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Body-size differences in a colonizing amphipod-mollusc assemblage

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Summary. We examined body size patterns in a colonizing assemblage of marine amphipods and molluscs. We collected animals over a 25 day period from an archipelago of pits that were drilled in brick surfaces. The percent of pits occupied, abundance, species richness, and body size of colonists all increased significantly through time. We compared size ratios of coexisting species with two null models, one that randomized individuals and one that randomized species-populations. For both models, observed overlap ratios usually did not differ from randomness, although species richness was consistently lower than expected for later samples. Results were similar for a subset of the data, a guild of suspension/deposit feeding amphipod species. Some assemblages did show significant deviations from the null models, but the results were spotty and varied among replicates. Overall, the evidence for non-random overlap ratios in body sizes of colonizers was weak.

Key words: Body-size – Colonization – Corophium – Mollusca amphipoda – Marine community

The distribution of body sizes in a population sometimes shifts in response to the presence of another co-occurring species. Where the shift occurs on an evolutionary time scale and results from natural selection for ecological or reproductive differences, it is called character displacement (Grant 1972; cf. Brown and Wilson 1956). Although character displacement is the mechanism invoked most commonly to explain body size shifts, other evolutionary processes, including ecological release, clinal or latitudinal variation in body size, and multiple invasions following differentiation may also result in body size shifts (Grant 1972).

Demographic processes may also lead to unexpected body size distributions. Differential colonization or extinction may prevent either the coexistence of species with overlapping body sizes, or the coexistence of certain size classes within species. These demographic changes may occur faster than evolutionary shifts in body size (Slatkin 1980).

In a community where competition has caused character displacement, body sizes should be more widely spaced than would be expected in the absence of competitive effects (Strong et al. 1979; Simberloff and Boecklen 1981; Schoener 1984). Competitive assortment during colonization and extinction could also lead to widely spaced body sizes in ecological time.

In this study, we investigated the body size distributions of amphipods and molluscs that colonized space-limited habitats over short time scales. The habitats consisted of holes drilled in bricks; these provided standardized and replicated mimics of holes and crevices in natural rock surfaces and barnacle shells. Animals rapidly colonized these habitats over a 25 day period.

Is it reasonable to expect non-random body size patterns on such small spatial and temporal scales? By the end of the experiment, all of the drilled holes were filled with animals, and there appeared to be little, if any, room left for subsequent colonization. Even if there were ongoing emigration, the probability of successful colonization might depend on the relative body sizes of the invaders and residents. Furthermore, we have casually observed behavioral interactions among amphipods that could lead to non-randomness. When displaced amphipods tried to enter occupied pits, they were sometimes repulsed by the large second antennae of the residents. If the outcomes of these encounters were determined by body size, there may have been constraints on the sizes of individuals that could successfully invade an occupied pit. These observations motivated our study of body size patterns of amphipods and molluscs during colonization.

Materials and methods

Study site

The study site was a shallow subtidal limestone outcropping at Wilson Beach, 2 miles east of Turkey Point, Franklin County, Florida, in the northeastern Gulf of Mexico. The outcropping was at 1.5 m depth, dominated by the compound ascidian *Aplidium stellatum*, the boring sponge *Cliona cellata*, and the gorgonian *Leptogorgia virgulata*. Most of the substratum was bare, although small patches of the bivalve mollusc *Brachiodontes exustus* and of amphipod tubes were common in rock crevices. These patches

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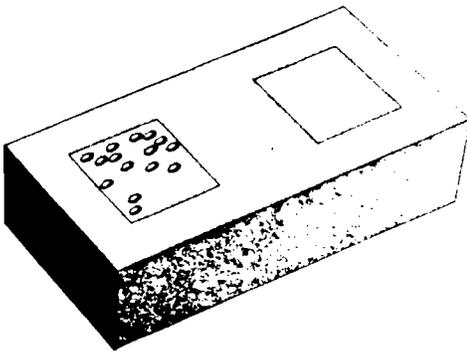
Fig. 1. Artificial substratum with drilled pits

may have served as colonization sources for animals collected in the experiment. Amphipods and molluscs were also common in the crevices of large. dead barnacle plates (*Balanus* spp.) on nearby pier pilings.

Sampling units

We used red building bricks (20 cm by 9.3 cm by 5.4 cm) as artificial substrata. On the large surface of each brick, we inscribed two 5 by 5 cm squares. We used a random number table to generate coordinates for 15 pits that were drilled in one of the squares (Fig. 1). Each pit measured 0.5 cm in diameter and 0.5 cm in depth, about the size of a lead pencil eraser.

