



# The control of the development of a marine benthic community by predation on recruits

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## Abstract

Recruitment is an important process in regulating many marine benthic communities and many studies have examined factors controlling the dispersal and distribution of larval immigrants. However, benthic species also have early post-settlement life-stages that are dramatically different from adult and larval stages. Predation on these stages potentially impacts measured recruitment and the benthic populations and communities that ultimately develop.

We examined the consequences of post-settlement predation on 1-day-old to 1-month-old recruits of sessile invertebrates at two field sites in southern New England. One site (Breakwater) was in a protected area with few predators and the other (Pine Island) was <1 km away in an open coast area with three different predator guilds: small and large invertebrates and fish. The Breakwater site had been dominated for >10 years by colonial and solitary ascidians. These species were absent from the Pine Island site which was dominated by bryozoans. Our goal was to examine whether post-settlement predation influenced the development and subsequent structure of the epifaunal community.

Here we examine long-term changes in community development resulting from post-settlement predation, and contrast these results to those of earlier experiments examining the reductions in observed recruitment by post-settlement predation. Our first long-term experiment examined natural community development at the two sites and whether transplanted communities changed when exposed to the different levels of predation at these sites. The communities that developed at both sites were consistently different from each other and similar to resident communities at their respective sites. On panels transplanted from the Breakwater to Pine Island, solitary ascidians and the colonial ascidian, *Botryllus schlosseri*, suffered high mortalities on both caged and uncaged treatments, indicative of predation by small predators that could enter cages. Some solitary ascidians

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did survive inside cages and the colonial ascidian, *Botrylloides violaceus*, became dominant on all transplanted treatments. On panels transplanted from Pine Island to the Breakwater, ascidians invaded and dominated all treatments except those that were originally caged at Pine Island.

In the second long-term experiment, natural communities were allowed to develop on panels exposed at the Breakwater for 1, 2, 3, and 4 weeks. Each set was transplanted to three treatments at Pine Island: open uncaged pilings, caged pilings to exclude fish and large invertebrates, and racks suspended above the bottom to exclude all predators. When 1-week-old communities were transplanted, after 2–3 weeks only bryozoans were found on the open and caged pilings, while colonial ascidians dominated the suspended rack treatment. When older 2-week-old communities were transplanted, colonial ascidians also became dominant in the caged piling treatment and when 3- and 4-week-old communities were transplanted colonial ascidians dominated all three treatments. Solitary ascidians were never abundant on open pilings exposed to fish and large benthic invertebrate predators.

Post-settlement predator–prey interactions involved newly settled and juvenile life-stages of a variety of prey species and many invertebrate and vertebrate predator species. The effects of these interactions on recruitment did result in differences in the development and eventual species composition of the communities, even though predators had little if any effect on the adults of the prey species.

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## 1. Introduction

Many studies examining the contribution of recruitment to the regulation of marine benthic communities have focused on processes controlling the dispersal and distribution of larvae and how these newly arrived individuals interact as adults with the existing community (e.g. Roughgarden et al., 1985; Menge and Sutherland, 1987; Underwood and Keough, 2001 for a recent review). However, benthic species often have post-settlement life-stages that are dramatically different from adult and/or larval stages. As such, these stages have a unique ecology which may have a strong impact on recruitment and its influence on community development (e.g. Thorson, 1966; Keough and Downes, 1982; Watzin, 1983; Luckenbach, 1984; Young and Chia, 1984; Connell, 1985; McGuinness and Davis, 1989; Stoner, 1990; Osman et al., 1990, 1992; Roegner, 1991; Olafsson et al., 1994; Osman and Abbe, 1994; Osman and Whitlatch, 1995, 1996, 1998; Caley et al., 1996). Their small size, if nothing else, makes them vulnerable to predators that may not interact with adults (e.g. Thorson, 1966; Sutherland, 1974; Watzin, 1983; Young and Chia, 1984; Stoner, 1990). Given that benthic systems are often limited by recruitment, post-settlement control may have a continuing influence on the composition of adult communities.

Our research has focused on a temperate subtidal marine benthic community composed principally of sessile invertebrates which, as adults, permanently attach to hard substrates such as cobbles, rocks, boulders, reefs, etc. These subtidal communities are often viewed as extensions of their intertidal counterparts (Witman and Dayton, 2001). Important

processes within intertidal systems such as (1) periodic disturbances of the community (e.g. Dayton, 1971; Sousa, 1979a,b, 1980), (2) strong competitive and trophic relationships controlled by one or a few key species (e.g. Connell, 1961a,b; Paine, 1966; Dayton, 1971; Underwood, 1980), and (3) recruitment into open space which is variable and often a function of large-scale hydrographic phenomena (e.g. Shanks, 1983; Wethey, 1986; Roughgarden et al., 1988; Farrell et al., 1991; Shkedy and Roughgarden, 1997) are also seen as important in these subtidal communities (e.g. Sutherland, 1974, Osman, 1977, 1978; Moran, 1980; Ayling, 1981; Witman, 1985). With larvae that are released into the water and presumably carried away from a site, the recruitment of many species within these communities is usually viewed as uncoupled from local changes in adult abundance and more dependent on the potentially unpredictable spatial and temporal variability of larvae produced throughout the whole region. In essence, these communities are viewed as open systems with competition among adults controlling local species dominance, physical disturbances and predation on various scales opening space for recruits, but the subsequent supply of new recruits (and, perhaps new species) uncoupled from local processes.

Because many of the species in these systems are relatively short-lived, recruitment is a critical component. Competition and predation may control dominance and disturbance may establish the extent of free space, but recruitment controls which species are present and their initial abundances. Key issues that have been foci of much research are the processes controlling the supply of available larvae, processes controlling their distribution, and factors affecting the selection of the substrate onto which they permanently attach. However, it is also critical to examine the degree to which post-settlement processes influence recruitment. Such processes have been examined infrequently in marine communities and their relative influence is largely unknown. Our previous research (Osman and Whitlatch, 1995, 1996, 1998; Osman et al., 1990, 1992) has indicated that on small, isolated substrates, predation on newly settled individuals has the potential to control recruitment, regardless of larval supply. The present research is directed at determining whether this predation can influence the development and subsequent structure of the prey community. To do this we examined the development of epifaunal communities under experimental conditions designed to contrast the effects of the predator guilds. The results of these experiments are also contrasted with those of 3–6-day experiments that examined predation on recruits of individual prey species.

## 2. Methods

### 2.1. Study sites

The studies were conducted at two field sites in eastern Long Island Sound (Groton, CT, USA) at the mouth of the Poquonnock River estuary (41°19'15" N, 72°2'40" W). One site was at the Avery Point Breakwater and the other was near Pine Island < 1 km from the Breakwater site. Although both sites are similar in their temperature and salinity regimes and tidal range, they differ in several important environmental parameters. Behind the protected Breakwater the bottom quickly grades into mud, water depth is 2.5 m below

MLW and tidal currents are generally  $< 15 \text{ cm s}^{-1}$ . During the study, hard substrates at the site were dominated by colonial and solitary ascidians and, except for green crabs, *Carcinus maenas* (Linnaeus), predators were rare or absent (Rogers, 1998, pers. obs.).

The Pine Island site is dominated by large boulders (1–2 m diameter) with much of the remaining bottom covered by smaller rocks and cobbles with a few pockets of sand. The site is more exposed to wind and waves and subject to strong tidal currents of  $\sim 70 \text{ cm s}^{-1}$  during peak flood or ebb flows. Our experiments were conducted at a depth of 5 to 6 m below MLW. The sessile invertebrate community at this site was dominated by bryozoans. Ascidians were extremely rare. On the other hand, both small and large invertebrate predators as well as benthic-feeding fish were extremely common (Rogers, 1998, pers. obs.).

## 2.2. Background data

### 2.2.1. Sessile epifauna

Our studies focused on the marine sessile invertebrate community found on hard substrates. Previous studies have shown that on individual substrates as small as  $100 \text{ cm}^2$ ,  $>25$  species can coexist for years (e.g. Osman, 1977, 1978). The dominant taxa were often colonial species, mostly bryozoans and ascidians. Although some colonies and individuals survive years, most live months to 1–2 years. The majority of species produce lecithotrophic larvae that live for only a few minutes to a day.

To test whether new recruits of species missing at the Pine Island site could survive there in the absence of predators, we exposed twelve  $100\text{-cm}^2$  PVC panels at the Breakwater site for 2 days after which all recruits were counted using a dissecting microscope. These panels were then exposed at the Pine Island site on racks suspended 2 m below a surface float ( $\sim 4$  m above the bottom) to eliminate exposure to invertebrate predators (Young, 1985). Four panels were also randomly assigned to cages ( $1\text{-cm}^2$  plastic-coated wire mesh) in order to test for effects of any fish predators that could reach the suspended panels. Panels were collected after 5 days and recounted to determine survival.

### 2.2.2. Predator guilds

Three guilds of predators can potentially impact the epifaunal community at the two sites: large invertebrates, small invertebrates, and benthic-feeding fish.

The most common large invertebrate predators were the seastar, *Asterias forbesi* (Desor 1848), and the crabs, *Libinia emarginata* (Leach, 1815), *Carcinus maenas*, and *Cancer borealis* (Stimpson, 1859). Adults of these species prey on both sessile species (particularly mussels and barnacles) and smaller motile invertebrates (e.g. Elnor, 1978; Hughes and Elnor, 1979; Jubb et al., 1983; Schneider and Mann, 1991; Cohen et al., 1995; Berger, 1998). In addition, as newly recruited juveniles they also prey on a wider array of sessile species (Cohen et al., 1995, pers. obs.).

