Early recruitment variation and an established dominant alter the composition of a temperate fouling community

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ABSTRACT: For marine organisms with complex life cycles, recruitment of dispersive propagules is highly variable in time and space, and can have important consequences for population and community dynamics. Recruitment often occurs in patches already occupied by adults that could alter its effects on communities. Using an experimental approach, we examined the effects of initial recruitment of a common bryozoan (*Conopeum seurati*) and barnacles in the presence/absence of a large and abundant solitary ascidian (*Pyura dalbyi*) on the composition of a marine fouling community occurring on artificial substrate. The presence of *P. dalbyi* and different initial recruitment patterns both influenced overall community composition, but did not interact. The main effect of *P. dalbyi* on communities was to reduce the amount of available primary space and alter the abundance and cover of other taxa. Different initial recruitment patterns also altered the abundance of a small number of taxa, but the direction of differences was variable. There were interactive effects of *P. dalbyi* and initial recruitment on 2 species. When there were no initial bryozoan or barnacle recruits, the colonial ascidian *Diplosoma listerianum* had a higher cover without *P. dalbyi* than when *P. dalbyi* was present, but when we inoculated plates with other recruits, *D. listerianum* was unaffected by the presence of *P. dalbyi*. In the first month of community development, *C. seurati* colonies had an overall higher cover on *C. seurati* recruitment treatments than on other recruitment treatments. *C. seurati* also had higher colony cover on the primary space of *C. seurati* recruitment treatments where *P. dalbyi* was present than on *C. seurati* treatments without *P. dalbyi*, but there was no interaction between other recruitment/*P. dalbyi* treatment pairs. Differences did not persist beyond one month, or lead to overall changes in community composition. The results of this experiment suggest that any combined effects of recruitment and the presence of established adults on individual taxa are likely to be complex and may not always alter overall community composition.

KEY WORDS: Recruitment · Sessile invertebrate · Community · Ascidian · Bryozoan · Barnacle

INTRODUCTION

In the marine environment, patterns of propagule recruitment are often highly variable in time and space and can play a key role in population and community dynamics. Variation in recruitment can influence density dependent interactions, rates of predation and population dynamics in a range of marine organisms including algae (Reed 1990, Wright 2002), barnacles (Caffey 1985, Gaines & Roughgarden 1985, Raimondi 1990, Minchinton & Scheibling 1993, Menge 2000) and other benthic marine invertebrates (Keough & Downes 1982, Keough 1984) as well as the overall composition of communities (Bingham 1992, Sams & Keough 2012a,b). The type of habitat in which recruits become established can also have

highly variable attributes, which may potentially interact with recruitment to influence community composition.

Most empirical studies of the effect of invertebrate recruitment variation on population and community dynamics have examined the effects of different recruitment patterns into unoccupied patches of habitat or primary space (Underwood & Keough 2001, Sams & Keough 2012a,b). Recruits will only experience this situation if they are the first to arrive in a newly created patch, or after an event that has removed all adult residents. Recruitment is more likely to occur in patches of habitat already occupied by at least some established adults, who may interact with recruits to influence subsequent population dynamics and community composition. For example, in benthic habitats, the presence of algal canopies can alter the assembly of species occurring in the understory by influencing recruitment and subsequent growth and survival of recruits (Duggins et al. 1990, Irving & Connell 2006). Kelp canopies can facilitate the recruitment and growth of algal spores (Graham et al. 1997, Bruno & Bertness 2001), while higher densities of some sessile invertebrates can enhance larval recruitment in adjacent areas (Russ 1982, Keough 1989, Todd & Keough 1994, Osman & Whitlatch 1995a,c). On intertidal rocky shores, gaps between individual mussels provide refuges for recruits and protection from desiccation, allowing diverse assemblages to form that could not form on bare rock (Tokeshi & Romero 1995). Alternatively, the presence of both macro-algae and/or sessile invertebrates can inhibit recruitment or increase post-recruitment mortality through direct and indirect competition (Sutherland & Karlson 1977, Kendrick 1994, Osman & Whitlatch 1995c, Hunt & Scheibling 1997).

Little is known about how established adults interact with recruitment patterns to influence the overall composition of communities. In particular, it is not clear whether the effects of different recruitment patterns on communities can be altered by the presence of resident adults. Here, we present the results of an experiment in a temperate marine fouling community dominated by sessile invertebrates and occurring on artificial substrate, where we manipulated the initial recruitment of commonly occurring species of barnacle and bryozoan in the presence/absence of a major space-occupying solitary ascidian, *Pyura dalbyi*. Our aim in this experiment was to test whether the effects of different initial recruitment patterns of barnacles and a bryozoan (*Conopeum seurati*) on communities were altered by the presence of these large ascidians. We predicted that where recruitment of *C. seurati* or barnacles caused changes in community composition, these effects would differ depending on whether *P. dalbyi* was present or absent.

