



An experimental test of the effects of variation in recruitment intensity on intertidal community composition

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Abstract

The rocky intertidal has been a model system for experimentally testing hypotheses regarding the factors that structure natural communities. Many ecologists have proposed that changes in the intensity of recruitment of individuals into a community should influence community structure. Past work investigating this hypothesis has primarily been surveys of recruitment and community structure across large spatial scales. Surprisingly, no researchers to date have manipulated recruitment into a rocky intertidal community to assess the response of interactions of the whole community to variation in recruitment intensity. We manipulated the densities of *Balanus glandula* and *Chthamalus* spp. recruits across a four-fold difference at two sites spanning the Monterey Bay, California, USA, to experimentally test if differences in recruitment intensity influenced initial changes in community composition and if these changes persisted through time. The results of this work indicate that differences in recruitment influence community composition initially, but that these changes can be short-lived.

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1. Introduction

The planktonic larval stage of many marine organisms introduces the potential for considerable spatial and temporal variation in recruitment to the benthic adult population.

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Such variation is driven by abiotic (e.g. waves, currents, tides and wind) and biotic (e.g. behavior, predation) factors, which vary markedly in space and time (Gaines and Roughgarden, 1985; Underwood and Fairweather, 1989; McEdward, 1995). Researchers have become interested in open life histories because so many marine organisms have dispersive larval stages and early work paid little attention to the potential effects of this life history phase on population dynamics or community structure (Underwood and Fairweather, 1989). Empirical research into “supply-side” ecology established that recruitment dynamics often influence adult distribution and abundance in reef fishes (Doherty, 1983; Doherty and Williams, 1988; Victor, 1983, 1986), barnacles (Caffey, 1985; Gaines and Roughgarden, 1985; Raimondi, 1990; Menge, 2000), and other benthic invertebrates (Keough, 1984; Keough and Downes, 1982). More recently, researchers have begun to investigate the effects of recruitment intensity on pairwise interactions (Underwood and Denley, 1984; Fairweather, 1985, 1988; Reed, 1990; Minchinton and Scheibling, 1993; Robles, 1997; Robles and Desharnais, 2002; Steele, 1997). The outcome of competition between two species can be influenced by recruitment (Reed, 1990), and several studies have demonstrated greater predation rates with higher rates of prey recruitment (Gaines and Roughgarden, 1985; Fairweather, 1988; Robles, 1997).

Much of the research on the relationship between recruitment intensity and community structure has been conducted as surveys of intertidal communities along recruitment gradients (Menge, 1991; Connolly and Roughgarden, 1998, 1999; Connolly et al., 2001). This research has consistently found, as expected, that sites with higher recruitment of invertebrates have less free space and a higher abundance of adult invertebrates than sites with low recruitment. Most marine ecologists have come to accept these associations as support for the hypothesis that differences in recruitment result in differences in community structure, at least across large spatial scales. However, these analyses suffer from the possible confounding influence of unrelated site-to-site covariation between recruitment variation and community variation. As far as we know, no research published to date has explicitly manipulated recruitment to test if recruitment variation alters interactions of the whole community (i.e., multiple species).

The broad goal of our research was to assess if experimentally enforced differences in recruitment of a dominant member in the community influenced species interactions and community composition, and if any such effects on community composition persisted through time. We manipulated the density of recruits of both of the dominant barnacle species in the high intertidal communities along the central California coast and monitored the response of the community through time. Our treatments (high and low density) reflected the largest difference in recruit density possible based on observed natural recruitment to the sites. Our alternative hypotheses were that differences in recruit density would influence community composition through effects on (1) competition for space or (2) facilitation. Under high levels of recruitment and/or limited available space, differences in recruit density should influence the outcome of competition. Alternatively, if space was not limiting, recruitment differences could affect community composition through facilitation. Past research has shown that facilitation can be important in the high intertidal zone, where dense assemblages can buffer group members from desiccation or heat stress (Lively and Raimondi, 1987; Bertness, 1989;

Bertness and Leonard, 1997). Therefore, we might actually see an increase in species abundances with increased recruit density. We conducted the experiments at two sites spanning the Monterey Bay that we expected to differ in barnacle recruitment rates and the processes likely to structure the community. Thus, we were able to test if differences in recruitment of two different barnacle species had effects on the community and address differences between sites in community-level processes that might be influenced by recruitment intensity.

