

## The influence of resident adults on recruitment: a comparison to settlement

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### Abstract

For species recruiting into established sessile communities, the adult colonies and individuals already present form a significant part of the environment and have the potential to alter both larval settlement rates and post-settlement mortality. Settlement rates can be reduced by predation on larvae, by the removal or addition of substratum space, or by stimulation or prohibition of larvae from settling on adjacent substratum. Once attached, the recruiting individual can still be influenced by predation or overgrowth by residents, by the added physical structure for firmer attachment, or by being camouflaged from motile predators. To examine those processes by which residents affect recruitment we exposed experimental substrata with three densities of adults of a single species at a site in eastern Long Island Sound, USA for a 1-wk period. Seven different species of common invertebrates were used in nine separate experiments. The major effect of most resident species was the usurpation of space and the restricting of recruitment to adjacent unoccupied areas. This was particularly true for resident ascidians and bryozoans, but less so for barnacles and oysters. In fact several species recruited in higher densities on or next to oysters and barnacles. Comparison to 1-day settlement experiments indicated that the encrusting ascidian species *Diplosoma* and possibly *Botryllus* reduced recruitment relative to settlement, probably by overgrowing newly-settled individuals. However, in the presence of most resident species, recruitment patterns were not greatly different from settlement patterns, indicating that the effects of the attached community on recruitment may result from influences on settlement.

**Keywords:** Recruitment; Settlement; Benthic communities; Sessile Invertebrates; Ascidians; Bryozoans

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## 1. Introduction

The link between larval settlement and successful recruitment into a benthic community is not always straightforward. Post-settlement events (e.g. predation, competition, environmental change) can greatly influence the survival and growth of newly-settled individuals, causing significant differences between settlement and recruitment patterns. Even with large numbers of available larvae and high settlement rates, the number of individuals of some dominant species that survive to become successful recruits can be reduced drastically or eliminated by small predators (e.g. Thorson, 1966; Watzin, 1983; Stoner, 1990; Osman et al., 1992) or by changes in the physical environment (e.g. Osman et al., 1990; Osman & Abbe, 1995). Because of ontogenetic changes in size, energy reserves, morphology, etc., the responses of newly-settled individuals to the environment often cannot be predicted from observations of adult life-stages. For example, the tiny gastropods that prey on post-settlement ascidians have no measurable effect on adults (Osman et al., 1992). Likewise, oyster mortality resulting from exposure to deep, hypoxic water that intrudes into nearshore shallow areas of Chesapeake Bay only occurs in the 1–2 wk after larval metamorphosis and settlement (Osman & Abbe, 1995).

For species recruiting onto substrata occupied by sessile communities, adult colonies and individuals already present form a significant part of the environment. As such these residents have the potential to alter both larval settlement rates and post-settlement mortality. Settlement rates can be reduced most directly by predation on larvae (Mileikovsky, 1974; Cowden et al., 1984; Young & Gotelli, 1988; Bingham & Walters, 1989; Osman et al., 1989, Stoner, 1990). However, attached adults can also influence larval settlement by either removing or adding substratum space, depending on whether larvae can attach to and survive on the surfaces of the residents (Stebbing, 1972; Moyse & Hui, 1981; Morse & Morse, 1984; Osman & Whitlatch, 1995), or by stimulating or prohibiting larvae from settling on adjacent substratum (Grosberg, 1981; Kent & Day, 1983; Jensen & Morse, 1984; Havenhand & Svane, 1989; Bingham & Young, 1991). In the extreme, adults of certain species may be the exclusive (Osman & Haugness, 1981) or the most frequent (Osman, 1987) surfaces to which other species attach. Once attached, the recruiting individual can still be influenced by residents. Predation or overgrowth by residents can increase the mortality of recruits (Grosberg, 1981; Osman et al., 1989, 1992, Stoner, 1990; Hurlbut, 1991a,b; Dalby & Young, 1992). On the other hand, residents can indirectly increase survivorship by adding physical structure for firmer attachment or by camouflaging recruits from predators (Osman & Haugness, 1981; Osman, 1987).

Many studies have investigated in detail the effects on settlement of specific parameters likely to be associated with resident species such as water flow (e.g. Butman et al., 1988; Denny & Shibata, 1989; Pawlik et al., 1991; Mullineaux & Garland, 1993), chemical stimuli (e.g. Crisp, 1974; Mihm & Banta, 1981; Morse & Morse, 1984; Johnson & Strathmann, 1989; Coon et al., 1990; Bingham & Young, 1991), or substratum characteristics (e.g. Crisp & Barnes, 1954; Raimondi, 1988).

In general, these studies have indicated that environmental characteristics can have a strong effect on settlement. Others have examined the potential patterns or rates of recruitment within a community by exposing clean substrata (e.g. Osman, 1977; Sutherland & Karlson, 1977; Sutherland, 1978) or examining cleared areas (e.g. Kitching, 1937; Bokenham & Stephenson, 1938; Moore, 1939; Connell, 1961; Dayton, 1971, 1975; Sousa, 1979; Sutherland, 1990). These studies have demonstrated strong temporal and spatial variability in overall recruitment but have not been able to distinguish whether this variability resulted from changes in larval availability, settlement rate, or post-settlement mortality.

Recently, a few field studies have tried to assess recruitment in the presence of particular resident species (Young & Gotelli, 1988; Young, 1989). In general, these studies have found that the effects of residents observed in the laboratory, such as larval predation, are difficult to detect in the field. Thus, despite detailed studies of specific mechanisms (mostly in the laboratory), it is still not clear to what extent recruitment is generally a function of larval production and distribution or of the conditions of the local environment into which larvae potentially recruit. If the local environment does influence recruitment it is also uncertain whether this results from influences during larval settlement or from post-settlement processes.

Given the potential variety and complexity of influences on recruitment, we have focused on whether any of a variety of dominant species measurably influenced the recruitment of sessile invertebrates in the field. We sought to examine individually the effects of each species established on a substratum on all species recruiting at the time of an experiment. Our objectives were to determine if and how resident species actually changed recruitment patterns in the field rather than role of any specific mechanism such as passive or active alteration of water currents or the responses of larvae to physical or chemical cues. By contrasting any pattern to settlement patterns measured in a separate set of experiments, we also estimated the contribution of post-settlement processes to measured recruitment. A detailed analysis of these settlement patterns as well as a general model are presented in a companion paper (Osman & Whitlatch, 1995).

## 2. Methods

The study was conducted in the eastern end of Long Island Sound at the mouth of the Poquonock River. The field site was a moored raft behind a breakwater near Avery Point, Groton, Connecticut, USA. As reported previously (Osman et al., 1992), the community on the raft and in its vicinity was dominated by ascidians, including the colonial ascidians *Botryllus schlosseri* (Pallas), *Botrylloides diegensis* Ritter and Forsyth, and *Diplosoma macdonaldi* Herdman and the solitary ascidians *Molgula manhattensis* (DeKay), *Styela clava* Herdman, and *Ciona intestinalis* (L.). Other common species included the bryozoans *Cryptosula pallasiana* (Moll), *Bowerbankia gracilis* Leidy, and *Bugula turrita* (DeSar), the serpulid polychaetes *Hydroides dianthus* (Verrill) and *Spirorbis* spp., the barnacles *Balanus amphitrite* Darwin, *Semibalanus balanoides* (L.), and *Balanus eburneus*

Gould, the sponges *Halichondria* sp. and *Leucosolenia* sp., and the hydroid *Obelia* sp.

The primary objectives of our experiments were to determine the effects of dominant species on the recruitment of all species recruiting at the time of the experiment and to contrast these observed patterns of recruitment with settlement patterns observed in separate experiments (Osman & Whitlatch, 1995). To compare recruitment and settlement patterns it was important to develop reasonable measurements of both processes. As we described previously (Osman & Whitlatch, 1995), larval settlement was measured for each species over 1 day, the shortest period over which we could reasonably collect data. In comparison, recruitment is the cumulative larval settlement over some longer period of time minus any post-settlement mortality during that same period. In most studies, the length of the recruitment period has usually been arbitrary, defined as the shortest reasonable period over which it can be measured in the context of the particular study. In most studies it was hoped or assumed that the period was sufficiently short to minimize any effects of post-settlement mortality.

However, to determine the significance of any post-settlement mortality, we needed a recruitment period of sufficient length to allow this mortality to occur, but short enough that the number of recruits or their growth did not reduce further settlement by limiting available space. We based our choice of a recruitment period on a preliminary experiment conducted in 1987 at the two sites in Woods Hole, Massachusetts, USA described by Osman et al. (1992). One site, Eel Pond, had settlement rates 2 to 3 orders of magnitude higher than the other, Vineyard Sound. At each site 100 cm<sup>2</sup> PVC panels were exposed on racks which held them horizontal and face-down,  $\approx$  1 m below MLW. To measure settlement, a pair of panels was sampled at each site every 2 days and replaced by a clean pair. After 8 and 16 days, two panels that were continuously exposed at each site were also sampled to measure recruitment. All individuals of all species were counted on the panels and cumulative means for the pairs of 2-day panels were compared to means for the 8- or 16-day panels. These comparisons (Fig. 1) suggest that recruitment measured over 8 days is not reduced from what is predicted from cumulative settlement. However, in the presence of high settlement rates (Eel Pond), recruitment measured over 16 days was significantly less than expected from cumulative settlement, suggesting space limitation. Therefore, based on these results, we used a 1-wk recruitment period in all of our experiments.

