

Effects of seasonality, length of immersion, locality and predation on an intertidal fouling assemblage in the Northern Gulf of Mexico

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Received 5 March 1997; received in revised form 5 August 1997; accepted 18 August 1997

Abstract

Recruitment of the intertidal fouling assemblage was studied by placing out tiles at four sites along the Louisiana Gulf of Mexico coast in fall, spring and summer, for immersion periods of one, two and three months. The dominant species were the barnacle *Balanus eburneus* (Gould), which recruited in all three seasons, but at highest densities in the spring; the oyster *Crassostrea virginica* (Gmelin), which recruited only in fall, and the bryozoan *Membranipora savartii*, which recruited in spring and fall. Thus, the species that recruited varied with the season, as in earlier studies of colonization of free space in intertidal fouling assemblages. However, unlike previous studies, barnacle abundances or oyster and bryozoan percentage cover tended to decrease with length of immersion. To determine if these post-settlement decreases were caused by predation, we enclosed tiles in mesh cages to exclude predators, and replicated experiments at both coastal and estuarine sites to determine site-specific differences in recruitment. Barnacles recruited at higher rates at coastal sites and oysters at estuarine sites, as predicted by the literature. For barnacles, densities after one month of colonization were lower on open or partially caged tiles than on caged tiles, supporting the hypothesis that predators, like blue and mud crabs, or southern oyster drills, may regulate barnacle abundance. Caging did not increase the percentage cover of either oysters or bryozoans. Oyster abundance may be limited by larval supply, as oyster recruitment never reached above 5% cover. Small predators, like flatworms, which were not excluded by cages, may also be important for the latter two prey. © 1998 Elsevier Science B.V.

Keywords: Colonization; Fouling; Seasonality; Predation

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1. Introduction

Succession in intertidal fouling assemblages is quite different than the classical, facilitative pattern seen in terrestrial plant assemblages (Sutherland, 1974; Sutherland and Karlson, 1977; Osman, 1977; Underwood and Anderson, 1994). For example, the species that initially colonize space, and eventually dominate the assemblage, are dependent on the seasonal reproductive periodicities of adults and on larval availability. There is little evidence of intermediate successional stages that facilitate invasion by subsequent stages and, instead, there are often multiple end-points that communities approach. Initial colonists are often efficient competitors for space and resist further invasions (Osman, 1977). For example, Underwood and Anderson (1994) found that the oyster *Saccostrea commercialis* was capable of dominating colonization plates set out in an estuarine bay during the summer, but was incapable of replacing barnacle and algal assemblages that had recruited onto surfaces the previous winter.

Studies of the American oyster, *Crassostrea virginica*, have revealed the importance of temporal and spatial variation in settlement and post-settlement mortality in determining recruitment patterns (Bushek, 1988; Osman et al., 1989; Michener and Kenny, 1991; Roegner, 1991). Oyster settlement is enhanced on surfaces enclosed by mesh (O'Beirn et al., 1996). Although the mechanism for such enhancement (e.g., reduced predation rates and desiccation stress, or increased larval entrainment) is not known, the facilitation evidently overrides any adverse effects of decreased water circulation or fouling of the mesh.

Our purpose in this paper was to report patterns in the recruitment of the intertidal fouling assemblage of the northern Gulf of Mexico, which had not been studied as extensively as assemblages along the Atlantic coast of the United States (Sutherland, 1974; Sutherland and Karlson, 1977; Osman, 1977). This intertidal fouling assemblage is fairly simple (Britton and Morton, 1989) and is composed primarily of the barnacle *Balanus eburneus* (Gould), the oyster *Crassostrea virginica* (Gmelin) and the bryozoan *Membranipora savartii* (Audouin). In general, northern Gulf of Mexico habitats are characterized by relatively warm water temperatures (averaging 25°C), variable salinities (averaging 25‰, but decreasing to 10‰ in estuarine habitats), muddy substrata and high turbidities.

Our specific questions included determining how much seasonal variation occurred in the recruitment rates of the three dominant species at a single site. We were also interested in whether or not successional patterns (over an immersion period of one to three months) varied depending on the season of immersion. Salinity and wave disturbance (Richardson and Brown, 1990), as well as availability of larvae (Underwood and Denley, 1984; Caffey, 1985; Connell, 1985; Gaines and Roughgarden, 1985; Underwood and Fairweather, 1989), vary between coastal and more estuarine sites. We were therefore also interested in whether or not consistent differences in recruitment occur between these coastal and estuarine sites. Finally, we were interested in whether or not predation was a major source of post-settlement mortality in this assemblage.