Epifaunal communities also harbor a great variety of small motile invertebrates (amphipods, isopods, pycnogonids, gastropods, polychaetes), some of which are active predators on one or more of the sessile species. Previously, we found that the very small predaceous gastropods *Mitrella lunata* (Say) ( $< 5$  mm shell length), *Anachis lafresnayi*

(P. Fischer and Bernardi, 1856), and *A. avara* (Say) (< 15 mm) are capable of consuming >200 newly settled gastropods snail<sup>-1</sup> day<sup>-1</sup> (Osman et al., 1990, 1992; Osman and Whitlatch, 1995). These gastropods also prey on new recruits of a variety of other epifaunal species including barnacles, mussels, and bryozoans, but the predation rates are either low or the prey species escape through a rapid increase in size or the production of external calcification.

Finally, benthic fish, particularly the cunner *Tautoglabrus adspersus* (Walbaum, 1792), can be extremely common and prey on a variety of sessile species (Olla et al., 1975; Green et al., 1984). In earlier studies (Osman et al., 1990) we found that juvenile solitary ascidians may be particularly vulnerable to predation by cunner.

Numbers and sizes of predators sampled on the experimental pilings (described below) at the end of every experiment at the Pine Island site (Osman and Whitlatch, 1996, 1998) were used to estimate temporal changes in the populations of these species at that site. To estimate predation rates of fish (cunner) we deployed 100-cm<sup>2</sup> panels with juveniles or adults of the solitary ascidian *Molgula manhattensis* (DeKay 1843) at the Pine Island site with a video camera mounted to record any activity of predators over a 40–60-min period. *Molgula* were spawned in the laboratory and panels were exposed to the larvae that developed. After larval settlement the panels were placed at the Breakwater site and periodically ‘gardened’ to remove other species. Juvenile panels had individuals approximately 2 weeks old and individuals on adult panels were 4 weeks old. Video recordings were analyzed by counting the number of *Molgula* removed and the number and sizes of fish present each minute.

### 2.3. Experiments

#### 2.3.1. Predation on recruits and juveniles of individual species

We exposed 1–3-day-old newly settled individuals and 1–3-week-old juveniles of dominant species to natural levels of predation at the field sites. In 1993 and 1994 over 20 recruitment experiments were conducted. Most experiments had four piling treatments with five pilings treatment<sup>-1</sup> and one to four substrates piling<sup>-1</sup>. Treatments were: (1) open, uncaged pilings, exposed to all three guilds of predators; (2) caged (1-cm<sup>2</sup> plastic-coated wire mesh) pilings designed to exclude larger invertebrate and fish predators but allowing access to *Mitrella* and *Anachis* and other small predators; (3) screened (1-mm<sup>2</sup> fiberglass mesh) pilings to exclude all predator guilds; and (4) partially screened pilings to control for potential artifacts (e.g. changes in water flow or sedimentation) associated with screening the pilings.

The pilings were 75-cm-tall, 28-cm-diameter sections of PVC pipe secured upright to weighted steel frames. All cages (including those used in screened and partially screened treatments) were cylinders 50 cm in diameter and 85 cm tall with sealed tops and bottoms. Cages completely enclosed individual pilings. Cages used in the partially screened treatments had a 10-cm-wide band at their bottom that was devoid of screening (but still covered by the 1-cm<sup>2</sup> mesh). Thus, this treatment was designed to exclude the same predators as the caged treatment and, in the absence of any artifacts, to produce similar effects on prey species as the caged treatment. Because no individual experiment lasted for more than a week, long-term artifacts resulting from caging or screening (e.g. reduced

larval settlement) were assumed to be minimal. All cages were periodically cleaned by divers and replaced monthly or if they needed repair.

For each experiment, clean substrates were exposed to larvae of the chosen species in the laboratory or the field. After exposure substrates were hung beneath a raft at the Breakwater site until the selected species had reached its proper life-stage. Panels were gardened periodically to remove all other species. Prior to beginning an experiment, all non-desired species were removed from each substrate and the substrates were photographed and randomly assigned to treatments. In addition, individuals or colonies of the chosen species were usually counted on each substrate before deployment. Experiments ran for 3–6 days after which substrates were retrieved, photographed, and surviving individuals counted. Estimates of mortality and/or growth were made by comparing the initial and final counts or by comparing photographs using computer-assisted image analysis (NIH Image).

### 2.3.2. Predation effects on community development

We conducted two 3-month experiments, one in 1993 and one in 1994, to test whether predation on post-settlement life-stages alters long-term development and species dominance within the sessile community. Both experiments used the experimental pilings. At the Pine Island site these pilings were placed among boulders and separated from each other by at least 3 m. At the Breakwater site the pilings were placed on the mud bottom within 2 m of the Breakwater and separated from each other by at least 2 m. In each experiment 100-cm<sup>2</sup> panels attached to the pilings were used as sampling units.

The 1993 study was conducted to measure (1) differences in community development at the two field sites, 2) whether excluding fish and large invertebrate predators influenced community development, and 3) whether established communities would change when transplanted between the two sites. To accomplish this, 20 panels were deployed in late July 1993 on caged and uncaged pilings at both sites. Tests for cage artifacts conducted at both sites were negative for all 14 species tested (unpublished data). After 2 weeks, 10 panels of each treatment were reciprocally transplanted between sites with five panels from each treatment transplanted to caged pilings and five transplanted to open pilings. At the time of transplant the remaining 10 panels at each site were also removed, photographed, and then returned to pilings at that site. All panels were periodically photographed in situ over a 3-month period and these photographs were analyzed to determine differences in species composition and abundance among treatments. NIH Image software was used to measure the area covered by each recognizable taxon in each photographic image.

The 1994 study examined how the age of the community when first exposed to predators influenced the development of the community and species. A total of sixty 100-cm<sup>2</sup> panels were initially exposed in early July at the Breakwater site. After 1, 2, 3, and 4 weeks, 15 of the panels were transplanted to the Pine Island site. A panel was assigned to one of: five uncaged, open pilings exposed to all predator guilds; five caged pilings exposed only to the small predators that could enter through the 1-cm<sup>2</sup> cage mesh; or five panel racks suspended 2–3 m above the bottom and located in sandy areas >5 m from the main boulder area to reduce (and usually eliminate) exposure to all predators (e.g. Young, 1985). To minimize handling, the selection and assignment of panels to treatments were both done haphazardly ('randomized' by being blindly chosen and assigned by different

groups of people). Unlike short-term experiments (Osman and Whitlatch, 1996, 1998), pilings could not be screened without potentially influencing other environmental parameters, particularly larval settlement. All panels were sampled weekly, transported to the laboratory, kept in filtered running seawater, photographed, and returned to the field in <1 day. During the experiment, only treatment conditions were maintained, i.e. assignment to a particular piling or rack, location on a piling (or rack), or site on the bottom was haphazard with panels blindly selected by one person and assigned to each treatment piling or rack by a second individual, and a separate group of divers placing the pilings or racks at bottom sites. This experiment was concluded after approximately 3 months of exposure. Weekly photographs were analyzed using NIH image software.

#### 2.4. Data analysis

All data were analyzed using analysis of variance (ANOVA), either as one-way analyses of treatment effects or as two-way analyses of treatment  $\times$  site effects. In each analysis a posteriori multiple comparisons of all pairs of means were done using the Tukey–Kramer HSD test. When variances were not homogeneous, data were log-transformed.

Both colonization experiments involved the repeated analysis of the same experimental panels over time. Our main goal was to characterize the progression over time in differences among treatment in the abundances of the dominant taxa. We used separate ANOVAs for each sampling period to compare these treatment differences. To compare overall treatment effects in the 1994 experiment in which experimental panels were analyzed 9–11 times, we also used a repeated measures ANOVA. We excluded data for the first sampling period of each series (pre-transplant data) in the repeated measure analyses. Each of the four series of transplants was analyzed separately.

### 3. Results

#### 3.1. Background data

##### 3.1.1. Recruit survival in the absence of predators

The survival of 2-day-old recruits on panels suspended  $\sim$  4 m above the bottom at the Pine Island site was generally high (Table 1). For most species the mean number of recruits observed increased after the 5-day exposure. The increases most likely resulted from larval settlement. Regardless, we analyzed both the change in the percentage of recruits of each species (which included increases from settlement) and the percentage surviving in which we assumed any additional individuals on a replicate were newly settled and that the survival of transplanted recruits on that panel was 100%.