A total of nine recruitment experiments were conducted between 1989 and 1992 using barnacles (*Balanus* spp.), the oyster *Crassostrea virginica*, the erect bryozoan *Bugula turrita*, or one of four dominant ascidians (*Botryllus schlosseri*, *Botrylloides diegensis*, *Diplosoma macdonaldi*, or *Molgula manhattensis*) as adult residents. Experiments were conducted in five groups; 1 group of 2 (*Balanus* and *Crassostrea*) in 1989, groups of 3 (*Botryllus*, *Balanus*, and *Crassostrea*) and 2 (*Botrylloides* and *Bugula*) in 1990, and 2 single experiments (*Diplosoma* and *Molgula*) in 1992. Within each group a common set of control treatments was

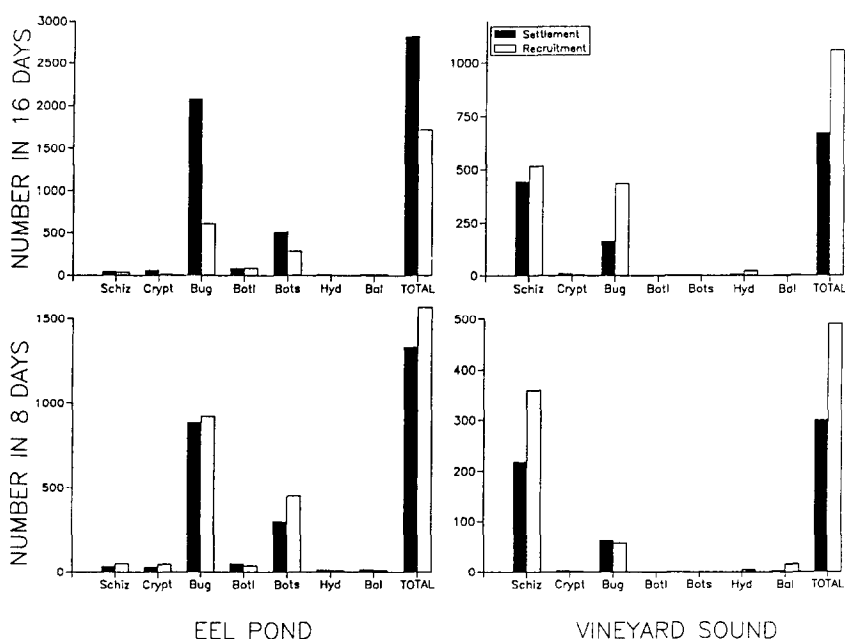


Fig. 1. Comparison of mean recruitment and cumulative settlement over 8- and 16-day periods on panels deployed at two sites (Vineyard Sound and Eel Pond) in Woods Hole, Massachusetts. Data are for the bryozoans *Schizoporella errata* (Schiz), *Cryptosula pallasiana* (Crypt), and *Bugula turrita* (Bug), the ascidians *Botrylloides diegensis* (Botl) and *Botryllus schlosseri* (Bots), the serpulid polychaete *Hydroides dianthus* (Hyd), and barnacles of the genus *Balanus* (Bal). Also shown are the total number of individuals of these and all other species (TOTAL).

used. The choice of test species was usually determined by which species were most abundant at the time of the experiment.

The general design of each experiment was to compare recruitment on equal-sized substrata which systematically varied in the percentage of their surface covered by a resident adult test species. Three cover treatments were used: (1) control substrata with no cover of the test species, (2) low-cover substrata with 30–50% cover of the test species, and high-cover substrata with 70–90% cover of the test species. Two methods were used to produce these treatments. For all but the oyster and *Molgula* experiments, 100 cm<sup>2</sup> PVC panels were exposed in the field 1–3 months prior to the beginning of an experiment. These substrata were examined weekly and all species except the chosen test species (usually the most abundant species) were removed. This was continued until most substrata had > 70% cover. At this time all substrata were carefully cleaned of all other species and assigned to one of the three treatments. Excess individuals or colonies of the test species were haphazardly removed until the assigned%-cover was reached. For the oyster experiments, juvenile oysters were obtained from a local grower, cleaned, and then glued onto clean 100 cm<sup>2</sup> substrata in densities of 0, 3, and 6

individuals. For the *Molgula* experiment, adult *Molgula* were collected in the field, cleaned, and then glued onto substrata in densities of 0, 10, and 20 individuals. All substrata were held for 24 h in filtered (5  $\mu$ m) running seawater before beginning an experiment.

In addition to the three cover treatments, high- and low-cover adult-mimic treatments were included in the 1989 and 1990 experiments. The mimic treatments were designed to simulate the potential changes in the local environment caused by the physical presence of the test species. Barnacle mimic treatments were created by removing a subset of barnacle panels from the water and drying them in the open air for 2 wk. In the 1990 experiments, the barnacle tests were also covered by a thin layer of epoxy. Oyster mimics were created by gluing together the clean valves of dead oysters and attaching these onto panels in the same densities as the regular oyster treatments. Encrusting ascidians were mimicked by covering parts of panels with a layer of silicone sealant approximately as thick as the colonies. Finally, shredded tufts of polypropylene rope glued to panels were used to mimic *Bugula*.

In 1989 and 1990, five panels of each treatment were used in each experiment while in the 1992 experiments eight panels were used per treatment. These panels were randomly assigned to positions on panel racks suspended from the field raft. Panel racks were similar in design to those used by Osman (1982) and Osman et al. (1989). When in the field the racks were suspended below the field raft such that they held the panels  $\approx$  1 m below the water surface (1–2 m above the bottom). All panels were oriented horizontally with the test surface facing the seafloor. In each experiment, panels were exposed in the field for 1 wk and then returned to the laboratory where all new recruits of all species were identified and counted. Individuals attached to the panel surface and those on the test species were counted separately.

No treatments were designed in which predators were excluded. Known benthic predators of newly-settled individuals (Osman et al., 1990, 1992) were not observed at the study site and we saw no evidence of removal of any of the test species from the panels during the course of any experiment. Even though our previous studies (Osman et al., 1990, 1992; Osman & Whitlatch, 1995) have shown no evidence of fish predation on newly-settled individuals of any species, we cannot rule out the possibility that predation could contribute to any observed differences between treatments. However, since all treatments would have been exposed equally to predators, any such differences would have resulted from the direct or indirect influence of the test species on predation of newly-settled individuals.

### 2.1. Analysis

Our primary goals were to test whether the attached adults of any test species affected recruitment and whether recruitment patterns differed from settlement patterns (see Osman & Whitlatch, 1995). Four groups of analyses were conducted to (1) examine the overall effects of each taxa of resident adults on recruitment,

(2) compare the responses of recruiting species to different resident taxa, (3) compare the effects on recruitment of resident taxa and mimics, and (4) contrast recruitment patterns with settlement patterns.

*Overall effects of adults on recruitment.* The effect of each of the seven taxa of adults on recruitment was examined separately for each of the recruiting species. Because the goal of these analyses was to determine the overall effect of living residents, mimic treatments were excluded from these analyses. Analyses were conducted using one-way ANOVA's (1) to test the effect of each adult species on the total recruitment of a species (numbers on panel and adult surfaces combined) and (2) to examine differences in recruitment onto adult surfaces and adjacent panel surfaces. In the latter analyses the density of recruits on each surface was used to correct for the differences in relative area of the available substrate types. In these analyses data were grouped by treatment and surface type, resulting in five groups of surfaces that were analyzed using a one-way ANOVA (panel and species surfaces on high-cover substrata, panel and species surfaces on low-cover substrata, and control panel surfaces). Densities were computed using estimates of the mean percent cover of adults (0, 40, or 80%) and open space (100, 60, or 20%) in each treatment (control, low-, and high-cover). Because of heterogeneity in variances, the data were log-transformed for all analyses.

*Response of recruits to different species of adults.* We also conducted analyses to examine whether recruitment for some species differed as a function of the species of adult that was present on the substratum. We examined this by comparing the recruitment of each species among all nine experiments. To correct for the variation in larval availability among the experiments, the density of individuals of each species recruiting onto panel or adult surfaces in each experiment was standardized to the mean density found on control panels in the same experiment. Data for recruitment onto panel surfaces and the surfaces of the adults were analyzed separately and differences among the six adult treatments were analyzed using ANOVA. Each recruiting species was analyzed separately.