We performed two experiments to address these questions. The first was a colonization study at an estuarine site, where settlement plates were set out in three seasons, and recruitment of the fouling assemblage was followed for periods of one, two and three

months in each season. Since abundances often decreased with time on substrata in this study (see Section 3), we designed a second experiment to assess the role of predation in determining such post-settlement mortality, with tiles enclosed in vexar mesh “cages”, in partial cages or unenclosed, as in the original study. This second experiment was also replicated at two coastal sites and two estuarine sites, to determine if there were any consistent site-based differences in recruitment. We reasoned that if predation were a significant source of mortality, caged tiles would have the highest recruitment rates. Partial cages would have recruitment rates similar to those of control tiles, or possibly even lower, if predators (for example, small blue or mud crabs) could use partial cages as refuges from their predators. If, however, caged tiles increased recruitment of larvae because of reduced currents, etc., we reasoned that partial cages would have intermediate recruitment.

In summary, our study is important because it was the first to document recruitment dynamics of the fouling assemblage of the northern Gulf of Mexico. It was also the first study, to our knowledge, to apply caging methods to ascertain the role of predation in causing post-settlement mortality in a fouling assemblage.

2. Methods

2.1. Site descriptions

We performed the initial colonization study at the Port Fourchon marine laboratory of the Louisiana Universities' Marine Consortium (Fig. 1). This site is 10 km from the mouth of Bayou Fourchon, on a side canal. Salinities average 20–22‰ at this site, and temperatures vary from lows of about 16°C in January, to as high as 32°C in late summer. The second estuarine site used in the caging study was at the Port Fourchon boat docks, about 1 km from the first site. The two exposed sites were Caminada Pass, at the mouth of Barataria Bay, and Belle Pass, at the mouth of Bayou Fourchon (both within 20 km of the estuarine sites). The latter two sites have higher average salinities (about 30‰) but have yearly fluctuations in temperature that are similar to those of the estuarine sites. Average tidal ranges at all sites are about 0.5 m. The coastal sites are exposed to moderate wave action, while the estuarine sites are more protected (Richardson and Brown, 1990). A further description of the sites can be found in Brown and Richardson (1987) and in Richardson and Brown (1990).

2.2. Colonization plates

We used 15 × 15 cm unglazed clay tiles as colonization plates, following Sutherland and Karlson (1977) as well as several other studies (Bingham, 1992; Dalbey and Young, 1993). Tiles were suspended subtidally from wooden docks or pilings with small-diameter braided nylon ropes. Tiles were tied in a crossing pattern (e.g., two lines tied at a right angle) with similar nylon ropes, creating four quadrants on each face of the tile, and then they were attached to the suspension lines. To limit disturbance by lines, only a 3 × 3 cm plot at the center of each quadrant was counted, with a dissecting microscope

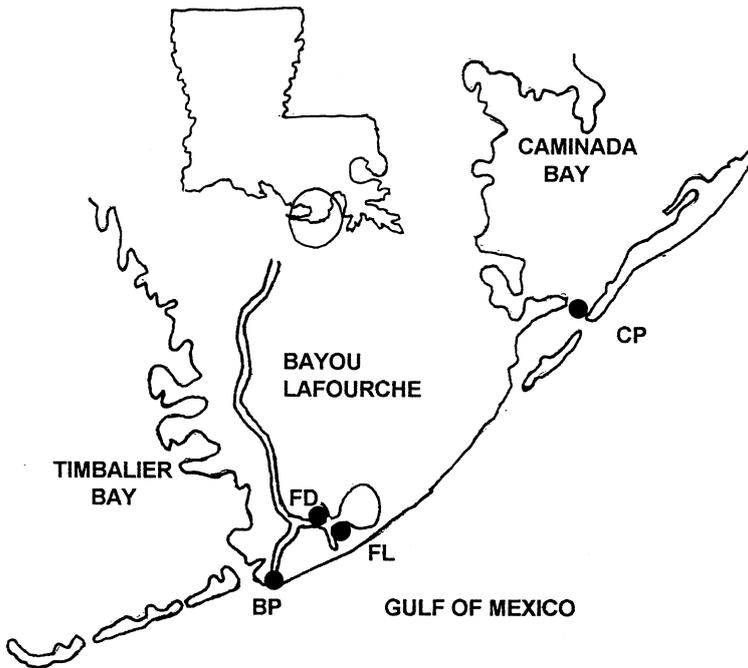


Fig. 1. Map of the study area with experimental sites indicated. CP = Caminada Pass, BP = Bell Pass, FL = Port Fourchon laboratory, FD = Port Fourchon boat docks.

at $7\times$ magnification and an optical micrometer. This size of plot was also chosen as it had been proven to be adequate in earlier studies of barnacle recruitment (Sutherland, 1990). To avoid pseudoreplication (Hurlbert, 1984), data from all four plots were pooled so that the individual tile was the experimental unit (total area counted to estimate barnacle density = 36 cm^2). Preliminary studies indicated higher settlement on the sides of the tile covered with protuberances, and only these plots were counted.

