Ecology, 69(3), 1988, pp. 624–634

LARVAL PREDATION BY BARNACLES: EFFECTS ON PATCH COLONIZATION IN A SHALLOW SUBTIDAL COMMUNITY[1]

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Abstract. Laboratory studies and gut-content analysis suggest that barnacles should be important predators on invertebrate larvae. To determine if predation on larvae limits settlement, we recorded recruitment in artificially produced patches of clear substratum surrounded by monocultures of either living or dead barnacles.

Living barnacles inhibited recruitment of colonial ascidians and bryozoans, but had no detectable effect on recruitment of barnacles, serpulid polychaetes, or solitary ascidians. Patch size did not influence the recruitment of any species. The presence of dead barnacle shells influenced spatial pattern of settlement in ascidians and serpulids. Comparison of blank control plates with barnacle-covered plates indicates that these spatial patterns are better explained by larval behavior than by small-scale hydrodynamic effects. Ascidians, which are dominant competitors in this community, settle primarily on shells of dead barnacles rather than on clear primary substratum.

Although predation on larvae by barnacles appears to inhibit recruitment of some species, its effects are variable and easily confounded with other determinants of settlement distribution.

Key words: Balanus; *community; disturbance; larval predation by barnacles; patch dynamics; power analysis; recruitment.*

INTRODUCTION

Studies of community development in marine epifaunal systems have demonstrated, with few exceptions (e.g., Mook 1981), that the first species to invade a site have important effects on subsequent colonization (Sutherland 1974, 1976, 1978, Menge 1976, Jackson 1977, Osman 1977, Sutherland and Karlson 1977, Lubchenco and Menge 1978, Dean and Hurd 1980, Russ 1980, Grosberg 1981, Kay and Keough 1981, Green and Schoener 1982). Where open substratum becomes available in the midst of established individuals ("type 1 patches" in the terminology of Connell and Keough 1985), colonization of the patch may be influenced significantly by its size and shape, as well as by the growth rates, feeding habits, and reproductive modes of surrounding organisms (Dayton 1971, Jackson 1977, Paine and Levin 1981, Palumbi and Jackson 1982, Dayton et al. 1984, Connell and Keough 1985). Although larvae may use established adults as attachment surfaces (Russ 1980, Dean 1981, Young 1986) or as settlement cues (Vance 1978, Grosberg 1981, Strathmann et al. 1981, Young and Chia 1981), prior colonists more often inhibit recruitment than enhance it (Connell and Slatyer 1977, Sutherland and Karlson 1977, Dean and Hurd 1980). Thus, marine epifaunal succession does not usually proceed according to the traditional "facilitation" model of terrestrial plant ecology (Clements 1916, Gutierrez and Fey 1980).

The mechanisms by which settlement is inhibited are not understood well. One mechanism of inhibition that has been invoked repeatedly, though rarely with experimental evidence, is consumption of larvae by established filter-feeders (Thorson 1950, 1966, Woodin 1976, Jackson 1979, Peterson 1979, Wilson 1980, Cowden et al. 1983, and many others). Many filter-feeders, including barnacles, bivalves, ascidians, etc. have been found with invertebrate larvae in their guts, and a few have been shown to consume larvae in laboratory experiments (reviewed by Young and Chia 1987). Nevertheless, community or population effects of predation on larvae are difficult to discern in the field. Most studies that have shown inhibition consistent with the larval predation hypothesis have failed to eliminate alternative hypotheses experimentally.

In the present study we designed an experiment to determine if patterns of distribution and abundance of newly settled epifauna were modified by surrounding fields of barnacles. The experiment was planned to test

[1] Manuscript received 10 September 1986; revised 20 July 1987; accepted 9 August 1987.

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four predictions that should hold if predators on larvae set patterns: (1) settlement should be greater in the presence of dead barnacle shells than in the presence of living barnacles; (2) settlement should increase with distance from feeding barnacles; (3) density of settlers should be greater in large open patches (surrounded by living barnacles) than in small patches because of the greater patch edge : surface area ratio of the latter; and (4) settlement directly on barnacle shells should be greater when the barnacles are dead. The predictions were tested by comparing recruitment in experimentally produced patches of two sizes that were surrounded by fields of living or dead barnacles, and by comparing cumulative recruitment on the living or dead barnacles surrounding the patches. We introduced blank plates as an additional control to estimate hydrodynamic effects that might be caused by the physical presence of barnacle shells (Bros 1987). We emphasize that this study was designed to seek patterns consistent with the larval predation hypothesis; we cannot infer predation on larvae from the patterns themselves without corroborative evidence on gut contents and feeding behavior. On the other hand, where the predicted small-scale patterns do not occur, we can state with some certainty that predation is not an important cause of distribution at that scale.

Materials and Methods

Study site and logistics

The experiment was run in a shallow seagrass (*Thalassia testudinum* and *Syringodium filiforme*) bed on Turkey Point Shoal, ≈1.6 km south of the Florida State University Marine Laboratory in the northeastern Gulf of Mexico. Water depth at the site was ≈1.5 m at MLLW, and flow was slight and bidirectional. Experiments could be serviced easily by snorkeling, but were never exposed by low tides. At this site, seagrass blades were the most common natural surface for the attachment of epifauna, but empty mollusc shells, emergent portions of polychaete (*Onuphis* sp.) tubes, and dead bryozoan colonies (*Schizoporella errata*) also supported epifaunal populations. In the northern Gulf of Mexico, most barnacle populations are found on pilings, floats, and other artificial substrata.