Survival for all five species was >95% on caged panels (Table 1), indicating that in the absence of predators these species can survive at the Pine Island site. In addition, we found no difference in survival between open and caged panels for the colonial ascidian *Botrylloides violaceus* (Oka, 1927), the erect bryozoan *Bugula turrata* (Desor, 1848), and the serpulid polychaetes *Spirorbis* spp. However, we found significantly lower

Table 1

Differences in survival of newly settled recruits on four caged and eight uncaged, open panels on racks suspended above the bottom at the Pine Island site

Species	Treatment	Initial	<i>F</i>	Final	<i>F</i>	% Change	<i>F</i>	% Survival	<i>F</i>
<i>Botrylloides</i>	CAGE	10.00 ± 2.04	0.11	12.00 ± 1.80	12.8	124 ± 15	6.4	100 ± 0	1.9
	OPEN	5.63 ± 1.44	<i>p</i> >0.10	4.13 ± 1.27	<i>p</i> <0.01	78 ± 11	<i>p</i> <0.05	80 ± 10	<i>p</i> >0.10
<i>Botryllus</i>	CAGE	101.25 ± 22.20	0.2	111.75 ± 18.22	7.2	116 ± 15	13.7	97 ± 3	10.7
	OPEN	112.75 ± 15.69	<i>p</i> >0.60	51.88 ± 12.88	<i>p</i> <0.05	47 ± 11	<i>p</i> <0.01	47 ± 10	<i>p</i> <0.01
<i>Bugula</i>	CAGE	18.50 ± 22.30	2.3	25.25 ± 24.49	0.6	157 ± 29	3.5	100 ± 0	3.1
	OPEN	60.00 ± 15.77	<i>p</i> >0.15	48.88 ± 17.32	<i>p</i> >0.40	91 ± 20	<i>p</i> >0.05	78 ± 9	<i>p</i> >0.10
<i>Cryptosula</i>	CAGE	10.75 ± 2.39	11.7	13.00 ± 3.88	0.8	130 ± 24	8.1	100 ± 0	5.1
	OPEN	20.75 ± 1.69	<i>p</i> <0.01	8.75 ± 2.74	<i>p</i> >0.35	44 ± 17	<i>p</i> <0.05	51 ± 15	<i>p</i> <0.05
<i>Spirorbis</i>	CAGE	30.50 ± 9.73	0.02	47.67 ± 10.62	0.7	117 ± 16	1.8	100 ± 0	2.4
	OPEN	42.25 ± 6.88	<i>p</i> >0.85	37.13 ± 6.51	<i>p</i> >0.40	92 ± 10	<i>p</i> >0.20	81 ± 7	<i>p</i> >0.10

Means ± SE are shown. Survival was calculated using 100% for all replicates in which the final number of recruits was equal to or greater than the initial number. *Spirorbis* was not present on one caged panel, reducing the number of caged replicates for this species to 3.

survival on open panels for the encrusting bryozoan *Cryptosula pallasiana* (Moll, 1803) and the colonial ascidian *Botryllus schlosseri* (Pallas), suggesting some predation by fish. Although this experiment was compromised by settlement of new individuals, the results do show that in the absence of predators, recruits of common epifaunal species not found at Pine Island (e.g. *Botrylloides*, *Botryllus*) will survive in that environment. In addition, recruits of the bryozoans *Schizoporella errata* (Waters, 1878) and *Bowerbankia gracilis* (Leidy, 1855), the ascidian *Molgula*, and the barnacles *Balanus* spp. that were in low abundance or found on only a few panels also survived on these panels.

### 3.1.2. Predator abundances

The most abundant predator species were the gastropods *Mitrella lunata*, *Anachis lafresnavi*, and *Anachis avara*. Abundances of *Mitrella* collected on experimental pilings at Pine Island increased from <50/piling in June to >400/piling in late August and then declined in early September (Fig. 1). The combined abundances of both species of *Anachis* (species-level field identifications were not always made) were much lower, more variable, and did not change systematically over the summer. The mean sizes of both gastropods increased in early July but then showed sharp declines in September reflecting the

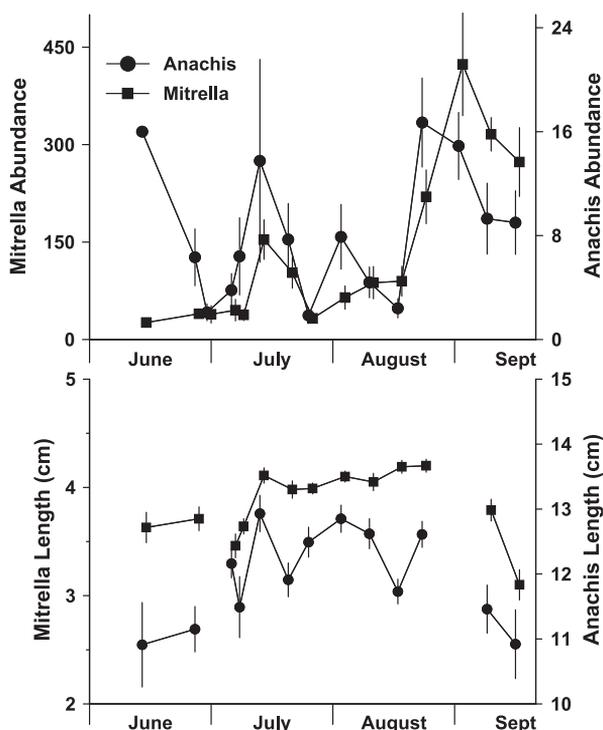


Fig. 1. Mean abundances and shell lengths of the gastropods, *Mitrella lunata* and *Anachis* spp. (*A. avara* and *A. lafresnavi*) on uncaged experimental pilings at the Pine Island field site. Data were collected each time an experiment was recovered and reflect the numbers on the pilings that had accumulated by the end of each deployment period of 3–6 days. Error bars represent standard errors.

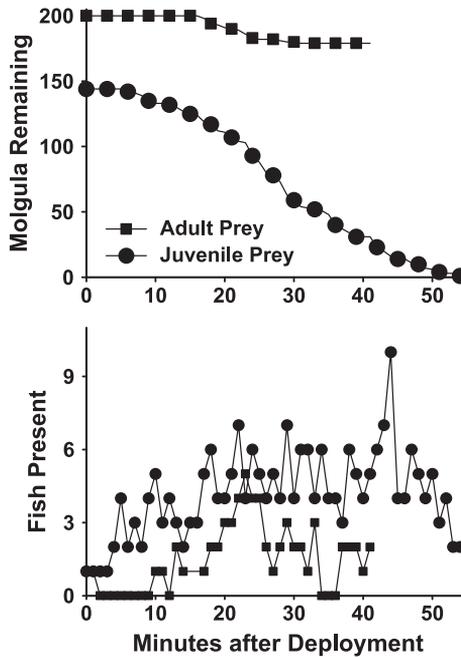


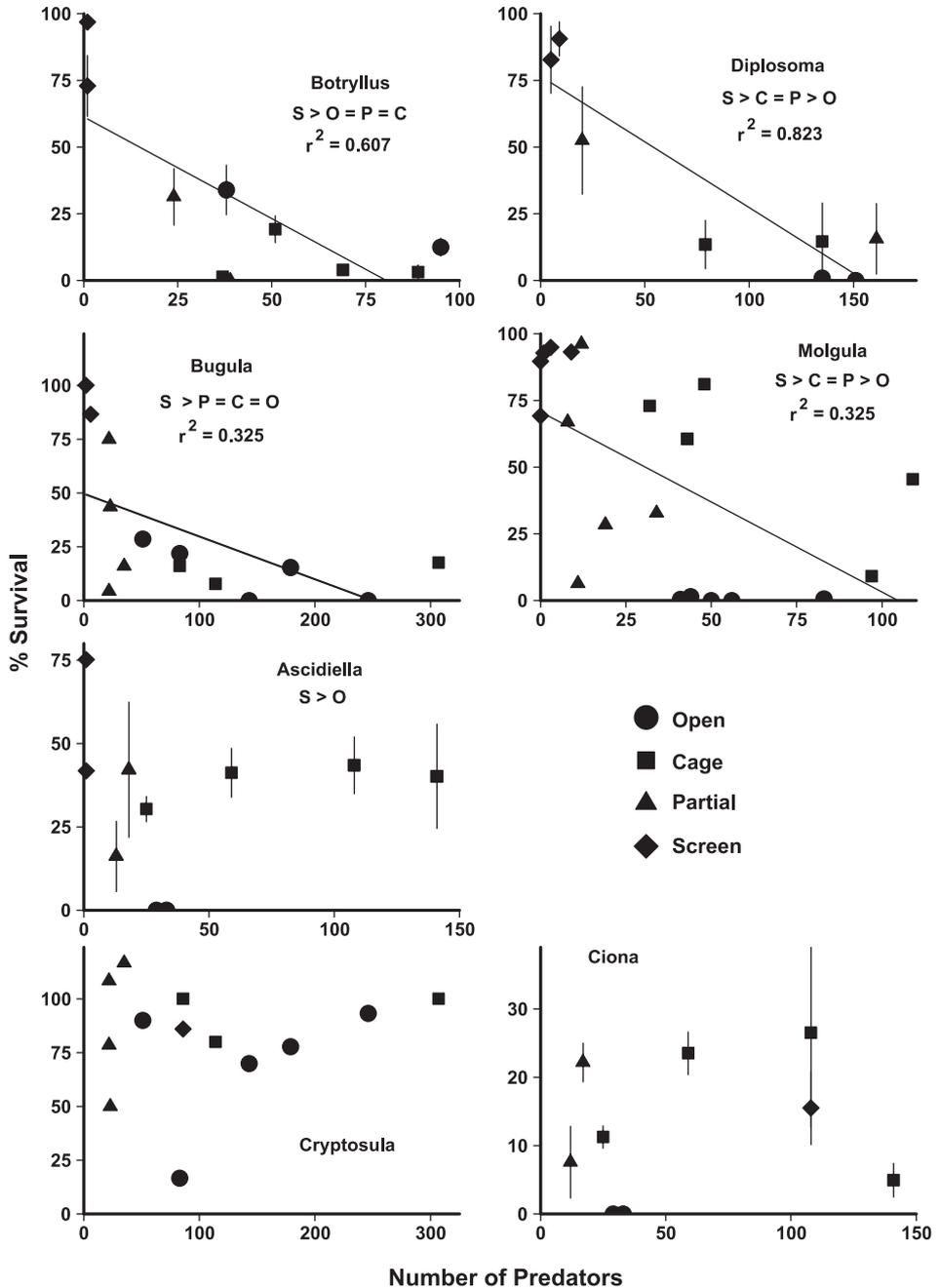
Fig. 2. Comparison of juvenile and adult *Molgula manhattensis* exposed to predation by the cunner, *Tautoglabrus adspersus*, at the Pine Island field site. The number of *Molgula* eaten and fish present were tabulated for each minute after the experiments were deployed at the field site. The data were collected from video recordings of the events. The juvenile experiment lasted 54 min and the adult experiment 42 min. Interference resulted in the loss of data for minutes 16 and 17 in the adult experiment.

recruitment of new cohorts. Thus these predators were very abundant during the late summer and early autumn when recruitment of many epifaunal species occurred.

