast, the diversity of the communities was less commonly a function of whether the crevice was natural or manipulated; the diversity of mimic crevices came to resemble that of controls within the three-month period between the initiation of the experiment and the collection of samples, thus supporting the structural-heterogeneity hypothesis. The dominant species (abundance) encountered were, in decreasing order, *L. saxatilis, Mytilus, L. obtusata, J. marina,* and *S. balanoides* for control crevices and *L. saxatilis, Mytilus, J. marina, L. obtusata,* and amphipods for mimic crevices. In terms of biomass, the dominant species were *Mytilus, Fucus, S. balanoides, L. saxatilis,* and *L. obtusata* for both control and mimic crevices. Because of the lack of variance in one or more of the cells for organisms >8 mm, this size class was dropped from all analyses. Similarly, cells for Stage = I were also dropped from the analyses of the barnacle and *Fucus* zones, as were those for organisms >4 mm for H'_{no} and H'_{wt} for the rock zone.

Total crevice community.—Except for a consistently higher value for control crevices at stage-I succession, indicated by a significant Size × Exco interaction (Table 5), H'_{no} of mimic and control crevices did not differ greatly for any given successional stage–mesh size combination and generally mirrored the size-dependent patterns for H'_{no} observed in the spring 1995 (compare Figs. 2 and 3, Table 5). Patterns of H'_{no} varied significantly with Stage, such that the increasing trend seen for Size > 0.5 mm and the peak in H'_{no} at stage II seen

Table 3. Extended.

	Barnacle			Fucus			Rock	
MS	F	P	MS	F	P	MS	F	P
0.2994	1.2	>0.3	0.1242	0.4	>0.6	0.1951	2.6	>0.05
0.2515	...	...	0.3318	...	...	0.0745	...	...
0.3638	10.7	<0.0005	1.1414	20.5	<0.0001	0.0774	3.8	<0.05
0.0179	0.5	>0.7	0.1538	2.8	>0.05	0.0273	1.3	>0.2
0.0341	...	...	0.0558	...	...	0.0206	...	...
0.0779	0.9	>0.4	0.1537	0.3	>0.7	0.1188	1.4	>0.2
0.0885	...	...	0.5419	...	...	0.0831	...	...
0.0176	8.5	<0.01	0.3224	9.9	<0.005	0.1038	4.8	<0.05
0.0026	1.3	>0.3	0.0669	2.1	>0.1	0.0511	2.4	>0.2
0.0021	...	...	0.0327	...	...	0.0216	...	...
0.5649	2.3	>0.1	2.7639	0.4	>0.7	0.6714	4.0	<0.05
0.2491	...	...	7.8694	...	...	0.1675	...	...
0.4446	26.9	<0.0001	44.6435	40.1	<0.0001	0.2211	4.2	<0.05
0.0027	0.2	>0.9	1.6157	1.5	>0.2	0.1287	2.5	>0.05
0.0165	...	...	1.1138	...	...	0.0522	...	...

for Size > 4 mm differ from every other size class as well as each other (Fig. 3a). Overall, H'_{wt} also follows the patterns seen in the spring 1995 data set and, except for a consistently higher value for stage-II mimic crevices, experimental and control crevices did not differ for any successional stage–mesh size combination. S also mirrors the pattern seen in the spring 1995 data set and increases through succession when the smallest organisms are included in the analyses, but levels out as the lower mesh size increases.

Mussel zone.—With the exception of consistently higher values for stage-I crevices (H'_{no}) and aberrant high values for stage-II mimic crevices (H'_{wt}), the patterns for all indices measured were similar to those seen in the spring of 1995 (Fig. 3). H'_{no} increased through succession when all size classes of organisms were included in the analysis, but was stable when only larger organisms were considered, as shown by the significant contrast for Age between Size > 0.5 mm and Size > 4 mm (Fig. 3d). Although contrasts for Exco between Size > 0.5 mm and all other mesh sizes were significant, it is not clear why visually. That H'_{wt} for mimic crevices at stage-II succession was always considerably higher than all other measures (Fig. 3e) is explained by a consistently higher number and biomass of both *L. obtusata* and *L. saxatilis* >4 mm associated with mimic crevices (data not shown). S typically increased through succession for all size groupings and the magnitude of the increase varied with Size (Fig. 3f). Again, Exco varied with Size for S (Table 5), but the source of this variation is not apparent.