Recruitment was monitored and manipulated on square red Italian floor tiles (15 cm on a side), held facing down within the seagrass bed. We do not pretend that these plates mimic any substratum more natural than a boat bottom. Rather than documenting population dynamics on a natural substratum, we hoped to determine whether or not barnacles could have an impact on settlement patterns under high-density conditions where larvae should be consumed at high rates. We deployed tiles on four parallel racks constructed of pressure-treated wood and fastened horizontally to a series of stakes. The racks were 2 m apart and were arrayed in an east-west direction, parallel to the shoal. Plates were fastened diagonally to the bottoms of the racks by stretching a loop of surgical rubber tubing from one corner of each plate, over the top of the rack, and under the opposite corner.

Twenty-four blank plates were deployed in February 1985 and were monitored every other week until the first pulse of barnacle settlement occurred near the end of March. Three weeks following initial settlement, cover of *Balanus eburneus* (average rostral–carinal length ± 1 SD: 5.04 + 1.07 mm, $n = 49$) was uniform and approached 100% on all plates. During the last week of April, barnacle-covered plates were transported in seawater to the laboratory, modified according to the experimental design (described below), and transported back into the field the same day. After 2 wk, we took the plates aboard a small boat one at a time, counted all recruits, photographed each plate, and scraped the settlement surface with a razor blade. Each plate was then replaced in its original position on the rack for a second 2-wk run.

We extracted spatial pattern data from the color slides with an Ikegami high-resolution black-and-white video camera linked to a Houston HiPad digitizer and a modified Kaypro PC microcomputer running Microcomp image analysis software. Settlement site was inferred differently for each recruitment species; barnacle and encrusting bryozoan distances were measured from the middle of the colony or individual, whereas serpulid distances were measured from the proximal (closed) ends of their tubes. The distance from each recruit to the nearest edge of the barnacle field was measured in the large-patch, live-barnacle treatment. Using the Kolmogorov-Smirnov goodness-of-fit test (Sokal and Rohlf 1981), we compared the resulting frequency distributions with two kinds of expected distributions: (1) distances from recruits to dead barnacles (empirical distribution taken from photographs of large-patch, dead-barnacle treatments), and (2) available area (distribution expected if recruits settled in accordance with the surface area available to them). The values for expected distribution (1) consisted of individual-to-nearest-barnacle distances taken from the dead treatments. The values for expected distribution (2) were calculated as areas available in concentric imaginary rings having diameters corresponding with the distance categories in the observed distributions. Thus, for a unit circle with radius = r, the area of the ring encompassed by a segment extending d units from the edge of the barnacle patch toward the center is:

$$\text{area} = 3.14\,[r^2 - (r - d)^2].$$

Experimental design

The experiment was designed as a balanced two-way ANOVA, with each factor (live/dead barnacles; patch size) having two levels. Round patches either 8.5 or 4.5 cm in diameter were cleared in the center of each plate as settlement areas to be monitored. Half of the

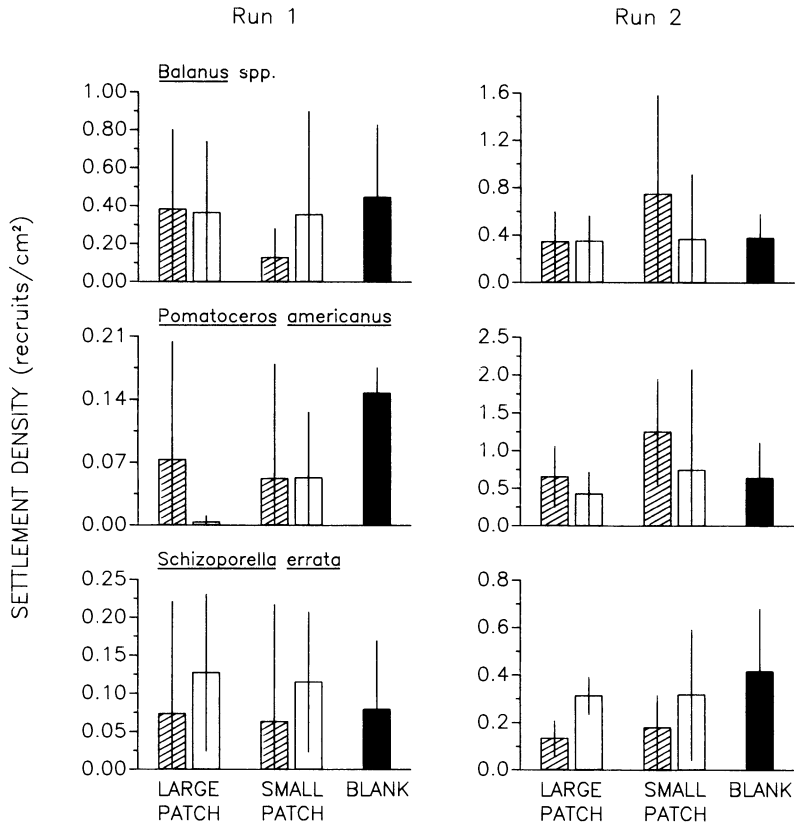

FIG. 1. Recruitment density of *Balanus* spp., *Pomatoceros americanus,* and *Schizoporella errata* to blank plates (solid bars), open patches surrounded by live barnacles (shaded bars), and open patches surrounded by dead barnacles (open bars). Error bars are standard deviations. Analyses of these data are given in Tables 1–3.

plates were then immersed for 10 min in hot fresh water to kill the barnacles. No barnacles survived this treatment. For each of the four treatment combinations, there were six replicate plates. In addition, we deployed six blank plates for use in a second analysis of the effect of barnacle shells on settlement. All treatments were assigned randomly to positions in the four-rack array.