*Comparison of mimics and regular panels.* As in the overall analyses, the data were grouped by treatment and surface type. This resulted in nine groups of surfaces (panel and species surfaces on high- and low-cover substrata with living species, panel and mimic surfaces on high- and low-cover mimic substrata, and control panel surfaces). Each of the recruiting species was analyzed separately for each of the seven experiments with mimics using one-way ANOVA's to compare the nine groups of recruitment densities. Four a priori contrast analyses were conducted to compare recruitment densities between: (1) mimic surfaces and the surfaces of living species, (2) panel surfaces on mimic and living species treatments, (3) species and panel surfaces in living species treatments, and (4) mimic and panel surfaces in mimic treatments. In addition, recruitment density on each of the two surface types within each of the four treatments was compared to densities on control panels using Dunnett's test.

*Comparison of recruitment and settlement patterns.* For those resident species used in both recruitment and settlement experiments (*Botryllus*, *Botrylloides*, *Diplosoma*, and *Molgula*) recruitment and settlement patterns were compared

directly using ANOVA. Because mimic treatments were not used in settlement experiments, these were not included in the analyses. Data were also standardized as a percentage of the mean settlement or recruitment densities observed on control panels in each experiment to correct for the obvious differences in absolute numbers for settlement and recruitment as well as any temporal differences in the availability of recruits. A one-way ANOVA, similar to that used in contrasting mimic and living species, was used to analyze the data. Similar to previous analyses, nine groups were used, consisting of recruitment and settlement densities on panel and species surfaces in high- and low-cover treatments ( $2 \times 2 \times 2$ ) plus controls. As in the mimic analyses, four a priori contrast analyses were conducted to compare: (1) recruitment and settlement between panel surfaces, (2) recruitment and settlement between the surfaces of resident species, (3) recruitment between species and panel surfaces, and settlement between species and panel surfaces.

Five basic assumptions were made in all analyses of the experiments. Firstly, it was assumed that the recruitment of each particular species was independent of all other species recruiting. The preliminary experiment conducted in Woods Hole (Fig. 1), suggests that this assumption is reasonable over the 1-wk recruitment period chosen.

Secondly, it was assumed that the effect of an adult test species on recruitment was independent of any temporal variation in the density of settling larvae. If a major effect of test species is usurpation of space and settling densities exceeded those observed in Eel Pond (Osman et al., 1992; Osman & Whitlatch, 1995, Fig. 1), then this assumption would not necessarily be valid. However, settlement densities at our study site did not reach these levels during any recruitment experiments.

Thirdly, to contrast the effects of the different test species on the recruitment of a particular species, we had to assume that no temporal differences existed in larval behavior, adult behavior, or the manner in which the test adults affected the local environment on a substrate. It was impossible to conduct all the experiments at the same time and even though environmental conditions did change somewhat between years, all experiments were conducted during the summer. We felt that the basic relationships between recruiting individuals and resident adults would remain the same.

Fourthly, we assumed that all substrata within an experiment were exposed to equal abundances of larvae contacting them.

Finally, we assumed that the any observed differences between recruitment and settlement patterns resulted from a significant influence of post-settlement processes.

### 3. Results

During the course of the experiments, at least 20 recognizable sessile invertebrate taxa recruited; including 2 sponges, 1 hydroid, 6 bryozoans, 2 barnacles, 6



ascidians, and 3 polychaetes. Of these, 6 taxa recruited in sufficient abundance to be analyzed; these included the ascidians *Botryllus schlosseri*, *Botrylloides diegenis*, and *Diplosoma macdonaldi*, the bryozoans *Bugula turrita*, serpulid polychaetes of the genus *Spirorbis*, and barnacles of the genus *Balanus*. For all six taxa, the number of recruits on control panels varied greatly among the different sets of experiments (see Figs. 2–7), reflecting, in part, within and between year changes in larval availability. Although this variability made it difficult to compare directly the results of experiments conducted at different times, it represents a range of recruitment densities and the effects that adults are likely to have on this recruitment.

### 3.1. Overall effects of adults on recruitment

Although the resident adults did have a significant effect on the total recruitment of some species, in most cases (67% of the analyses) no significant differences were found among the three treatments (Table 1). In particular, none of the six recruiting species exhibited any differences among treatments in the *Botrylloides* and *Molgula* experiments or in the 1989 barnacle and oyster experiments. Opposite to this, all six species recruited in significantly higher numbers onto control substrata in the *Diplosoma* experiment. In the remaining experiments recruitment patterns were mixed. In the *Botryllus* experiment the recruitment of *Botryllus*, *Bugula*, and *Spirorbis* were all significantly higher on control substrata while *Balanus* recruitment was highest in the high-cover treatment. Only *Bugula*, which is known to aggregate (Buss, 1981), exhibited any difference among treatments in the *Bugula* experiment, recruiting in significantly higher numbers in the presence of adults. *Botryllus*, as in other experiments, recruited in significantly higher numbers onto control treatments in both the 1990 barnacle and oyster experiments while *Spirorbis* displayed significantly increased recruitment in the low-cover treatments of these experiments. Finally, in the 1990 barnacle experiment, *Diplosoma* exhibited the same pattern as *Spirorbis* and *Balanus* recruited in significantly higher numbers onto high- and low-cover treatments.

The causes for the different patterns are more apparent when the abundance of recruits is partitioned between panel and adult surfaces (Table 2). In general there appear to be two distinct types of patterns; those with little, if any, recruitment onto attached adults (ascidian and *Bugula* experiments) and those in which substantial recruitment onto adult surfaces occurred (barnacles and oyster experiments).

Recruitment onto *Diplosoma* and arborescent *Bugula* colonies was never observed for any species and recruitment onto *Botryllus*, *Botrylloides*, and *Molgula* was universally low. For all species in the *Diplosoma* experiment except *Balanus*, and recruiting *Botryllus* in the *Botryllus* experiment, the recruitment density on controls was significantly higher than onto other surfaces (Table 2). The density of recruitment for most of the remaining species in the ascidian and *Bugula* experiments was significantly higher onto panel surfaces (including control

Table 1  
Differences among treatments within experiments in total recruitment

Recruit	93 <i>Borysthus</i>			90 <i>Borysthodes</i>			90 <i>Bugula</i>			89 <i>Balanus</i>			90 <i>Balanus</i>			89 <i>Oyster</i>			90 <i>Oyster</i>			92 <i>Diplosoma</i>			92 <i>Molgula</i>		
	Low	High	Cntl	Cntl	Low	High	Cntl	Low	High	Cntl	Low	High	Cntl	Low	High	Cntl	Low	High	Cntl	Low	High	Cntl	Low	High	Cntl		
<i>Diplosoma</i>	4	4	4	3	3	2	3	2	1	31	27	17	6	4	2	29	25	17	13	7	4	349	27	16	556	523	508
<i>Borysthus</i>	Cntl	Low	High	Cntl	Low	High	Cntl	Low	High	Cntl	Low	High	Cntl	Low	High	Cntl	Low	High	Cntl	Low	High	Cntl	Low	High	Cntl	Low	Cntl
	59	6	4	43	20	11	43	22	13	7	6	4	59	25	6	6	4	2	59	34	15	16	1	0	23	18	15
<i>Borysthodes</i>	Cntl	Low	High	Cntl	Low	High	Cntl	Low	High	Cntl	Low	High	Cntl	Low	High	Cntl	Low	High	Cntl	Low	High	Cntl	Low	High	Cntl	Low	Cntl
	4	2	1	19	10	7	19	14	13	35	26	21	4	4	1	21	20	15	4	3	2	13	2	1	20	17	16
<i>Bugula</i>	Cntl	Low	High	Cntl	Low	High	Cntl	Low	High	Cntl	Low	High	Cntl	Low	High	Cntl	Low	High	Cntl	Low	High	Cntl	Low	High	Cntl	Low	High
	30	7	4	45	28	21	139	44	28	66	45	36	30	9	7	74	45	38	30	17	16	22	4	2	95	76	64
<i>Sporobolus</i>	Cntl	Low	High	Cntl	Low	High	Cntl	Low	High	Cntl	Low	High	Cntl	Low	High	Cntl	Low	High	Cntl	Low	High	Cntl	Low	High	Cntl	Low	Cntl
	198	65	43	97	72	34	95	74	72	73	57	29	279	198	120	123	100	74	315	265	198	131	8	4	94	64	47
<i>Balanus</i>	High	Low	Cntl	Low	High	Cntl	High	Low	Cntl	High	Low	Cntl	High	Low	Cntl	High	Low	Cntl	High	Low	Cntl	Cntl	Low	High	High	Low	Cntl
	7	2	0	7	2	2	6	4	2	215	169	103	8	5	0	22.4	176	103	5	3	0	4	1	1	0	0	0

Total recruitment includes recruitment onto panel surfaces and onto the surfaces of the resident adults. Treatments were High and Low percent cover of the resident species and controls with the resident species removed. Each column represents a separate experiment and is identified by year and resident species used. Analyses based on log-transformed data, but untransformed means in numbers of individuals recruiting are shown in the table.

*Botrylloides* experiment. These patterns suggest that recruitment onto panel surfaces adjacent to *Bugula*, *Molgula*, and *Botrylloides* was equal to or higher than that observed on control panels. Thus, the data indicate that some species have the general effect of removing available space or “shading” underlying space from recruitment with many of those individuals that do not attach to adult colonies possibly moving and attaching onto adjacent panel surfaces.