Barnacle zone.—Although both H'_{no} and S varied with respect to Size × Stage, and that the contrast between Size > 0.5 mm and Size > 4.0 mm for this effect was significant for H'_{no} (Table 5), the source of

these differences is not evident visually (Fig. 3g,i). In contrast, H'_{wt} increased with successional stage for all size groupings, and the magnitude of this trend differed with Size such that the Size > 4 mm pattern differed from that of all others (Fig. 3h).

Fucus zone.—No significant trends were detected for this zone (Table 5) despite the fact that, except for the stage-I mimic crevices, the patterns observed agree reasonably well visually with those of the total crevice community (data not shown), as was seen for the spring 1995 data sets. The lack of recruitment of algae and the organisms associated with it to the stage-I mimic crevices is probably explained by the burning of the crevice walls (see *Methods*) done in the creation of mimic crevices.

Rock zone.—Again, no significant shifts in trends were observed for any of the indices of diversity measured for this zone (Table 5), although a decreasing trend is apparent visually for the S data that becomes less pronounced as smaller organisms are included in the data set. This is the same pattern that was observed for the spring 1995 data set (Fig. 2). Also, H'_{no} of control crevices was, overall, significantly lower than that of mimics (univariate $P = 0.01$ for Exco).

The nonparametric multivariate analyses were done including only those organisms or size classes of organisms that were not manipulated. That is, all mussels >4 mm (the size added to the crevices) and barnacles were excluded from the analyses. The multidimensional scaling (MDS) ordination plot represents the raw data fairly well (stress = 0.17) and is shown in Fig. 4. Although control and mimic crevices were significantly different ($R = 0.109$, $P = 0.04$), the source of this difference was not apparent either statistically within successional stages or visually, as there is a complete
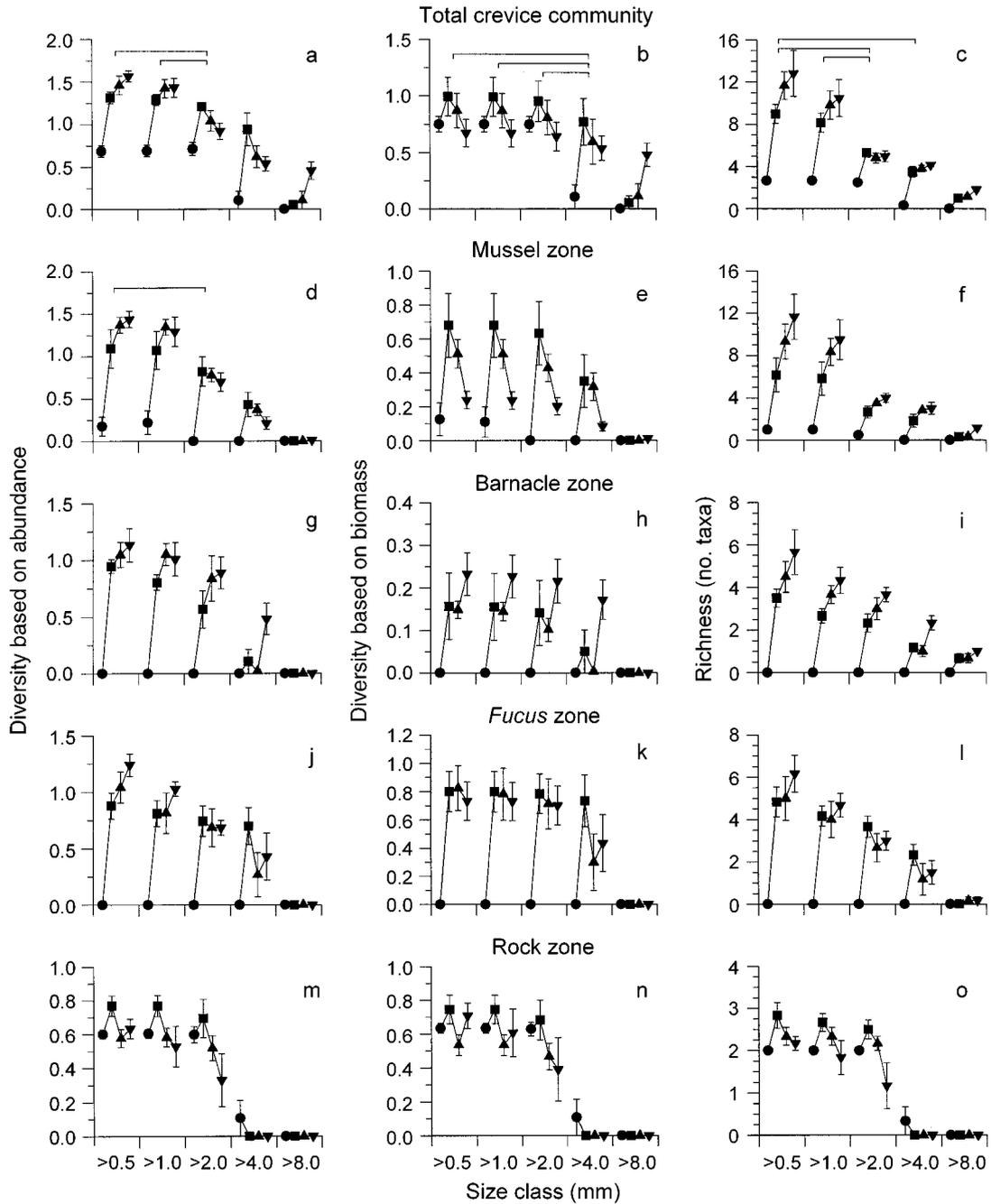
FIG. 2. Mean (± 1 SE) Shannon-Weiner diversity (calculated using abundance [a, d, g, j, and m] and biomass [b, e, h, k, and n] data) and richness (number of taxa; c, f, i, l, and o) of total crevice communities and each of the four zones comprising them, in the spring of 1995, for size groupings of organisms >0.5, 1, 2, 4, and 8 mm. Circles, squares, triangles, and upside-down triangles represent crevices at stages I, II, III, and IV of succession, respectively. Data were analyzed using repeated-measures ANOVAs with size class as the repeated measure and using a Huynh-Feldt adjustment for significance testing. Horizontal brackets at the tops of panels indicate Size × Stage contrasts that differ significantly using sequential Bonferroni corrections. See text for details about which stages and size groupings were excluded from the analyses and Table 3 for transformations used. Note that all data shown have been back-translated and that the ordinates have variable scales.