Collection methods

On November 11, 1982 we placed 24 drilled bricks horizontally on the limestone outcropping. Each brick was at least 0.5 m from any other and 1 m or more from the nearest sponge or ascidian colony. Four bricks were chosen randomly and collected at each of four times: 4 days, 11 days, 18 days, and 25 days after the beginning of the experiment. Bricks were transported horizontally in 5-gallon plastic containers of fresh seawater. Within 6 h of collection, we examined the contents of each pit under a dissecting microscope, transferred the resident animals to individual glass vials, and fixed them in 70% ethanol. The animals from each pit were counted, identified to species, and measured to the nearest hundredth of a mm with an ocular micrometer in a dissecting scope. We measured head and total lengths (excluding antennae) of amphipods and total lengths of molluscs. Thirty-two polychaetes and two brittle stars (less than 2% of the total) were collected but excluded from the analysis. We lost the amphipods from two pits of Brick #16. so we excluded these data from all analyses except the regression of percentage of pits occupied.

We could not identify juvenile amphipods of the genus *Corophium*, so they were grouped and counted as a single "species". In addition, the taxonomic status of some individuals of *Corophium ascherusicum* presented problems. They were initially retained as a separate species for the analysis of the entire assemblage. Later, we determined that this "species" actually comprised small individuals of *Corophium ascherusicum*. We combined the two groups for the guild analyses.

Null models

We used several measurements to test for size assortment. The sample variance of body sizes (s^2) in a community was used as an overall index of body size assortment. If the species (or individuals) of an assemblage are segregated by size, the observed variance should be significantly larger than the variance of randomly constructed assemblages (Poole and Rathke 1979). We also considered three specific pairwise size ratios as measures of assortment: RMAX, the ratio of the largest to the second largest species (or individual); RMIN, the ratio of the second smallest to the smallest species (or individual); and RANGE, the ratio of the largest to the smallest species (or individual). For pits that had only two species (or individuals), only RMAX was calculated. We calculated size differences, as well as ratios, for these three statistics. In all cases, the results of the tests on size differences were nearly identical to the results of tests on size ratios; therefore, only the ratio tests are presented.

Because we knew the identity and sizes of all individuals in each pit, we were able to search for size assortment among species and among individuals. We reasoned that the same mechanism that separates similar-sized species may also separate similar-sized individuals. Therefore, we constructed two null models, one that randomly combined individuals and one that randomly combined species-populations. For both models, each pit in a brick was compared independently to a null distribution of 1,000 random assemblages. Observed statistics were compared to this null distribution, and the upper and lower probabilities were calculated.

Model I. For the n individuals in a particular pit, n individuals were drawn randomly from the source pool, sampling with replacement. The source pool comprised all individuals from pits of the same brick. All size ratios and statistics were calculated among individuals. Species identity was ignored in this model (except for the calculation of species richness). This model tested for displacement among similar-sized individuals, both within and between species.

Model II. For the k species in a particular pit, k species populations were drawn randomly from the source pool, which consisted of all species populations from the brick. Each "population" was the set of individuals of the same species from the same pit (Case and Sidell 1983). Sampling was without replacement: once a species was represented in a randomly constructed community, it could not be drawn again. Thus, species number was held constant for each simulation, in contrast to Model I. Species were not drawn equiprobably, but in proportion to the number of species-populations represented in the archipelago. The average body size of each species-population was used in the calculation of ratios and other size statistics.

To insure independence of the results, we used a different random number sequence for each simulation. The simulations were written in Fortran V and performed on the CYBER 760, at the Florida State University Computing Center.

Guild analyses

Non-random size patterns are most likely to be detected in a particular subset of an assemblage, the guild of species competing for limiting resources (Root 1967). Guilds should be defined on the basis of resource use, but this is rarely done (Jacsic 1981). Instead, groups of taxonomi-

cally related species are treated as guilds because their similar morphologies make it likely that they compete for similar resources (Diamond 1975). This is the approach we have taken. We included 7 amphipod species in a suspension/deposit feeding guild. *Paracaprella tenuis, Amphithoe longimana, Cymadusa compta,* and the tanaid *Hargeria rapax* were excluded because these genera and families include species thought to be carnivores or macroalgal feeders (Barnes 1980; Cain 1974; Holmes 1902; Skutch 1926; Zimmerman et al. 1979). We also excluded *Stenothoe minuta* because we could find no information on its feeding habits. The genera in our suspension/deposit feeding guild are common fouling organisms and are characteristic of turbid con-

ditions (Barnard 1958; Barnard and Reisch 1959; Moore 1978). For the guild analyses, we used head lengths, rather than total body lengths. We analyzed guild patterns using both Model I and Model II.