We randomly chose 40 barnacles on each tile and measured an average basal diameter that was used to calculate individual basal area (hereafter referred to as barnacle size), assuming that the barnacle was circular. However, individual oyster spat and young bryozoan colonies initially had circular shapes, but eventually had quite irregular outlines. We therefore estimated oyster and bryozoan percentage cover by overlaying each of the four plots on the tile with a grid with 25 intersecting points, and multiplying the number of points intersecting oysters or bryozoans by four (as in Underwood and Anderson, 1994), to estimate the percentage cover. The resulting four values were then averaged.

Before analysis, all data were examined for heteroscedacity and normality (Procedure Univariate, SAS Institute, 1988). Barnacle densities and sizes were ($\log + 1$) trans-

formed in some cases, and oyster and bryozoan percentage covers were arc–sin square root transformed. The original means and standard errors are portrayed in figures.

2.3. Seasonal study

We suspended tiles on September 15, 1992 (hereafter referred to as fall), February 15, 1993 (referred to as spring) and June 15, 1993 (referred to as summer). In each season, twelve tiles were set out and four were retrieved after one, two and three months, respectively. The tiles were thus independent sampling units, which allowed application of standard analysis of variance methods to data (Underwood, 1981; Underwood and Anderson, 1994). Since three of the four seasons and nine of twelve months were sampled [a fairly high fraction, see Underwood (1981)] and specific immersion periods were chosen (e.g., we were not sampling all possible times), we considered both season and immersion time to be fixed effects. The design was thus a two-way factorial with three seasons and three immersion lengths. Following suggestions in Underwood (1981), if an interaction effect was significant, all pair-wise comparisons of means were tested (procedures GLM and PDIFF, SAS Institute, 1988) to determine which individual means were different. Significance levels ($P = 0.05$) were divided by the number of comparisons, to be conservative. We first stated what level of significance is required (based on the number of comparisons) and then noted what specific comparisons are significant.

To test for any preemptive use of space by colonists, we also regressed the abundances or percentage covers of each of the three species (the dependent variables) against each of the other two groups (the independent variables) in simple linear regressions, as well as performing a multiple linear regression for each species, with the other two species as joint predictors. All regressions were pooled over all three seasons and immersion times ($n = 36$ tiles).

2.4. Caging study

In this study, two thirds of the tiles at each site were enclosed in 3 mm vexar mesh, following O'Beirn et al. (1996). Enclosures were constructed by cutting vexar sheets with 1.5 times the dimensions of the tile, and hot-gluing their margins so that they formed a pillow surrounding the tile. A cable tie was used to gather the vexar together and to provide greater space on the side of the tile that would later be counted, to limit any abrasion of the surface. Partial cages were further modified by cutting two 10×5 cm windows on the side of the cage above the tile surface that was counted. There were six replicate tiles for each treatment (e.g., cage, partial cage and control). Tiles were immersed on May 15, 1996, cleaned with a stiff brush after two weeks and retrieved after four weeks immersion, to limit fouling of mesh. Tiles were counted as in the seasonal study. We considered the site (see Section 2.1) and caging treatments as fixed effects, and the data were analyzed in a two-way analysis of variance (four sites \times three caging treatments), using the same types of a posteriori comparisons as in the seasonal study. Sites were considered fixed because we were comparing only the four sites, and not considering them to be a sample of all possible sites.

3. Results

3.1. Seasonal study

Both season and immersion period had significant effects on the number of barnacles recruiting to tiles (Fig. 2A; Table 1). Contrasting the seasons, a posteriori comparisons suggested that spring recruitment was significantly higher ($P < 0.05/3$ or 0.02) than both fall and summer, but that fall and summer were not significantly different from each other. Contrasting immersion times within seasons, barnacle abundances at one month were marginally greater than those at three months ($P = 0.02$), but not greater than those at two months. Thus, barnacle recruitment was significantly greater in the spring, but there was also a trend for densities to decrease with longer immersion periods.

Average barnacle sizes differed significantly among seasons and colonization periods, and there was also a significant two way interaction (Fig. 3; Table 1). Contrasting all nine possible combinations of immersion periods within seasons (e.g., for significance, $P < 0.05/9$ or 0.006), there were no significant differences among immersion periods in the fall. In Spring, barnacles grew significantly larger only between one and three months. In the summer, barnacle sizes were significantly smaller after three months than after two months or one month, suggesting a significant settlement of barnacles at the end of the summer colonization period, or size-specific mortality.