MATERIALS AND METHODS

Our experiment was conducted from late February until late September 2010 at Workshops Jetty, Williamstown, Port Phillip Bay, Australia (37° 51′ 39.78″ S, 144° 54′ 34.17″ E), a shallow 2000 km^2 embayment, of which more than two-thirds is less than 8 m deep. Workshops Jetty is situated at the northern end of Port Phillip Bay, Australia, near the mouths of the Yarra and Maribyrnong rivers, in a sheltered estuarine environment characterised by high loads of muddy sediment. The sessile community found at Workshops Jetty extends from the low water mark to approximately 4–5 m depth (the maximum depth around the jetty). It is a typical 'fouling' community found in shallow sheltered estuarine environments, consisting of the spatially dominant native solitary ascidian *Pyura dalbyi* abundant native species such as the bryozoan *Bugula dentata*, the barnacle *Elminius modestus*, the serpulid *Pomatoceros taeniatus* and many abundant invasive species, including colonial ascidians (*Botryllus schlosseri*, *Botrylloides leachii* and *Diplosoma listerianum*), solitary ascidians (*Styela plicata*, *Styela clava*, *Ascidiella aspersa*, *Ciona intestinalis*), bryozoans (*Watersipora subtorquata*, *Bugula neritina*, *Bugula stolonifera*, *Bugula flabellata*), barnacles (*Amphibalanus variegatus* and *Balanus trigonus*) serpulids (*Hydroides ezoensis*, *Ficopomantus enigmaticus*) as well as didemnid ascidians, whose status as invasive or native is unknown.

We manipulated the recruitment of 2 common but ecologically and taxonomically distinct sessile taxa: the encrusting bryozoan *Conopeum seurati*, and the closely related barnacles *Amphibalanus variegatus* and *Balanus trigonus* (henceforth referred to as barnacles) onto settlement substrates on which a large space-occupying solitary ascidian, *Pyura dalbyi* (formerly *Pyura stolonifera*, Rius & Teske 2011) was either present or absent. *P. dalbyi* is found on natural and artificial hard substrates throughout southern Australia, and often grows in dense aggregations, such as those found at Workshops Jetty (Dalby 1997). It is numerically dominant in most sheltered artificial hard substrata of Port Phillip Bay and is large and long-lived relative to co-occurring sessile taxa. Given its abundance and longevity, it is likely to be fre-

quently encountered by larvae of a range of subtidal sessile species attempting to settle onto hard surfaces. *C. seurati* and barnacles were chosen for this experiment because they were recruiting in high abundances at the time our experiments were being set up, and represent common but very different types of sessile taxa. *C. seurati* is a fast growing but short-lived encrusting bryozoan that can cover substantial areas, with individual colonies usually up to 5–6 cm^2. *A. variegatus* and *B. trigonus* are the most common and largest barnacles at our particular study site. As very early recruits they are difficult to distinguish in the field, which is why both species were included in a single treatment. As adults, individuals can be up to 1.5 cm^2 in basal diameter and 1 cm high. They can occupy large areas and change the surface topography substantially.

Settlement surfaces were made of opaque acrylic plates (125 × 100 mm) attached in an evenly spaced array to weighted PVC backing (600 × 600 mm). Panels were suspended horizontally by rope so that they floated at a depth of approximately 2.5 m below the low water mark, with settlement plates oriented downwards. Settlement plates were designed to act as small patches of habitat and are readily colonised by sessile invertebrates, developing diverse communities over time.

Pyura dalbyi treatments consisted of plates that had either 2 adult *P. dalbyi* (approximately 5 cm length, 3 cm width and 6 cm in height) attached to them, or had no *P. dalbyi* present. Established *P. dalbyi* were approximately 2 years old and had been grown on artificial settlement surfaces before being removed as adults and re-attached in random locations on the surface of plates with cyanoacrylate adhesive. After approximately one month of being submerged on the underside of panels at Workshops Jetty, these adult *P. dalbyi* had attached to plates with their own adhesive structures and did not suffer any obvious adverse effects. Established *P. dalbyi* that were attached to panels as experimental treatments occupied approximately 35% of space on surfaces throughout duration of the experiments.

Recruits of *Conopeum seurati* and barnacles were collected on roughened acetate sheets that were suspended in the water from downward-facing backing panels for approximately 3 weeks. This ensured that recruits had recently settled whilst still obtaining them in adequate numbers for experiments. After this collection period, recruitment was artificially manipulated by cutting and gluing sections of acetate with single colonies of *C. seurati* or single barnacle recruits onto settlement surfaces. Prior to

the addition of recruits on acetate, all primary space on the plates was thoroughly cleaned to remove any species that may have established over the time they were submerged during *Pyura dalbyi* attachment.

Plates that had either adult *Pyura dalbyi* or no *P. dalbyi* received one of 4 'recruitment' treatments: (1) 15 *Conopeum seurati* recruits; (2) 15 barnacle recruits; (3) acetate controls; or (4) no initial recruitment. Acetate controls consisted of 15 squares of acetate of roughly the same size as those that had barnacle recruits or *C. seurati* glued onto the plates. By comparing *C. seurati,* barnacles and acetate treatments to the no recruitment treatments we could determine if the presence of initial recruits had an effect on communities, and also separate these from any effects of acetate squares or glue that were used to transplant them into communities. There were 3 replicates of each treatment (limited by the number of recruits we were able to collect). Replicate plates were spread across 3 individual panels, each with 1 *Pyura dalbyi*/recruitment combination and arranged in an evenly spaced 2 × 4 array.