TABLE 4. Pearson correlations of total crevice community diversity (calculated in terms of abundance [H'_{no}], and biomass [H'_{wt}]) and richness (S) to the corresponding measure for each of the four zones for each of the five size groupings studied.

Zone	0.5–8 mm	1–8 mm	2–8 mm	4–8 mm	8 mm
Diversity (H'_{no})					
Mussel	0.85	0.88	0.59	0.52	···
Barnacle	0.56	0.32	0.14	−0.11	···
Algae	0.46	0.024	0.06	0.55	···
Rock	−0.22	0.19	−0.23	···	···
Diversity (H'_{wt})					
Mussel	0.46	0.46	0.47	0.76	···
Barnacle	−0.24	−0.22	−0.22	−0.15	···
Algae	0.45	0.45	0.48	0.55	···
Rock	0.32	0.26	0.17	···	···
Richness (S)					
Mussel	0.96	0.96	0.33	0.59	0.54
Barnacle	0.40	0.42	−0.10	0.28	0.54
Algae	0.49	0.42	0.45	0.46	0.10
Rock	0.10	0.39	−0.05	···	···

Note: In all cases, only crevices at stages greater than zero years are included in the analyses. Blanks in the table represent blocks that contained only zeros for one or both variables in the pair.

overlapping of the two crevice types for each of the successional stages. Crevices at different stages of succession differed significantly ($R = 0.195$, $P < 0.0005$), such that crevices at stage-I succession cluster to the right of the figure and differ significantly from those at stages III and IV of succession (Fig. 4). Stage-II crevices were more or less evenly distributed over the plot and did not differ from any other cluster.

Influence of ecological time and structural heterogeneity: spring 1996 data

During the winter of 1995–1996, many of the crevices, both mimic and control, and particularly those at the most advanced stages, were reset at less advanced stages of succession (data not shown), presumably by ice scour or heavy wave action. For example, only three of the 18 unsampled stage-IV crevices remained at that stage for both the mimic and control crevices. Other crevices at differing stages advanced and regressed in various ways. Nonetheless, sampling was done as planned (six crevices for each stage crevice type, except for the advanced stages where only three could be sampled). Analysis of the data using the classification of the crevices to specific stages done in the spring of 1995 showed no trends (univariate or multivariate) with respect to crevice type or successional stage (data not shown).