Contrasting all nine possible combinations of seasons within months of immersion, there was no difference in barnacle size between one or two months immersion in any season, but barnacle size after three months was significantly lower in summer than in either spring or fall. Thus, the general pattern was evidently for growth of the individual barnacles to increase the average size on tiles, except in late summer, when recruitment of a cohort of barnacles during the third month depressed the average size.

Oysters recruited only during the fall, and the seasonal effect was highly significant. However, even in the fall, oyster percentage covers were below 5% (Fig. 2B). Although average percentage cover tended to decrease with time (Fig. 2B), neither the immersion length nor interaction effects were significant (Table 1).

By comparison, bryozoan recruitment occurred both in fall and spring, but not in summer (Fig. 2C), and the season as well as the immersion time and interaction effects were significant (Table 1). The general pattern was for percentage cover to increase from one to two months of colonization, but to remain stable or decrease thereafter. For example, contrasting colonization times within seasons (e.g., significant $P < 0.05/9$ or 0.006), percentage cover increased significantly in the fall between one and two months, but dropped somewhat by the third month, so that there was no significant difference between months two and three or one and three. In spring, the percentage cover increased significantly between months one and two and between months one and three, but the difference between months two and three was not significant. Contrasting colonization times among seasons, there were no differences in cover after one month, but cover was significantly lower after both two and three months in summer than in either fall or spring.

Although oysters were not successful in monopolizing space, bryozoans occupied from 40 to 60% of the available space after two months, although only in fall or spring.