2. Materials and methods

2.1. Study system

Experiments were conducted during 2000 in the high intertidal zone at two sites within the Monterey Bay on the central California coast, USA (Fig. 1). Hopkins Marine Station is at the southern end of the bay (HMS; N36.621', W121.903') and Sand Hill Bluff is to the north end of the bay (SHB; N36.977', W122.151'). The high intertidal zone in this region is relatively simple compared to zones lower in the intertidal, typically including eight common species of sessile or somewhat motile organisms. Acorn barnacles *Balanus glandula* and *Chthamalus fissus/dalli* are the dominant space occupiers in the high rocky intertidal community. (*C. fissus* and *C. dalli* cannot be distinguished in the field without dissecting individuals). The red algae *Endocladia muricata* and

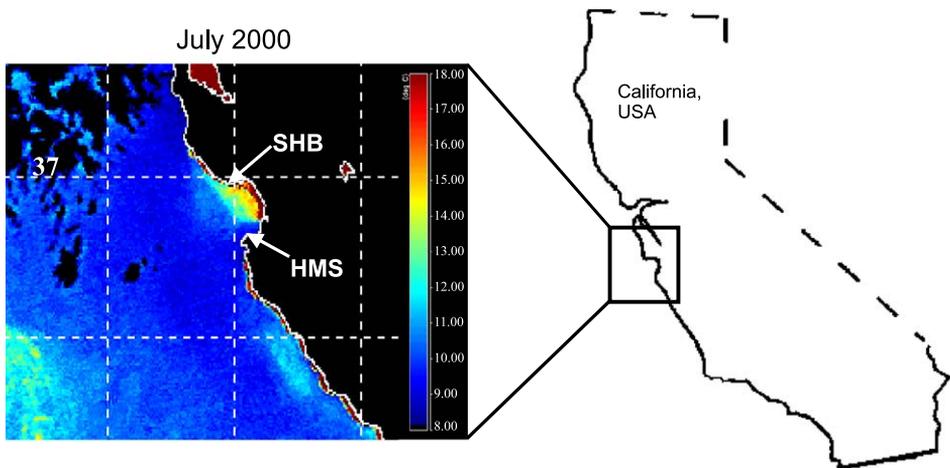


Fig. 1. Locations of the study sites in central California, USA. The color image shows the sea surface temperatures in July 2000. Note the differences in sea surface temperature offshore of Sand Hill Bluff (SHB) vs. Hopkins Marine Station (HMS), which are representative of general patterns in sea surface temperature in spring and summer (Graham and Largier, 1997). White numbers on the map indicate latitude and longitude (images obtained from the Biological Oceanography Group, MBARI; http://www.mbari.org/bog/Projects/Satellite/seawifs_br/default.html).

Mastocarpus papillata are also common and compete with barnacles for space. The ephemeral algae, *Ulva* spp. is sometimes found in the winter and early spring. The limpets *Macclintockia scabra* and *Collisella paradigitalis* are also present. *M. scabra* occurs primarily on horizontal surfaces, whereas *C. paradigitalis* occurs on vertical rock. When the two species co-occur, they compete for food (algae; Dayton, 1971). Both species of limpets have been observed scraping juvenile barnacles off the rock surface while grazing (Dayton, 1971; Farrell, 1991). The majority of limpets in the experimental plots in this study were *M. scabra* (the experiment was conducted on horizontal rock benches). The main barnacle predators at our study sites were the snails, *Acanthina punctulata* and *Acanthina spirata*.