In contrast, most species were able to recruit onto the shells of barnacles and oysters, resulting in a broader range of recruitment patterns exhibited in these experiments (Table 2). No consistent significant differences among treatments in recruitment density were seen for *Diplosoma*, *Botrylloides*, *Bugula*, and *Spirorbis*. Contrary to this pattern, *Botryllus* recruitment density was significantly higher on control panels in both the 1990 barnacle and oyster experiments and thus were similar to that observed in other experiments. However, in 1989, when *Botryllus* recruitment was very low, no significant patterns were observed. Finally, barnacles exhibited the strongest recruitment patterns in the presence of adult barnacles and oysters. Barnacle recruitment was enhanced in the presence of adults of both species. In the barnacle experiments recruitment densities were highest on the panel surfaces with adults present while in the oyster experiments barnacle recruitment densities were highest on surfaces of the oysters.

Even though some patterns can be discerned it is important to note that in many analyses significant differences in recruit densities were not observed. In addition, there was a high degree of variability, both among replicates within groups as well as between the results of experiments that were repeated in both years. However, recruitment patterns seemed to be a consequence of whether recruits responded to resident adults as either alternative substratum or not. If a resident adult was avoided, it reduced available attachment sites which may have reduced overall recruitment to the whole substrate but may also have enhanced recruitment density on panel surfaces adjacent to the resident species. If recruits responded to resident adults as additional substrate, overall recruitment may have been unchanged or even enhanced.

### 3.2. Response of recruits to different species of adults

When recruitment was compared among the different experiments (Table 3), the most consistent patterns observed were that (1) all species recruited in significantly lower numbers onto panels surfaces when *Diplosoma* was present and (2) most species recruited in low numbers onto the surfaces of adults other than *Balanus* and oysters.

The recruitment patterns of the three species of ascidians did not differ greatly from the general pattern. As well as recruiting in lower numbers near *Diplosoma*, both *Botryllus* and *Botrylloides* exhibited low recruitment onto panel surfaces adjacent to *Botryllus*. With only a few exceptions, all three also recruited in universally low numbers onto adult surfaces. Recruitment for all three species was significantly higher on barnacles and oysters than on *Diplosoma*, *Botrylloides*, and *Bugula*. Ascidian recruitment onto *Molgula* and *Botryllus* was generally inter-

panels) than onto the surfaces of resident adults. In the *Bugula*, *Molgula*, and *Botrylloides* experiments, recruitment was usually densest on panel surfaces in the high-density treatment. However, this pattern was usually not significant in the *Botrylloides* experiment. These patterns suggest that recruitment onto panel surfaces adjacent to *Bugula*, *Molgula*, and *Botrylloides* was equal to or higher than that observed on control panels. Thus, the data indicate that some species have the general effect of removing available space or “shading” underlying space from recruitment with many of those individuals that do not attach to adult colonies possibly moving and attaching onto adjacent panel surfaces.

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Even though some patterns can be discerned it is important to note that in many analyses significant differences in recruit densities were not observed. In addition, there was a high degree of variability, both among replicates within groups as well as between the results of experiments that were repeated in both years. However, recruitment patterns seemed to be a consequence of whether recruits responded to resident adults as either alternative substratum or not. If a resident adult was avoided, it reduced available attachment sites which may have reduced overall recruitment to the whole substrate but may also have enhanced recruitment density on panel surfaces adjacent to the resident species. If recruits responded to resident adults as additional substrate, overall recruitment may have been unchanged or even enhanced.

### 3.2. Response of recruits to different species of adults

When recruitment was compared among the different experiments (Table 3), the most consistent patterns observed were that (1) all species recruited in significantly lower numbers onto panels surfaces when *Diplosoma* was present and (2) most species recruited in low numbers onto the surfaces of adults other than *Balanus* and oysters.

The recruitment patterns of the three species of ascidians did not differ greatly from the general pattern. As well as recruiting in lower numbers near *Diplosoma*, both *Botryllus* and *Botrylloides* exhibited low recruitment onto panel surfaces

Table 3  
Comparison of the effects of the seven species of resident adults on the recruitment density of six taxa

Species recruiting	Recruitment onto panels						Recruitment onto species							
	Oyster	Molgula	Boryllioides	Balanus	Boryllus	Bugula	Diplosoma	Oyster	Balanus	Boryllus	Molgula	Diplosoma	Bugula	Boryllioides
Diplosoma	98	96	73	68	61	53	6	112	71	48	6	0	0	0
Boryllus	Molgula	Balanus	Bugula	Boryllioides	Oyster	Boryllus	Diplosoma	Balanus	Oyster	Molgula	Boryllioides	Diplosoma	Boryllus	Bugula
	56	42	42	34	31	8	2	21	16	16	1	1	1	0
Boryllioides	Molgula	Bugula	Boryllioides	Balanus	Oyster	Boryllus	Diplosoma	Balanus	Oyster	Molgula	Boryllus	Diplosoma	Bugula	Boryllioides
	83	70	43	42	32	12	11	60	37	21	18	1	0	0
Bugula	Bugula	Boryllioides	Molgula	Oyster	Balanus	Boryllus	Diplosoma	Oyster	Balanus	Molgula	Boryllioides	Boryllus	Diplosoma	Bugula
	310	97	55	32	31	12	12	58	39	19	17	6	1	0
Spirorbis	Molgula	Bugula	Boryllioides	Oyster	Balanus	Boryllus	Diplosoma	Oyster	Balanus	Molgula	Boryllus	Boryllioides	Diplosoma	Bugula
	159	119	85	60	46	24	5	89	34	10	4	0	0	0
Balanus	Boryllus	Balanus	Bugula	Boryllioides	Molgula	Diplosoma	Oyster	Oyster	Balanus	Bugula	Boryllus	Diplosoma	Molgula	Boryllioides
	430	260	241	222	167	28	20	277	154	0	0	0	0	0

To correct for differences in larval abundances between experiments data were analyzed as a percentage of the control during each experiment. Data were log-transformed for analyses but untransformed means (in % of control) are shown. Lines connect species of resident adults which had no significant difference on the recruitment of each larval species either onto panel surfaces or species surfaces.

adjacent to *Botryllus*. With only a few exceptions, all three also recruited in universally low numbers onto adult surfaces. Recruitment for all three species was significantly higher on barnacles and oysters than on *Diplosoma*, *Botrylloides*, and *Bugula*. Ascidian recruitment onto *Molgula* and *Botryllus* was generally intermediate between these extremes. *Diplosoma* and *Botrylloides* did exhibit a fair amount of recruitment onto *Botryllus* while *Botryllus* and *Botrylloides* showed a similar pattern for *Molgula*.

*Bugula* recruitment was not greatly different from that seen for the ascidians. The bryozoan recruited in significantly higher numbers onto oysters, barnacles, and *Molgula* than onto *Diplosoma* and *Bugula*. However, *Bugula* did recruit in significantly higher numbers near adult *Bugula* than near most of the other species; again confirming its tendency to aggregate.

Recruiting *Spirorbis* exhibited strong differences in their reactions to resident adults. *Spirorbis* avoided recruiting onto ascidians and *Bugula* while recruiting in significantly higher numbers onto oysters and *Balanus*. The residents also influenced *Spirorbis* recruitment onto adjacent panel surfaces in contrasting ways. Recruitment near *Molgula* and *Bugula* was significantly higher than near all other adults except *Botrylloides*. The results suggest that the *Spirorbis* that avoided recruiting onto the surfaces of *Bugula*, *Molgula*, and *Botrylloides* recruited onto adjacent substrate, enhancing numbers there. However, in the presence of *Botryllus* and *Diplosoma* this enhancement either did not occur or the recruits on adjacent panel surfaces may have suffered higher mortalities. Finally, because *Spirorbis* recruitment onto oysters and barnacles was not inhibited, numbers on adjacent substrata apparently were not elevated and thus were lower than seen in the *Molgula* or *Bugula* experiments.

Finally, recruiting barnacles responded to the resident species as two distinct groups. As with other recruiting species they avoided recruiting onto ascidians and *Bugula* and recruited in significantly higher densities on oysters and adult barnacles. Recruitment onto adjacent panel surfaces was partially influenced by this pattern with the lowest recruitment in the oyster experiments and highest in the *Botryllus* experiment. Recruitment onto panel surfaces in all the remaining experiments except *Diplosoma* was higher than onto control panels, but intermediate from the extremes. The high recruitment onto both panel and species surfaces in the barnacle experiments suggests that there may have been some kind of attraction or aggregation response.