### 3.1.3. Fish predation rates

When 144 juvenile *Molgula* were deployed at Pine Island only 1 remained after 54 min (Fig. 2). Conversely, when larger adult *Molgula* were placed at the same location 179 of 200 individuals remained at the end of the 42-min deployment. Large numbers of cunners were attracted to the *Molgula*, often five or six at a time. Initially, small 2–4-cm fish were observed attacking the ascidians, but larger individuals (8–16 cm) soon followed. The main difference between the two deployments was that fish numbers increased more rapidly and remained high longer in the juvenile *Molgula* experiment. After 25 min few

Fig. 3. The mean survival of new 1–2-day-old recruits of seven species at the Pine Island field site. Separate experiments were conducted for each species in 1993 and 1994. The means are plotted as a function of the total abundance of *Mitrella lunata*, *Anachis lafresnayi*, and *Anachis avara* on each experimental piling. The results of Bonferonni a posteriori tests based on one-way ANOVAs of treatment effects with experimental panels nested by piling are shown. Treatments were: O=open, uncaged pilings, C=caged pilings (fish and large invertebrate predators excluded), P=partially screened pilings (fish and large invertebrate predators excluded, control for screening), and S=fully screened (all predators excluded) pilings. Error bars represent standard errors.



fish visited the adult *Molgula* and no *Molgula* were removed. This contrasted with the continued predation of the juvenile *Molgula*, regardless of their density.

### 3.2. Experiments

#### 3.2.1. Predator effects on recruits of individual species

The survival of recruits of individual prey species was analyzed using a one-way ANOVA of the four piling treatments (see also Osman and Whitlatch, 1996, 1998) and as a function of the measured abundances of the predators, *Mitrella* and *Anachis* (Fig. 3). The number of surviving recruits of the colonial ascidians *Botryllus schlosseri* and *Diplosoma listerianum* (Milne Edwards, 1841) (previously identified by us as *Diplosoma macdonaldi* (Herdman, 1886)) and the erect bryozoan *Bugula turrita* (weakly) varied inversely with

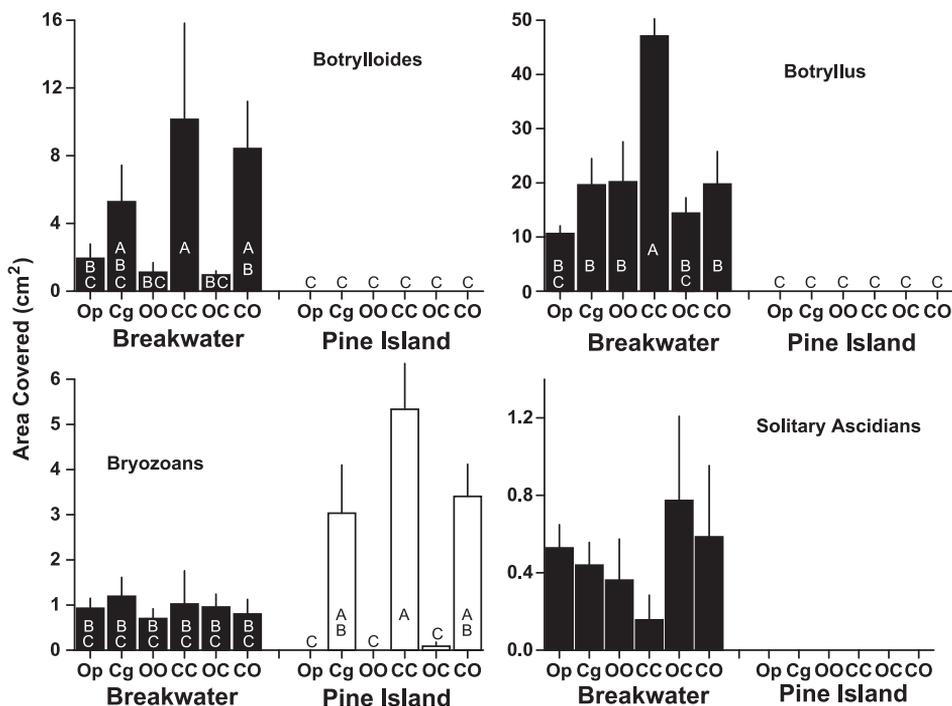


Fig. 4. Mean abundances in the 1993 Colonization Experiment after 1 month of exposure. Means are for four taxa on 100-cm<sup>2</sup> panels attached to experimental pilings at the Avery Point Breakwater and Pine Island sites. These data represent abundances on six piling treatments at each site prior to the reciprocal transplanting of some panels between the two field sites. The treatments are: Op = control or untransplanted panels on open, uncaged pilings, Cg = control panels on caged pilings, OO = transplanted panels from open pilings at the source site to open pilings at the receiving site, CC = transplanted panels from caged pilings at the source site to caged pilings at the receiving site, OC = transplanted panels from open pilings at the source site to caged pilings at the receiving site, and CO = transplanted panels from caged pilings at the source site to open pilings at the receiving site. Open bars represent treatments at Pine Island and black bars represent treatments at the Breakwater. Letters indicate means for treatments that are not significantly different. Bars without letters were not significantly different from one another but were significantly different from those with letters. Error bars represent standard errors.

the abundances of predators on the pilings, showing high survival only on screened pilings which excluded these small predators (Fig. 3). The survival of the solitary ascidian, *Molgula manhattensis*, also varied inversely (weakly) with predator abundance, but two other solitary ascidians, *Ascidiella aspersa* (Müller, 1776) and *Ciona intestinalis* (Linnaeus, 1767), showed no relationship to snail abundances. However, none of these species survived on open pilings exposed to large invertebrates and fish. Finally, survival of non-prey species such as the encrusting bryozoan, *Cryptosula pallasiana*, showed no significant variation with predator abundance and no differences among treatments.

3.2.2. Community development differences and transplant effects

After 1 month and prior to any transplanting, the panels at the two field sites generally had less than 50% of their available surface covered by the sessile community. Individuals and colonies that had recruited onto them were still fairly small. Nevertheless, panels on pilings at the Breakwater were dominated by ascidians and those at Pine Island were dominated by encrusting bryozoans (Fig. 4). No ascidians occurred on any of the panels on pilings at Pine Island. Although covering less than 10% of any panel, encrusting

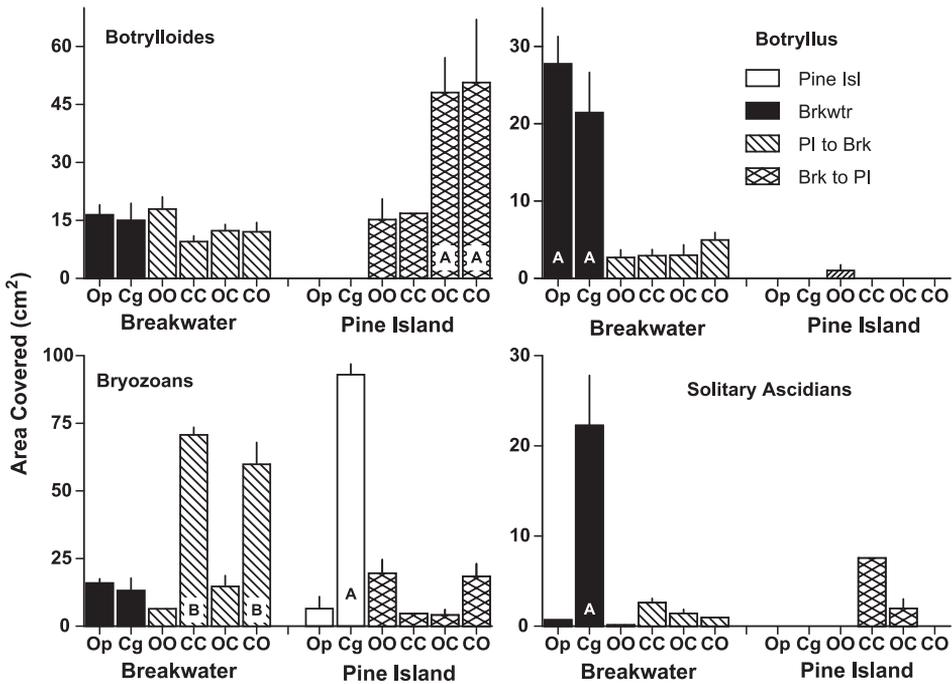


Fig. 5. Mean abundances in the 1993 Colonization Experiment 1 month after the reciprocal transplanting of panels between sites (2 months after initial exposure). The symbols are the same as those in Fig. 3. Data are shown by their destination site. Therefore, the means for four treatments transplanted from the Breakwater to Pine Island (OO, CC, OC, and CO, cross-hatched bars) are shown at Pine Island, and those treatments transplanted from Pine Island to the Breakwater (diagonally lined) are shown at the Breakwater. Error bars represent standard errors.

bryozoans were significantly more abundant on the three caged piling treatments at Pine Island than on the three open piling treatments.