The power of ANOVA tests was computed using tables and formulas in Cohen (1977) for an alpha value of .05. Because we had no a priori expectation of the effect size desired, we used Cohen's measure of effect size, *f,* which is the standard deviation of the population means divided by the common standard deviation of the populations of interest. Even though the plates were deployed on four separate racks, the experiments were not analyzed as a randomized block design, since plates were initially randomized without respect to racks, leaving some treatments without representation in all racks. However, after the data were analyzed, it became important to know if spatial variability among racks might be important. For this unplanned analysis, we pooled nonsignificant treatments within "blocks" (racks) and reanalyzed the data as a series of one-factor ANOVA.

We made four predictions. (1) If the filtering activities of a field of barnacles reduces the number of larvae entering an open patch, the effect should be clearly demonstrated by lower recruitment on "live" plates than on "dead" plates. (2) With respect to animals settling on the barnacles themselves, settlement should be greater on dead barnacles than on living ones. (3) The predation effect should be stronger in small patches than in large ones, because small patches have a relatively larger edge zone that should be influenced by barnacles. (4) Settlement should be lower near the edges of the living barnacle fields than in the middle of the patches. Prediction 4 (and to a lesser extent, prediction 3) are based on two assumptions concerning flow characteristics and supply of larvae. First, we assume that flow effects (e.g., eddies near the edges of the barnacle stands) do not modify the probabilities of larvae encountering different regions of a patch; such modification would obscure the effects of predators. Second, we assume that barnacles draw larvae from the overlying and adjacent portions of the water column, not just from laminar, horizontal currents passing across the plate. By assuming that larvae are well mixed in the water column and supplied vertically as well as

TABLE 1. Two-way analyses of variance to test the effects of patch size and living vs. dead barnacles for the three most abundant species recruiting to the open patches during each of the sequential 2-wk runs. Blank plates are not included in the analyses.

Species	Run no.	Source of variation	df	SS	MS	F	P
Balanus spp.	1	Live/dead	1	0.0627	0.0627	0.390	.5389
		Patch	1	0.1009	0.1009	0.630	.4370
		Interaction	1	0.0871	0.0871	0.540	.4697
		Error	19	3.0407	0.1600	...	...
	2	Live/dead	1	0.1917	0.1917	0.670	.4253
		Patch	1	0.2402	0.2402	0.830	.3732
		Interaction	1	0.2018	0.2018	0.700	.4136
		Error	18	5.1857	0.2881	...	...
Pomatoceros americanus	1	Live/dead	1	0.0069	0.0069	0.670	.4221
		Patch	1	0.0011	0.0011	0.110	.7433
		Interaction	1	0.0072	0.0072	0.700	.4134
		Error	19	0.1945	0.0102	...	...
	2	Live/dead	1	0.7351	0.7351	1.250	.2779
		Patch	1	1.1387	1.1387	1.940	.1807
		Interaction	1	0.1039	0.1039	0.180	.6789
		Error	18	10.5670	0.5871	...	...
Schizoporella errata	1	Live/dead	1	0.0162	0.0162	0.990	.3323
		Patch	1	0.0007	0.0007	0.040	.8356
		Interaction	1	0.0000	0.0000	0.000	.9912
		Error	19	0.3113	0.0164	...	...
	2	Live/dead	1	0.1533	0.1533	6.230	.0225
		Patch	1	0.0064	0.0064	0.260	.6154
		Interaction	1	0.0053	0.0053	0.210	.6496
		Error	18	0.4429	0.0246	...	...

horizontally, we can predict that encounters of larvae with the substratum would be higher in the middle of a patch than near the edge. The strength of the last prediction is predicated upon these unverified assumptions concerning small-scale flow processes around the plates.

RESULTS

At the beginning of the first experimental run, cover of live barnacles outside the cleared patch was 100% on all plates. During this 2-wk run, barnacles experienced an average daily mortality of 1.23%/d, resulting in a population with 82.66 ± 0.07% ($\bar{X}$ ± SD) of the initial population remaining. Mortality of barnacles was higher during the second 2-wk run as more predatory snails colonized the plates. When the second run was terminated, only 28.89% of the barnacles remained alive; average daily mortality during the second run was 3.84%/d.

Fig. 1 shows the settlement densities of the three most abundant recruit species in open patches of runs 1 and 2. There were no significant effects of barnacle treatment, patch size, or interactions in run 1 (Table 1). Living and dead barnacle treatments differed in their effect on recruitment of the cheilostome bryozoan *Schizoporella errata* in run 2. The direction of the difference was consistent with the predation hypothesis (Fig. 1).