Sampling and data analysis

After manipulations of recruitment, we followed community development by photographing all plates 1, 5 and 8 mo after recruits were added to plates. Photos were taken using a standardised camera setup (Canon G8 12.1 megapixel with a WP-DC21 underwater housing) 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 seawater on Workshops Jetty.

To determine the structure of communities on each plate, we estimated % cover of species by identifying the taxa beneath 200 points placed randomly over photos of the plates. Points analysis was performed using the program CPCe (Kohler & Gill 2006).

To test for the effects of initial recruit type and the presence of established *Pyura dalbyi* on overall community structure, we analysed % cover data using PERMANOVA (Anderson et al. 2008); ANOVA was used to examine changes in the abundance of individual taxa. For both PERMANOVA and ANOVA, we used the same linear mixed model with 4 factors: (1) *Pyura* (fixed at 2 levels: established *P. dalbyi* or no *P. dalbyi*), (2) Recruitment (fixed at 4 levels: *Conopeum seurati* recruitment, barnacle recruitment, no recruitment or acetate controls, and crossed with *Pyura*), (3) Time (fixed at 3 levels: 1, 5 and 8 mo)

and (4) Plate (random with 3 levels and nested within *Pyura* × Recruitment). *Pyura*, Recruitment and Time (P, R and T, respectively) were crossed factors. In this analysis we were particularly interested in significant P × R interactions (including P × R × T), as they potentially indicate cases where the effects of recruitment on communities or individual species were altered by the presence of *P. dalbyi*. For example, a P × R interaction of interest might occur when different communities develop on treatments that initially received barnacle recruits compared to other recruitment treatments, and also on barnacle recruitment treatments with different *P.dalbyi* treatments (i.e. there is an effect of barnacle recruitment on community composition which is also altered by the presence/absence of *P. dalbyi*).

We tested community structure using the models above, firstly using % cover of taxa found on total space (i.e. on *Pyura dalbyi* tunics and on primary space together), and secondly only using % cover of taxa found on primary space (i.e. excluding space occupied by established *P. dalbyi* and taxa growing on *P. dalbyi* tunics). We used these 2 measures of space occupation because, unlike many other species of sessile animals, the surfaces of *P. dalbyi* are colonised by many kinds of species and act as an additional, secondary habitat to the surfaces of plates. *Pyura dalbyi* also had the potential to alter the abundance of taxa in communities simply by making less primary space available to those species that do not settle on *P. dalbyi* tunics. Our measure of % cover of taxa on primary space was corrected for the different amounts of primary space available between *P. dalbyi* and no *P. dalbyi* treatments and provided a standardised measure of abundance that allowed us to determine whether community and species responses were altered by differences in available primary space or growth on the tunics of *P. dalbyi*.

Where significant results were found, PERMANOVA or ANOVA results were followed by post-hoc pairwise comparisons between recruitment treatments at the appropriate level using PERMANOVA pairwise comparisons or Tukey's HSD, respectively. For univariate analysis, we have only presented results for taxa that showed significant differences in the amount of space they occupied as a result of *P. dalbyi* and recruitment treatments.

Principal co-ordinates ordination (PCO) based on the Bray-Curtis dissimilarity matrix of % cover of all taxa recorded were also used to visualize differences in overall community structure between treatments through time on total space (*P. dalbyi* and primary space) and primary space only. This is considered one of the most suitable visual complements to PERMANOVA output (Anderson et al. 2008).

In all of the analyses outlined above, % cover data of individual *Conopeum seurati* or barnacles that were part of initial recruitment treatments were included in community measures and measures of those particular species. The % cover of established *Pyura dalbyi*/available secondary space provided by resident ascidian treatments and free primary space was not included in analyses.

RESULTS

Over the course of this experiment, diverse communities (consisting of approximately 42 taxa) formed on settlement surfaces and a range of taxa recruited onto both the tunics of established *Pyura dalbyi* and primary space. All taxa occurring on *P. dalbyi* tunics were also found on primary space, but a range of taxa occurred only on primary space. Only a few taxa dominated available space. The most abundant taxa occurring on all available space were the colonial ascidian *Botrylloides leachii*, didemnid ascidians (consisting of 1 or 2 species of ascidian in the family Didemnidae belonging to *Tridemnum* and *Didemnum* that are difficult to distinguish from one another, but easily distinguished from *Diplosoma listerianum*; also in the same family and common at our site) and the bryozoans *Conopeum seurati*, *Bugula dentata*, *Bugula flabellata*, and *Bugula neritina* — all of which varied in the amount of space they occupied through time, and in some cases between experimental treatments. The amount of free space (i.e. unoccupied by any taxa) decreased as communities aged but was not limiting at any time during these experiments. Approximately 59, 34 and 20 % of space was free of any taxa on treatments without *P. dalbyi* at 1, 5 and 8 mo, respectively. Slightly less space was available on treatments with established *P. dalbyi* with 29, 20 and 19 % of overall space (uncorrected for differences in primary space caused by established *P. dalbyi*) remaining free of any taxa at 1, 5 and 8 mo, respectively.