### 3.3. Comparison of mimics and regular panels

The rationale for using mimics was to duplicate the structural changes created by the presence of a particular species without any of the potential biological interactions (e.g. predation on larvae, post-settlement overgrowth, alteration of water currents resulting from resident feeding activities). Unfortunately, the response of recruits to the mimics was varied and difficult to interpret. For example, recruitment onto the thin layer of silicone cement used to mimic cover by ascidians in two separate experiments was generally lower than onto control

panels as well as higher (but usually not significantly different) from recruitment onto live ascidians (Figs. 2–7). It is likely that the silicone was not perceived as substrate equal to that of panel surfaces and this could have altered any effect of physical structure. Likewise in the 1989 barnacle experiment, black, anoxic areas developed around the bases of the dead barnacles used as mimics and could have affected results. The coating of barnacles in the 1990 experiment resulted in both the removal of any response to the shell material of the barnacles as well as presenting recruits with another type of unnatural substrate. No species recruited onto the polypropylene tufts used to mimic *Bugula*. As in the ascidian experiments, this altered the ability of the mimic treatments to test for the influence of structure alone. Finally, in the oyster experiments mimics were identical to the live oysters except for their lack of a living organism. However, oyster shell may have been more or less attractive as a substrate than panel surfaces, causing differences within treatments. Differences between treatments should have resulted from the activities of the oysters and any larval response to them.

Figs. 2–7 compare recruitment densities of each of the six recruiting species in the seven experiments which had mimic treatments. For comparison, the results of the *Diplosoma* and *Molgula* experiments, which had no mimic treatments, are also shown.

The results for *Botryllus* recruitment are shown in Fig. 2. In all experiments the *Botryllus* recruitment pattern suggested a negative effect of structure. *Botryllus* densities were consistently lower on the surfaces of species and mimics than on control and adjacent panel surfaces. In three of the experiments (*Botryllus*, *Botrylloides*, and 1989 *Balanus*), significant differences were found in recruitment between mimic and species surfaces. Lower densities on the surfaces of *Botryllus* and *Botrylloides* compared to mimic surfaces suggest that these encrusting ascidians had a negative effect on *Botryllus* recruitment in addition to that of structure. The opposite pattern was seen in the 1989 *Balanus* experiment, suggesting a positive effect of the barnacle coupled with a negative structural effect. Given the lack of a similar pattern in the 1990 *Balanus* experiment suggests that the development of anoxic areas on panel surfaces around the bases of the barnacles in the 1989 experiment may have been the cause rather than any positive effect of the adult barnacles. Finally, a strong reduction in recruitment density was also seen on panel and species surfaces in the *Diplosoma* experiment and suggests a strong negative effect of this species on recruitment.

The recruitment patterns of *Botrylloides* (Fig. 3) and *Diplosoma* (Fig. 4) are similar to those for *Botryllus* but the effect of structure on both species seems to be fairly weak. No significant differences were found for either species in the 1990 *Balanus* or oyster experiments. However, both species did recruit in higher densities on adjacent panel surfaces than on species and/or mimic surfaces in the *Botrylloides*, *Diplosoma*, *Molgula*, *Bugula*, and 1989 oyster experiments. Similar to *Botryllus*, both species recruited in significantly higher densities on barnacles than on mimics in the 1989 experiment, again suggesting a positive barnacle (or negative anoxia) effect. Also, negative species effects were indicated by significantly lower *Botrylloides* recruitment onto adult *Botrylloides* than onto mimics

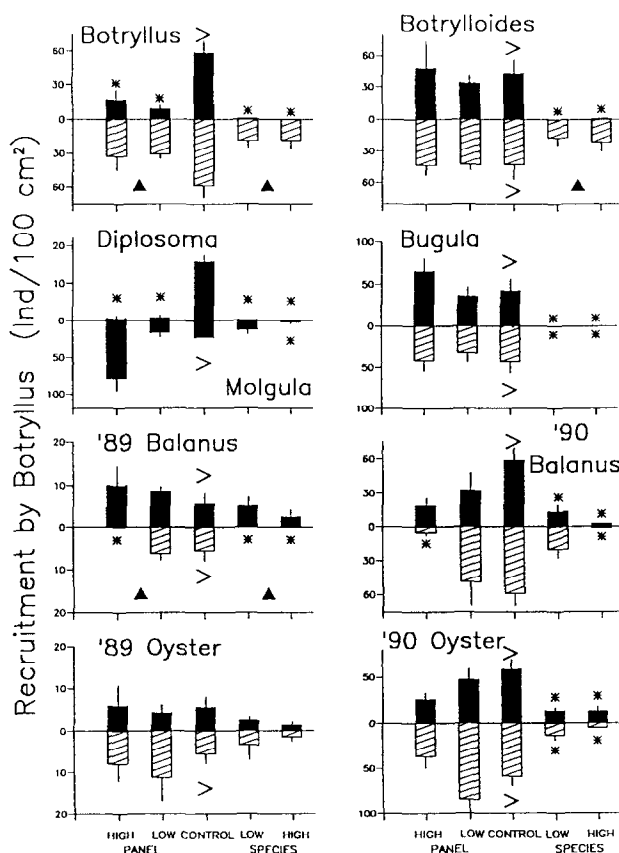


Fig. 2. Recruitment densities of *Botryllus* in the nine experiments conducted between 1989 and 1992. Graphs are labelled by the resident test species used with 1989 and 1990 *Balanus* and oyster experiments shown separately. All graphs show the mean density ( $\pm$  SE) of *Botryllus* recruits on each of the nine substrate groups consisting of panel and species (or mimic) surfaces in high and low density treatments of living species or mimics ( $2 \times 2 \times 2$ ) plus controls. Except for the 1992 experiments in which *Diplosoma* and *Molgula* were resident on the panels, each graph shows the mean density of *Botryllus* for living resident (top—solid bars) and mimic (bottom—hatch bars) treatments. The mean density on control panels is plotted on both the top and bottom. The *Diplosoma* and *Molgula* experiments had no mimics and these two experiments are plotted together. Symbols are: \*, significant difference from control panel surfaces based on Dunnett's test; > or <, panel surfaces with significantly greater or lesser densities than adjacent surfaces of the resident species (or mimics) based on a priori contrast analyses, and ▲, significantly different densities between panel and/or species surfaces on living resident and mimic treatments based on a priori contrast analyses. Analyses were based on log-transformed data but means and standard errors shown are for untransformed data.

and significantly lower *Diplosoma* recruitment onto *Botryllus* than onto mimic surfaces.

*Bugula* recruitment (Fig. 5) seemed to exhibit a mixed response to structure or resident species. No significant differences in recruitment were found in *Balanus* or oyster experiments which could be attributed to structure. Significantly lower



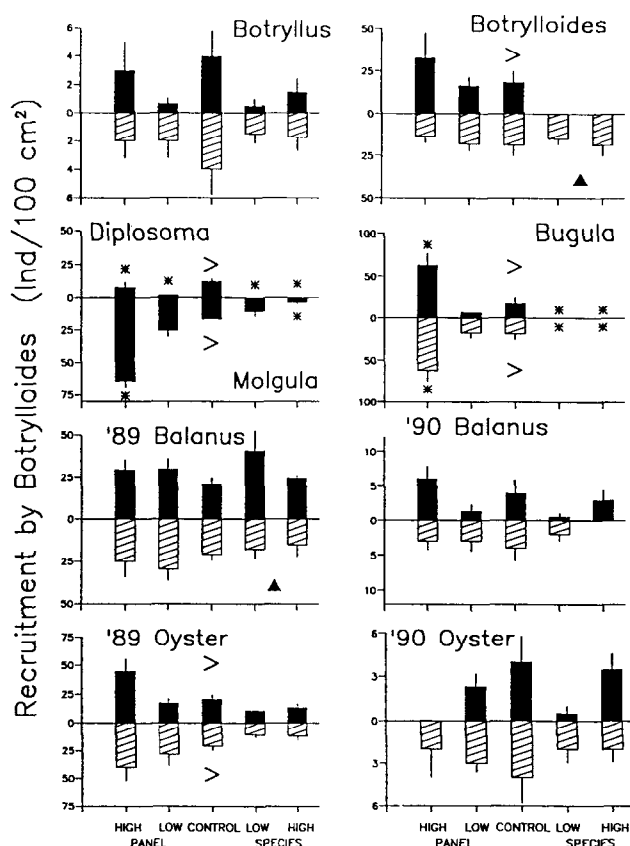


Fig. 3. Recruitment densities of *Botrylloides* in the nine experiments conducted between 1989 and 1992. Description the same as Fig. 2.

recruitment onto mimic surfaces than onto species in the 1989 *Balanus* and oyster experiments suggest a possible positive effect of these species, but no overall structural effect. In the remaining experiments *Bugula* did recruit in significantly lower densities on species and mimic surfaces than on adjacent panel and control surfaces, suggesting an effect of structure in the presence of ascidians and *Bugula*. Finally, a fairly strong effect was seen in the *Bugula* experiment in which *Bugula* recruited in significantly higher densities on panel surfaces adjacent *Bugula* than adjacent mimics. This result is consistent with *Bugula*'s known aggregated recruitment behavior (Buss, 1981).