Beta probabilities of the main effects were calculated for each nonsignificant result in order to determine if we could confidently accept the null hypothesis of no predation effect. When based upon Cohen's effect-size index, f, and an alpha value of .05, beta values were all large, ranging from 0.45 to 0.99 (Table 2). Although there are no strict conventions that dictate acceptable beta values, we conclude from this analysis that our power for detecting significant predation effects was less than might be desired, given the inherent variability in recruitment rates.

To determine if the presence of barnacle shells influenced recruitment (by, for example, flow entrainment), we pooled all nonsignificant live and dead treatments across patch sizes and compared them with the blank treatments using one-way ANOVA. In run 1, pooling was justified for *Balanus* spp. and *Pomatoceros* sp. Blank plates did not differ from barnacle treatments for either species (Table 3). Because of a significant live/dead effect, only dead treatments were contrasted with blank treatments in *Schizoporella errata*. Again, the effect of barnacle shells was not significant. In run

TABLE 2. Beta values from power tests of the main effects in analyses of variance from Table 1. Beta, the probability of incorrectly accepting the null hypothesis of no effect on recruitment, is related to power as $\beta = 1 - \text{power}$.

	Run 1		Run 2	
Species of recruit	Live/dead	Patch size	Live/dead	Patch size
Balanus spp.	0.99	0.88	0.88	0.86
Pomatoceros americanus	0.89	0.93	0.81	0.73
Schizoporella errata	0.85	0.95	0.45	0.99

TABLE 3. One-way analyses of variance comparing recruitment on blank plates with recruitment on treatment plates, which were partly covered with barnacles. All nonsignificant treatments (Table 1) were pooled for the analysis.

Species	Run no.	Source of variation	df	SS	MS	F	P
Balanus spp.	1	Treatment	1	0.0930	0.0930	0.6237	.4366
		Error	27	4.0255	0.1941	...	...
	2	Treatment	1	0.0287	0.0287	0.1190	.7330
		Error	25	6.0287	0.2410	...	...
Pomatoceros americanus	1	Treatment	1	0.0050	0.0050	0.6301	.4342
		Error	27	0.2127	0.0079	...	...
	2	Treatment	1	0.0774	0.0774	0.1421	.7094
		Error	25	13.6060	0.5442	...	...
Schizoporella errata	1	Treatment	1	0.0009	0.0009	0.0672	.7975
		Error	27	0.3688	0.0137	...	...
	2	Treatment	1	0.0340	0.0340	0.7793	.3923
		Error	14	0.6102	0.0436	...	...

2, where pooling was justified in all species, the presence of barnacles or barnacle shells had no significant impact on recruitment (Table 3).

Given the unexpected nonsignificance of treatments, we wanted to know whether spatial variability in abundance of larvae among racks might be important. When nonsignificant treatments were pooled within blocks (racks) and analyzed as a series of one-factor ANOVAS (Table 4), only one significant treatment effect was detected: *Schizoporella errata* in run 1. Settlement densities of *S. errata* differed by an order of magnitude between racks III (0.049 individuals/m^2) and IV (0.005 individuals/m^2), indicating spatial variation on a scale of metres.

The influence of barnacles on within-patch spatial patterns was studied by measuring distances between settlement sites and barnacle fields in large patches only. There were insufficient recruits in small patches to undertake this kind of analysis. The spatial pattern of barnacle recruitment differed between living and dead treatments (Fig. 2). The pattern appears consistent with the predation hypothesis; more barnacles attached near the patch edge in dead treatments than in living ones. However, recruit-to-adult distances in living treatments were indistinguishable from the predicted pattern that would have been produced by random settlement within the patch (Table 5). Thus, the difference seen in Fig. 2 probably resulted not from predation in the living treatments, but from enhanced settlement near the edge of the patch in dead treatments.

The distribution of distances from recruits of *Schizoporella errata* to the patch edge also did not differ significantly between living and dead barnacle treatments, suggesting no predation effect. As in the case of barnacles, the observed distribution was not significantly different from the predicted random settlement distribution (Table 5).

The distribution of distances from recruits to live animals did not differ significantly from the recruit-to-dead animal distances in *Pomatoceros americanus*. However, the distribution was significantly different from that predicted on the basis of surface area (Table 5). This was either a small-scale flow effect or the result

TABLE 4. One-way analyses of variance to test the null hypothesis H_0: settlement is not different among blocks (racks) of plates. Data were pooled across all treatments (justified by nonsignificant main effects; Table 1) except in *Schizoporella errata*, run 2, where there was a significant live/dead effect. In the latter experiment, only the dead treatments were analyzed, though these were pooled across patch sizes.

Species	Run no.	Source of variation	df	SS	MS	F	P
Balanus spp.	1	Blocks	3	0.0526	0.0175	2.172	.1248
		Error	19	0.1533	0.0081	...	...
	2	Blocks	3	0.0301	0.0100	0.557	.6502
		Error	18	0.3242	0.0180	...	...
Pomatoceros americanus	1	Blocks	3	0.0028	0.0009	1.719	.1969
		Error	19	0.0103	0.0005	...	...
	2	Blocks	3	0.0972	0.0324	0.3864	.7641
		Error	18	1.5099	0.0839	...	...
Schizoporella errata	1	Blocks	3	0.0074	0.0025	3.3726	.0334
		Error	19	0.0131	0.0007	...	...
	2	Blocks	3	0.0172	0.0057	0.3708	.7750
		Error	18	0.2786	0.0155	...	...

