

Contrasting effects of variable species recruitment on marine sessile communities

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Abstract. The species composition, density, and frequency of recruitment into any given habitat are highly variable in most biological systems that rely on dispersive propagules (larvae, seeds, spores, etc.). There are few direct experimental studies of how recruitment variation between single species influences the composition and assembly of whole communities in many of these systems. We manipulated recruitment of a variety of single taxa and followed their effects on the subsequent development of hard-substrate communities of sessile animals living in temperate marine waters. The effects of recruitment on communities were complex. Patterns of recruitment of individual species influenced community structure, but these effects varied greatly depending on the identity of species recruits, the time of community development, and location across three different sites. Variable recruitment of arborescent bryozoans and didemnid ascidians had little effect on community structure. At one site, recruitment of the colonial ascidian *Botryllus schlosseri* had short-lived effects on community structure, while barnacles had more persistent effects. At another site, recruitment of *B. schlosseri* and the bryozoan *Watersipora subtorquata* had strong persistent effects on community structure, dominating space where they recruited and influencing the abundances of a variety of different taxa. Differences in the effects of species recruitment on communities appear to be caused by differences between the ecology and life history of recruiting species as well as differences in background processes between sites. These results demonstrate that discrete recruitment events that vary between single species can be important drivers of community composition but are likely to be heavily influenced by the local environment, even within a single species.

Key words: *ascidian; barnacle; bryozoan; community; marine; recruitment variation; sessile.*

INTRODUCTION

Communities of sessile organisms that reproduce with dispersive propagules (e.g., seeds, spores, and larvae) are characterized by high variability in the identity and density of recruits that colonize a patch of habitat. This variability is often predicted to have an important role in determining community dynamics and composition. However, post-recruitment processes such as disturbance, competition, facilitation, predation, and physical gradients can decouple initial colonization from later composition, and the relative importance of recruitment is not clear in many systems.

Direct evidence of the role of propagule recruitment in communities has largely come from experimental studies of terrestrial plant communities (e.g., Myers and Harms 2009). For example, the composition of initial seedlings can determine species composition and create divergent community types years after establishment in grassland communities (Tilman 1997, Turnbull et al. 1999, Fukami et al. 2005) and tropical forest systems (Paine

and Harms 2009). It is not clear how well plant communities represent other community types that also rely heavily on dispersive propagules, such as in hard-substrate marine habitats, where dispersal distances of propagules and propagule pressure can be extremely high and variable and where larvae play a more active role in habitat selection (Morgan 2001, Kinlan and Gaines 2003).

Despite a long history of “supply-side” ecology in marine systems dominated by sessile animals, there is surprisingly little direct experimental evidence of the effects of recruitment variation on whole communities. Influential, but indirect, evidence has argued that recruitment plays an important role in structuring intertidal invertebrate populations, where areas of high larval recruitment consistently have more adults and less free space than areas of low recruitment (Menge 1991, Connolly and Roughgarden 1998, Connolly et al. 2001).

Studies of succession on subtidal hard surfaces from a limited number of sites have demonstrated that experimental surfaces submerged at different times develop very different communities of sessile invertebrates, which were attributed to seasonal variations in larval recruitment patterns (Sutherland 1974, Osman 1977, Sutherland and Karlson 1977). In contrast, other studies adopting comparable methods in other locations have

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shown that succession in subtidal benthic habitats can be predictable, with communities converging upon a similar structure within months despite high levels of variation in the identity, number, and time of recruitment (Dean and Hurd 1980, Mook 1981, Bram et al. 2005). The experimental design of the aforementioned studies means the effects of recruits were not decoupled from important post-recruitment processes that also regulate community composition (e.g., competition for limited space, predation on larvae and recruits, early post-settlement mortality, food availability, and temperature; reviewed in Wahl [2009]) that can often covary with recruitment over time, environmental gradients, seasons, and in some cases depth, and may have contributed to differences between communities that were attributed primarily to recruitment.

In one of the few studies to directly manipulate recruitment in marine habitats, Forde and Raimondi (2004) found that different recruit densities of intertidal barnacles led to short-lived initial differences in communities that converged after a short time, but could not directly compare the effects of different species. Another experimental approach demonstrated that differences in the distribution of epifaunal communities growing on red mangrove (*Rhizophora mangle*) roots correspond most closely to differences in recruitment, and were not strongly affected by variation in physical factors (Bingham 1992). Consequently, the importance of particular recruitment patterns for whole communities is still poorly understood.

We used a direct experimental approach to investigate whether recruitment of particular taxa as discrete events at the start of community development can drive differences in the composition of temperate subtidal marine communities. Patches of habitat exposed to recruitment of different individual species could experience very different community dynamics where they alter species interactions and other post-recruitment processes. However, it is largely unknown whether discrete recruitment of single species is capable of driving community-level differences given the complex array of other processes that can regulate communities.

We manipulated the identity and density of early recruits of individual species/taxa on small uniform patches of subtidal habitat (settlement plates) to test (1) if variation between different species of initial recruits causes differences in community development and composition and (2) at what recruit densities such changes occur.

We directly manipulated the recruitment of multiple different species at the same time within a site, so that we were able to decouple the effects of recruitment treatments from other processes that covary with seasons and/or time. We also ran experiments at three geographically distant sites with different attributes and at two different times at one of these sites to test how widespread and consistent the effects of these types of recruitment events are on communities.

METHODS

Study sites

Experiments were done subtidally at Workshops Jetty, Williamstown (37°51'39.78" S, 144°54'34.17" E) and at St Leonard's Pier (38°10'13.46" S, 144°43'15.09" E) in Port Phillip Bay, a large shallow embayment in southeastern Australia, and at Santa Cruz Harbor (36°57'50.76" N, 122°0'9.49" W), a manmade boat harbor in Monterey Bay, central California, USA. The hard artificial structures of each of the sites support diverse assemblages of sessile marine animals, including ascidians, bryozoans, sponges, barnacles, serpulids, and hydroids and are similar to those found on subtidal rocky reefs and hard artificial substrata in temperate waters. Each of the sites had different physical environments, and sessile communities were quite different, even though all were a mixture of native and nonnative species (for a more comprehensive list of taxa present in experiments see Appendix A and for details of the study sites see Appendix B).