We chose the two study sites for a number of reasons. First, past research in the region (Grantham, 1997; Connolly and Roughgarden, 1999; Connolly et al., 2001), along with our own work (Forde, 2002), has shown that recruitment rates of *B. glandula* and *Chthamalus* spp. often differ between the north and south ends of Monterey Bay. Second, oceanographic factors, such as sea surface temperature, often differ between the northern and southern tips of the bay, particularly during the barnacle recruitment season (Graham and Largier, 1997; Fig. 1). Finally, sites to the north of the bay are typically composed of sandstone, whereas south of the bay the rock is primarily granite, and rock-type can influence the structure of rocky intertidal communities (Lewis, 1964; Raimondi, 1988, but see Caffey, 1982). Thus, conducting the experiment in two different communities provided us with potentially more information regarding how communities might respond to differences in recruitment in general than if we conducted the experiment at one site.

2.2. Experimental design

We followed the same general procedure at both sites. The experimental design included a series of plots used for manipulations of acorn barnacle recruitment and a series of plots used to monitor natural variability in recruitment. This was done to determine if our manipulations reflected the natural levels of recruitment at each site. We chose acorn barnacles as our target species for the manipulations for a number of reasons. First, acorn barnacles are the dominant space occupiers of high intertidal communities in the region and past research has shown that both barnacle species interact with other sessile species in the community (Gaines and Roughgarden, 1985; Forde, 2002). Second, past research in the region indicated that acorn barnacles are reliable settlers (Gaines and Roughgarden, 1985; Grantham, 1997; Connolly and Roughgarden, 1999; Forde, 2002). Finally, acorn barnacles can be induced to settle, which aided our recruitment manipulations in that we could potentially increase the range of recruit densities used in our experimental treatments (Knight-Jones, 1953; Raimondi, 1988).

The most abundant barnacle species at each site was targeted for the recruit density manipulations (i.e., either *Chthamalus* spp. or *B. glandula*). The recruit density treatments were based on the maximum number of either *Chthamalus* spp. or *B. glandula* recruits at each site that allowed for random allocation of the treatments. Recruit densities were maintained for 2 months by removing excess recruits. This design simulated recruitment dynamics characterized by a pulse in recruitment followed by periods of little to no

recruitment. The recruitment manipulations, combined with our data on natural variability in recruitment (methods detailed below), allowed us to determine the effects of recruitment on community composition within a typical recruitment range at each site.

2.2.1. Effects of *Chthamalus* spp. recruitment at HMS

Ten 8×12 cm plots were permanently marked in the high intertidal and cleared of all organisms in March 2000. We crushed adult barnacles with a mortar and pestle and applied the crushed adults to all of the plots after clearing to enhance barnacle settlement (Raimondi, 1991). The number of barnacle recruits and other species present in the plots were counted and crushed barnacles were reapplied to the plots during each low tide series (about every 2 weeks) until July.

In June 2000, we initiated recruitment manipulations. Recruitment to HMS of *Chthamalus* spp. was higher than *B. glandula*, so here we manipulated the density of *Chthamalus* spp. recruits. Recruit density treatments were 200 *Chthamalus* spp. recruits per plot (high density) or 50 recruits per plot (low density; five replicates per treatment). The treatments were maintained by removing any recruits in excess of the treatment densities from the rock with forceps during each low tide series through the end of August 2000, when the majority of recruitment ended.

We followed the development of the community during and after the recruitment manipulations to determine if these early events influenced other species and if these influences persisted through time. To accomplish this, we collected data on the percent cover of barnacles, limpets and *E. muricata*, and the amount of free space in August and December using a 8×12 cm quadrat with 100 randomly placed points. We rarely encountered *C. paradigitalis* in the plots so we combined data on the cover of both limpet species into 'limpets' for the data analyses. Although *Acanthina* spp. were present at HMS, they were never found in our experimental plots.