After 2 months of exposure (1 month after transplanting), control panels on caged and open pilings at the Breakwater were still dominated by ascidians (Fig. 5). *Botryllus* was more abundant on these panels than on all other treatments while solitary ascidians were significantly more abundant on Breakwater caged control panels than on all other treatments. Both taxa were absent or in low abundance on panels transplanted to pilings at Pine Island with solitary ascidians only occurring on caged pilings. On the other hand, both taxa did colonize panels transplanted from Pine Island to open and caged pilings at the Breakwater. *Botrylloides* reached significantly higher abundances on two groups of panels transplanted from the Breakwater to Pine Island. *Botrylloides* abundance was not significantly different among any of the other treatments, but it did remain absent from control panels at Pine Island. Finally, control panels on caged pilings at Pine Island were dominated by encrusting bryozoans. Bryozoan abundances on these panels were significantly greater than in all other treatments. Panels transplanted from Pine Island caged pilings to the Breakwater were also dominated by bryozoans, and bryozoan abundances were significantly greater than in all the remaining treatments.

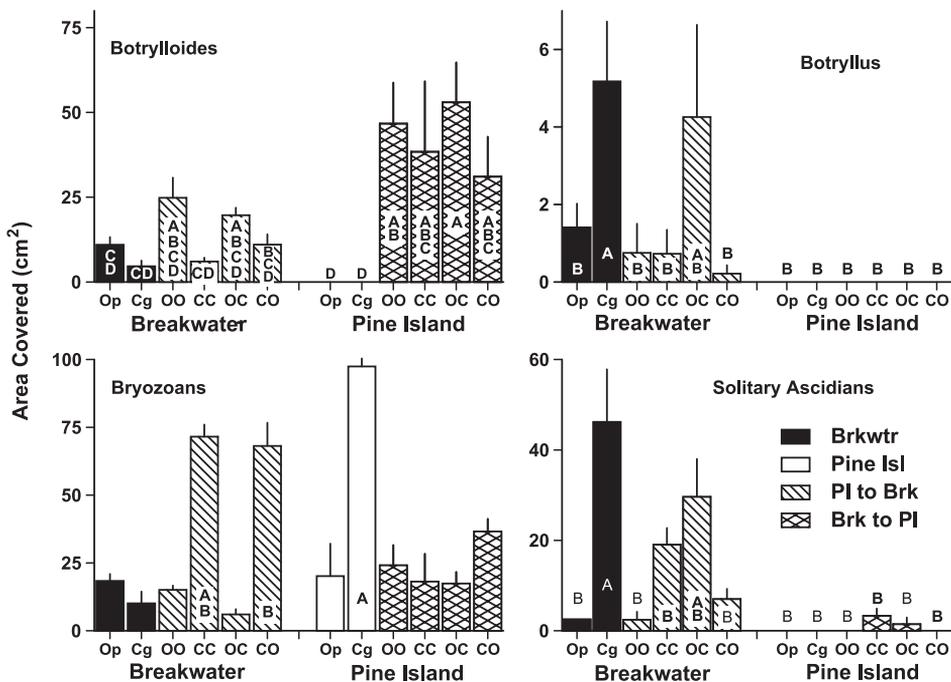


Fig. 6. Mean abundances in the 1993 Colonization Experiment 2 months after the reciprocal transplanting of panels between sites (3 months after initial exposure). The symbols and bar shading are the same as those in Fig. 5. Error bars represent standard errors.

After 3 months (Fig. 6), *Botryllus* was found only on pilings at the Breakwater and was significantly more abundant on caged pilings. Solitary ascidians had a distribution similar to *Botryllus* and were dominant on control panels on caged pilings at the Breakwater. However, a few solitary ascidians also remained on panels transplanted to caged pilings at Pine Island. *Botrylloides* was in greatest abundance on all treatments transplanted from the Breakwater to Pine Island. It was also abundant on all other treatments except the Pine Island control panels. Finally, the pattern of bryozoan abundance did not change substantially from the previous month; abundances on panels originally on caged pilings at Pine Island were significantly greater than on other treatments. The large difference in bryozoan abundance on control panels on caged and open pilings at Pine Island did not result from the presence of other species on the open pilings. The control panels on these pilings had 50–75% of the remaining space unoccupied.

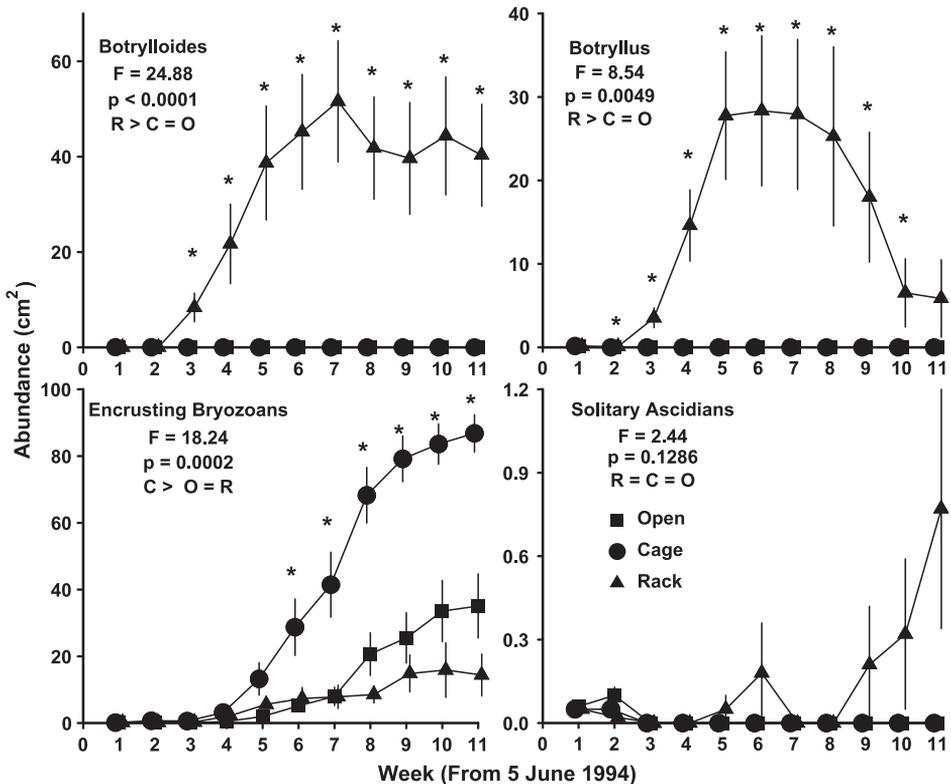


Fig. 7. The change in the mean abundances on the 1-week series panels in the 1994 Colonization Experiment. Data are for panels transplanted to Pine Island after 1 week of exposure at the Avery Point Breakwater site. The mean abundance  $\pm$  S.E. on each of three treatments is compared for each taxon. Treatments were open (O) = open, uncaged experimental pilings, cage (C) = caged pilings, and rack (R) = racks suspended above the sea floor. Week 1 represents the initial mean abundance prior to transplanting. Significant results of repeated measures ANOVA for each taxon are shown and time periods in which a significant difference (one-way ANOVA) was found among the treatments are indicated by an asterisk (\*). Error bars represent standard errors.

### 3.2.3. Variation in response to predation with initial community age

In the 1994 experiment, all colonies and individuals on panels transplanted to the Pine Island site after a 1-week exposure at the Breakwater site were still extremely small and could only be identified and counted using a dissecting microscope. The total area covered by all species was never greater than 2% of the available surface area of any panel. However, after transplanting, striking differences among the treatments developed. The colonial ascidians, *Botryllus* and *Botrylloides*, dominated the panels on the racks but were absent from the caged and open pilings (Fig. 7). Although solitary ascidians never became abundant and did not differ significantly among the treatments, they survived only on panels suspended on racks. *Botryllus* abundance declined near the end of the study, but this probably resulted from the post-reproductive loss of adult colonies. In the absence of ascidians, encrusting bryozoans dominated both open and caged pilings. Bryozoan abundance differed significantly between the caged and open pilings with panels on caged pilings becoming almost completely covered by bryozoans (Fig. 7). Mean bryozoan cover on the open pilings reached only 40% of the available surface area and did not differ

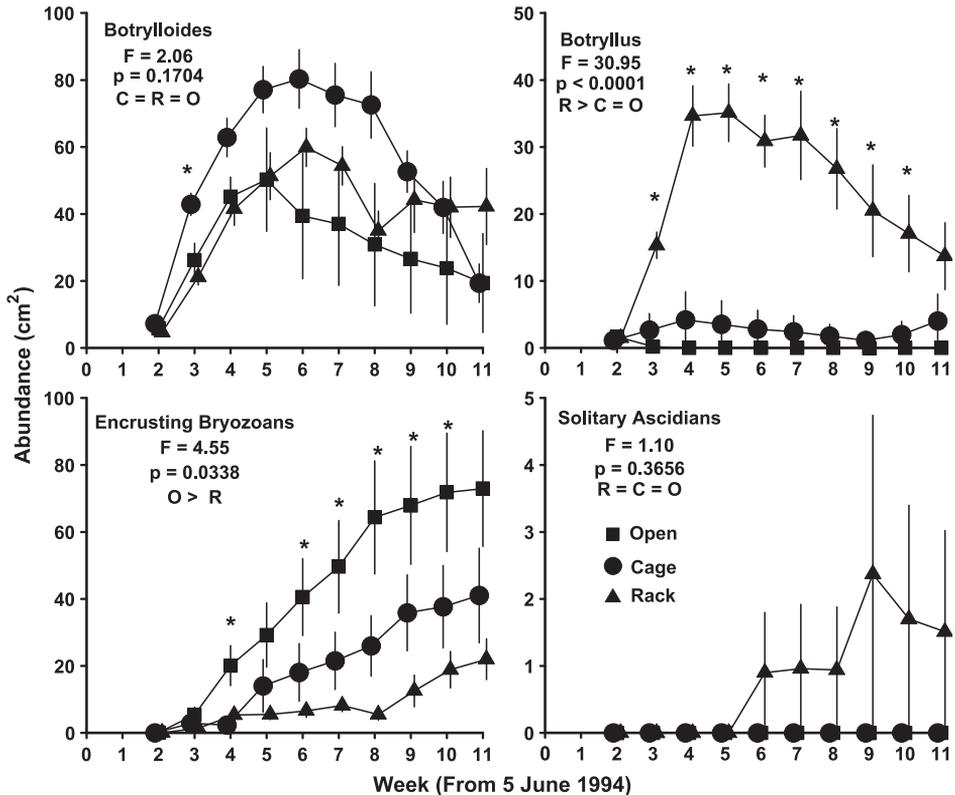


Fig. 8. The change in the mean abundances on the 2-week series panels in the 1994 Colonization Experiment. Data are for panels transplanted to Pine Island after 2 weeks of exposure at the Avery Point Breakwater site. Week 2 represents the initial mean abundance prior to transplanting. Descriptions and symbols are the same as in Fig. 7. Error bars represent standard errors.

significantly from that on racks. Similar to the 1993 experiment, most of the remaining surface on open-piling replicates still remained open and devoid of epifaunal invertebrates by the end of the experiment.