Experimental design

Experiments followed the same general procedure at each site. Opaque acrylic settlement plates were sanded on one side and attached to large weighted PVC backing panels that were suspended from horizontal pier pylons so that plates faced downward at a depth of approximately 2.5 m below the low water mark. Experiments at Williamstown and St Leonards used 125 × 100 mm settlement plates attached to 600 × 600 mm backing panels. Experiments at Santa Cruz used 100 × 100 mm plates attached to 600 × 600 mm backing panels. These settlement plates act as hard substrata that sessile organisms readily recruit onto and support diverse communities. Each panel had plates of all treatment types attached, equally replicated across panels (see Appendix B for further details of experimental setup).

In order to manipulate initial recruitment patterns, plates were left in the water for two weeks at Williamstown, where recruitment rates are high, or for four weeks at St Leonards and Santa Cruz, where recruitment rates were lower. This provided enough recruits for manipulations while ensuring that they were recently settled. Panels were then removed from the water and submerged in large tubs of seawater. Recruitment was manipulated by removing individuals from plates with tweezers or scraping them off with small chisels to create particular patterns of interest.

The basic design of all of the experiments in this study was to create treatment plates that initially received recruits of only a single target taxon at multiple densities at the beginning of community development. The number of species treatments used in each experiment varied from one to three, depending on the availability of recruits. Controls consisted of plates completely cleared of initial recruits in all experiments. This allowed us to compare the effects of initial recruitment of (1)

TABLE 1. Summary of details of experimental treatments, sites, and dates (including the period of recruit collection before experimental manipulations) for each of the experiments in this study.

Experiment, dates, and species treatment	Density treatment	No. individuals	No. replicates
1. Williamstown A, mid Nov–late May 2009			
<i>Botryllus schlosseri</i> (colonial ascidian)	high	70	6
	medium	40	6
	low	20	6
Didemnid (colonial ascidian)†	low	20	6
No initial recruits	none	0	6
2. Williamstown B, late Dec–mid Jun 2009			
<i>Botryllus schlosseri</i> (colonial ascidian)	medium	40	8
	low	20	8
<i>Balanus trigonus</i> , <i>Amphibalanus variegatus</i> (barnacles)	medium	80	8
	low	40	8
Arborescent bryozoans (<i>Bugula</i> spp.)	low	10	8
No initial recruits	none	0	8
3. St Leonards, early Mar–early Sep 2009			
<i>Tricellaria occidentalis</i> (arborescent bryozoan)	medium	10	8
	low	5	8
No initial recruits	none	0	8
4. Santa Cruz, early Aug–mid Feb 2010			
<i>Botryllus schlosseri</i> (colonial ascidian)	low	20	15
	very low	10	15
<i>Watersipora subtorquata</i> (encrusting bryozoan)	very low	5	15
No initial recruits	none	0	15

Notes: For each experiment, each replicate plate received one species/taxon listed under treatment at one of the density levels outlined. For some species/taxa treatments, early recruits of closely related species could not be distinguished and treatments were a mixture of closely related and morphologically similar species rather than a single species (e.g., didemnids, barnacles, and arborescent bryozoans; see Appendices A and B for further details).

† Family Didemnidae.

different species and (2) different densities of those species on the subsequent development and structure of communities. The specific treatments of each experiment in this study are summarized in Table 1.

The taxa used in these experiments were largely determined by availability at the time experiments were run, but in all experiments we used a range of species that are abundant as adults and important contributors to community structure. They are also commonly found in high abundance relative to other species as recruits during the early stages of community development, and therefore potentially important for influencing communities. The highly variable nature of recruitment during these experiments meant that it was impossible to set up experiments with completely orthogonal species and density treatments. However, where possible we used multiple density treatments for all initial recruitment species. We used densities that were relative to typical recruitment levels for a species at each particular site, rather than forcing uniform, and possibly unrealistic, standardized densities across all sites. Our intent was to ask the same ecological question at several places, rather than to formally compare a given density of recruits.

Sampling and data analysis

After initial recruitment patterns were set up, community development was followed by photographing all plates two weeks after manipulations (only at Williams-

town and Santa Cruz) and then monthly for the first three months of experiments and then again after six months (at all sites). Sampling was done using a standardized camera setup (Canon G8 with a WP-DC21 underwater housing; Canon, Tokyo, Japan) with a framer to ensure that all photos were taken at the same distance and orientation. All photos were taken while plates were submerged in large tubs of sea water at the surface of the pier they were suspended from.

To determine the structure of communities on each plate we estimated percent cover (henceforth referred to simply as cover) of species by identifying the taxa beneath 200 points randomly placed over photos using the program CPCe (Kohler and Gill 2006).

To test for differences in overall community structure, we analyzed cover of all taxa present on plates with the PERMANOVA add-on for PRIMER 6 (Anderson et al. 2008). Differences between treatments were analyzed by partly nested PERMANOVA for each experiment using unrestricted permutations of data with 9999 permutations, followed by PERMANOVA pairwise comparisons if significant differences were detected among treatments. To determine which species were likely to be driving community level patterns, as well as to examine the influence of different recruitment treatments on individual species we used repeated-measures ANOVA (analogous to the partly nested analysis used in PERMANOVA). A summary of the statistical model(s)