Communities occupying total space (both primary space and the surface of *Pyura dalbyi* tunics) as well as those found exclusively on primary space were influenced by the presence of established *P. dalbyi* and different recruitment treatments, but the effects of recruitment treatments were not altered by the presence of *P. dalbyi* (i.e. there was no significant interaction between *P. dalbyi* treatments and recruitment treatments; Fig. 1, Tables 1 & 2).
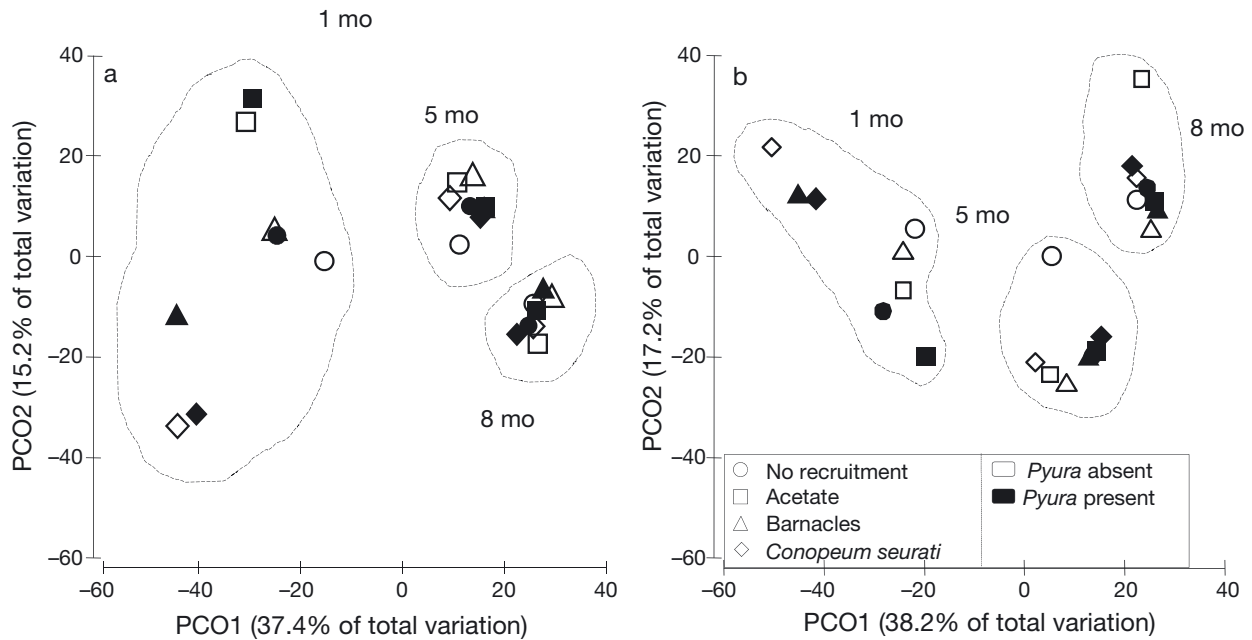
Fig. 1. Principal co-ordinates ordination (PCO) of % cover of all taxa colonizing settlement plates at Williamstown on (a) total space or (b) primary space only that were exposed to either recruitment of *Conopeum* or barnacles, no recruitment, or received acetate controls at 1 month, 5 months and 8 months after experimental manipulations (see key above). To increase the clarity of PCO plots, we have only shown a single object representing the average distances among centroids sampled on the basis of the Bray-Curtis measure of % cover of taxa for each treatment at each time. Increasing distances between treatments represent increasing differences in community structure. Details of differences between individual treatments are described in the 'Results'

Table 1. Results of partly-nested ANOVA on the % cover of major space-occupying taxa or taxa that showed differences between experimental treatments and partly-nested PERMANOVA on the % cover of all taxa found on total space (on both *Pyura dalbyi* tunics and primary space). Numbers under each factor and factor combination are p-values, and the 2 columns at the right show the denominators used to construct the relevant *F*-ratios, with MS$_{plate(P \times R)}$ used to test overall effects of *Pyura* and Recruitment. Differences between treatment groups associated with significant p-values (p < 0.05, in **bold**) in the main analysis were tested for individual species with Tukey's HSD or PERMANOVA pairwise comparisons and are shown on relevant figures for individual species. Details for PERMANOVA pairwise comparisons are shown below, as they are difficult to show clearly on an ordination plot. No pairwise comparisons were done for significant *Pyura* effects with no interactions in any analysis (as there were only 2 levels), or for Time on its own. P = *P. dalbyi*, N = No *P. dalbyi*, Br = *Conopeum*, Ba = Barnacles, Ac = Acetate Controls, C = No Recruitment Controls