A reanalysis of the data using a reclassification of the crevices made in the field in the spring of 1996 showed the general patterns observed mirrored those of spring and fall 1995. The analyses of effects involving Exco and those evaluating how closely mimic crevices resembled controls mirrored the results seen

in fall 1995. Nonparametric multivariate analyses showed more clear-cut differences between successional stages, but no differences with respect to Exco. Once more, both analyses support the structural-heterogeneity and not the ecological-time hypothesis. For the sake of brevity, we do not present the results and refer the interested reader to McKindsey (1999).

Summary

Overall, the results are consistent with the hypothesis that the patterns of diversity observed through succession are a function of the lower size limit of the organisms included in the analyses. Diversity for the total community typically peaked or plateaued at intermediate stages of succession when only the larger organisms were considered, but continued to increase with advancing successional stage when the entire community was considered. The patterns observed in the mussel zone typically mirrored those observed for the total community but the other zones did so only to a lesser degree. Thus, knowledge of what occurs in the mussel zone provides a good idea of what happens in the community as a whole. Differences between control and experimental crevices were typically minimal, suggesting that the structural heterogeneity rather than the age per se of the communities determines diversity.

DISCUSSION

Body size and diversity in succession

Many authors have stressed the importance of selecting the appropriate physical and temporal scales at which experiments on or observations of ecological communities are made (Palumbi 1985, Wiens 1989, Farnsworth and Ellison 1996). Our results suggest that the scale of the animals themselves, the community constituents, must also be considered when interpreting studies. Studying communities at different resolutions may yield different results.

Trends in diversity through succession were a function of the size of the organisms studied. Both diversity in terms of abundance (H'_{no}) and species richness (S) typically increased through succession when all size classes of macrofauna were included in the analyses, but were either stable or declined when only the largest organisms were used. In contrast, as dominance in terms of biomass changes little with the addition of smaller individuals or species, diversity by biomass (H'_{wt}) varied little among size groupings but considerably among successional stages, often peaking at intermediate stages. This peak is consistent with most models of succession for rocky intertidal systems (see Dean and Connell [1987a] and references therein), many of which use percent cover to describe community structure. If it is assumed that H'_{wt} is a better indicator of community diversity because it reflects the partitioning of energy in a system (Harvey and Godfray 1987), then the additional effort required to measure

TABLE 5. Results of repeated-measures ANOVA on the effect of the lowest mesh size used (Size), successional stage (Stage), and crevice type (experimental or control, Exco) on the diversity (calculated from species counts [H'_{no}] and biomass [H'_{wt}]) and richness (S) of crevice communities (total) and each of the four zones comprising them, in the fall of 1995.

Source of variation	Total			Mussel		
	MS	F	P	MS	F	P
Diversity (H'_{no})						
Stage	1.475	7.1	<0.001	0.3535	1.7	>0.1
Exco	0.050	0.2	>0.6	0.0235	0.1	>0.7
Stage × Exco	0.981	4.7	<0.01	0.6912	3.4	<0.05
Error1	0.208	...	...	0.2033	...	...
Size	1.789	44.7	<0.0001	4.5580	120.5	<0.0001
Size × Stage	0.193	4.8	<0.001	0.1281	3.4	<0.01
Size × Exco	0.148	3.7	<0.05	0.1979	5.2	<0.01
Size × Stage × Exco	0.029	0.7	>0.6	0.0539	1.4	>0.2
Error2	0.040	...	...	0.0378	...	...
Diversity (H'_{wt})						
Stage	0.476	1.7	>0.1	1.5104	6.7	<0.001
Exco	0.022	0.1	>0.7	0.3891	1.7	>0.1
Stage × Exco	0.647	2.3	>0.5	0.8837	3.9	<0.05
Error1	0.280	...	...	0.2260	...	...
Size	0.327	120.7	<0.0001	0.2266	86.4	<0.0001
Size × Stage	0.016	6.1	<0.0005	0.0071	2.7	<0.05
Size × Exco	0.000	0.1	>0.8	0.0009	0.3	>0.6
Size × Stage × Exco	0.003	1.3	>0.2	0.0007	0.3	>0.9
Error2	0.002	...	...	0.0026	...	...
Richness (S)						
Stage	2.751	21.7	<0.0001	71.3663	6.7	<0.001
Exco	0.056	0.4	>0.5	0.4188	0.0	>0.8
Stage × Exco	0.402	3.2	<0.05	21.5608	2.0	>0.1
Error1	0.126	...	...	10.5823	...	...
Size	5.076	287.5	<0.0001	196.6857	153.4	<0.0001
Size × Stage	0.017	1.0	>0.4	4.9080	3.8	<0.005
Size × Exco	0.062	3.5	<0.05	4.5469	3.6	<0.05
Size × Stage × Exco	0.072	4.1	<0.0001	0.5006	0.4	>0.9
Error2	0.017	...	...	1.2823	...	...