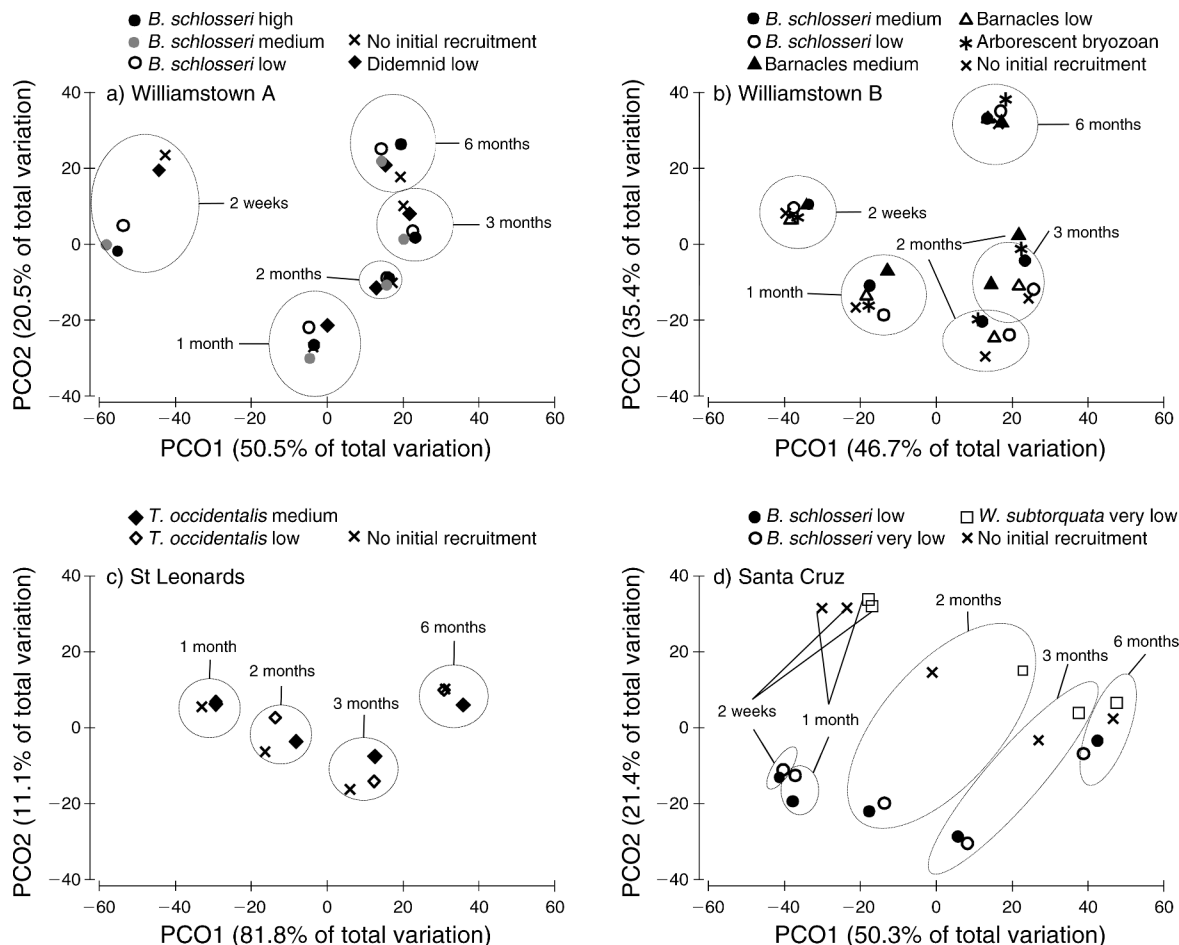


FIG. 1. Principal coordinates ordination (PCO) of distances among centroids on the basis of the Bray-Curtis measures of percent cover of taxa four experiments at three sites: (a, b) Williamstown A and B, (c) St Leonards, and (d) Santa Cruz. Communities initially had different species recruits present at different densities and were sampled at two weeks (except St Leonards), one month, two months, three months, and six months. Centroids represent average distances between recruitment treatments at each time sampled within each experiment. Abbreviated taxa are *Botryllus schlosseri*, *Tricellaria occidentalis*, and *Watersipora subtorquata*. For details of differences between treatments, see statistical analysis and results for PERMANOVA in Appendix B.

used in each experiment is given in Appendix B. Detailed results of PERMANOVA and ANOVA for the major space occupying species in each experiment and those species that showed significant differences in cover between treatments can also be found in Appendix B.

Principal coordinates ordinations (PCO) based on the Bray-Curtis dissimilarity matrix of percent covers of taxa were also used to visualize differences in overall community structure through time, as recommended by Anderson et al. (2008). To increase the clarity of PCO plots we have only shown a single object representing the centroid for each treatment at each time.

RESULTS

Experiment 1 (Williamstown A)

Differences in initial species recruitment did not have a strong persistent effect on overall community structure or on any of the eight major space occupying taxa,

during Experiment 1 (Williamstown A; Figs. 1a and 2; Appendix B: Table B1 and Fig. B1). The main space occupiers were the ascidians *Botryllus schlosseri*, *Diplosoma listerianum*, and other didemnids (consisting of two ascidian species in the family Didemnidae belonging to *Trididemnum* and *Didemnum* that were too difficult to accurately distinguish, but not *Diplosoma listerianum*, also in the same family but easily distinguishable), plus several bryozoans (*Watersipora subtorquata*, *Bugula dentata*, and *Bugula stolonifera*), polyps of the jellyfish *Cyanea capillata*, and tube-dwelling corophiid amphipods. Two weeks after manipulations, community structure differed between treatments that received *B. schlosseri* recruits and controls that had no initial recruits present and *B. schlosseri* recruits and didemnids, but not between control treatments and plates that initially received didemnid recruits (Fig. 1a; Appendix B: Table B1). These differences did not persist and one month after manipulations, overall community structure