The relationships among the three treatments in the communities that developed on panels that were transplanted to Pine Island after a 2-week exposure at the Breakwater were different than those seen in the 1-week transplants. *Botryllus* and *Botrylloides* continued to be the dominant species on the suspended racks (Fig. 8). *Botrylloides* also dominated the two piling treatments and was not significantly different among the treatments. Some *Botryllus* were present in the caged piling treatment, but its abundance remained significantly higher on the racks than on the other two treatments. Bryozoan abundance also differed among the treatments, with their abundance on open pilings (reaching almost 80% cover) being significantly different from the racks with bryozoan abundance on caged pilings being intermediate. The abundance of bryozoans on the open pilings also contrasted with their much lower abundance on open pilings in the 1-week series.

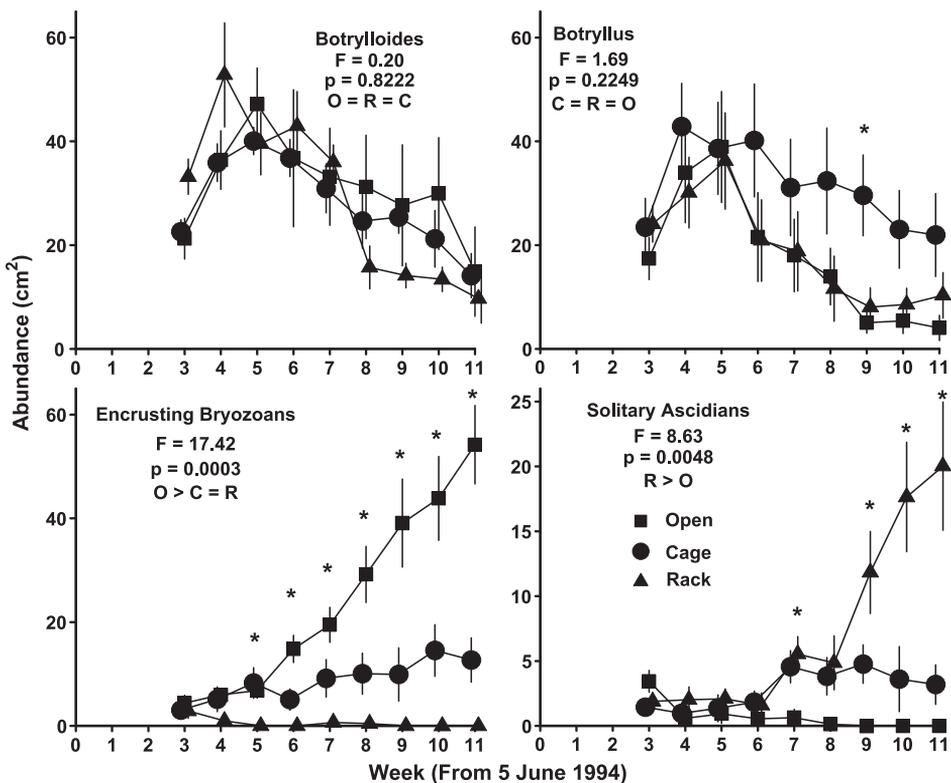


Fig. 9. The change in the mean abundances on the 3-week series panels in the 1994 Colonization Experiment. Data are for panels transplanted to Pine Island after 3 weeks of exposure at the Avery Point Breakwater site. Week 3 represents the initial mean abundance prior to transplanting. Descriptions and symbols are the same as in Fig. 7. Error bars represent standard errors.

Three major changes occurred on the panels transplanted after 3 weeks. First, *Botryllus* as well as *Botrylloides* became dominant on piling treatments as well as on the suspended racks with no significant differences among the three treatments in the abundance of either species (Fig. 9). Secondly, solitary ascidians increased to 20% cover on the panels in the rack treatment and were significantly more abundant than in the open piling treatments with caged pilings being intermediate. Thirdly, colonial hydroids became abundant on the panels on suspended racks and significantly different from the two piling treatments (Fig. 10). Finally, as in the 2-week series, encrusting bryozoans were significantly more abundant on open pilings, probably as a consequence of the reduced abundance of *Botryllus* and solitary ascidians.

The results of the 4-week series (Fig. 11) were fairly similar to those of the 3-week series. The major difference was the significantly greater abundance of solitary ascidians on caged pilings than on the open pilings. In addition, *Botryllus* decreased to significantly lower abundances on open pilings, contributing to significantly higher abundances of

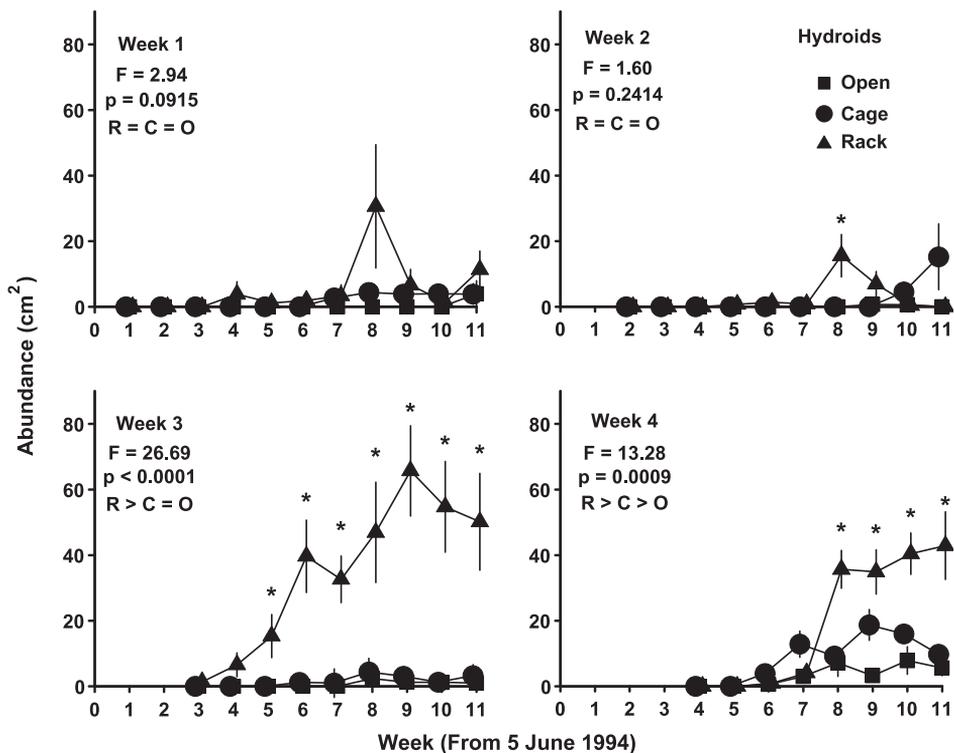


Fig. 10. The change in the mean abundances of colonial hydroids on each of the four transplant series in the 1994 Colonization Experiment. Data are for panels transplanted to Pine Island after 1, 2, 3, and 4 weeks of exposure at the Avery Point Breakwater site. Descriptions and symbols are the same as in Fig. 7. Error bars represent standard errors.

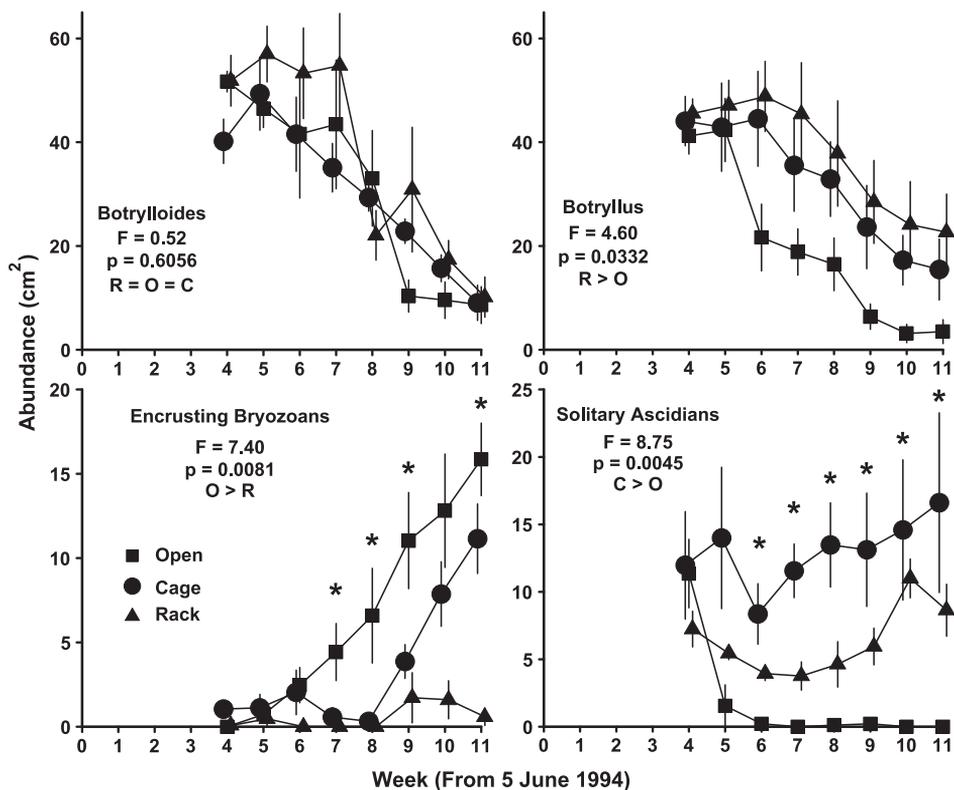


Fig. 11. The change in the mean abundances on the 4-week series panels in the 1994 Colonization Experiment. Data are for panels transplanted to Pine Island after 4 weeks of exposure at the Avery Point Breakwater site. Week 4 represents the initial mean abundance prior to transplanting. Descriptions and symbols are the same as in Fig. 7. Error bars represent standard errors.