Notes: In order to have fully orthogonal models that obeyed the assumptions of ANOVA, it was necessary to exclude entire levels of some variables from the analyses. Probabilities given for the repeated factor are those calculated using a Huynh-Feldt adjustment for nonsphericity. Data for S were ln($x + 1$)-transformed for both the total crevice community and the rock zone prior to analysis. The degrees of freedom for Stage, Exco, Stage × Exco, Error1, Size, Size × Stage, Size × Exco, Size × Stage × Exco, and Error2 were 3, 1, 3, 40, 3, 9, 3, 9, and 120 for Total and Mussel; 2, 1, 2, 30, 3, 6, 3, 6, and 90 for Barnacle, *Fucus*, and Rock S; and 2, 1, 2, 30, 2, 4, 2, 4, and 60 for Rock H'_{no} and H'_{wt}.

biomass, which commonly precludes its use in studies of species abundance patterns (Tokeshi 1993), may be unnecessary. However, models for interaction webs based on energy flow assume that importance may be measured by energy flux and ignore the competitive cross-links that are important in structuring communities (Paine 1980). Such functional links between macroscopic and microscopic organisms (Peters 1983, Stone 1995, Thompson et al. 1996) have rarely been included in studies of community regulation on rocky shores (Menge et al. 1995).

We believe our finding that the size of organisms examined influences the outcome of studies may be general and not limited to species-poor systems with a small size range of organisms, as is the one examined in this study. Indeed, our results most likely underestimated the magnitude of the true differences in trends in succession between the different size groupings. While all of the largest species were identified to the species level, this was not true of the smaller organisms (oligochaetes, nematodes, etc.), which were also more

abundant in later stages of succession. The effect may in fact be more pronounced in more speciose systems, or in those displaying a greater range of body sizes, and should be equally applicable to ecological processes other than succession as well as in terrestrial systems. For example, within terrestrial grassland systems, recent work has shown distinct peaks in richness for terrestrial arthropods of intermediate body sizes (Siemann et al. 1996, 1999), although such peaks have usually been attributed to differences in sampling effort and a poorer knowledge of the taxonomy of smaller organisms (May 1978). Siemann et al. (1999) suggest this may not always be the case, as the patterns they observed remained constant for different orders of species with mean body sizes ranging over more than two orders of magnitude. While such relationships may hold true for the orders studied, they most probably do not for the sum of all the different species within the environment under observation. Mites, for example, may partially fill the overall decline in arthropod species richness for smaller body sizes and are often un-

TABLE 5. Extended.

	Barnacle			*Fucus*			Rock	
MS	F	P	MS	F	P	MS	F	P
0.003	0.0	>0.9	0.5916	1.5	>0.2	0.0539	0.4	>0.7
0.712	3.6	>0.5	0.1969	0.5	>0.2	1.0689	6.9	<0.05
0.024	0.1	>0.8	0.5193	1.3	>0.2	0.0528	0.3	>0.7
0.198	...	...	0.4404	...	...	0.1548	...	...
3.814	106.7	<0.0001	1.7970	36.0	<0.0001	0.0099	0.8	>0.4
0.166	4.7	<0.005	0.0150	0.3	>0.9	0.0082	0.6	>0.5
0.113	3.2	>0.05	0.0170	0.3	>0.7	0.0321	2.6	>0.1
0.065	1.8	>0.1	0.0076	0.2	>0.9	0.0152	1.2	>0.3
0.035	...	...	0.0499	...	...	0.0126	...	...
2.250	12.2	<0.0001	0.9748	2.4	>0.1	0.7798	2.5	>0.05
0.717	3.9	>0.05	0.0684	0.2	>0.6	0.0244	0.1	>0.7
1.137	6.1	<0.01	0.3578	0.9	>0.4	0.2261	0.7	>0.4
0.185	...	...	0.4121	...	...	0.3091	...	...
0.147	86.1	<0.0001	0.4041	18.6	<0.0001	0.0447	19.0	<0.0001
0.009	5.3	<0.005	0.0056	0.3	>0.8	0.0018	0.8	>0.5
0.000	0.4	>0.6	0.0076	0.35	>0.6	0.0015	0.7	>0.4
0.001	0.6	>0.6	0.0083	0.38	>0.7	0.0027	1.2	>0.3
0.007	...	...	0.0217	...	...	0.0024	...	...
32.5278	3.0	>0.05	0.7897	1.7	>0.2	5.0486	0.7	>0.5
3.361	0.3	>0.5	1.0821	2.3	>0.1	14.6944	2.0	>0.1
20.8611	1.9	>0.1	1.0402	2.2	>0.1	15.2569	2.1	>0.1
11.0194	...	...	0.4720	...	...	7.4167	...	...
170.5556	127.8	<0.0001	2.2830	72.6	<0.0001	45.2870	64.9	<0.0001
5.638	4.2	<0.005	0.0032	0.1	>0.9	0.0856	0.1	>0.9
3.138	2.4	>0.05	0.0136	0.4	>0.6	0.5463	0.8	>0.4
0.583	0.4	>0.8	0.0196	0.6	>0.6	0.7755	1.1	>0.3
1.334	...	...	0.0314	...	...	0.6981	...	...