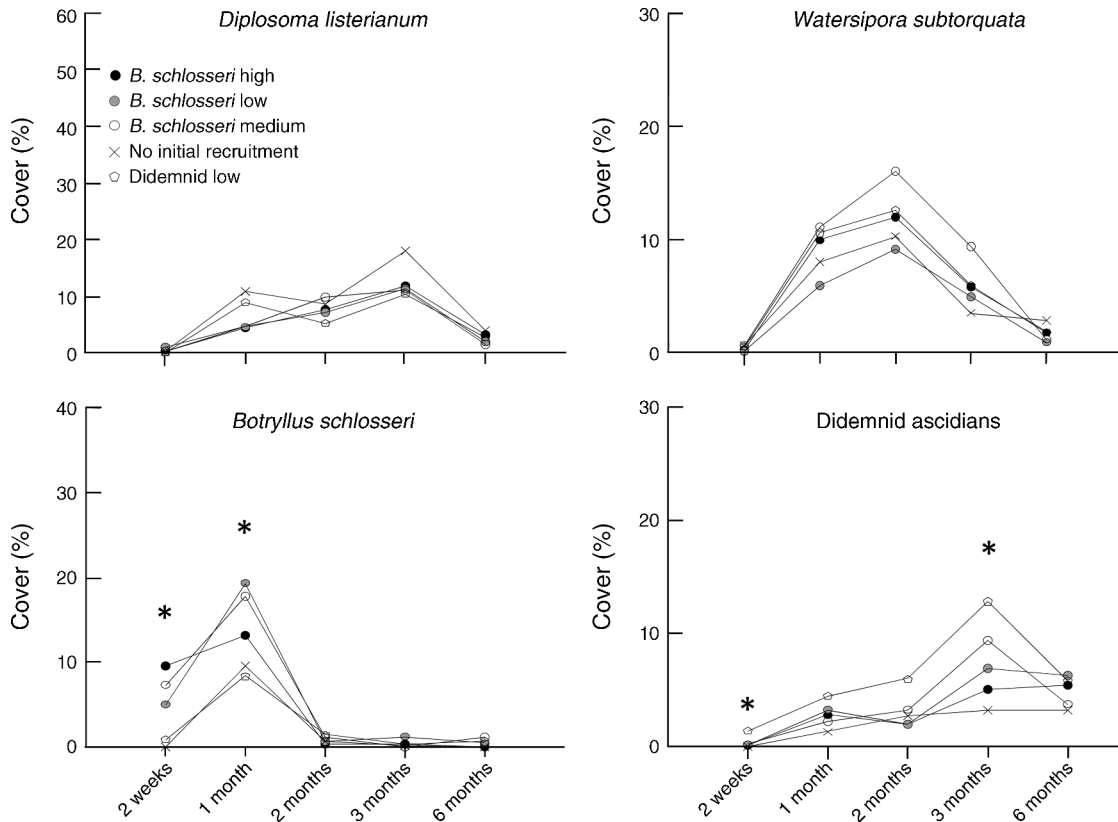


FIG. 2. Percent cover of two of the most abundant taxa, the colonial ascidian *Diplosoma listerianum* and encrusting bryozoan *Watersipora subtorquata*, and the two species that were influenced by recruitment treatments, the colonial ascidians *Botryllus schlosseri* and didemnid ascidians, found on settlement plates exposed to initial recruitment of either *B. schlosseri* in high, medium, or low densities, didemnid ascidians at low densities or no initial recruitment at Experiment 1 (Williamstown A) at samples taken two weeks, and one, two, three, and six months after manipulations. Asterisks denote times when there were significant differences ($P < 0.05$) in cover between treatments according to repeated-measures ANOVA. For details of analysis, see Appendix B: Table B1.

no longer differed among treatments. This pattern persisted for the rest of the experiment, even though overall community structure continued to change, with the different treatments being similar to each other.

Early differences in community structure were largely driven by differences in the abundance of *Botryllus schlosseri* and didemnid ascidians, both of which were abundant during Experiment 1 (Fig. 2; Appendix B: Table B1). In two-week-old communities, colonies of *B. schlosseri* occupied approximately 5% more cover on plates that initially received recruitment of *B. schlosseri*, but occupied <1% of space on plates that initially received recruits of didemnid and were not present on plates that received no initial recruitment. After one month, *B. schlosseri* occupied twice as much space on plates that initially received recruits of *B. schlosseri* than on plates that initially received didemnid ascidian recruits and occupied <1% of space on plates that received no initial recruits. Differences at one month did not have any influence on overall community structure and disappeared permanently by two months. Didemnid ascidians showed opposite and more persistent differences in cover between species treatment than *B. schlosseri* (Fig.

2; Appendix B: Table B1). In two-week communities, plates that initially received didemnid recruits had a slightly higher cover of didemnid than plates that were initially exposed to recruits of *B. schlosseri* or had no initial recruits. In one- and two-month communities, these differences were not apparent and didemnid ascidians occupied a similar amount of space on all treatments. By three months, didemnid ascidians occupied twice as much space on plates that initially received didemnid recruits than on plates that initially received *B. schlosseri* recruits, and three times the amount of space on plates that received didemnid recruits than on plates that received no initial recruitment, although these differences did not have a strong effect on overall community structure. The cover of didemnid ascidians became similar across all treatment six months after manipulations.

There was also a weak temporary effect on overall community structure caused by different initial densities of *Botryllus schlosseri* (Fig. 1a; Appendix B: Table B1). After two weeks, communities on plates exposed to high and medium densities of *B. schlosseri* recruits had a different overall community structure from plates that

received no initial recruits, but no density treatments differed after this (Appendix B: Table B1).

Although different initial densities of *Botryllus schlosseri* recruits did not influence community structure, they did weakly affect the abundance of *B. schlosseri* itself (Fig. 2; Appendix B: Table B1). In two-week communities, treatments that received recruits of *B. schlosseri* had more *B. schlosseri* occupying space than plates that received initial recruits of didemnids or no initial recruits, but cover was not affected by initial densities of *B. schlosseri*. In three-month communities, plates that received initial recruits of *B. schlosseri* in low abundance had a higher percent cover of *B. schlosseri* than any other treatment. Even then *B. schlosseri* only occupied approximately 1% of space on plates.