	Pyura (P)	Recruit-ment (R)	Time (T)	P × R	P × T	R × T	P × R × T	Plate (P × R)	MS (plate(P × R))	MS (Error)
df	1	3	2	3	2	6	6	16	16	32
Didemnids ascidians	0.705	**0.045**	**0.000**	0.170	0.246	0.884	0.378	0.734	10.706	14.470
Diplosoma listerianum	0.094	0.131	0.548	**0.045**	0.470	0.163	0.605	**0.020**	13.142	5.593
Amphibalanus variegatus	**0.001**	0.152	**0.000**	0.349	0.052	**0.049**	0.382	0.066	3.359	1.797
Balanus trigonus	0.203	0.800	**0.011**	0.678	**0.007**	0.822	0.521	0.106	0.131	0.078
Conopeum seurati	0.982	**0.000**	**0.000**	0.177	0.728	**0.000**	**0.030**	0.291	13.045	10.423
Bugula dentata	0.116	0.801	**0.027**	0.843	0.463	0.886	0.313	0.383	65.387	58.560
Bugula flabellata	0.093	0.120	**0.000**	0.287	0.071	0.130	0.312	0.523	17.838	18.674
Bugula neritina	0.832	0.061	**0.004**	0.892	0.314	0.085	0.809	0.177	7.303	4.993
Cyanea capillata	**0.001**	0.083	**0.000**	0.077	**0.001**	0.567	0.244	**0.029**	18.262	8.295
Community (PERMANOVA)	**0.004**	**0.000**	**0.000**	0.626	0.078	**0. 000**	0.828	**0.008**	1984.6	1492.0

Community (PERMANOVA) pairwise comparisons: **1 mo** Br≠Ba Br≠Ac Br≠C Ba≠Ac C≠Ac Ba=C; **5 mo** Br≠Ba Ba≠C Br=C=Ac Ba=Ac; **8 mo** Br=Ba=Ac=C

Table 2. Results of partly-nested ANOVA on the % cover of major space-occupying taxa or taxa that showed differences between experimental treatments and partly-nested PERMANOVA on the % cover of all taxa found on primary space only (excluding space occupied by *Pyura dalbyi* and taxa found growing on *P. dalbyi* tunics). Numbers under each factor and factor combination are p-values, and the 2 columns at the right show the denominators used to construct the relevant *F*-ratios, with $MS_{plate(PxR)}$ used to test overall effects of *Pyura* and Recruitment. For further details, see Table 1

	Pyura (P)	Recruit-ment (R)	Time (T)	P × R	P × T	R × T	P × R × T	Plate (R × T)	MS (plate (P × R))	MS (wthn)
df	1	3	2	3	2	6	6	16	16	32
Didemnids ascidians	**0.000**	0.120	**0.000**	0.104	**0.011**	0.896	0.436	0.952	13.703	30.415
Diplosoma listerianum	0.308	0.228	0.388	**0.046**	0.356	0.274	0.939	0.099	20.310	9.420
Amphibalanus variegatus	**0.020**	0.157	**0.000**	0.495	0.431	**0.043**	0.420	0.103	4.259	2.497
Balanus trigonus	0.999	0.922	0.114	0.609	**0.037**	0.741	0.360	**0.029**	0.306	0.137
Conopeum seurati	**0.022**	**0.000**	**0.000**	0.310	**0.000**	**0.000**	**0.037**	0.275	24.798	19.421
Bugula dentata	**0.040**	0.820	**0.044**	0.779	0.206	0.946	0.788	0.244	315.979	237.271
Bugula flabellata	0.919	0.139	**0.000**	0.443	0.940	0.267	0.665	0.651	46.683	56.650
Bugula neritina	0.447	**0.049**	**0.009**	0.642	0.292	0.169	0.881	0.312	14.233	11.680
Cyanea capillata	0.139	0.348	**0.000**	0.143	0.606	0.847	0.500	**0.022**	56.665	19.937
Community (PERMANOVA)	**0.002**	**0.02**	**0.0001**	0.788	0.0697	**0.0004**	0.884	**0.0026**	2259.4	1657

Community (PERMANOVA) pairwise comparisons: **1 mo** Br≠Ba Br≠Ac Br≠C Ba≠Ac C≠Ac Ba=C; **5 mo** Br=Ba=Ac=C; **8 mo** Br=Ba=Ac=C

On both total and primary space, the influence of *Pyura dalbyi* persisted into later community stages. Communities on plates without established *P. dalbyi* differed from those with *P. dalbyi* throughout the experiment, as shown by a significant *Pyura* effect but non-significant P × T interaction (Tables 1 & 2).

The influence of recruitment treatments on community composition changed over time, as indicated by a significant R × T interaction; these effects differed between total and primary space (Fig. 1, Tables 1 & 2). In the first month after manipulation, communities on both total space and exclusively on primary space that received different recruitment treatments all differed in overall structure, with the exception of those that received barnacle recruitment and no recruitment treatments. At 5 mo, communities occupying total space differed between treatments that initially received *Conopeum seurati* and those that received barnacles; and those that received barnacles differed from those that received no initial recruitment, but no other recruitment treatments differed from each other. In contrast, communities found exclusively on primary space did not differ at 5 mo. Initial effects of recruitment treatments did not persist, and at 8 mo there were no differences between communities on total or primary space that had received different recruitment treatments. Communities on both total and primary space that received different recruitment treatments became more similar as they aged, and by 8 mo had converged on a similar structure and did not differ significantly (Fig. 1). Communities at 8 mo were comprised of a variety of species, the most abundant of which still occupied an average of less than 10% of both total and primary space, and were not dominated by any one particular species.

Differences in community structure due to the presence of established *Pyura dalbyi* and recruitment treatments were associated with complex effects on individual taxa that varied depending on the taxon, and whether cover was measured across total or primary space.