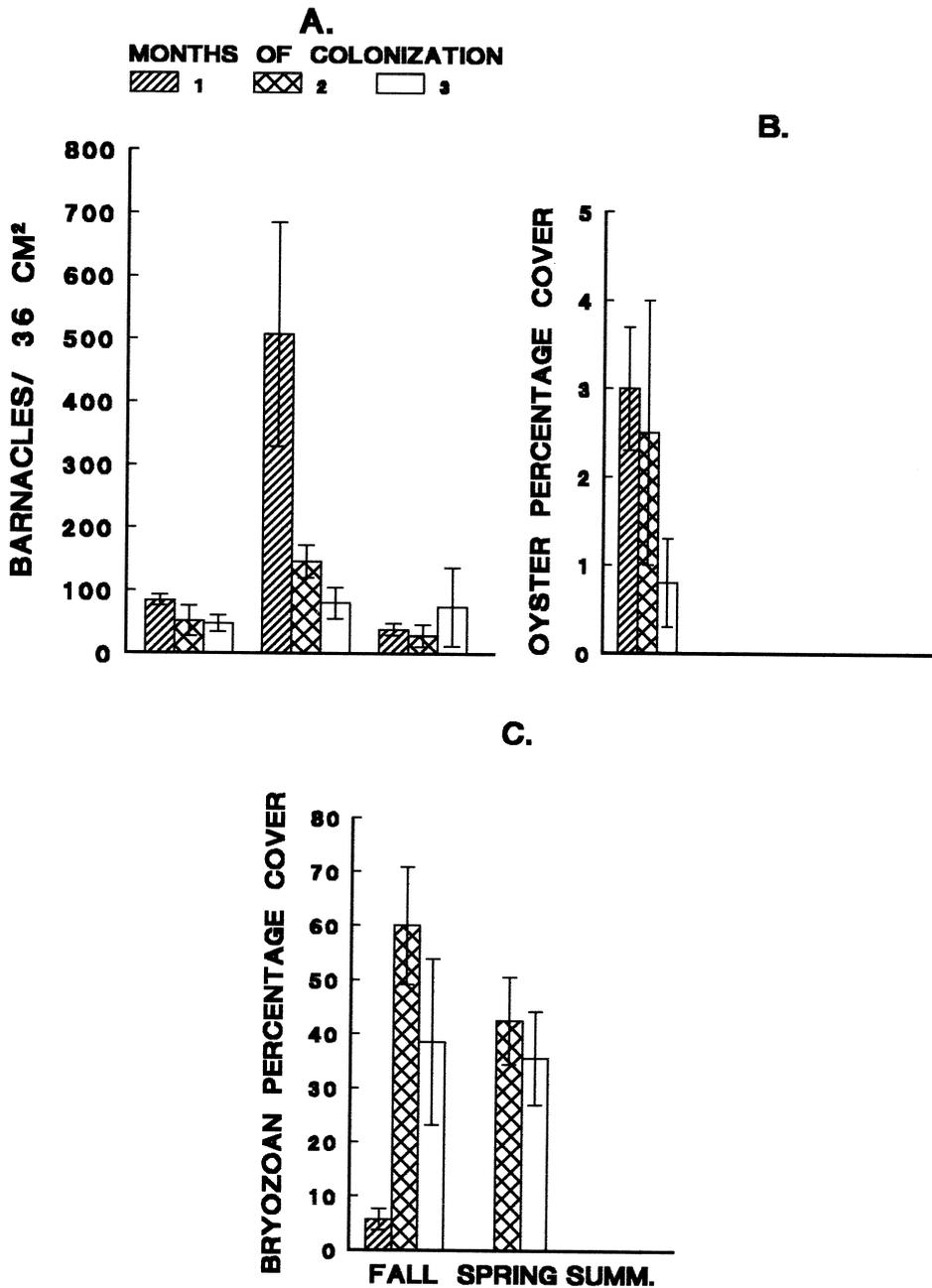


Fig. 2. (A) Colonization densities (mean \pm SE, $n = 4$) of the barnacle *Balanus eburneus* in three seasons for three immersion time periods. (B) Percentage cover (mean \pm SE, $n = 4$) of the oyster *Crassostrea virginica* in three seasons for three immersion periods. (C) Percentage cover (mean \pm SE, $n = 4$) of the bryozoan *Membranipora savatii* in three seasons for three immersion periods.

Table 1
Analysis of variance results for the seasonal colonization study

S.O.V.	Barnacle density ^a			Barnacle size ^a			Oyster cover ^b			Bryozoan cover ^b		
	M.S.	F	P	M.S.	F	P	M.S.	F	P	M.S.	F	P
Season	11.94	10.51	0.0004	3.50	8.46	0.002	144.08	20.31	<0.0001	2891.4	27.97	<0.0001
Time	3.94	3.47	0.046	3.44	8.32	0.002	8.91	1.26	0.30	1807.5	17.46	<0.001
Season × time	0.49	0.43	0.785	4.35	10.53	<0.0001	8.91	1.26	0.31	482.5	4.67	0.005

Sources of variation (S.O.V.), Mean squares (M.S.), *F* statistics and their associated probabilities are given. There were two degrees of freedom for season and immersion period (= time), four degrees of freedom for the interaction, and 27 error degrees of freedom

^a log transformed.

^b arc-sin square root transformed.

We observed numerous cases of bryozoans overgrowing barnacles, although, in most cases, the barnacles were still capable of extending their cirri and feeding. However, in no case was there any evidence of a significant negative correlation between the abundance of barnacles and the percentage coverage by either oysters or bryozoans in the regressions (Table 2).

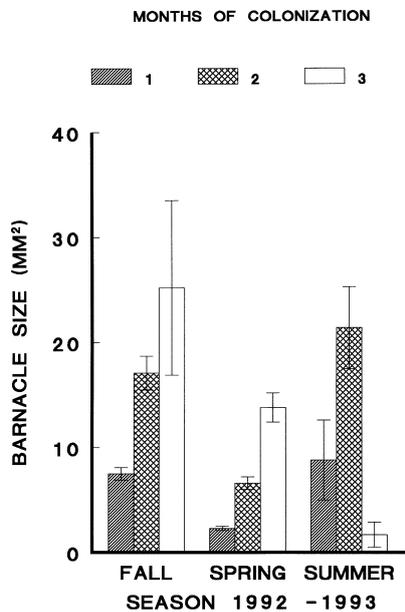


Fig. 3. Basal area (mean ± SE, *n* = 4) of the barnacle *Balanus eburneus* in three seasons for three immersion time periods.

Table 2

Regression statistics for univariate and multiple linear regressions of the dependent variables against the independent variables

Dependent variable	Independent variable	β	t	P
Barnacle density	Oyster cover	-12.4	-0.60	0.55
	Bryozoan cover	-1.3	-1.11	0.28
	Bryozoan + ^a	-1.2	-0.97	0.34
	oyster cover	-6.69	-0.31	0.76
Oyster cover	Barnacle density	-0.001	-0.60	0.55
	Bryozoan cover	0.02	1.66	0.11
	Barnacle +	-0.0004	-0.31	0.76
	bryozoan cover	0.016	1.55	0.13
Bryozoan cover	Barnacle density	-0.03	-1.11	0.28
	Oyster cover	4.76	1.65	0.11
	Barnacle +	4.48	1.54	0.13
	oyster cover	-0.02	-0.97	0.34

Statistics are the regression coefficient or partial regression coefficient (β), the value of the t statistic testing $\beta = 0$ and its associated level of probability. $n = 36$.

^a Multiple linear regression.