Experiment 2 (Williamstown B)

Similarly to Experiment 1, initial differences in recruitment had no effect on overall community structure or the 10 major space occupying taxa in Experiment 2 (Williamstown B; Figs. 1b and 3; Appendix B: Table B2 and Fig. B2). As for the first Williamstown experiment, community composition changed through time independently of recruitment treatments, even though the main space occupiers were different, consisting of several ascidians (*Botryllus schlosseri*, *Diplosoma listerianum*, other didemnids), *Watersipora subtorquata*, *Cyanea capillata*, corophiid amphipods, the barnacles *Amphibalanus variegatus* and *Balanus trigonus*, and serpulid polychaetes (*Ficopomatus enigmaticus* and "medium" serpulids, that consisted of individuals *F. enigmaticus* and *Hydrooides ezoensis* that were too small to easily distinguish between species).

Only two major space occupiers were affected, *Botryllus schlosseri* and *Balanus trigonus* (Fig. 3; Appendix B: Table B2). In two-week communities, *B. schlosseri* had a higher cover on plates that initially received recruits of *B. schlosseri* than those that received recruits of arborescent bryozoans and it was absent from plates that initially received barnacle recruits or received no initial recruits. In one-month communities, the cover of *B. schlosseri* declined and there were no longer any differences among treatments. *B. trigonus* occupied approximately twice the amount of space on plates that initially received barnacle recruits than on plates that received *B. schlosseri*, arborescent bryozoan recruits or no recruits, and these differences were apparent two weeks, one month, and six months after manipulations.

Unlike Experiment 1, there was no difference in the overall structure of communities on plates that received different initial densities of *B. schlosseri* (Fig. 1b; Appendix B: Table B2). Different initial densities of *Botryllus schlosseri* recruits also did not have a strong effect on any other individual taxon (Appendix B: Table B2 and Fig. B2). Those plates that received low initial densities of *B. schlosseri* recruits had a higher cover of the serpulid, *Ficopomatus enigmaticus*, than those that received no *B. schlosseri*, but there were no differences

between plates that received medium initial densities to those that received low or no recruitment of *B. schlosseri* (Appendix B: Table B2 and Fig. B2).

In contrast, there were differences in the overall structure of communities when barnacles were present initially (Fig. 1b; Appendix B: Table B2). Two weeks after manipulations, plates that received initial recruitment of barnacles at medium densities had a different community structure from control plates that received no initial recruits, but there was no difference between plates that received barnacles at medium density or low density (Fig. 1b, Appendix B: Table B2). Differences in community structure were not apparent at one month, but they reemerged. Plates exposed to initial recruitment of barnacles at medium densities had a different community structure from plates that received initial recruitment of barnacles at low densities or no initial recruitment at both two and three months, but not at six months (Fig. 1b, Appendix B: Table B2).

Differences in communities caused by initial densities of barnacles were influenced by differences in the amount of space occupied by *Botryllus schlosseri*, the encrusting bryozoan *Watersipora subtorquata*, corophiid amphipod tubes, and *Balanus trigonus* (Fig. 3; Appendix B: Table B2). In two-week communities, *B. schlosseri* occupied twice the amount of space on plates that received medium barnacle recruits than on those that had no initial recruits present, whereas plates that received low initial recruitment of barnacles had a similar cover of *B. schlosseri* to plates that received no initial recruitment. These differences did not persist through time. Amphipod tubes also occupied twice as much space on plates that initially received medium recruitment of barnacles than on low initial barnacle recruitment plates and 10 times more than when there were no initial recruits at two months. They covered twice as much space on medium barnacle treatments than on low barnacle and control treatments three months after manipulations. In contrast, *W. subtorquata* occupied almost twice the amount of space on plates that received no initial recruitment of barnacles as on plates that initially received medium barnacle recruitment but did not differ between plates that initially received medium and low barnacle recruits, at two and three months after manipulations. *B. trigonus* occupied more space in treatments that initially received barnacles than on plates that received no initial recruits at two weeks, one month, and two months after manipulations but there was no effect of initial barnacle density.

Across the two experiments, we saw no evidence of convergence to a common community state, whether comparisons were made at the same age (Appendix C) or at same time of the year (January, February, and May; Appendix C).

Experiment 3 (St Leonards)

Initial recruitment of arborescent bryozoans had no significant effect on overall community structure or on