The presence of established *Pyura dalbyi* altered the abundance of the barnacle *Amphibalanus variegatus* and arborescent bryozoan *Bugula dentata* over the entire sampling period, as indicated by a significant *Pyura* effect. *A. variegatus* occupied 2.27 ± 0.43% (mean ± SE) of both total space and primary space when adult *P. dalbyi* were absent, but only 0.57 ± 0.18% of total space and 0.98 ± 0.30% of primary space where *P. dalbyi* was present (Tables 1 & 2). In contrast, the arborescent bryozoan *Bugula dentata* had a higher proportional cover on primary space where *P. dalbyi* was present, covering 11.02 ± 3.7% of primary space on *P. dalbyi* treatments but only 2.1 ± 0.7% of primary space on treatments without *P. dalbyi*, although its cover over total space did not significantly differ between *P. dalbyi* treatments (Tables 1 & 2).

Resident *Pyura dalbyi* also had an effect on the cover of 3 taxa that varied over time, as indicated by a significant P × T interaction. The barnacle *Balanus trigonus* covered 6 and 3 times more total and primary space, respectively, on treatments without *P. dalbyi* than on treatments where *P. dalbyi* was present at 5 mo, but not at other times (Fig. 2, Tables 1 & 2). Polyps of the
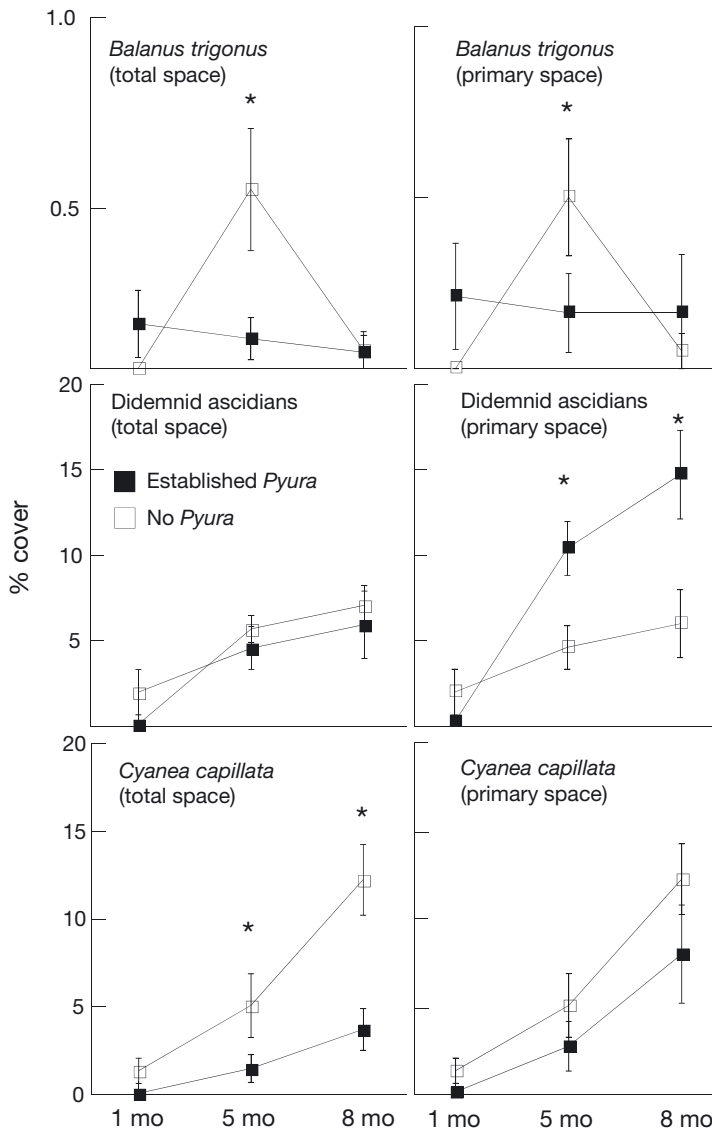
Fig. 2. Percent cover of taxa that showed an interaction between *Pyura dalbyi* treatments and time. Asterisks denote treatments that were significantly different from each other according to partly-nested ANOVA (tested in the term P × T; see Tables 1 & 2)

sea-jelly *Cyanea capillata* did not differ in cover at 1 mo but covered approximately 4 times more total space on treatments without *P. dalbyi* than on treatments where *P. dalbyi* was present at 5 and 8 mo (Fig. 2, Table 1). There were no differences in the % cover of *C. capillata* on primary space alone for any treatments or interactions between them (Table 2). In contrast, didemnid ascidians did not show differences in abundance between *P. dalbyi* treatments across total space, but covered 2 and 3 times more primary space on treatments where established *P. dalbyi* was present than on treatments without established *P. dalbyi* at 5 and 8 mo, respectively (Fig. 2, Tables 1 & 2).

Different recruitment treatments influenced the abundance of didemnid ascidians and the arborescent bryozoan *Bugula neritina*, but these recruitment effects were not altered by the presence/absence of established *Pyura dalbyi* as indicated by a significant Recruitment effect but non-significant P × R interactions. Didemnids occupied approximately twice as much total space on plates that received barnacle recruitment treatments than no-recruitment treatments (Fig. 3, Table 1). However, these effects were not apparent when we compared the % cover of didemnids on primary space only (Fig. 3, Table 2). *B. neritina* had a % cover that was 3 times greater on barnacle and acetate control treatments than on no-recruitment and *Conopeum seurati* treatments on primary space only, but these effects did not occur across total space (Fig. 3, Tables 1 & 2).