3.2. Caging study

Barnacle recruitment varied both among sites and among caging treatments, but the interaction was not significant (Table 3). The general trend was for coastal sites to have higher recruitment rates than estuarine sites, although the two coastal sites also had different recruitment rates (Fig. 4A). A posteriori contrasts indicated Caminada Pass had significantly higher recruitment rates than both estuarine sites as well as Belle Pass ($P < 0.05/4$ or 0.01). Belle Pass also had higher recruitment rates than both estuarine sites. Recruitment rates were similar between the two estuarine sites.

Table 3

Analysis of variance results for the caging study

S.O.V.	Barnacle density ^a			Barnacle size			Oyster cover ^b			Bryozoan cover ^b		
	M.S.	F	P	M.S.	F	P	M.S.	F	P	M.S.	F	P
Site	26.08	35.76	< 0.0001	197.06	4.79	0.005	35.60	5.40	0.003	262.56	3.26	0.028
Trt	3.50	4.79	0.012	43.96	1.07	0.35	14.65	2.22	0.12	258.68	3.21	0.048
Site \times Trt	1.10	1.50	0.19	151.50	3.68	0.004	11.06	1.68	0.14	136.82	1.70	0.139

Sources of variation (S.O.V.), mean squares (M.S.), F statistics and their associated probabilities are given. There were three degrees of freedom for site and two degrees of freedom for caging (= Trt), six degrees of freedom for the interaction and 66 error degrees of freedom

^a log transformed.

^b arc-sin square root transformed.