Table 1

Recruitment of *Chthamalus* spp. and *B. glandula* to HMS from May through December in 2000 and 2001 at (A) HMS and (B) SHB

Barnacle species	2000 (per 96 cm ²)	2001 (per 100 cm ²)
<i>(A) HMS</i>		
<i>Chthamalus</i> spp.		
Range	0–109	0–55
Mean (\pm S.E.)	9.27 (3.94)	10.18 (2.27)
<i>B. glandula</i>		
Range	0–29	0–33
Mean (\pm S.E.)	1.67 (0.99)	3 (0.98)
<i>(B) SHB</i>		
<i>Chthamalus</i> spp.		
Range	4–212	0–640
Mean (\pm S.E.)	54.1 (10.9)	77 (20.65)
<i>B. glandula</i>		
Range	0–153	0–448
Mean (\pm S.E.)	16.62 (6.21)	42 (15)

Table 2

Results from the MANOVA on the percent cover of all species and free space at (A) HMS and (B) SHB

Effect	F-statistic	df	p-value
<i>(A) HMS (n = 10)</i>			
Recruit density	6.549	5, 12	0.004
Month	19.992	5, 12	0.000
Recruit density \times month	2.686	5, 12	0.075
<i>(B) SHB (n = 16)</i>			
Recruit density	238.723	6, 12	0.000
Month	37.401	6, 12	0.000
Recruit density \times month	23.997	6, 12	0.000

2.2.2. Effects of *B. glandula* recruitment at SHB

At SHB, we took advantage of a large recruitment event of *B. glandula* to the high intertidal zone in June 2000. Sixteen 8×12 cm plots were randomly selected and permanently marked in areas with high cover of *B. glandula* recruits (mean recruits per plot = 350; range = 200–600/plot). Density treatments were randomly assigned to the plots and *B. glandula* recruitment was manipulated to either 400 recruits/plot (high density) or 100/plot (low density). To control for any confounding effects of initial size of *B. glandula* recruits, the length of the opercular opening of at least 100 recruits per plot (randomly chosen in the high-density treatment) were measured to ensure that the size structure was similar for all treatments at the start of the experiment. We collected data on the percent cover of all members in the community (plus *Ulva* spp.) as described for HMS.

Finally, we wanted to be sure that our recruitment manipulations were within the range of natural variability in recruitment to each site so that we could evaluate the relevance of the results of our recruitment manipulations to general community composition and development at each site. To do this, we monitored natural levels of barnacle recruitment to both sites. In May 2000, 8×12 cm plots were permanently marked in the high zone and cleared of all organisms so that new recruits could easily be counted (HMS: $n = 13$; SHB: $n = 5$; the unbalanced design was due to a limited area for establishing plots at SHB). The number of *B. glandula* and *Chthamalus* spp. recruits was counted on a monthly basis through December. Plots were again cleared after sampling each month. Similar recruitment data (although plots were 10×10 cm rather than 8×12 cm) were collected from May through December 2001 (Partnership for Interdisciplinary Studies of Coastal Oceans, unpublished data), which allowed us to assess if our recruitment manipulations were within the range of natural variability in recruitment to each site in the following year. This information allowed us to better determine if barnacle recruitment patterns observed during the experimental phase of this project were typical or unusual, and thus whether or not the effects of our recruitment manipulations could be interpreted more generally.

Fig. 2. (A) Ninety-five percent confidence ellipses around score 1 vs. score 2 from the MANOVA on data collected at HMS in August and December. The high-density treatment was 200 *Chthamalus* spp. recruits/plot and the low-density treatment was 50 recruits/plot. (B) Correlations between each dependent variable and score 1 and score 2 from the MANOVA. The length of the arrow indicates the strength of the correlations. (C) Mean percent cover of each species in the high and low recruit density communities in August and December.