dersampled, even with directed sampling (Walter and Behan-Pelletier 1999). The idea that patterns of diversity may vary with the size of organisms studied is intuitive, and many researchers stress that their findings should not be extended beyond the system studied (e.g., Paine 1966, 1991). However, this is commonly overlooked and many authors talk loosely about influences of various processes on "community structure" and overgeneralize their findings with respect to the macrospecies studied to the community as a whole. Hurlbert (1997) discusses this point at length in a recent critique.

Ecological time vs. structural heterogeneity

The diversity of the communities examined in this study was a function of their structural heterogeneity, rather than their age. Each index of diversity calculated was similar for mimic and control crevices at the same successional stage, three months after manipulation. Further, when the manipulated organisms were removed from the nonparametric multivariate analyses, no differences between control and mimic crevices were detected, but significant differences were observed among crevices at different successional stages. That the structural heterogeneity of communities is

responsible for increasing diversity is not novel (MacArthur and MacArthur 1961). For mussel communities, most studies (e.g., Dye 1992, Tokeshi and Romero 1995, Günther 1996) have shown their presence to increase the diversity of macrofauna over that of adjacent areas, and those that have not done so (Paine 1974, Lohse 1993) have considered only those species that could be observed in the field. Furthermore, field studies comparing mussel communities with increasing structural heterogeneity usually report concomitant increases in diversity (e.g., Suchanek 1979, Tsuchiya and Nishihira 1985, 1986). This has also been shown experimentally using plastic mimics of *M. californianus* (Suchanek 1979). A number of studies (e.g., Dean and Connell 1987b, c, Gee and Warwick 1994b) have also found positive correlations between the structural heterogeneity of algae (and artificial algae) and the richness of the associated invertebrates. Data regarding the influence of barnacles on diversity is rare. However, both real and fake barnacles have been shown to increase the recruitment of various species over that of surfaces without barnacles (e.g., Petraitis 1990, Miron et al. 1996).