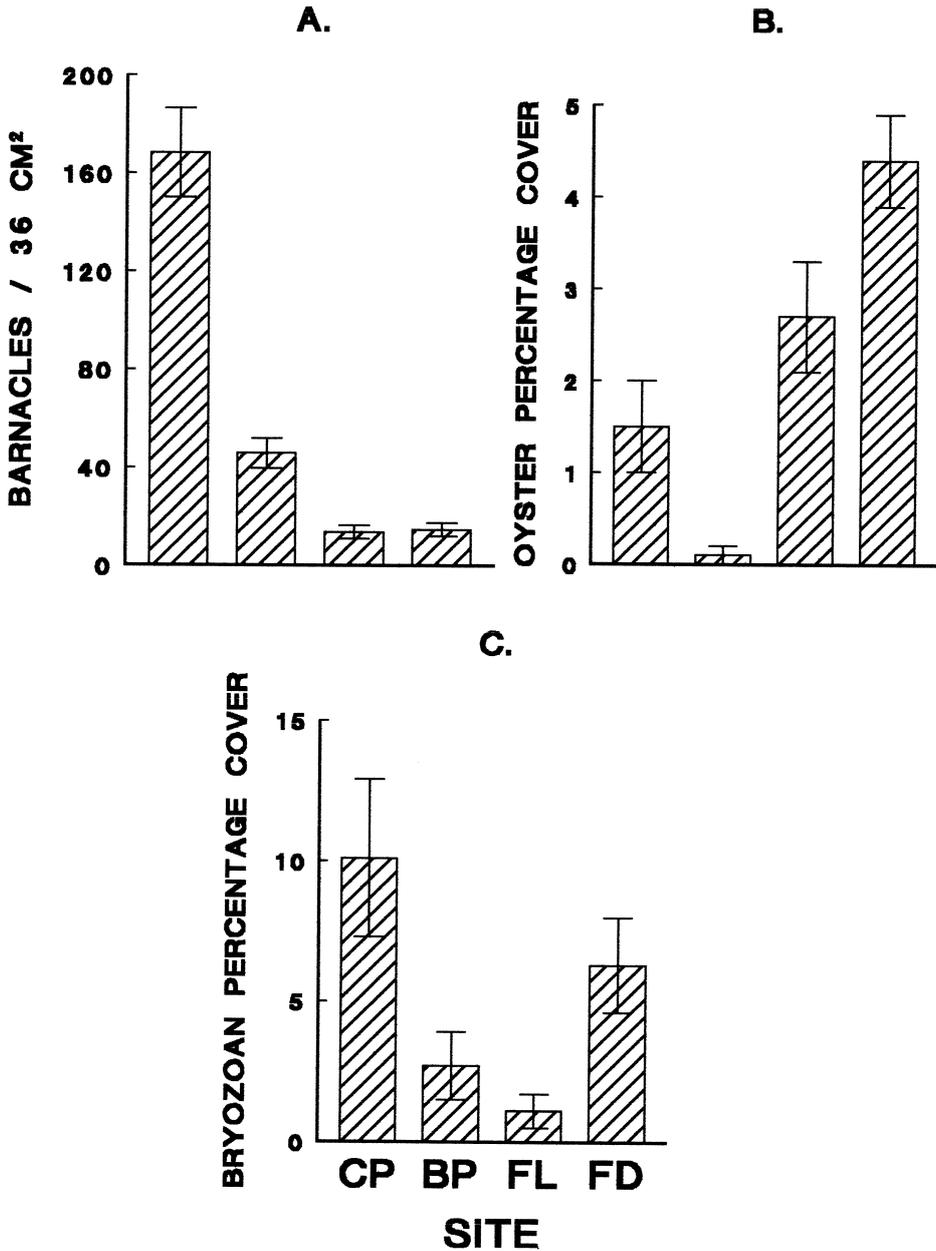


Fig. 4. (A) Colonization densities (mean±SE, n = 18) of the barnacle *Balanus eburneus* at four sites along the coast of Louisiana, pooled across all caging treatments. (B) Percentage cover (mean±SE, n = 18) of the oyster *Crassostrea virginica* at four sites along the Louisiana coast, pooled across caging treatments. (C) Percentage cover (mean±SE, n = 18) of the bryozoan *Membranipora savartii* at four sites along the Louisiana coast, pooled across all caging treatments. See legend to Fig. 1 for site acronyms.

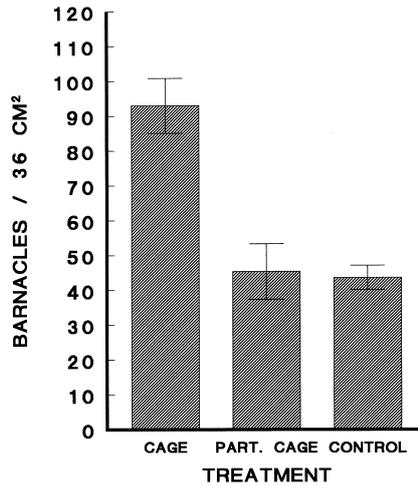


Fig. 5. Colonization densities (mean±SE, $n = 24$) of the barnacle *Balanus eburneus* on tiles completely or partially enclosed with vexar versus control (open) tiles, pooled across sites.

The differences in barnacle recruitment among the caging treatments conformed to the predictions if predation was important (Fig. 5). Caged tiles had significantly higher recruitment than either partially caged tiles or control tiles ($P < 0.05/3$ or 0.02). There was no significant difference between partially caged and control tiles.

Barnacle size also differed among sites (Fig. 6), but not treatments, although the

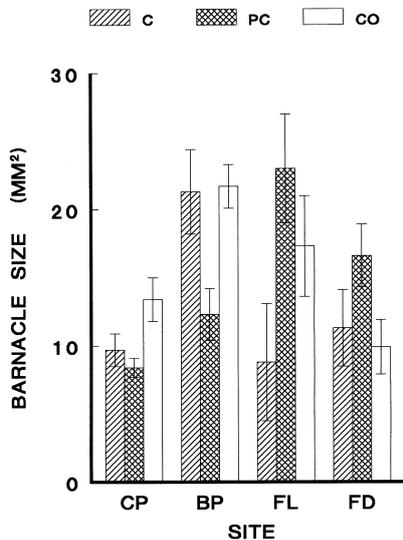


Fig. 6. Basal area (mean±SE, $n = 6$) of the barnacle *Balanus eburneus* at four sites along the Louisiana coast (see acronyms in the legend to Fig. 1) under three caging treatments (C = cage, PC = partial cage, CO = control).

interaction was significant (Table 3). The a posteriori contrasts indicated that barnacles were significantly greater in size at Belle Pass than at Caminada Pass ($P < 0.05/9$ or 0.006), but there were no other site-based differences. The significant interaction occurred because barnacles were significantly larger on control tiles than on partially caged tiles at exposed sites, but larger in partial cages at estuarine sites (Fig. 6).

For oysters, site-based differences in recruitment also occurred, and they were essentially the opposite of those observed in barnacles (Fig. 4B): The highest percentage cover occurred at the estuarine sites. The a posteriori contrasts indicated that recruitment was higher ($P < 0.05/4$ or 0.01) at both the Port Fourchon laboratory and Port Fourchon boat docks than at Belle Pass. Oyster recruitment at Caminada Pass was not significantly different than at any of the other sites. There was no effect of caging on oyster recruitment, nor was there an interaction between site and caging effects (Table 3).

Bryozoan percentage cover was significantly different between both sites and treatments (Table 3). The a posteriori contrasts indicated that recruitment differed ($P < 0.05/4$ or 0.01) only between Caminada Pass and the Fourchon laboratory (Fig. 4C). Comparisons among caging treatments indicated that percent coverages on control tiles were marginally lower (e.g., $P = 0.02$ or the same as $P = 0.05/3$) than those in partial cages.