encrusting bryozoans in this treatment. As in the 3-week series, hydroids colonized and dominated on the suspended racks (Fig. 10).

#### 4. Discussion

Taken together the results from two colonization experiments demonstrate that the predation on recruits observed in short-term transplant experiments (Fig. 3; Osman and Whitlatch, 1995, 1996, 1998) has predictable consequences on the communities that develop at the two sites. In the 1993 experiment (Figs. 4–6), bryozoans dominated panels that remained at the Pine Island site for the entire length of the experiment and ascidians dominated controls at the Breakwater. When panels were transplanted from Pine Island to the Breakwater, absent ascidians rapidly colonized the communities on them. However, panels from caged pilings at Pine Island with higher abundances of bryozoans when transplanted became dominated by bryozoans rather than ascidians. This suggests that

some established encrusting bryozoans can successfully compete with the ascidians and maintain dominance. Panels transplanted from the Breakwater to Pine Island (Figs. 4–6) suffered losses of *Botryllus* and solitary ascidians from both caged and open pilings, indicating the effects of the small and abundant snail predators that could enter cages. Some solitary ascidians survived on caged pilings, suggesting that larger individuals do escape predation by smaller invertebrates but not large invertebrates and fish. The large difference in the abundance of solitary ascidians between caged and open pilings at the Breakwater indicates that some losses to large predators (probably green crabs) occurred at that site. Because *Botryllus* is usually semelparous (Grosberg, 1988) its overall decline on all treatments was a consequence of the post-reproductive mortality of adult colonies and the lack of subsequent recruitment. Finally, the dominance of *Botrylloides* on all panels transplanted to Pine Island is consistent with the results of recruitment experiments (Osman and Whitlatch, 1996) in which colonies greater than 1 week old were not affected by predators.

The results from the 1994 experiment emphasize how predation by different predator guilds on different life-stages of different species influences recruitment and overall community development (Figs. 7–11). All of the ascidian species were vulnerable to predation when newly settled or less than 1 week old (Fig. 7). When predation was reduced or removed by using suspended racks, even the 1-week transplants (Fig. 7) with the smallest and youngest prey developed an ascidian-dominated community. However, no ascidians survived on either piling treatment and bryozoans were the dominant taxon. When the transplanted community was older (Figs. 8,9 and 11), *Botrylloides*, as in the 1993 experiment, became a dominant species in all treatments. *Botryllus* was absent from open pilings in the 2-week series (Fig. 8) and was rare on caged pilings. Only when the transplanted community was 3 weeks old did this species become abundant on pilings (Figs. 9 and 11). Bryozoan abundance reflects the differences among treatments in ascidian abundance. On racks where both *Botrylloides* and *Botryllus* dominated, bryozoan abundance remained low (Figs. 7–9 and 11). It was somewhat higher in the caged treatment where only *Botrylloides* was dominant and highest on open pilings where *Botrylloides* abundance was lower. The bryozoans also increased in abundance as ascidian abundance declined near the end of the study. The decline in both species of colonial ascidians reflects their mortality after reproduction coupled with an absence of subsequent recruitment at the Pine Island site. Finally, solitary ascidians never survived on open pilings and only became abundant on caged pilings when the transplant community was 4 weeks old (Fig. 11). This progression of additions of species to the community is what we would expect based on the earlier predation studies (Osman and Whitlatch, 1995, 1996). In addition, the ascidians appeared to become part of the community on caged pilings at an earlier age than on open pilings. This is consistent with earlier experiments that suggested that as prey grew older they first escaped predation by the small predators and then by the macro-predators.

It appears that for the most part the short-term effects of predators on the survival of early life-stages of the dominant species do have a longer term effect on the development of the community. We did not follow the experiment into the winter and do not know whether the treatments would have remained different. Because the predators are likely to prevent recruitment by any of the ascidians, we would expect that all treatments would

become dominated by bryozoans as the transplanted ascidians died. In fact, this can be seen as in the decline of *Botryllus* and *Botrylloides* in all three treatments. Nevertheless, the experiments show that ascidians can thrive as part of the community at the Pine Island site if recruits and young juveniles can escape predation, which seems unlikely unless there are habitat refuges from the predators. It should also be noted that the hydroids that became dominant in the 3- and 4-week series on suspended racks (Fig. 10) may have also escaped the effects of predators, since they never became abundant in either of the piling treatments.

Earlier studies of subtidal marine epifaunal communities stressed the importance of temporal and spatial variation in larval recruitment coupled with competition for space and predation on established adults in controlling the development and structure of these communities (e.g. Osman, 1977, 1978; Sutherland and Karlson, 1977; Karlson, 1978). Our present study demonstrates that when examined more closely, predation on the earliest post-settlement life-stages rather than larval supply can control recruitment completely and the community that develops. Because post-settlement predation occurs so early in the development of communities it was largely unnoticed in those earlier studies in which recruitment was measured over longer time periods (e.g. monthly). Hixon et al. (2002) have pointed to similar effects of unnoticed post-settlement predation on estimates of fish recruitment and an increasing number of studies (e.g. Carr and Hixon, 1995; Hixon and Carr, 1997; Cowen et al., 2000; Steele, 1997; Steele et al., 1998; Searcy and Sponaugle, 2001; Carr et al., 2002; Taylor and Hellberg, 2003) document the importance of local control of early life-stages to recruitment and populations. In their review, Hunt and Scheibling (1997) showed that post-settlement mortality from various causes can be important in numerous other marine benthic communities. Thus, the post-settlement control of recruitment and subsequent community development by predators is not unique to our system and may actually be fairly common.

The strong control of these New England subtidal epifaunal communities by predation on recruits is the consequence of the cumulative influence of a number of generalist invertebrate and vertebrate predators feeding on early post-settlement life-stages of species that vary sharply in their susceptibility to the different predators. The results of the experiments reported here (also see Osman and Whitlatch, 1996, 1998; Whitlatch and Osman, 1998) as well as earlier work examining individual predator species (Osman et al., 1990, 1992; Osman and Whitlatch, 1995) all suggest that *Anachis* and *Mitrella* have broad diets, but they exert their greatest influence on newly settled ascidians. Likewise, the cunner has a broad diet (Olla et al., 1975; Green et al., 1984) and in the epifaunal communities at our sites exerts its greatest influence on recruitment by solitary ascidians. Vulnerability to these predators not only varies among prey species but also among life-stages of the same species.

For most species vulnerability to predation is high immediately after metamorphosis and attachment to the substrate. Small invertebrates, similar in size to the newly settled prey, are the likely predators. Some prey taxa, particularly calcified ones (e.g. barnacles, mussels, some bryozoans), remain vulnerable for only a short period of time (hours to days). For example, in an experiment in which different densities of recruits of the bryozoan *Schizoporella errata* were exposed to *Mitrella*, mean survival was reduced to approximately 50% of that observed in controls (Table 2). The observed mortality

Table 2

Comparison of the mortality of recruits of the encrusting bryozoan *Schizoporella errata* on control surfaces and surfaces exposed to *Mitrella lunata*

Treatment	% Mortality	% Ancestrula mortality	% Survivors with ancestrula
Control	15.07 ± 7.76	18.13 ± 8.59	95.91 ± 1.70
<i>Mitrella</i>	52.83 ± 5.85	78.45 ± 6.40	37.81 ± 8.51

Also shown is the percent mortality of the first zooid or ancestrula of the colonies and the percentage of surviving colonies in which the ancestrula was alive.

resulted from predation exclusively on the first zooid or ancestrula of each *Schizoporella* colony. The ancestrulae are both smaller than normal zooids and uncalcified (Waters, 1924), making them more vulnerable to predators (Harvell, 1984). Less than 50% of the surviving colonies exposed to *Mitrella* predation had a living ancestrula. All observed dead recruits were ancestrulae without other zooids. Thus for *Schizoporella*, there is an escape from *Mitrella* predation with the formation of the second zooid of the colony, which should make recruits vulnerable to these small predators for only a 1–2-day period.