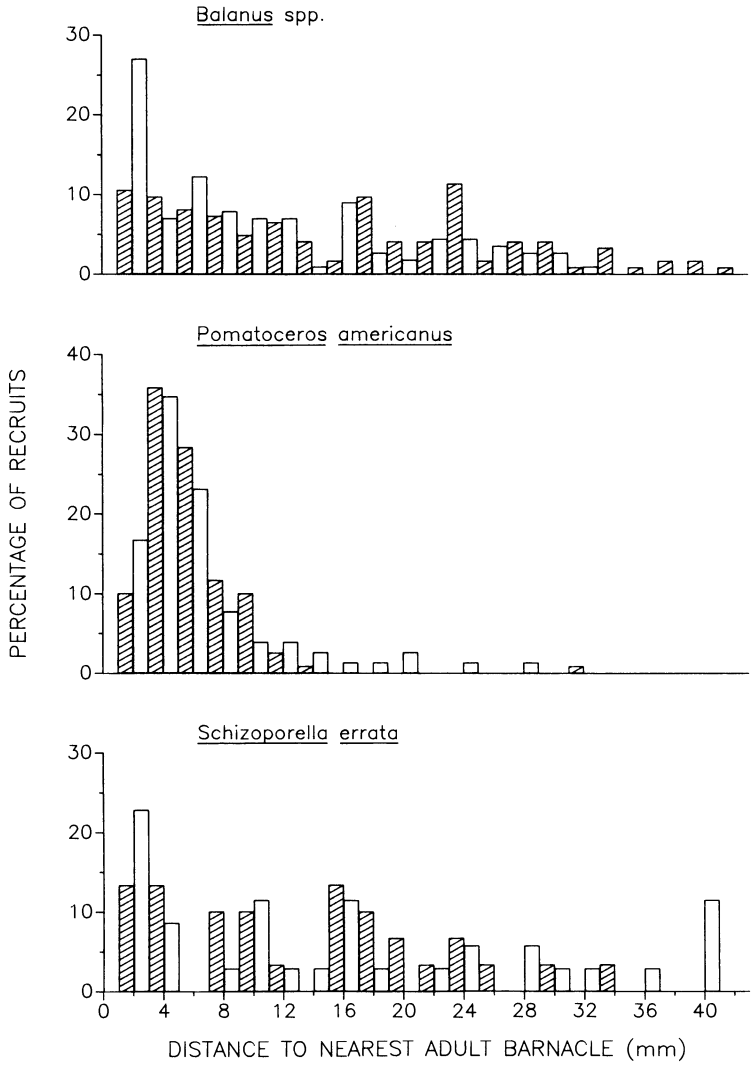

FIG. 2. Frequency distributions of *Balanus* spp., *Pomatoceros americanus,* and *Schizoporella errata* recruits as a function of distance to the edge of the barnacle field. Shaded bars: live barnacle treatment. Open bars: dead barnacle treatment. Actual barnacle-to-recruit distances are grouped in 2-mm classes for the graph and also for the analysis in Table 5.

of a strong preference for settlement near the patch edge. The pattern of distribution was virtually indistinguishable between plates with dead and those with live barnacles, so chemical attraction to barnacles is probably not a factor. Perhaps the pattern can be attributed to larval rugophilia. In any case, if predation on larvae of *Pomatoceros americanus* by barnacles were important, the opposite pattern (more recruitment in the center of the patch) would be expected.

Four species of ascidians recruited in numbers large enough to analyze. All four species were more abundant on the living or dead barnacles than in the open patches (Fig. 3; Table 6). Because ascidians were not removed from the barnacle surfaces after the first run, analyses were run on cumulative numbers of recruits after run 2. The three species of colonial ascidians, *Didemnum* sp., *Diplosoma glandulosum,* and *Distaplia bermudensis,* showed the same general pattern: there were more recruits on the dead barnacle fields than on the living ones, a pattern consistent with the larval predation hypothesis. The reverse was true for the one species of solitary ascidian, *Styela plicata*: there were significantly more recruits on living than on dead barnacles. The effect of patch size, a reflection of the total surface area of barnacle shell available for settlement on the plates, was not significant in any of the species (Table 6).

DISCUSSION

Gut contents of many barnacle species contain invertebrate larvae including echinoderms (Barnes 1959, Crisp and Southward 1961, Kuznetsova 1974), molluscan veligers (Barnes 1959, Crisp and Southward 1961, Hadfield 1963, Potts 1970, Kuznetsova 1974),

TABLE 5. Results of Kolmogorov Smirnov goodness-of-fit tests comparing the frequency distributions of recruit-to-live-barnacle distances (Fig. 2) with expected distributions generated by two different hypotheses.