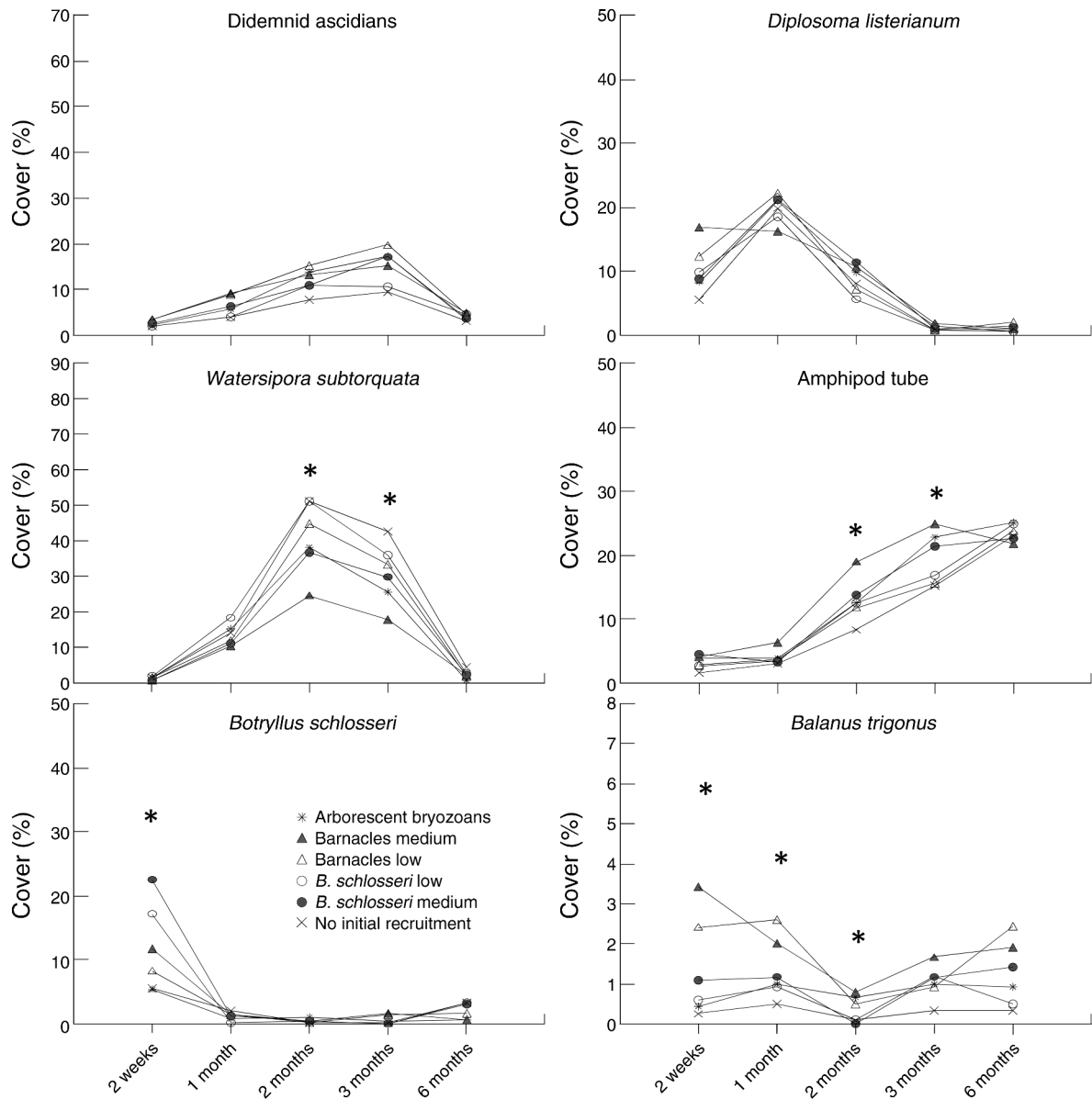


FIG. 3. Percent cover of two of the most abundant taxa, the colonial ascidians *Diplosoma listerianum* and didemnids, as well as taxa that were influenced by recruitment treatments, the encrusting bryozoan *Watersipora subtorquata*, tube-building amphipods, the colonial ascidians *Botryllus schlosseri*, and the barnacle *Balanus trigonus*, found on settlement plates exposed to initial recruitment of either *B. schlosseri* in medium or low density, a mixture of barnacles (*Amphibalanus variegatus* and *Balanus trigonus*) in medium or low density, a mixture of arborescent bryozoans (*Bugula* spp.) at low density or no initial recruitment at Experiment 2 (Williamstown B) at samples taken two weeks, and one, two, three, and six months after manipulations. Asterisks denote times when there were significant differences ($P < 0.05$) in cover between treatments according to repeated-measures ANOVA. For details of analysis, see Appendix B: Table B2.

the abundance of any of the six most common taxa at St Leonards (Fig. 1c; Appendix B: Fig. B3 and Table B3), which were the bryozoans *Bugula dentata*, *Biflustra perfragilis*, and *Tricellaria occidentalis*, didemnid ascidians, hydroids (mainly *Phialella quadrata*, *Halecium delicatum*, and *Monotheca flexuosa*; see Appendix B) and an unidentified sponge with a tube-like growth form. Approximately 41 individual taxa were found in St Leonards communities, and their identity and

abundances were very different from those found at Williamstown (Appendix A).

Experiment 4 (Santa Cruz)

Unlike previous sites in this study, differences in initial recruitment of species had a strong persistent effect on the overall structure of communities at Santa Cruz, which comprised approximately 32 species, 7 of which were common enough to be analyzed individually