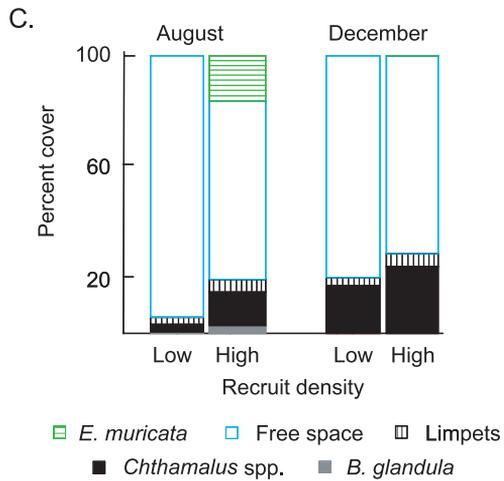
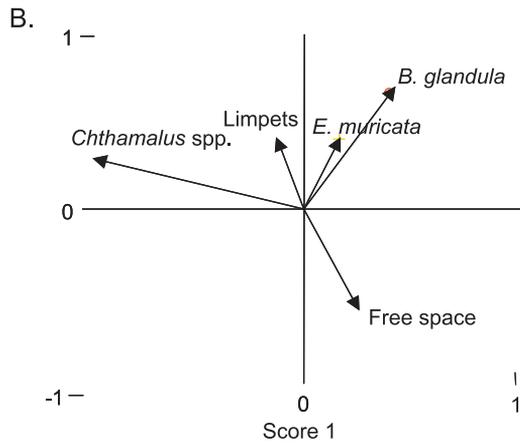
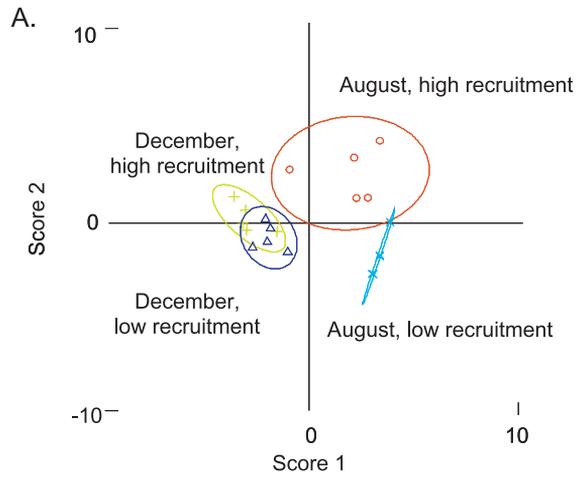


Table 3

Correlations between the scores from the MANOVA and the dependent variables for data collected at (A) HMS and (B) SHB

Dependent variable	Score 1	Score 2
<i>(A) HMS</i>		
<i>Chthamalus</i> spp.	– 0.913	0.312
<i>B. glandula</i>	0.396	0.679
Free space	0.249	– 0.576
<i>E. muricata</i>	0.17	0.408
Limpet	– 0.118	0.389
<i>(B) SHB</i>		
<i>B. glandula</i>	0.622	0.749
<i>Ulva</i> spp.	– 0.998	0.032
Free space	0.875	– 0.476
Limpet	0.578	0.648
<i>Chthamalus</i> spp.	0.636	0.361
<i>E. muricata</i>	0.288	0.536