Expected distribution*	Recruit species	*D*	*P*
Distances to dead barnacles	*Balanus* spp.	0.25	NS
	Pomatoceros americanus	0.09	NS
	Schizoporella errata	0.19	NS
Available area	*Balanus* spp.	0.09	NS
	Pomatoceros americanus	0.54	<.01
	Schizoporella errata	0.09	NS

* Comparison with the first expected distribution (distances to dead barnacles) tests a potential predation effect on spatial distribution. The second expected distribution (available area) tests the hypothesis that larvae are not influenced by proximity to adults, but settle in proportion to the surface area available to them.

ascidian tadpoles (Standing 1976; C. M. Young, *personal observation*), and barnacle cyprids and nauplii (Barnes 1959, Kuznetsova 1974). In laboratory feeding experiments, *Balanus eburneus* adults clear water of various types of larvae very quickly (C. M. Young, *personal observation*). However, the fact that barnacles consume invertebrate larvae does not mean that predation is necessarily a factor that limits invertebrae recruitment. In our controlled field experiments, patterns consistent with the larval predation hypothesis were detected in four species, *Schizoporella errata* (experiment 2 only), *Didemnum* sp., *Distaplia bermudensis,* and *Diplosoma glandulosum,* but not in three others, *Balanus* spp., *Pomatoceros americanus,* and *Styela plicata.* In the latter cases, we could only conclude that if predation occurs in the field, its effects are overshadowed by other factors that have a much greater influence on recruitment. We hasten to add that this conclusion is valid only for our experimental conditions (i.e., patches surrounded with only 3–5 cm wide bands of barnacles). Predation effects could be much greater in the rocky intertidal or in other areas with more expansive fields of barnacles. Broader generalizations must await experiments in such areas.

Even in circumstances where predation on larvae occurs, we might expect nonsignificant main effects in the ANOVA tests if our sample size was too small with respect to the observed variation in settlement density. Power analysis (Cohen 1977) verifies that samples size may limit our ability to detect predation effects in this system. Unfortunately, the level of replication that would be required to accept the null hypothesis is prohibitively large. For example, in the cases where means were closest together and alpha was highest (*Balanus* spp., run 1, live/dead; *Schizoporella errata,* run 2, patch size), >2000 plates would have had to be deployed in order to say with 95% certainty that larval predators do not affect settlement density. Field experiments of this magnitude are logistically difficult, if not impossible. Moreover, because a 45 × 45 array of plates would sample a much larger water mass than our 4 × 6 array, the likelihood of encountering greater meroplankton patchiness would be high, rendering even this level of replication inadequate. Some workers have touted the desirability of using power analysis to support null results in ecology (Toft and Shea 1983), while others (Rotenberry and Wiens 1985) have pointed out its limitations. The power of analysis of variance tests is a function of three variables: alpha (*P,* or the probability of type I error), sample size (*n*), and effect size. With these three values, power (and hence beta) can be determined easily from published tables (Cohen 1977). However, a major problem in ecological studies is the determination of effect size (Rotenberry and Wiens 1985). If one sets a high enough effect size criterion, relatively few replicates are required, but if one bases

TABLE 6. Two-way analyses of variance testing effects of live vs. dead barnacles and patch size on cumulative settlement of ascidians during both runs of the experiment (Fig. 3). Only recruits settling directly on live or dead barnacle shells (i.e., outside open patches) are included in the analysis. Data were transformed as $\log(y + 1)$ in order to equalize variances.

Species	Source of variation	df	SS	MS	*F*	*P*
Didemnum sp.	Live/dead	1	0.0380	0.0380	41.66	.0000
	Patch	1	0.0024	0.0024	2.66	.1195
	Interaction	1	0.0006	0.0006	0.68	.4215
	Error	19	0.0173	0.0009	...	...
Diplosoma glandulosum	Live/dead	1	0.0008	0.0008	21.38	.0002
	Patch	1	0.0000	0.0000	0.50	.4891
	Interaction	1	0.0001	0.0001	1.39	.2534
	Error	19	0.0007	0.0000	...	...
Distaplia bermudensis	Live/dead	1	0.0021	0.0021	17.69	.0005
	Patch	1	0.0002	0.0002	1.40	.2513
	Interaction	1	0.0007	0.0007	5.77	.0266
	Error	19	0.0022	0.0001	...	...
Styela plicata	Live/dead	1	0.0001	0.0001	7.57	.0127
	Patch	1	0.0000	0.0000	0.30	.5922
	Interaction	1	0.0000	0.0000	2.72	.1152
	Error	19	0.0002	0.0000	...	...