Recent theoretical and applied papers have stressed the importance of positive interactions in structuring
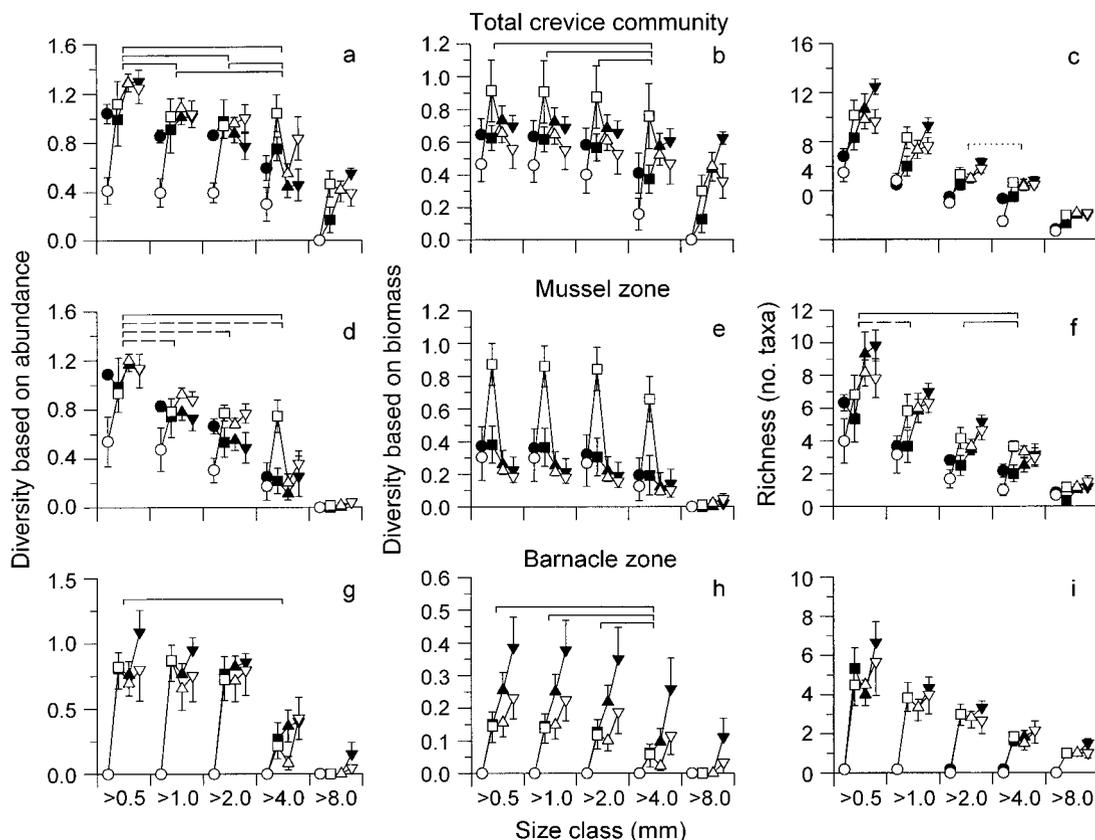
FIG. 3. Mean (±1 SE) Shannon-Weiner diversity (calculated using abundance [a, d, and g] and biomass [b, e, and h] data) and richness (number of taxa; c, f, and i) of total crevice communities and two of the four zones comprising them, in the fall of 1995, for size groupings of organisms >0.5, 1, 2, 4, and 8 mm. Solid and hollow symbols represent control and experimental crevices, respectively. Circles, squares, triangles, and upside-down triangles represent crevices at stages I, II, III, and IV of succession, respectively. Data were analyzed using two-way repeated-measures ANOVAs, with size class as the repeated measure and using a Huynh-Feldt adjustment for significance testing. Horizontal solid, dashed, and dotted brackets indicate Size × Stage, Size × Exco, and Size × Stage × Exco contrasts, respectively, that differ significantly using sequential Bonferroni corrections. See text for details about which stages and size groupings were excluded from the analyses and Table 5 for transformations used. Note that all data shown have been back-translated and that the ordinates have variable scales.

communities (Witman 1987, Bertness and Callaway 1994, Bertness and Leonard 1997, Hacker and Gaines 1997, Jones et al. 1997). Mussels alter their local environment and increase local diversity by filling each of the engineering roles outlined in Jones et al. (1994). They act as a food source (Menge 1976, Davenport and Moore 1996), and their physical bodies create novel habitat for organisms that could not otherwise exist, both directly (Ong Che and Morton 1992, Ricciardi et al. 1997) and indirectly (Tsuchiya 1982, Iwasaki 1995), as well as preventing erosion during storms (Bell and Gosline 1997). They also modify temperature and desiccation regimes (Helmuth 1998), along with nutrient fluxes (Tsuchiya 1980, Asmus and Asmus 1991). The same could also be said for both *S. balanoides* and *Fucus,* the two other engineering species present in crevice communities. Thus, each of these species may alter the dynamics, structure, and diversity of crevice communities.

However, the three engineering species examined were not equal in promoting diversity within crevice communities. Richness and diversity were consistently highest within the mussel fraction of the crevices, despite the fact that their biomass rivaled that of barnacles and *Fucus* only in the last stage of succession (data not shown). Furthermore, only the diversity associated with the mussel zone consistently mirrored that of the crevice community as a whole, and an equivalent diversity was also observed in crevices where mussels were the only engineering species present (C. W. McKindsey, *unpublished data*). If this holds true for mussel communities in other systems, then an increase to a final stage where mussels are the only engineering species present may in fact increase diversity rather than decrease it, as most studies have suggested.