Statistical tests

Because the simulations generate many tail probabilities, some are likely to be significant by chance alone. We have used Fisher's combined probabilities (Sokal and Rohlf 1967) to test for a consistent tendency towards non-randomness. Probabilities were summed across pits for each statistic. Summing across bricks tests for a consistent effect at one time of collection. The test statistic is:

$$-2 \sum_i \ln(p_i)$$

where p_i is the tail probability for each pit. The statistic has a chi-square distribution with 2n degrees of freedom. Because Fisher's test is one-tailed, we performed it for both upper and lower tail probabilities. All results are reported with reference to a two-tailed test.

We established the size ratios, simulation models, and significance tests *before* the data were treated in any way. This point is important in reducing the probability of Type II error (Selvin and Stewart 1966).

Table 1. Assemblage changes through time. For each statistic, the average value of occupied islands was calculated for the archipelago. These values were regressed against $\log_{10}$ (number of days). Dependent variables were also log transformed before analysis except for percent pits occupied, which was arcsin (square root) transformed

Dependent variable	Slope	r^2	Significance
Body size	0.106	0.248	$P < 0.05$
Abundance	0.490	0.400	$P < 0.01$
Species richness	0.243	0.434	$P < 0.01$
Percent pits occupied	0.500	0.454	$P < 0.01$

Table 2. Species composition of island assemblages. For each species, the proportion of the total number of individuals collected at that time is listed. A " + " indicates species in the suspension/detritus feeding guild

Species	4 days	11 days	18 days	25 days
Amphipoda				
+ *Corophium ascherusicum* Costa, 1857	0.237	0.225	0.139	0.121
+ *Corophium ascherusicum*[1]	0.155	0.111	0.115	0.101
+ *Corophium* juveniles	0.319	0.281	0.251	0.140
+ *Corophium bonnelli* (Milne-Edwards, 1830)	0.043	0.024	0.002	—
+ *Corophium tuberculatum* Shoemaker, 1934	0.034	0.033	0.034	0.039
+ *Corophium baconi* Shoemaker, 1934	—	0.002	—	0.002
+ *Erichthonius brasiliensis* (Dana, 1853)	0.004	0.144	0.098	0.198
Paracaprella tenuis Mayer, 1903	0.009	0.005	0.009	0.004
+ *Lembos smithi* (Holmes, 1905)	—	0.002	0.022	0.056
+ *Photis macromanus* McKinney, Kalke, and Holland, 1978	—	—	0.003	0.004
Stenothoe minuta Holmes, 1905	—	—	0.007	0.004
Amphithoe longimana Smith, 1873	—	—	—	0.009
Cymadusa compta (Smith, 1873)	—	—	—	0.002
Tanaidacea				
Hargeria rapax (Harger, 1879)	—	0.002	0.019	0.006
Bivalvia				
Brachiodontes exustus (Linne, 1758)	0.159	0.116	0.273	0.306
Musculus lateralis (Say, 1822)	0.022	0.005	0.007	—
Anadara transversa (Say, 1822)	0.022	0.005	0.002	0.004
Argopecten irradians (Lamarck, 1819)	—	—	—	0.002
Gastropoda				
Bittium varium (Pfeiffer, 1840)	0.004	—	0.002	0.003
Astyris lunata (Say, 1826)	0.004	0.024	0.003	—
Crepidula plana Say, 1822	0.004	0.019	0.012	—
Caecum floridanum Stimpson, 1851	—	0.002	0.002	—
N	232	423	582	536[b]

[a] These small individuals were originally classified as a distinct species (see Materials and methods)
[b] Two samples from Brick no 16 excluded

Table 3. Significant deviations from Model 1, which randomized individuals. If the observed value was greater than expected by chance, a " + " is shown. If the observed value was less than expected, a " − " is shown. One symbol means $p < 0.05$; two symbols mean $p < 0.01$. If no entry is given, then $p > 0.05$. All tests were two-tailed. Archipelago chi-squares were summed to give an overall test for each time period. Values in parentheses are significant deviations for the suspension/deposit feeding guild. XBAR = average body size; SVAR = sample variance of body sizes; RMAX = ratio of the largest to the second largest individual; RMIN = ratio of the second smallest to the smallest individual; Range = ratio of the largest to the smallest individual; S = species number. Archipelagoes are listed separately to emphasize the variability among sets of identical islands

Brick	No	XBAR	SVAR	RMAX	RMIN	Range	S
	1						
	2						
	3						
	4						
Total	4 days						
	5						
	6	+			−		
	7						
	8						
Total	11 days						
	9						
	10					(−)	
	11						
	12						−
Total.	18 days						
	13						
	14			+ +			=
	15						(=)
	16						
Total.	25 days			+ +			=