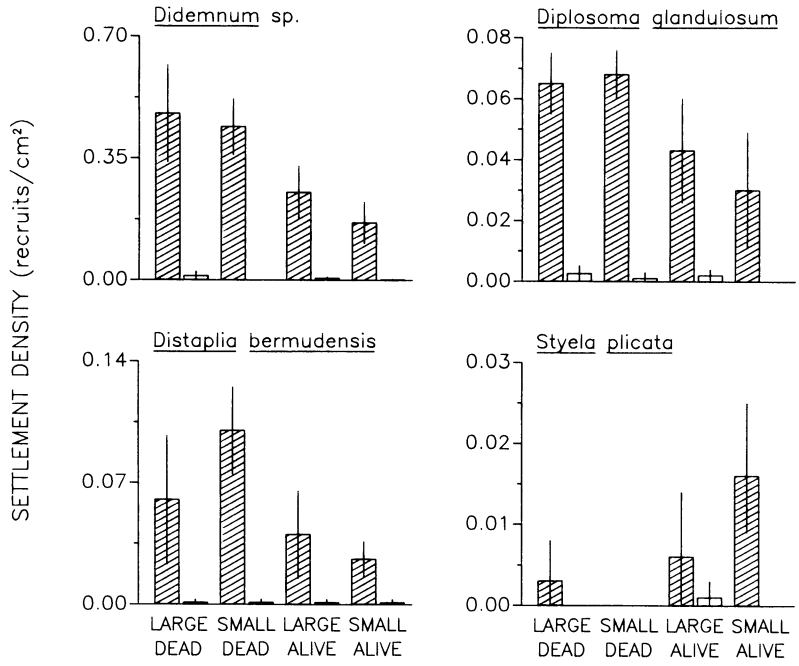

FIG. 3. Recruitment densities of colonial ascidians (*Didemnum* sp., *Diplosoma glandulosum, Distaplia bermudensis*) and solitary ascidians (*Styela plicata*) on barnacle fields (shaded bars) and on open patches surrounded by barnacle fields (open bars). Error bars are standard deviations. Analysis of these data is given in Table 6.

the effect size variable on actual observed differences between means, the power of any given statistical test decreases substantially as means get closer together. This is correct from a statistical point of view, but runs contrary to and frustrates a naturalist's intuition. As stated by Rotenberry and Wiens (1985), "in order to use power analysis to estimate beta to support a null hypothesis, one must estimate a magnitude for the very effect that one seeks to demonstrate has no effect at all." From a biological standpoint, it may be irrelevant to say with a high level of confidence that two nearly identical means do in fact come from the same statistical population, particularly where differences cannot possibly be measured because of logistical constraints or real-world variability.

Quinn and Dunham (1983) have observed, "Postulated ecological causes or relationships can rarely be strictly disproven, although they may often be shown to be unimportant or improbable." Having run power analyses on our field experiments, we concur strongly. We were never able to show that predation has no effect; only that the effect is probably trivial for several species. Few other ecological studies have included power analyses to estimate the validity of accepting a null hypothesis. A notable exception is the study by Doherty and Sale (1985), of predation on fish on the Greater Barrier Reef. They had reasonably high replication for an underwater experiment (10 replicates per treatment), but their power tests revealed that 90 replicates would be needed in order to reduce the probability of a type II error to .05. Because the philosophical relevance of power analysis has been questioned (Rotenberry and Wiens 1985) and empirical studies have now demonstrated its impractical aspects (this study; Doherty and Sale 1985), it seems clear that a better method is needed for evaluating "nonsignificant" results in ecological field experiments. Power analysis will be useful only if much more liberal rejection criteria are accepted by convention, and if methods are developed to estimate ecologically relevant effect sizes.

Variation in recruitment resulting from processes occurring on many scales (Caffey 1985, Gaines and Roughgarden 1985) could obscure the effects of larval predators. In a general sense, recruitment variation results either from patchiness in supply of larvae or from differential postsettlement mortality occurring before the first census. Because our experiments were only 1 wk long, and because three of the four species that settle commonly in open patches secrete calcareous structures that persist when the animals die, mortality is the least likely of the two possibilities. Empty shells (of which there were relatively few) were included in our counts. The important processes influencing recruitment pattern more probably occur in the presettlement stages than after settlement. Thus, spatial variability in locations of adult source populations, mortality in the plankton, and advective or diffusive dispersal processes (reviewed by Young and Chia 1987) may all create patchiness of larvae at settlement. Such pro-

cesses still need to be studied in detail for virtually all larval types and in most marine systems.

The only species in which settlement varied on a between-rack scale was *Schizoporella errata.* As in other ascophoran bryozoans, larvae of this species are released from the parent already competent or nearly competent to settle (C. M. Young, *personal observation*). They are likely to remain near the adults because of their very short dispersal phase. Thus, location of the adult source population coupled with local current patterns should be particularly important as a factor influencing recruitment pattern. Barnacles, *Pomatoceros,* and solitary ascidians disperse for longer periods of time (Costlow and Bookhout 1957; C. M. Young, *personal observation*), so the effect of origin of the larvae should be masked to some extent by later dispersal. Indeed, settlement did not vary among racks in any of these latter species. Patchiness in supply of larvae on a "within-rack, between plate" scale (see large standard deviations in *Pomatoceros americanus,* run 1; Fig. 1) could have caused our failure to detect significant predation effects in these species.