*Spirorbis*, which recruited in high densities in all experiments (Fig. 6), showed a consistent negative response to structure. In the *Botryllus*, *Botrylloides*, *Bugula*, and 1989 oyster experiments, recruitment densities were lower on mimic and species surfaces than on adjacent panel surfaces. In addition, recruitment densities were lower on species than on adjacent panel surfaces in the *Diplosoma*, *Molgula* and 1990 *Balanus* experiments and lower on mimics than on adjacent panel

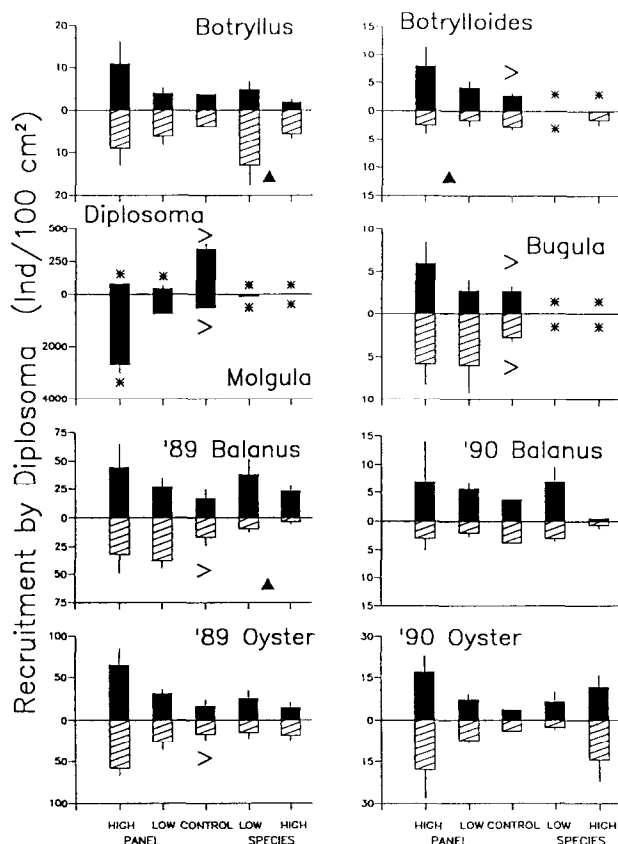


Fig. 4. Recruitment densities of *Diplosoma* in the nine experiments conducted between 1989 and 1992. Description the same as Fig. 2.

surfaces in the 1989 *Balanus* and 1990 oyster experiments. Species effects were also seen in several experiments. In the *Botryllus* experiment significantly higher recruitment onto all surfaces on mimic panels than onto *Botryllus* or adjacent surfaces suggested a negative effect of this species. Although no mimic treatments were used in the *Diplosoma* experiment, the significant reduction in recruitment on this species and adjacent surfaces suggests a similar negative effect. An opposite pattern was seen in the oyster and 1989 *Balanus* experiments where *Spirorbis* recruitment was higher on the resident species than on the mimics. Also, in the 1990 oyster experiment recruitment was significantly higher on oysters than on adjacent panel surfaces. These patterns suggest a positive effect of both oysters and barnacles on *Spirorbis* recruitment.

Finally, barnacle recruitment (Fig. 7) was fairly similar to that exhibited by *Spirorbis*. Barnacle recruitment was strongly influenced by structure in all but the oyster and *Molgula* experiments. In the remaining 6 experiments, *Balanus* recruitment was significantly less on species and/or mimics than on adjacent panel

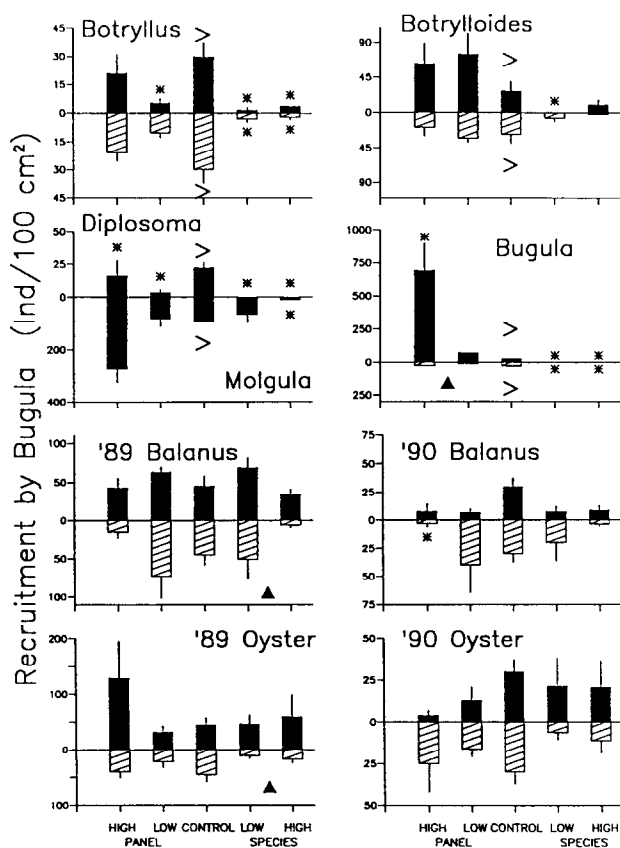


Fig. 5. Recruitment densities of *Bugula* in the nine experiments conducted between 1989 and 1992. Description the same as Fig. 2.

surfaces. In the presence of both barnacles and oysters, barnacle recruitment was higher on species surfaces than on the surfaces of mimics, indicating a positive effect of these species. The effect of living oysters was particularly strong with recruitment onto oysters significantly higher than on adjacent panel surfaces as well as onto mimics.

#### 3.4. A comparison of recruitment and settlement patterns

Because separate settlement studies (Osman & Whitlatch, 1995) had been conducted using resident adult *Botryllus*, *Botrylloides*, *Diplosoma*, and *Molgula*, direct comparisons between settlement and recruitment in the presence of these species could be made. In the presence of resident *Botrylloides*, *Molgula*, and to some extent *Botryllus*, the general patterns between settlement and recruitment were quite similar for the 6 recruiting species. For the most part both settlement and recruitment densities were higher on panel surfaces than on species (Figs.

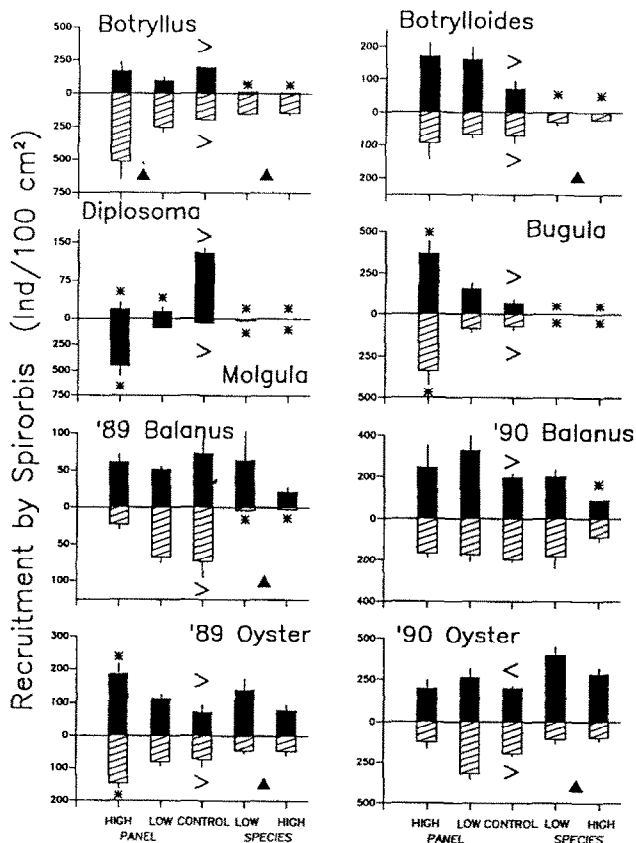


Fig. 6. Recruitment densities of *Spirorbis* in the nine experiments conducted between 1989 and 1992. Description the same as Fig. 2.

8–10). These similarities indicate that these resident species influenced settlement but had little effect on the post-settlement mortality of recruits.

In the presence of *Botrylloides* (Fig. 8), *Botryllus*, *Bugula*, *Balanus*, and *Spirorbis* all recruited onto adjacent panel surfaces in significantly higher densities (relative to controls) than they settled. Again, these data suggest possible aggregation of settling larvae, but no post-settlement mortality resulting from the presence of *Botrylloides*. Only *Diplosoma* recruited in significantly lower densities than it settled onto the surface of *Botrylloides* colonies, indicating some possible post-settlement mortality. However, the differences are small and there was no similar effect on adjacent panel surfaces.