2.3. Data analysis

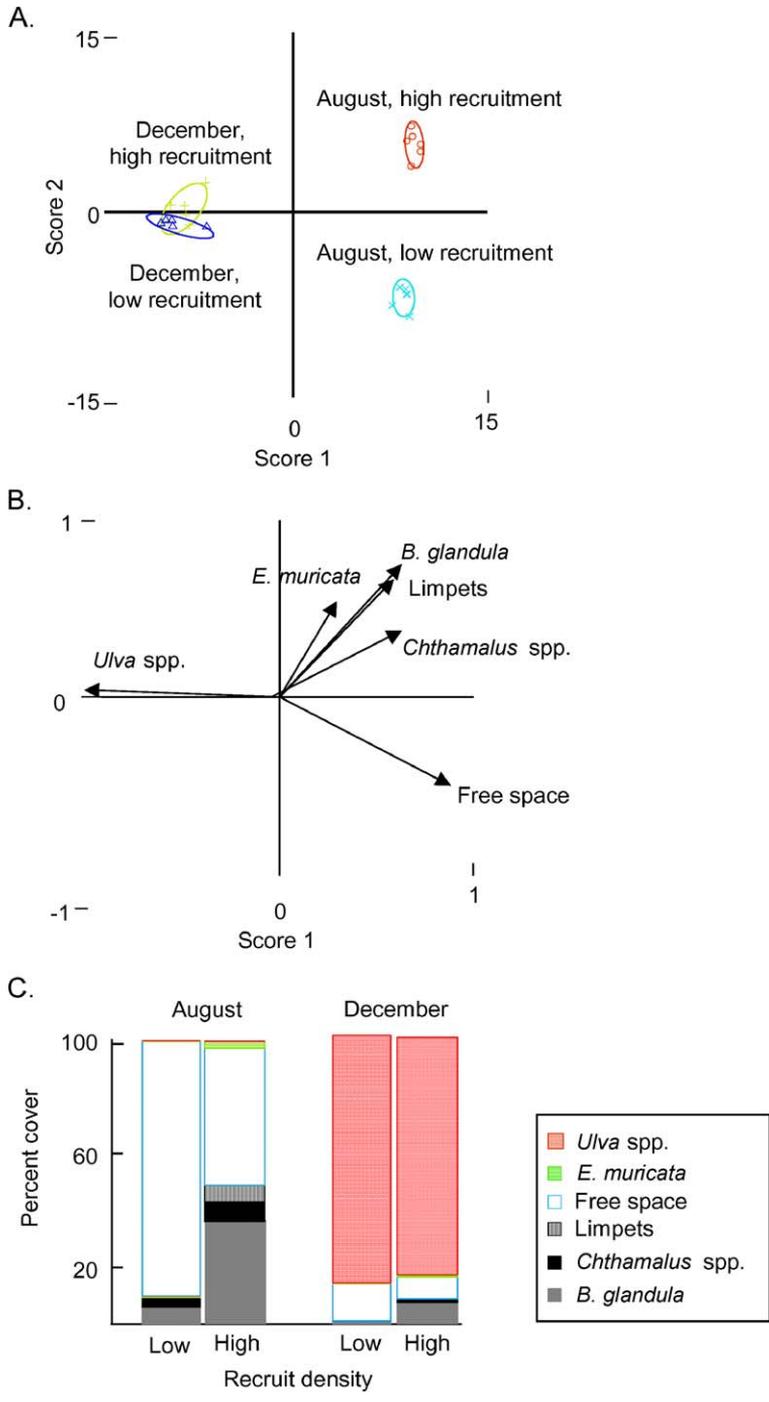
Analyses were done separately for each site. To test for the effects of differences in recruit density on community structure, and whether community composition changed through time, we analyzed the percent cover data collected during the manipulations (August) and 4 months after the manipulations ended (December) using multivariate analysis of variance (MANOVA), with recruit density and month as the independent variables. Assumptions were tested following Quinn and Keough (2002). We used the interaction term from the MANOVA (recruit density \times month) as the independent variable in a canonical discriminant analysis to generate canonical scores. These scores were then correlated with the percent cover data to interpret what was driving any differences in community composition.

3. Results

3.1. Effects of *Chthamalus* spp. recruitment at HMS

Our recruitment manipulations were within the range of natural recruitment to the site in both 2000 and 2001 (Table 1A). In 2000, recruitment of *Chthamalus* spp. ranged between 0 and 109 recruits per 96 cm², and from 0 and 55 recruits per 96 cm² in 2001.

Fig. 3. (A) Ninety-five percent confidence ellipses around score 1 vs. score 2 from the MANOVA on data collected at SHB in August and December. The high-density treatment was 400 *B. glandula* recruits/plot and the low-density treatment was 100 recruits/plot. (B) Correlations between each dependent variable and score 1 and score 2 from the MANOVA. The length of the arrow indicates the strength of the correlations. (C) Mean percent cover of each species in the high and low recruit density communities in August and December.