In many marine communities, small-scale hydrodynamic processes may influence the distributions of organisms (Russ 1980, Dean 1981, Eckman 1983, Hannan 1984, Thistle et al. 1984). Whenever evaluating the effect of a living animal, therefore, it is now customary to provide an inert mimic in a separate treatment to determine how disruption of flow might bias the results. We ran an appropriate flow control using dead barnacle shells as a "mimic," but comparison with blank plates showed no significant effects on density. This result contrasts with the findings of Bros (1987), who ran a similar study in Tampa Bay, Florida, $\approx$350 km southeast of our study site. Bros examined the effects of living and dead barnacles on species number in the fouling community. He found that dead barnacle shells enhance species number, and that they have their greatest effect on motile organisms. In agreement with our findings, living barnacles did not generally inhibit recruitment. In our study, the presence of barnacle shells influenced only the within-plate spatial pattern of settlement in ascidians and serpulids. Populations of *Pomatoceros americanus* larvae initially settled in sites near the edge of the barnacle patches, then grew toward the middle. Turbulence and eddies driven by ambient currents near the edges of the barnacle fields might have increased the probability of larvae encountering this region. However, we consider behavior to be a more viable explanation, since the difference between settlement in edge and in middle sites was seen in only a single species. Perhaps settlement near barnacle shells enables *Pomatoceros* to exploit the open areas as adults while receiving some protection when the tubes are small. Ascidians, both compound forms and solitary forms, preferred to settle on the barnacle shells themselves. None settled on open spaces in any significant numbers. Rugophilic larval responses are very common among larvae of many invertebrate phyla (Meadows and Campbell 1972) including ascidians.

Recruitment patterns of all three compound ascidians were consistent with predictions of the larval predation hypothesis. We found it surprising that the solitary ascidian *Styela plicata,* which has small larvae and should have been susceptible to predation by barnacles (C. M. Young, *personal observation*), was more abundant on living barnacles than on dead ones, whereas colonial ascidians, which originate from much larger tadpoles, were more abundant on dead than on living barnacles. Laboratory work is needed to determine if barnacles feed on large tadpoles of compound ascidians. If they do, larval predation may be the cause underlying the observed pattern. Otherwise, several alternative hypotheses must be considered. One is that colonial ascidian tadpoles are more strongly rugophilic or negatively phototactic than the larvae of *Styela plicata.* In this case, the colonial forms would be more likely to locate suitable settlement sites in the shells of dead barnacles than on living barnacles. Comparative behavioral data with which to test this hypothesis are not yet available. A second alternative is that organisms associated with dead barnacle shells (e.g., corophiid amphipods) prey selectively on the smaller larvae of *Styela plicata* and fail to take the larger larvae of colonial ascidians. Such a reduction in settlement of *Styela plicata* on the dead plates, coupled with greater surface area for settlement of colonial ascidians on the same plates could explain the observed pattern at least as well as larval predation by barnacles.

It is noteworthy that our results were split along lines of coloniality. Solitary species were never inhibited by the presence of living barnacles, but all four colonial species were affected in at least one of the two runs. However, the colonial and solitary species in this study differed not only in their capacity for asexual reproduction, but also in many attributes of their larvae that could influence recruitment rate: life span, feeding mode, size, and swimming speed (Jackson 1977, 1983). Moreover, many colonial invertebrates, including ascidian larvae (Young and Bingham 1987), are known to contain chemical defenses against predators (Green 1977, Stoecker 1980). It is therefore surprising that larvae of colonial species were inhibited by barnacles more often than the larvae of solitary species.

One might imagine that since barnacles inhibit recruitment of colonial organisms (which tend to be superior competitors: Jackson 1977, 1979), barnacles should be able to dominate a subtidal surface for a relatively long time. However, substantial ascidian recruitment occurs even on living barnacles (Fig. 3). This ascidian colonization is balanced somewhat by the fact that predation by barnacles apparently impacts barnacle cyprids less than ascidian tadpoles. Nevertheless, from a competitive standpoint, the scales tip in favor of colonial ascidians. Cumulative cover values of as-

cidians following the two runs (1 mo total) often exceeded 50%. One species in particular, *Diplosoma glandulosum,* grew very quickly; single colonies were often >5 cm in diameter after 2 wk of growth. Predation by snails and overgrowth by ascidians were so intense in our experiments that we would be surprised to see persistent monocultures of barnacles subtidally in the northern Gulf of Mexico. Indeed, most populations on natural substrata (e.g., empty cockle shells) consist of small and/or isolated individuals, and subtidal barnacles on boats and pilings are often overgrown by ascidians. Although long-term monitoring is needed, casual observations suggest that barnacle patches persist only in the high intertidal.

Established invertebrates often reduce recruitment of subsequent colonists by preempting space (Sutherland 1978, Jackson 1979, 1983, Dean and Hurd 1980). Our experiments were designed to determine whether established barnacles have effects on recruitment densities in open patches, where space does not limit settlement. For most solitary sessile invertebrates, effects of predation by barnacles were either nonexistent or indetectable in small-scale field experiments. Potential effects of larger fields of barnacles (e.g., on intertidal rocks) demand further investigation. For colonial invertebrates, especially ascidians, recruitment patterns were consistent with the predictions of larval predation, but may also be explained by alternative hypotheses involving behavior of larvae and surface-area effects. In almost every case where barnacles or barnacle shells influenced recruitment, the patterns observed were not the patterns expected. Generalizations in the tradition of Thorson (1950) on the importance of predation on larvae by benthic filter-feeders are clearly not warranted by the evidence at hand.

Acknowledgments

We thank B. M. S. Mahoney and J. Schmidt for asssistance in the field. J. L. Cameron, R. R. Olson, W. Sousa, and two anonymous reviewers provided useful comments on the manuscript. C. and F. Monniot graciously assisted with the identification of compound ascidians. This paper is Contribution Number 1041 of the Florida State University Marine Laboratory, and Harbor Branch Contribution Number 595. Supported by N.S.F. Grants OCE-8400406 and OCE-8544845.

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