The differences between recruitment and settlement in the *Molgula* experiments (Fig. 9) are similar to those found in the presence of *Botrylloides*. All species except *Diplosoma* and *Botryllus* recruited in higher densities than they settled onto panel surfaces adjacent *Molgula*. In addition, *Botryllus*, *Spirorbis*, and *Bugula* recruited onto the surfaces of *Molgula* in higher relative densities than

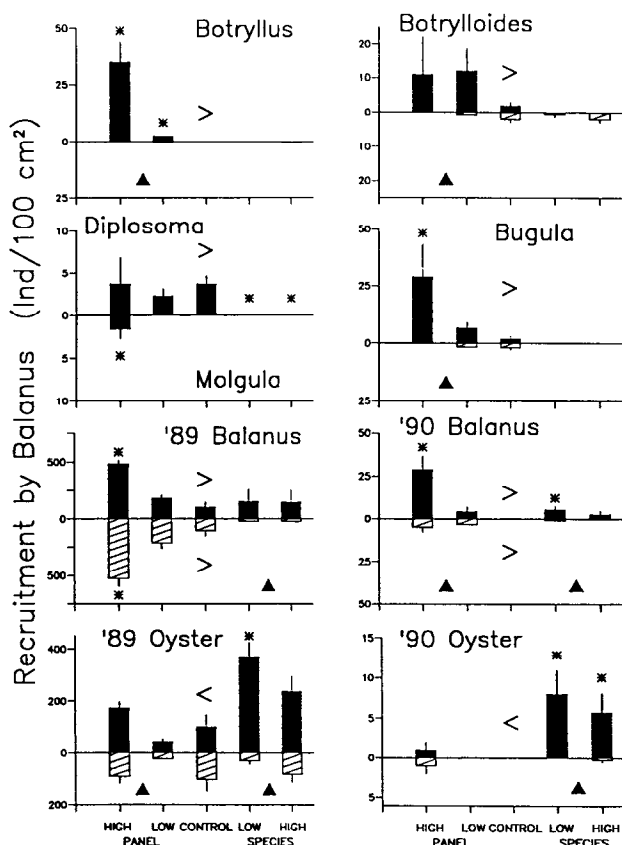


Fig. 7. Recruitment densities of *Balanus* in the nine experiments conducted between 1989 and 1992. Description the same as Fig. 2.

they settled onto these surfaces. None of these patterns indicate any significant post-settlement mortality that could be attributed to the presence of *Molgula*.

In the presence of *Botryllus* (Fig. 10) two additional patterns were observed; significantly higher recruitment densities were observed for *Balanus* and *Botrylloides* and significantly lower recruitment densities were observed for *Botryllus* and *Spirorbis*. For *Balanus* recruitment densities were significantly higher than settlement densities on adjacent panel surfaces and for *Botrylloides* higher recruitment was observed directly on *Botryllus* colonies. Both patterns indicate possible aggregation of settling larvae, but certainly no significant post-settlement mortality. On the other hand, *Botryllus* had significantly lower recruitment densities than settlement on adjacent panel surfaces and *Spirorbis* had lower recruitment densities on both panel and species surfaces. These patterns probably resulted from post-settlement mortality, but in the case of *Botryllus* could also have resulted from fusion of some newly settled individuals with older colonies (Rinkevich & Weissman, 1987).

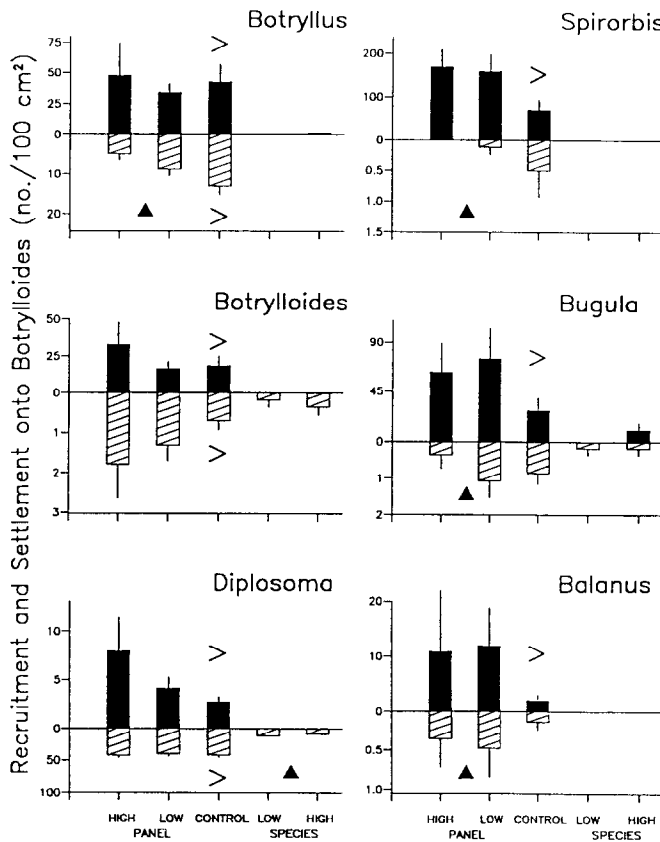


Fig. 8. Comparison of recruitment (top—solid bars) and settlement (bottom—hatched bars) mean densities ( $\pm$  SE) of six taxa onto panels with *Botrylloides* as the resident test species. Because all densities were scaled to control treatments for analyses, settlement and recruitment control means were plotted with the same height. Each graph shows the mean density of a species settling and recruiting onto each of the five substrate groups (panel surfaces on the control, high-, and low-density treatments and species surfaces in the high- and low-density treatments). Based on ANOVA and a priori contrast analyses, symbols are: > or <, panel surfaces with significantly greater or lesser recruitment or settlement densities than adjacent surfaces of the resident species and  $\blacktriangle$ , significant differences between recruitment and settlement densities on panel and/or species surfaces. Analyses were based on log-transformed data but means and standard errors are for untransformed data.

Opposite to recruitment in the presence of the other three ascidians, recruitment in the presence of *Diplosoma* was significantly less than settlement for all species recruiting except *Botryllus* and *Spirorbis* (Fig. 11) and these two species showed the same pattern. All species avoided settling onto resident *Diplosoma* while settling in significantly higher densities on adjacent panel surfaces. However, in the recruitment experiment few individuals of any species were found in the presence of *Diplosoma*. The pattern suggests very high post-settlement mortality. This is confirmed by observations made during the experiment. *Diplosoma* grew

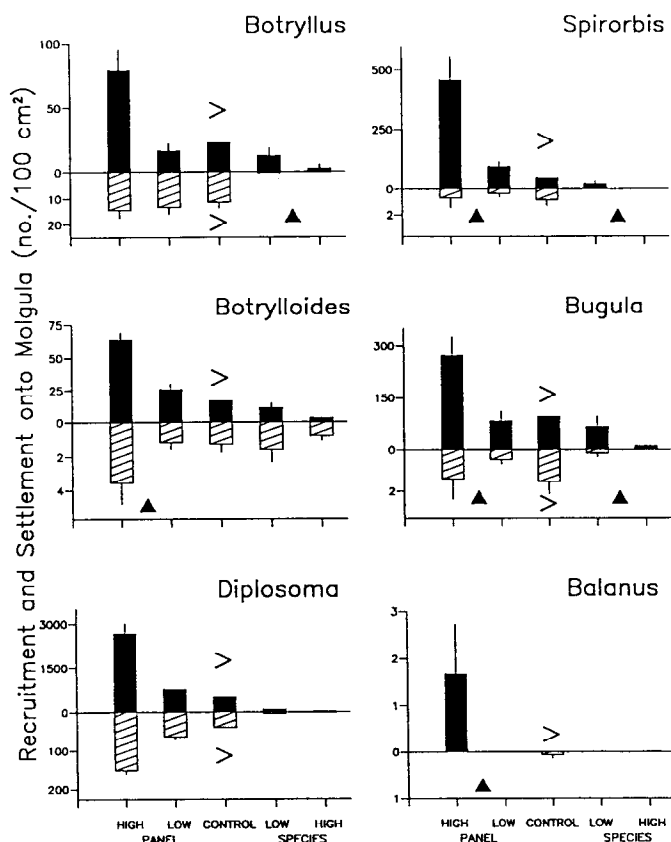


Fig. 9. Comparison of recruitment (top—solid bars) and settlement (bottom—hatched bars) mean densities ( $\pm$  SE) of 6 taxa onto panels with *Molgula* as the resident test species. Description the same as Fig. 8.

very rapidly during the 1-wk recruitment experiment, overgrowing most of the available space (and any newly settled individuals) on most replicates.