Recruit density had a significant effect on community composition and this effect varied through time (Table 2A). Community composition was different in the high vs. the low recruit density treatments in August, but composition converged by December (Fig. 2A). Relatively strong correlations between the scores from the MANOVA and the dependent variables indicated that aside from the cover of *Chthamalus* spp., which was manipulated, the cover of *B. glandula*, *E. muricata* and the amount of free space were driving differences in community composition (Table 3A). In August, the low recruit treatment was characterized by more free space than the high-density treatment, whereas the high-density treatment was characterized by *B. glandula* and *E. muricata* (Fig. 2). By December, community composition converged and this convergence was primarily driven by an increase in the cover of *Chthamalus* spp. in both treatments and a decrease in the cover of *E. muricata* in the high-density treatment (Fig. 2B, C).

3.2. Effects of *B. glandula* recruitment at SHB

Again, our recruitment manipulations were within the range of natural recruitment to the site in both 2000 and 2001 (Table 1B). *B. glandula* recruitment ranged from 0 to 448 recruits per 96 cm² in 2000 and 2001.

Analyzing the data on community composition using a MANOVA indicated that there was a significant interaction between recruit density and month (Table 2B). In August, community composition in the high recruit density treatment was clearly different from that in the low-density treatment, but the communities converged by December (Fig. 3A).

The correlations between the scores from the MANOVA and the dependent variables indicated that the abundance of all species and the amount of free space drove differences in community composition (Table 3B). The low recruit density treatment was characterized by more free space than the high-density treatment in August (Fig. 3). The high-density treatment was characterized by cover of both barnacle species, limpets, and *E. muricata*. In December, community composition converged (Fig. 3A), and both the high and low recruit density communities were characterized by high *Ulva* spp. cover (Fig. 3C).

4. Discussion

Our results indicate that differences in recruitment of the dominant members of a community may initially influence community composition, but that these differences are short-lived. At both of the sites used in this study, differences in community composition during our manipulations were driven, not surprisingly, by more free space in the low recruit density treatment than in the high-density treatment. In addition, the high recruitment communities were characterized by a higher abundance of all species at both sites, and thus were relatively more complex (i.e., had more species) than the low recruitment communities. Four months later, these differences in community composition were no longer apparent, and community convergence was driven by a decrease in complexity in the high density communities at both sites. At HMS, the high and low

recruit density plots converged on a community dominated by *Chthamalus* spp. and free space, whereas a bloom of *Ulva* spp. dominated both the high and low density plots at SHB.

We found no evidence to suggest that differences in recruitment influenced community composition through effects on competition for space. In contrast, we found an increase in species abundances with increased recruit density at both sites in August. Our results point toward the role of facilitation in structuring the communities, which is consistent with some past research. In the early stages of succession, facilitation can be important to structuring rocky intertidal communities (Jernakoff, 1983, 1986; Underwood et al., 1983; Farrell, 1991; Bertness and Leonard, 1997). For example, acorn barnacles can enhance algal recruitment (Farrell, 1991). In addition, positive interactions can be important in the high intertidal zone, where dense assemblages can buffer group members from heat or desiccation stress (Lively and Raimondi, 1987; Bertness, 1989; Bertness and Leonard, 1997). It was unlikely that space was a limiting resource during our recruitment manipulations, and therefore competition for space was relatively unimportant to community structure. Instead, the initial effects of recruitment intensity on community composition were mediated by facilitation.

Since this experiment was only conducted over one recruitment season, we were concerned that the dramatic increase in *Ulva* spp. cover in December that led to community convergence at SHB may have been an anomaly. If so, our results would not be generally applicable to the community dynamics at this site. We evaluated data on community composition collected in 2001 and 2002 from five replicate 1 m² plots that were established in the high intertidal zone at SHB as part of an ongoing long-term monitoring program (Partnership for Interdisciplinary Studies of Coastal Oceans). Data were sampled in the late winter/early spring (March of 2001 and 2002), late summer (August 2002), and fall (November 2001) at SHB. Thus, the sampling periods roughly corresponded with the seasons in which we first collected data in our experiment in 2000, but the data from the monitoring plots provided us with information about patterns in community composition over multiple years. This allowed us to put the results of our experiments into a more general context of seasonality in the community dynamics at SHB. Data from the monitoring plots from SHB showed a spring increase in the cover of *Ulva* spp. that was similar to our experimental results from December 2000 (Fig. 4). Thus, the mechanism that drove community convergence in our experiments (i.e., domination by *Ulva* spp., which overwhelmed any effect of recruitment) may be common characteristic of seasonality in community composition at this site.