Different recruitment treatments also influenced the abundance of the barnacle *Amphibalanus variegatus*, but these effects varied through time and were not altered by the presences of established *Pyura dalbyi* as indicated by a significant R × T interaction but non-significant P × R and P × R × T interactions. In the 1 month samples, % cover of *A. variegatus* was 4 and 3 times greater for total and primary space, respectively, on barnacle treatments than on acetate control treatments, but did not differ from *Conopeum seurati* treatments or no recruitment treatments — which also did not differ from acetate control treatments on total or primary space, although these differences did not persist into 5 and 8 mo communities (Fig. 4, Tables 1 & 2).

Only the colonial ascidian *Diplosoma listerianum* and the bryozoan *Conopeum seurati* were influenced by a combination of recruitment treatments and established *Pyura dalbyi*, as indicated by significant P × R or P × R × T interactions. Across both total and primary space, *D. listerianum* covered 7 times more space on plates that received no initial recruitment and had no established *P. dalbyi* than on plates that received no initial recruitment but had established *P. dalbyi* present; its cover did not differ between other *P. dalbyi* and other recruitment treatment combinations (Fig. 5, Tables 1 & 2).

When the % cover of *Conopeum seurati* colonies was compared across primary space only, the presence of established *Pyura dalbii* altered the effects
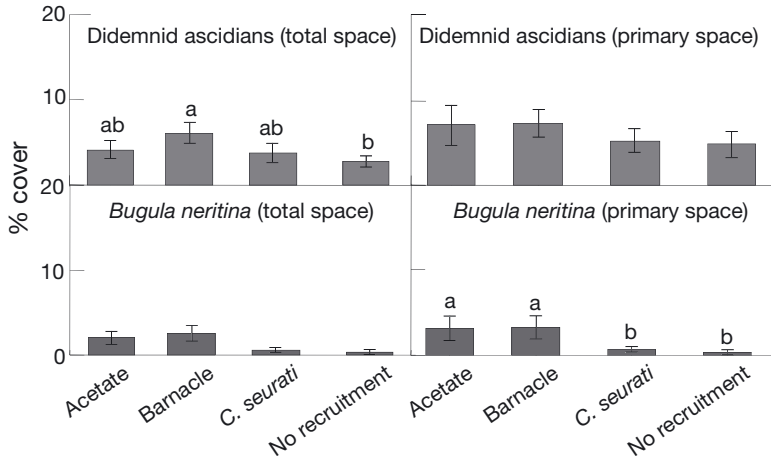
Fig. 3. Percent cover of taxa that showed differences between initial recruitment patterns across all times sampled, regardless of the presence/absence of *Pyrua dalbyi,* and pooled over time (tested in the term Recruitment). Letters above bars represent differences between treatments and those without letters in common were significantly different from each other according to partly-nested ANOVA
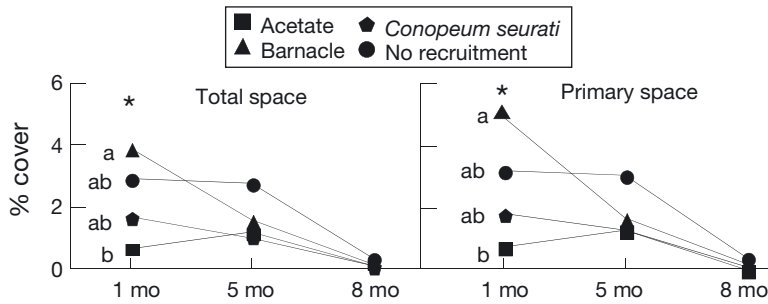