On the other hand, recruits of most colonial and solitary ascidians remain vulnerable to small predators for much longer (usually weeks). Even for these species vulnerability to predators can vary as a function of size. For example, we exposed 0.5-, 1.0-, and 4.7-mm-diameter recruits of the solitary ascidian *Molgula* to predation by individual *Anachis* and *Mitrella*. For the two smallest size classes, <10% of the *Molgula* survived predation by *Mitrella* compared to >85% survival in controls (Table 3). However, for the 4.7-mm recruits we found >90% survival in both the control and *Mitrella* treatments. *Molgula* survival in the *Anachis* treatment decreased from 63% to 36% as the size of the recruits increased. Thus, as *Molgula* recruits increase in size they escape predation by *Mitrella* only to suffer increased predation by the larger *Anachis*. The only exception to this several week-long period of vulnerability seems to be the colonial ascidian *Botrylloides* which remains vulnerable to predators for only a few days to a week. We have observed partially eaten recruits of this bright orange species, suggesting that it may be defended chemically, as in some other ascidians (e.g. Young and Bingham, 1987; Pisut and Pawlik, 2002; Tarjuelo et al., 2002).

Ultimately, most prey species reach a size at which the small predators have no measurable effect on them. However, some species then become vulnerable to predation

Table 3

Comparison of the survival of different sized *Molgula manhattensis* when preyed on by *Mitrella lunata* and *Anachis* spp.

<i>Molgula</i> size	% <i>Molgula</i> survival			A posteriori test	$F_{2,27}$	$p$
	Control	<i>Mitrella</i>	<i>Anachis</i>			
0.53 ± 0.03	99.3 ± 0.5	2.7 ± 1.2	61.4 ± 8.6	C>A>M	90.5	<0.0001
1.00 ± 0.06	85.4 ± 5.6	7.2 ± 3.0	53.6 ± 11.7	C>A>M	26.4	<0.0001
4.65 ± 0.20	95.0 ± 1.6	94.3 ± 1.4	36.2 ± 7.2	C = M>A	50.0	<0.0001

In each experiment thirty 2.5 × 7.5-cm panels with at least 40 *Molgula* were exposed to no predator (control), a single *Mitrella*, or a single *Anachis* (10 panels per treatment). After 2 days survival was estimated as the percentage of *Molgula* remaining. Data were transformed (arcsine square root) before analysis.

by larger invertebrates (e.g. sea stars, crabs) and fish. Juveniles of all species of solitary ascidians, as well as mussel recruits (Osman and Whitlatch, 1998), were found to be vulnerable to fish predation. In addition, mussels and barnacles are known prey of sea stars, gastropods, and crabs (e.g. Connell, 1961a; Paine, 1966; Menge, 1976, 1978; Elner, 1978; Jubb et al., 1983). Eventually, even the solitary ascidians can reach a size at which they escape predation from fish (Osman et al., 1990). Barnacles and mussels, which can find refuge from some predators in the intertidal zone, may remain vulnerable to some predators in these subtidal communities.

Most of our inferences regarding the particularly strong effects of predators on post-settlement life-stages and thus on recruitment have resulted from observations of three small species of gastropods. These species can be extremely abundant and their recruitment occurs when prey recruitment is highest (Rogers, 1998; Fig. 3). There is clearly a wide array of other similarly sized species that potentially function as predators of the epifaunal communities. Some of these (e.g. nudibranchs) prey on particular species (e.g. Thompson, 1964; Clark, 1975; Bloom, 1981; Lambert, 1991) while others (e.g. flatworms, nemerteans, small crustaceans, some polychaetes) may be more general in their prey selection (e.g. Bell, 1980; Watzin, 1983; Palmer, 1988; Ejdung and Elmgren, 1998). In addition, new recruits of larger predators (e.g. crabs, sea stars, whelks) are often similar in size to epifaunal recruits and may feed on them or juveniles (e.g. Hughes et al., 1992; Cohen et al., 1995). For example, in two 1-week experiments contrasting epifaunal recruitment onto 20 sets of paired panel surfaces, one exposed to a newly settled spider crab, *Libinia emarginata*, and one acting as a control (see Osman et al., 1992; Osman and Whitlatch, 1995 for methods) we found significantly reduced recruitment of *Botryllus*, *Diplosoma*, *Bugula*, *Cryptosula*, and *Botrylloides*, but not *Spirorbis* or *Molgula* (Table 4). These recruiting predators often eat different prey species than adults (Birkeland et al., 1971, Barker, 1979) and even those species that are herbivorous as adults can be predators as juveniles (Barker, 1979). Given the wide array of likely predators of epifaunal recruits and their potential to influence community development, it is likely that our results provide a conservative estimate of the influence of post-settlement mortality resulting from predation.

Table 4

Comparison of the recruitment of seven epifaunal species in the presence and absence of newly recruited *Libinia emarginata*

Species	Control	<i>Libinia</i> present	<i>t</i>	<i>p</i>
<i>Botrylloides</i>	1.45 ± 0.21	0.78 ± 0.15	2.37	0.0229
<i>Botryllus</i>	2.15 ± 0.27	0.30 ± 0.11	5.91	< 0.0001
<i>Diplosoma</i>	0.92 ± 0.21	0.15 ± 0.08	3.44	0.0014
<i>Molgula</i>	0.30 ± 0.11	0.18 ± 0.07	0.96	0.3423
<i>Bugula</i>	1.08 ± 0.21	0.05 ± 0.03	4.95	< 0.0001
<i>Cryptosula</i>	4.62 ± 0.61	2.65 ± 0.36	2.86	0.0067
<i>Spirorbis</i>	1.28 ± 0.18	1.55 ± 0.26	0.96	0.3434

Means are for two experiments conducted in September–October 1993 each with twenty 2.5 × 7.5-cm panels with each panel having one surface exposed to *Libinia* and a paired surface acting as a control. A paired *t*-test was used to contrast the two treatments.

Ultimately, the strong effect of these predators on the community as a whole can be seen in our colonization experiments (Figs. 4–11). When all predators were excluded the most vulnerable ascidians were common or dominant members of the communities. This occurred regardless of the age of the transplanted community and implies that their absence from sites with predators is not a consequence of their inability to survive in these more exposed habitats (also Table 1). The presence of solitary ascidian larvae in larval traps at Pine Island (Rogers, 1998) and small numbers of ascidian larvae in plankton samples from this site (unpublished data) demonstrate that larvae of these species do reach this site. The dominance of these species in the 1-week series suspended rack treatment (Fig. 7) indicates that if these larvae settle at this site they can survive if predators are absent.

It remains that dominance within these communities is controlled by differences in recruitment. However, the control of recruitment is at the post-settlement stage. This control is so strong that the same communities develop at the same sites year after year despite the ephemeral nature of several dominants and the almost certainty that propagules of all species reach all the habitats. We observed clear differences in dominant species at the Pine Island and Breakwater sites over more than 10 years, yet many of the dominants are short-lived with individuals surviving much less than a year. For these sessile species, larval recruitment is critical for maintaining a population at a particular site. Given the potential of larvae to be well-dispersed and be distributed among the sites, this long-term maintenance of distinctly different communities at the sites which are <1 km apart is both remarkable and a testament to the strength of the predators in exerting strong local control on recruitment into these communities, altering any patterns that would result from changes in the supply of larval settlers. This strong control would seem to differentiate this subtidal system from intertidal ones that are more closely linked to larval supply.

Although we can document the role of predators in determining the development of different communities at different sites, we have not determined what controls the distribution of the predators and why they are rare at the Breakwater site. In earlier work (Osman et al., 1990, 1992; Osman and Whitlatch, 1995) we used both *Anachis* and *Mitrella* in experiments conducted at the Breakwater site. The snails were often held at this site for several months, with only incidental mortality. Thus adult snails can survive at this site, and given the large ascidian populations found there an ample food supply exists. Although all three species produce benthic egg capsules, larvae that hatch from these capsules still spend several weeks in the plankton (Scheltema and Scheltema, 1963; Scheltema, 1969; Thiriot-Quievreux, 1983; Rogers, 1998). We would expect larvae to be transported to both sites and that the long-term maintenance of differences in population densities between sites must result from post-settlement differences in mortality.

Another difference between the sites is the higher abundance of green crabs (*Carcinus maenas*) at the Breakwater (Berger, 1998). This corresponds to previous studies that have shown green crabs are often more abundant in protected areas (Menge, 1983, 1991; Moksnes et al., 1998). In addition, Berger (1998) found an inverse correlation between the abundance of green crabs and the densities of *Anachis* and *Mitrella* based on habitat type. In laboratory experiments *Carcinus* readily preyed on *Anachis* and *Mitrella* (Berger,

1998). It is possible that green crabs or other predators influence the distribution of the small predators which in turn influence the epifaunal community.

## 5. Conclusions

Our experimental studies demonstrate that post-settlement predator–prey interactions can involve multiple early-ontogenetic life-stages of a variety of prey species and many predator species, both invertebrate and vertebrate. There is no single dominant prey nor a single key predator species. These dominant processes are the most likely cause of the striking and persistent differences in species composition between sites that are inversely correlated with the presence of predators which consume newly settled and juvenile (post-settlement) life-stages. At sites without abundant predators, ascidians dominate adult populations and recruitment. At sites where predators are present ascidians are rare or absent and bryozoans dominate.

We feel that post-settlement predation needs to be recognized as a generally important process affecting community composition. For those systems in which recruitment is a dominant or controlling process, post-settlement predation may often be the most important process. In this light, the intertidal barnacle–mussel communities in which supply often seems to control recruitment (e.g. Gaines and Roughgarden, 1985; Raimondi, 1990; Sutherland, 1990; Minchinton and Scheibling, 1991) may be viewed as an end member of a continuum. In such harsh environments the diversity of possible prey and predators is greatly reduced, limiting both the potential number of post-settlement predators as well as their ability to control recruitment. However, even within intertidal systems there have been indications that predation on recruiting life-stages can be important (e.g. Palmer, 1990; Gosselin and Qian, 1996).

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