Clearly our results are contingent on the recruitment levels used in our experiments and are specific to the sites used in this study. The rapid convergence of community composition in both of our treatments may be due to the range of recruit densities we used (as dictated by natural levels of recruitment to the sites). In other words, the high and low-density treatments may not have been different enough to impose a long-lasting influence on species interactions, and thus on community composition. At intertidal sites characterized by higher recruitment rates, such as those seen in past research evaluating the role of recruitment intensity on community structure (e.g. Connolly and Roughgarden, 1999; Connolly et al., 2001), a more dramatic difference in recruit densities could potentially lead to larger differences in community composition that might persist over

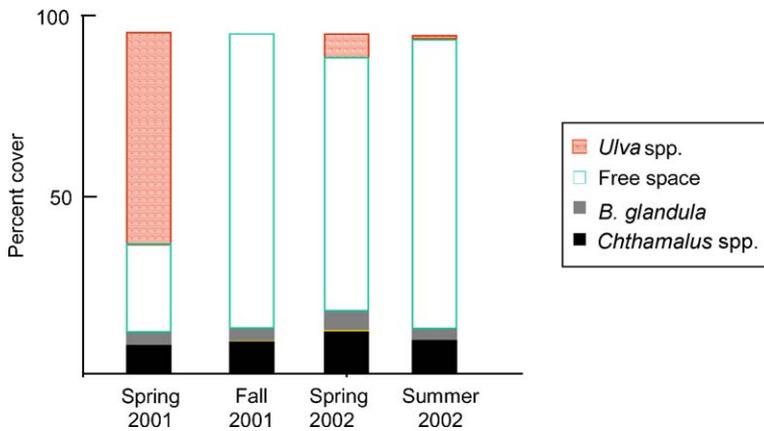


Fig. 4. Mean percent cover data from long-term monitoring of community composition at SHB. Total cover does not equal 100% because taxa irrelevant to the analysis were omitted (e.g. dead *B. glandula* and *Chthamalus* spp.).

longer periods of time than seen in our study. Similarly, experiments in which *Tesseropora* spp. were manipulated showed an effect of variation in recruitment on predatory whelks that persisted for 4 months (Fairweather, 1988). Alternatively, continually high amounts of recruitment to a site through time might actually swamp any initial effects of differences in recruitment on community structure, also resulting in community convergence as we saw in our experiment. Thus, more work needs to be done investigating both the initial and the chronic effects of variation in recruitment on community structure across a broad range of recruitment rates through time and in space.

Past work asking if recruitment variability influences the structure of rocky intertidal communities has often been surveys of community composition at sites with known differences in recruitment rates (Menge, 1991; Connolly and Roughgarden, 1999; Connolly et al., 2001). This research has shown that sites with higher amounts of invertebrate recruitment tend to have higher cover of adult invertebrates and less free space than sites with low recruitment. The results of our research suggest that whether or not differences in recruitment rates correlate with differences in community composition may depend on the dynamics of community composition through time. Past surveys of community composition were often conducted at one point in time during the recruitment season (e.g. Connolly and Roughgarden, 1999; Connolly et al., 2001), which was when differences in community structure were apparent during our experiment. Our results suggest that differences in community composition driven by differences in recruitment may not be evident if survey data were collected during other seasons, particularly winter or early spring. In fact, our monitoring data indicates that the communities used in this study show changes in the abundance of the same species each season, and that these species (e.g. *Ulva* spp.) eliminated any effects of differences in community composition resulting from our recruitment manipulations. Thus, the relative similarity in community structure at sites with different amounts of recruitment may vary through time. In addition, we found community convergence at two sites that were characterized by differences in the underlying recruitment and community dynamics. Therefore, the short-lived effects

recruitment variability on community composition seen in our experiments might be common to other rocky intertidal communities.

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