4. Discussion

Our results were similar to those found in earlier studies of recruitment in other intertidal fouling assemblages in several ways. The species colonizing free space, as in those studies (Sutherland and Karlson, 1977; Osman, 1977; Underwood and Anderson, 1994), differ among seasons. In fall, all three of the most common species recruit to tiles, while in the spring, only bryozoans and barnacles recruit and, in the summer, only barnacles. Nor does there appear to be any unidirectional sequence of succession, also similar to earlier studies. Seasonal differences in recruitment rates are evidently caused by seasonal periodicities in adult reproduction and, thus, larval supply in the water column. Warm-water balanoid barnacles can reproduce throughout the year and produce as many as three broods (Moore and Frue, 1959; Patel and Crisp, 1960). Although oysters as a group are thought to recruit throughout the summer (Britton and Morton, 1989; Underwood and Anderson, 1994), Supan (1983) also found oysters to recruit most heavily in late summer and fall in Mississippi Sound. Similarly, several studies have also found bryozoans to reproduce mostly in fall or winter (Beaven, 1947; McGraw, 1980; Underwood and Anderson, 1994). Thus, our study suggests, as have earlier ones, that recruitment and successional patterns in marine fouling assemblages are heavily influenced by reproductive periodicities and lack of facilitation among intertidal fouling species.

Our results also corroborate the predicted differences in recruitment rates for barnacles between coastal and estuarine sites that are expected because larval abundances decrease as most larvae settle on the first available sites (Caffey, 1985; Gaines and Roughgarden, 1985; Raimondi, 1990; Sutherland, 1990; Minchinton and Scheibling,

1991). Oysters, on the other hand, recruited at higher rates to estuarine sites, also as expected from earlier studies, because they may survive better at the lower salinities found in estuarine areas along the Louisiana coast (Chatry et al., 1983).

Our results, however, also differed from past studies of intertidal fouling assemblages. We found little evidence that barnacle densities or percentage covers of oysters and bryozoans increased monotonically with time and, thus, that free space for colonization became limiting. Densities in several cases actually decreased with longer periods of immersion. We could, therefore, detect little evidence from our data that the abundances of the three dominant groups of organisms, barnacles, oysters and bryozoans, were negatively correlated on tiles. There appears to be little chance that species can competitively dominate space, as in other studies of intertidal fouling assemblages (Osman, 1977; Osman et al., 1989, 1992; Underwood and Anderson, 1994).

Our observations of natural substrata (e.g., rocks or pilings) indicate that the same patterns occur there as well. For example, there appear to be seasonal shifts in abundance (oysters and bryozoans are obvious in fall and winter, and barnacles in the spring and summer). Abundances of all three species are low overall, suggesting that there are high levels of post-settlement mortality. Thus, occupation of free space varies seasonally, similar to the “lottery” hypothesis proposed for coral reef fish (Sale, 1978).

The cage experiment suggested that this post-settlement mortality, at least for barnacles, could be caused by predation. The most likely predators are small xanthid and portunid crabs, which chip away barnacle shell (Britton and Morton, 1989), or the southern oyster drill, *Stramonita haemastoma*, which drills the shells (Brown and Richardson, 1987). We collected numerous small mud and blue crabs when tiles were retrieved, and oyster drill egg cases were collected on tiles retrieved in the spring, indicating that the snails can also colonize the tiles.

The lack of caging effects on abundance of oysters or bryozoans could be caused by a number of factors. Oyster percentage cover never reached above 5% over even the three month immersion periods. Perhaps over a longer time scale, growth of settled spat could eventually result in a higher percentage of cover, causing limitation of space, or predation on these larger oysters might become more important over long time scales. Oyster abundance was so low and variable in this study that we may thus simply not have been able to detect any effects of predators. Predators of bryozoans may include very small oyster drills (Garton, 1986) or predatory flatworms (Pearse and Wharton, 1938), which our mesh sizes would not exclude. Alternatively, these latter two species of colonizers may simply have been less susceptible to predation, although oysters are considered to be quite vulnerable to predation by oyster drills (Butler, 1985; Brown and Richardson, 1987).

In summary, patterns in the recruitment of the Gulf of Mexico fouling assemblage were similar to those occurring in other fouling assemblages. Seasonal periodicity in reproduction and, hence, larval availability, determined the final assemblage. Recruitment of barnacles and bryozoans was also greater at coastal sites, indicating that declining larval abundances limited recruitment at more estuarine sites, as in other studies (see above). However, abundances of colonists never reached the point where preemption of available space occurred, and, at least for barnacles, predation was an important part of the post-settlement mortality that limited the use of free space.

Acknowledgements

We acknowledge the assistance of D. McCoy in setting out tiles and T. Tran for counting the tiles. Funding for this study was provided by Louisiana Sea Grant.

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