It is informative to contrast our observation that the presence of engineering species other than *Mytilus* did not increase community diversity over the amount due
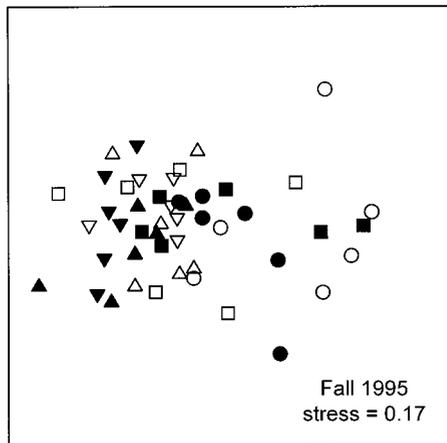
Fig. 4. Two-dimensional multidimensional scaling (MDS) ordination plots for all macrofauna and mussels <4 mm from control (solid symbols) and experimental (open symbols) crevices at four stages of succession in the fall of 1995. Circles, stage I; squares, stage II; triangles, stage III; and upside-down triangles, stage IV.

directly to the addition of the engineering species in question (i.e., no novel species were observed) with other studies examining the interaction between mussels and co-occurring algae. Albrecht and Reise (1994) reported that canopies of *F. vesiculosus* have a positive effect on the diversity of organisms associated with *M. edulis* on soft sediments. They found most of the difference between communities (with and without *F. vesiculosus* cover) could be attributed to differences in the herbivores associated with the algae, thus highlighting the importance of both species in structuring the community. This increase in diversity, however, was due to an increase in evenness; as compared to mussel communities without *F. vesiculosus* cover, only one novel species was found in those with *F. vesiculosus* cover, and richness and abundance actually decreased. In the system examined in this study, all the herbivores observed in the *Fucus* zone were also present in the mussel zone, possibly because of differences between where organisms are found during high and low tides (Peake and Quinn 1993). However, these species were also found in crevices where mussels were the only engineering species present (C. W. McKindsey, *unpublished data*) and an alternative explanation is that they also consume epiphytic algae that grow on the mussels themselves. McCook and Chapman (1991) manipulated both mussel densities and *F. vesiculosus* canopies and found the latter to be much more important in structuring the community. However, this study evaluated the populations studied as percent cover and field counts of abundance. It would have been interesting to compare the results had the entire macrofaunal community been considered.

The increase in diversity through succession in the mussel zone and the constant levels observed for the

other two zones may be explained in part by differing growth rates. Barnacles and *Fucus* approximately attain mature size within one growing season, whereas mussels continue to grow and increasingly alter their environment throughout their lives. Furthermore, except for the addition of surface area, the habitat modifications created by Barnacles and *Fucus* are not as pronounced as in mussel communities (i.e., *Fucus* holdfasts, stipes, and thalli and barnacle walls vs. matrix of mussel shells, byssal threads, and accumulated sediment; see review in Seed and Suchanek [1992]). Thus, mussels may increase diversity directly at successive stages of succession by increasing the number of niches (Hutchinson and MacArthur 1959, Huston 1979) or indirectly through complex ecological interactions that are only manifest with an increase in physical heterogeneity (Downes et al. 1998).

There has recently been increasing interest in using higher taxonomic level surrogates for species richness to identify locations of high biodiversity for conservation purposes (Oliver and Beatie 1993, Williams and Gaston 1994, Gray 1997). In the same spirit, recent discussions have centered on the identification of "keystone species" (sensu Mills et al. 1993) or the study of interaction strengths and "community importance" (sensu Power et al. 1996) to identify the conditions under which different species are most important in structuring communities (Mills et al. 1993, Power et al. 1996, Ruckelshaus and Hays 1998). While this approach may often be appropriate, an organism's "importance" may vary both spatially and temporally (Underwood and Denley 1984, Dethier and Duggins 1988, Elner and Vadas 1990), and an emphasis on "keystoneness" creates an artificial dichotomy between rare and common (foundation) functionally important species (Hurlbert 1997), both of which may influence diversity. This study showed that while patterns in diversity of large structural species may not be indicative of those of the total assemblage of animals in communities, the presence of one of these species, in this case, mussels, might be a useful indicator of locations with high diversity. We suggest that rewards would follow efforts directed toward understanding such relationships and the conditions under which extrapolations of this sort prove valid.

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