Results

Colonization patterns are summarized by regressions that use time as the independent variable (Table 1). Percent of pits occupied, average abundance and species richness per pit, and average body size of individuals increased significantly through time. However, r^2 values are usually less than 0.50, suggesting that variation among bricks was at least as important as variation among times. The fauna also showed marked changes in species composition through time (Table 2). For example, the amphipod *Corophium ascherusicum* was common at early collection times, whereas the mollusc *Brachiodontes exustus* was numerically dominant in later samples. Each collection time was considered separately because of these differences in size and composition of the assemblages.

Relative to Model 1, species number per pit decreased significantly in the 25 day old collections (Table 3). The ratio of the largest to the second largest individual (RMAX) was also significantly greater than expected for the last collection time. For one of the bricks from the 8 day collection (no 6), the average body size of coexisting individuals was larger than expected by chance. The ratio of the largest

to the smallest individual (RANGE) was also smaller than expected. All other ratios were within the range predicted by Model 1.

From Model II, which randomized species-populations, there were even fewer significant deviations than from Model I, which randomized individuals. The ratio of the second smallest to the smallest species (RMIN) was larger than expected for one brick from the first time period (Brick no 2). No other pattern was distinguished from randomness.

The guild analyses generated similar results. The ratio of the largest to second largest individual (RANGE, Model I) was smaller than expected for one collection (Brick no 10). Species number was also depressed in one of the 25 day samples (Table 3). No significant deviations from Model II were detected for the suspension/detritus feeding guild.

Discussion

Although we were unable to distinguish most body size patterns from randomness, two patterns were strong for the 25-day old assemblages: a decrease in species number and an increase in the ratio of the largest to the second largest individual. A skeptic might argue that even those patterns are marginal. If we adjust the overall error rate for all of the summed brick tests in Table 3 ($n = 24$), the species richness pattern is still significant ($X^2_{116} = 186$, $P = 0.0004$); the ratio pattern is marginally not ($X^2_{116} = 164$, $P = 0.003$; critical value for the 0.05 level is $P = 0.0021$). Both patterns arose after 25 days, when all pits were occupied, abundance and total species richness was greatest, and animals were larger than at earlier times. Competitive effects are most likely to be expressed under these conditions. Perhaps if the study had been of longer duration, size ratios would have shown more deviations from randomness. On the other hand, size ratios from a two year study of coexisting intertidal amphipods (Croker 1967) were not significantly larger for a subset of strongly co-occurring species pairs (Simberloff and Boecklen 1981: 1221).

The Model II simulation produced only one significant result out of 80 patterns tested. There was no evidence of any nonrandomness in the body sizes of coexisting species. Case and Sidell (1983) would argue that our Model II was biased towards failure to reject the null hypothesis because species were not weighted equally in the simulation. Whether or not this bias exists, the relative abundance of many species changed dramatically between the start and the end of the study (Table 2). Most likely this pattern was due to differential colonization ability and responses to the habitat, which could have been modified both physically and biologically by early settlers (Dean and Hurd 1980). Unless one is willing to ascribe these successional changes to competition, an equiprobable model of species colonization seems unrealistic for this assemblage.

Results for the guild analyses were similar to results for the total assemblage. From this similarity we infer that competitive interactions may not be restricted to a subset of species with similar morphologies. If food resources are limiting, coexistence may have resulted not from an assortment of similar sized species, but from shifts in feeding mode. Crawford (1937) discussed suspension and deposit feeding in *Corophium volutator* and noted that:

"The form of the limbs chiefly used in feeding... is so constant throughout the genus that it is probable that other

species differ only in the proportions of the food supply drawn from those two food sources."

Such feeding differences could promote local coexistence of similar sized species. Coexisting benthic invertebrate species often display distinct feeding preferences (Fenchel et al. 1975; Zimmerman et al. 1979), but it is uncertain whether these preferences reflect resource partitioning. For example, Zimmerman et al. (1979) documented feeding differences among several seagrass amphipod species. However, they argued that resource partitioning was unimportant because of an overabundance of food and because amphipod populations were limited by predation.

If resource partitioning was important in the assemblage we studied, its effects were not manifest in the overlap ratios of the particular species and individuals that coexisted locally. Although competition for space limited the numbers of individuals that could occupy a crevice habitat, body size patterns of colonizing amphipods and molluscs appeared to be determined more by the size distribution of individuals in the source pool, and perhaps by growth after colonization, than by interactions among similar-sized species or individuals.

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