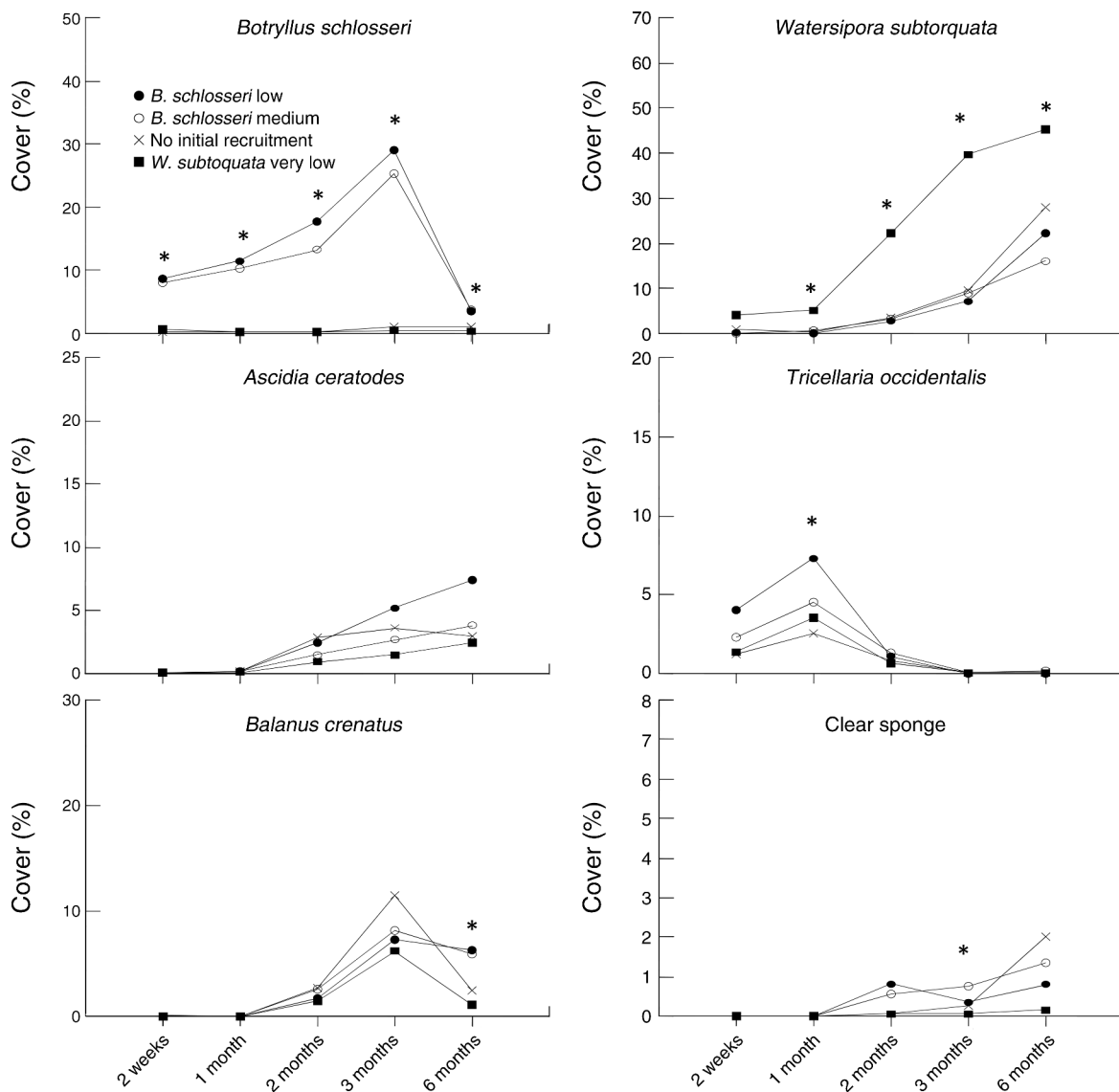


FIG. 4. Percent cover of the six most abundant taxa found on settlement plates exposed to initial recruitment of *Botryllus schlosseri* in low or very low density, *Watersipora subtorquata* in very low density or no initial recruitment at Experiment 4 (Santa Cruz) from samples taken two weeks, and one, two, three, and six months after manipulations. Asterisks denote times when there were significant differences ($P < 0.05$) in cover between treatments according to repeated-measures ANOVA. For details of analysis, see Appendix B: Table B4.

(Figs. 1d and 4; Appendix B: Table B4). Communities that initially received recruitment of *Watersipora subtorquata* were always different from those that received *Botryllus schlosseri*. Two weeks after manipulations, *W. subtorquata* treatments did not differ from those that received no initial recruitment, but they diverged after one month, and these differences still persisted at six months. Plates that initially received recruitment of *B. schlosseri* differed from plates that received no initial recruitment for the first three months, but were not different after six months.

Initial recruitment of both species resulted in their taking over large amounts of space as the communities

developed. The greatest difference in the cover of *W. subtorquata* occurred after two months, where initial recruitment increased its cover by seven times (Fig. 4; Appendix B: Table B4). By six months, *W. subtorquata* occupied 45% of space on treatments that initially received *W. subtorquata* recruitment, which was two to three times higher than on plates without such recruitment.

The greatest increase in the cover of *B. schlosseri* occurred at three months where colonies occupied over 25 times more space than when no initial ascidian recruitment occurred. (Fig. 4; Appendix B: Table B4). After six months, differences between treatments still

existed but the amount of space occupied by *B. schlosseri* had declined dramatically. Even so, *B. schlosseri* occupied over five times more space on treatments that initially received recruitment of *B. schlosseri*.

Initial recruitment of *B. schlosseri* also resulted in increased abundance of the barnacle *Balanus crenatus*, which, after six months, occupied three to six times more space than on plates that initially received recruits of *Watersipora subtorquata* or no recruitment. Cover of an unidentified pale sponge was also enhanced by *B. schlosseri*, occupying twice as much space after three months as on the other two treatments.

Initial recruit densities of *Botryllus schlosseri* had little influence on communities at Santa Cruz. Treatments that initially received recruitment of *B. schlosseri* in low and very low density differed from plates that received no initial recruitment but not from each other at two weeks up to three months, and all treatments no longer differed at six months.

Initial densities of *Botryllus schlosseri* only influenced the abundance of two individual taxa (Appendix B: Table B4). In one-month communities, the arborescent bryozoan *Tricellaria occidentalis* occupied approximately seven times more space on treatments that initially received low recruitment of *B. schlosseri* than on treatments that received no recruitment (Fig. 4; Appendix B: Table B4). Very low initial recruitment of *B. schlosseri* had no effect on *T. occidentalis*. *Watersipora subtorquata* also occupied slightly more space when there was very low recruitment of *B. schlosseri* than when there was low recruitment of *B. schlosseri*. The cover of *W. subtorquata* did not differ from controls for either *B. schlosseri* recruitment treatments. Colonies of *B. schlosseri* also occupied more space on treatments where *B. schlosseri* recruits were initially present, but there were no differences in the amount of space colonies occupied between treatments that received low or very low recruitment of *B. schlosseri* colonies at any time. This pattern was the same for hydroids and *Balanus crenatus*.

DISCUSSION

Initial recruitment had very different effects across our four experiments, ranging from no detectable effect to strong persistent changes in community structure. Where differences in initial species influenced community composition they did so through both positive and negative interactions that varied between species. We also saw the same species, *Botryllus schlosseri*, having quite different effects at Williamstown and Santa Cruz.

We found the weakest effects at St Leonards, where only recruits of the arborescent bryozoans *Tricellaria occidentalis* were present initially. We also saw little effect of arborescent bryozoans at Williamstown, with a different group of bryozoans represented (*Bugula* spp.). Arborescent bryozoans are generally weak interference competitors for space, which may potentially explain the

lack of difference in communities that received different amounts of arborescent bryozoan recruits. Adult arborescent bryozoans can increase the recruitment of conspecifics and colonial ascidians and settlement of serpulid polychaetes (Russ 1980, Osman and Whitlatch 1995, Bryan et al. 1998), so they might be able to influence community structure as they mature in some habitats. Such interactions were not observed in this study, however.