#### 4. Discussion

Although there were some differences between species of recruits in their responses to sessile adults as well as differences among residents in their overall affect on recruitment, the main conclusion that can be drawn from the nine recruitment experiments is that the principal way in which resident sessile species affect recruitment is by changing the quantity of available space. Some species such as colonial ascidians and bryozoans have surfaces which do not appear to be perceived as habitable substrate. On the other hand, recruitment onto the calcareous surfaces of other species such as oysters and barnacles suggests that

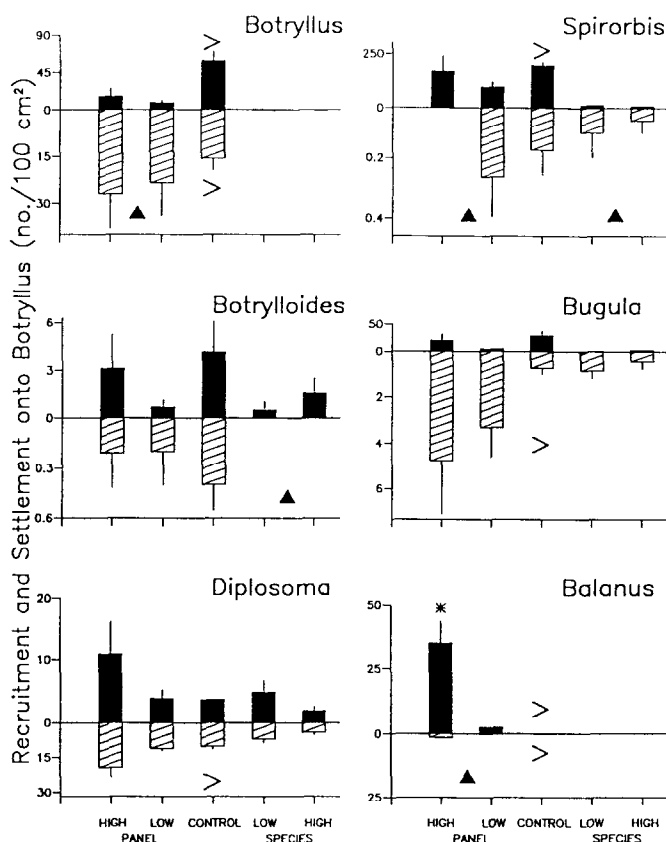


Fig. 10. Comparison of recruitment (top—solid bars) and settlement (bottom—hatched bars) mean densities ( $\pm$  SE) of six taxa onto panels with *Botryllus* as the resident test species. Description the same as Fig. 8.

these surfaces are generally not distinguished as different from other hard substrata.

To a great degree, the patterns that we observed in these experiments can be most easily explained by assuming that living resident species represent different substratum types to which settling larvae respond. Except in the presence of *Diplosoma* and, to a lesser extent, *Botryllus*, few differences were seen between settlement and recruitment patterns suggesting that in most experiments recruitment was largely a function of settlement. There were some indications of possible aggregation by barnacles and *Bugula* near adults (as previously reported by Buss, 1981) and possible avoidance by *Botryllus* of conspecifics (Grosberg, 1981) and/or structure, but little indication of either predation on larvae (Osman & Whitlatch, 1995) or any significant post-settlement mortality resulting from the presence of any of the sessile adults. This is not to deny that either of these processes occur or that they have the potential to influence recruitment. Larval predation has been



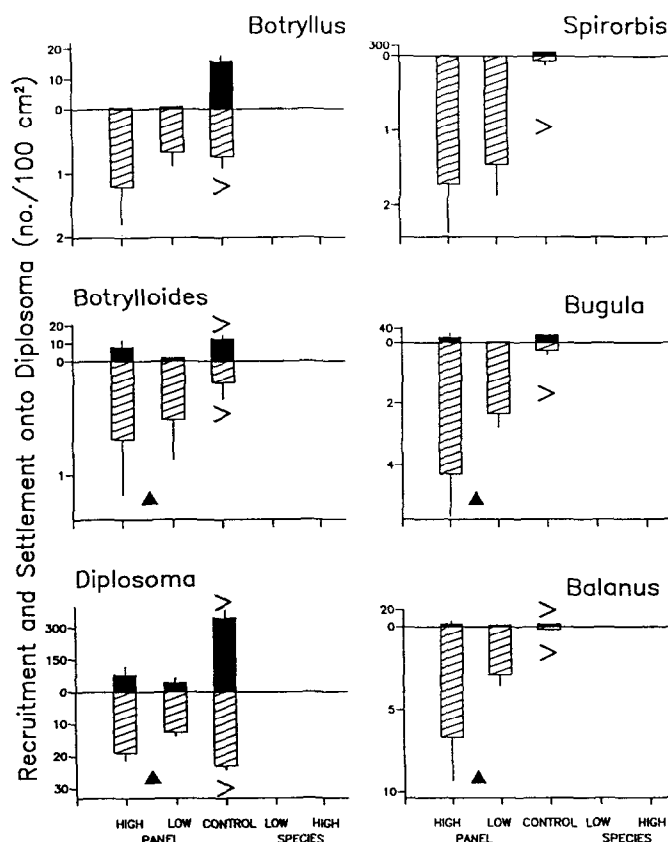


Fig. 11. Comparison of recruitment (top—solid bars) and settlement (bottom—hatched bars) mean densities ( $\pm$  SE) of six taxa onto panels with *Diplosoma* as the resident test species. Description the same as Fig. 8.

observed in a variety of studies (Young & Gotelli, 1988; Davis & Butler, 1989; Osman et al., 1989; Young, 1989; Stoner, 1990) and surmised from field data in others (Thorson, 1950; Woodin, 1976). However, in field experiments designed to measure larval predation (Young & Gotelli, 1988; Young, 1989), no significant effects on recruitment were found.

In earlier laboratory and field studies we did observed post-settlement mortality of recruiting oysters that apparently resulted from overgrowth (Osman et al., 1989) by colonial ascidians and in this study we observed large numbers of newly-settled individuals of a variety of species under transparent *Diplosoma* colonies. The greatly reduced recruitment relative to settlement that we observed in the presence of *Diplosoma* suggests that this and perhaps other fast growing species influence recruitment patterns by overgrowing newly-settled individuals and causing high post-settlement mortality.

Nevertheless, most of the various recruitment patterns seen probably resulted

as a consequence of larval settlement and the reaction of larvae to the resident adults as substrate. In the presence of resident species such as *Botryllus*, *Botrylloides*, *Molgula*, and *Bugula*, recruitment of most species was extremely low on the species but often increased on adjacent substrate. As we have demonstrated for settlement (Osman & Whitlatch, 1995), this can result when some larvae which fail to attach to the residents settle onto the adjacent substrate. This process can actually result in recruitment densities being higher on the panel surfaces of treatments with residents than on control panels. On the other hand, only *Botryllus* seemed to avoid recruiting onto barnacle and oyster surfaces. These residents exhibited little negative effect on the recruitment of most species. Some species such as *Spirorbis* and *Balanus* may actually have been “attracted” to the surfaces of oysters and barnacles, potentially reducing recruitment onto adjacent “less-attractive” panel substratum. Whether this attraction resulted from the increased physical structure provided by these species, their calcareous chemistry, or simply the increase in surface area their shells produce (the presence of barnacles can triple the available surface area of the space they occupy), they nonetheless can influence local settlement and recruitment.

Perhaps some of the strongest recruitment-resident effects observed were intraspecific. *Botryllus* recruitment was reduced the most on or near adult *Botryllus* suggesting that either settling larvae avoid adult colonies or some newly-settled *Botryllus* fused with the resident adults (Rinkevich & Weissman, 1987). *Bugula* and *Balanus* clearly recruited in higher numbers near, but not on, conspecific adults, confirming earlier studies that demonstrated aggregation in these species (e.g. Barnett & Crisp, 1979; Buss, 1981). However, *Botrylloides* recruitment was equally unaffected by adult *Botrylloides* or any other species.

Overall our results are fairly consistent with earlier studies. Field experiments examining the effects of solitary ascidians (Young, 1989) and barnacles (Young & Gotelli, 1988) have demonstrated the difficulties of observing any strong effects of resident sessile species on recruitment, even when the results of laboratory studies suggest intense interactions. The major patterns that we have seen in our experiments appear to result mostly from the usurpation of substratum by residents and not from either direct effects such as larval predation or overgrowth of newly-settled individuals or indirect effects such as changes in current flows. Likewise, our earlier laboratory and field studies examining oyster recruitment suggested that the presence of resident adults could enhance settlement and recruitment on adjacent substrate (Osman et al., 1989). We have also observed this in many of our recruitment and settlement experiments (Osman & Whitlatch, 1995). However, this again can be attributed to a removal of available substratum followed by increased settlement in adjacent areas by some fraction of the larvae that originally attempted to settle on the adults.

There has been some indication that attached residents can influence post-settlement mortality through processes such as intra-and interspecific competition (Caffey, 1985; Bertness, 1989; Reed, 1990). Our experiments would suggest that in some communities most dominant species may not have such strong effects, at least over the first week after settlement. The species that appeared to cause

significant post-settlement mortality, *Diplosoma* and possibly *Botryllus*, were encrusting species that have the greatest potential to overgrow adjacent individuals. It is possible that over a longer time period, the still small recruits will suffer higher mortality when near other species of resident adults. Also special relationships can exist whereby survivorship can actually be enhanced by recruiting onto particular species (Osman & Haugsness, 1981; Osman, 1987). However, the overall generality may be that recruitment is much less affected by the resident sessile community than it is by other factors such as predation (e.g. Keough & Downes, 1982; Watzin, 1983; Young & Chia, 1984; Stoner, 1990; Osman et al., 1992), herbivory (Underwood, 1980; Dean et al., 1984, 1988), desiccation (Hruby & Norton, 1979; Brawley & Johnson, 1991), siltation (Dayton, 1973, 1975; DeVinny & Volse, 1978), or other changes in the physical environment (Dayton & Tegner, 1984; Deysher & Dean, 1986; Osman & Abbe, 1995).

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