In contrast the colonial ascidians, *Botryllus schlosseri* and didemnids, are competitive dominants in many communities, capable of usurping and occupying large amounts of space and thereby altering community structure (e.g., Russ 1982, Nandakumar et al. 1993, Osman and Whitlatch 2004, Dijkstra and Harris 2009). Despite this, recruitment of these ascidians did not have a particularly strong effect on communities at Williamstown. Colonial ascidians such as didemnids often have plastic life histories and are capable of changing growth rates and reproductive output depending on their local environment (Stoner 1992). At Williamstown, didemnid colonies persisted throughout experiments but did not occupy large amounts of space and may interact more like colonizing species, rather than strong competitors, by only growing to small sizes and possibly directing effort into sexual reproduction.

Unlike didemnids, *Botryllus schlosseri* grows rapidly and undergoes senescence after one or a small number of periodic larval spawnings (Grosberg 1988). At Williamstown, the disappearance of *B. schlosseri* during the early stages of community development is likely to be due to the reduction of colonies after reproduction as well as a failure to recruit into patches containing established adults of other species. Despite showing a dramatic decrease in cover while communities were still young, early differences in the cover of *B. schlosseri* still could have influenced community structure by altering larval settlement patterns or the survival and growth of subsequent recruits (e.g., through overgrowth, inhibition of settlement, allelopathy, and facilitation). The lack of strong overall differences in community structure where *B. schlosseri* had a higher cover as a result of initial recruitment suggests that it did not have strong interactions with other species at Williamstown during experiments.

Barnacles were the only species present as initial recruits to influence community structure at Williamstown. The effects of barnacles only occurred during the first few months of development but did not persist into older communities. The higher amount of space occupied by *Balanus trigonus* in barnacle treatments was most likely due to the growth of initial recruits present in barnacle treatments, as well as the subsequent recruitment of new individuals near established recruits. Barnacle larvae will often settle in the presence of conspecifics or settle in higher numbers in particular flow conditions, causing increased recruitment and aggregations of juveniles near adults (Raimondi 1988,

Wright and Boxshall 1999). Barnacles can also create cavities and interstices that provide habitat and increase abundances of amphipods in other habitats, and may have caused higher abundances of amphipods through similar mechanisms in this experiment (Lewis 1992). The lower cover of *W. subtorquata* on barnacle treatments may have been due to increased competition for space or food between colonies and barnacles or tube building amphipods, or as a result of decreased settlement near barnacles. Barnacles can also prey on larvae of a range of invertebrates and may have reduced larval settlement of *W. subtorquata* through such predation (Young and Gotelli 1988). However, most barnacle recruits were probably too small to consume the relatively large larvae of *W. subtorquata* during early community stages.

In contrast, *Watersipora subtorquata* and *Botryllus schlosseri* went on to become dominant space occupiers at Santa Cruz, largely through the colony growth of initial recruits, and caused strong community level differences. *Botryllus schlosseri* colonies may have differed in their life histories at Santa Cruz (e.g., Grosberg 1988) as they were longer lived and persisted for much longer, increasing their influence. Community differences at Santa Cruz were also enhanced by differing effects of these species on other taxa. *Balanus crenatus* had a higher cover on plates with *B. schlosseri* than on plates with *W. subtorquata*, suggesting that *B. schlosseri* enhanced recruitment or *W. subtorquata* inhibited it. The higher cover of *B. crenatus* coincided with a decrease in the cover of *B. schlosseri* at six months, and the opening up of space previously occupied by colonies at three months may have facilitated barnacle recruitment and growth.

We repeated our basic experiment in several locations over a broad spatial scale. Our aim was to see whether the effects of individual recruitment events were generally consistent, so we chose locations that differed in many respects. Our aim was not to explain why the results differed (which would have required a different study design), but we can identify some important ecological differences between them.

There was little evidence of predation (e.g., fish bite or scrape marks, partially eaten colonies, empty tests) at any site, nor did we see many predators active on plates when they were sampled. Previous work at Williamstown has shown that predation occurs but has little effect on developing communities during early stages (Sams and Keough 2007), but little is known about the effects of predators at St Leonards or Santa Cruz.

At Williamstown, recruitment rates were one to two orders of magnitude higher than at St Leonards and Santa Cruz. High rates of ongoing recruitment may lead to increased propagule pressure and competition between recruits. At Williamstown, approximately 80% of space was occupied by the first month of sampling in Experiment 1 and the second month of sampling in Experiment 2. Approximately 40% of space was occupied at St Leonards after two months, and 30% of

space at Santa Cruz, suggesting that competition for space was lower at both of these sites than at Williamstown (Appendix B: Fig. B3). Higher propagule pressure and subsequent competition for space may have reduced any effects of initial recruitment, particularly if recruits encounter high competition before they have become established. At Santa Cruz, where ongoing recruitment rates were lower and there was more free space, initial differences in recruitment may have had more persistent effects on communities because early recruits have more time to grow and establish themselves as adults without encountering strong competition, giving them an advantage over later arriving recruits. However, this was not observed at St Leonards, where the first three months of community development was characterized by high recruitment of *T. occidentalis* and hydroids but few other species, potentially reducing differences initially created by experimental manipulations and the effects of treatments.

We have shown that variation in discrete recruitment events of different species can influence the composition of communities, but the strength of this influence depends on the exact taxa involved, and even the same species can have dramatically different effects in different communities. In these experiments, we used small isolated patches of habitat to manipulate recruitment, where most species are often small, complete their life cycles well within six months, and abundances are typically driven by larval recruitment (e.g., Keough 1984). In habitats where long-lived, large, colonial species dominate (e.g., where patches are larger, more continuous, and less disturbed), competitive interactions can be stronger determinants of species abundances or community. Recruitment variation may have a weaker effect on the composition of such communities but may persist for longer if they occur. This is not clear, however, and our results suggest that the local environment is likely to have a strong influence on recruitment effects.

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SUPPLEMENTAL MATERIAL

Appendix A

A table of taxa found in experimental communities (*Ecological Archives* E093-099-A1).

Appendix B

Details of study site, experimental setup, statistical methods, and supplementary results, including tables of statistical analysis and figures of common species (*Ecological Archives* E093-099-A2).

Appendix C

Comparisons of community structure of experiments 1 and 2 at Williamstown (*Ecological Archives* E093-099-A3).