Fig. 4. Percent cover of *Amphibalanus variegatus* between plates that received recruitment of barnacles, the encrusting bryozoan *Conopeum seurati,* acetate controls or no recruitment across total space or primary space at each time sampled. Asterisks denote times where treatments were significantly different from each other according to partly-nested ANOVA (tested in the term R × T). Letters adjacent to symbols represent differences between treatments and those without letters in common were significantly different from each other at that particular time sampled according to partly-nested ANOVA. We have not shown error bars around mean values as they do not represent error terms used to compare groups within factors of interest in partly-nested ANOVAs
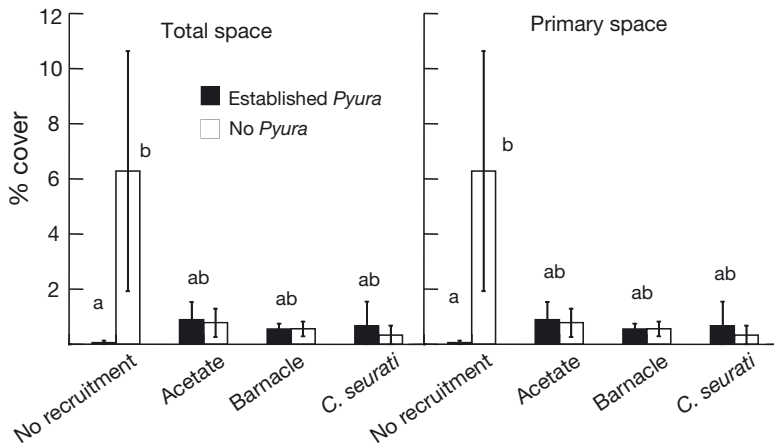
of recruitment treatments, but this effect varied through time as indicated by a significant P × R × T interaction. At 1 mo, the % cover of *C. seurati* on primary space was 1.5 times higher on plates that received *C. seurati* recruitment treatments and had established *P. dalbyi* present than on those that received *C. seurati* recruitment treatments but had no *P. dalbyi* present; both of these treatments had higher cover of *C. seurati* colonies than other recruitment/*P. dalbyi* treatment combinations (Fig. 6, Table 2). There were no differences between other recruitment/*P. dalbyi* treatment pair combinations 1 mo. When pooled over *P. dalbyi* treatments, the abundance of *C. seurati* colonies was also higher on *C. seurati* recruitment treatments at 1 mo, where they occupied 4 to 17 times as much primary space as other recruitment treatments (indicated by a significant R × T interaction). None of the differences between treatments detected at 1 mo persisted into the 5 and 8 mo communities, and *C. seurati* occupied very little primary space at this time (Fig. 6, Table 2). Although there was a significant P × R × T interaction for *C. seurati* across total space, post-hoc comparisons revealed that these differences were not because *P. dalbyi* altered its abundance a meaningful way (i.e. the abundance of *C. seurati* did not differ between different *P. dalbyi* and recruitment treatment combinations within each time sampled but were driven by interactions between treatments across different times; Table 1). While there was not a strong combined effect of *P. dalbyi* and recruitment treatment across

Fig. 5. Percent cover of *Diplosoma listerianum* between *Pyura dalbyi* and recruitment treatments, pooled across all times sampled (tested in the term P × R). Letters above bars represent differences between treatments, and those without letters in common were significantly different from each other according to partly-nested ANOVA
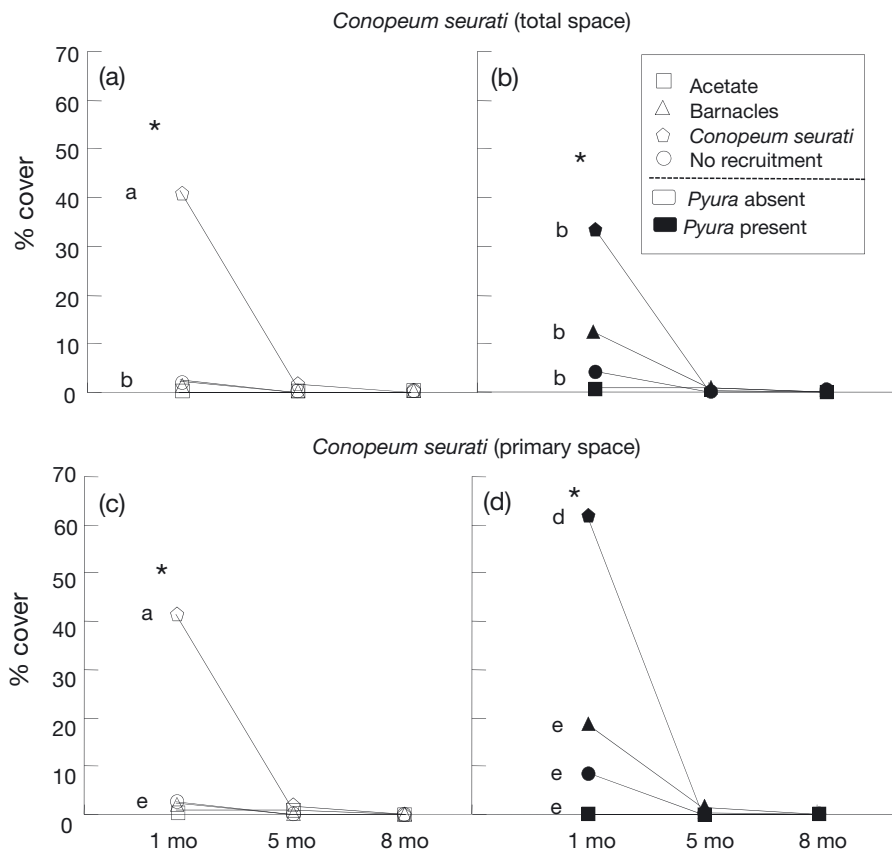
Fig. 6. Percent cover of the encrusting bryozoan *Conopeum seurati* at each time sampled on (a,b) total space or (c,d) primary space only. Asterisks denote times when there were differences in cover between treatments according to partly-nested ANOVA (tested in the term P × R × T). Letters adjacent to symbols represent differences between treatments and those without letters in common were significantly different from each other at that particular time sampled according to partly-nested ANOVA. Recruitment treatments are shown on separate axes for different *Pyura dalbyi* treatments for clarity, but were directly compared between *P. dalbyi* treatments in a single partly-nested ANOVA within each different measure of space. Letters, therefore, also represent differences between recruitment treatments on different *P. dalbyi* treatments (on different axes) within each different measure of space. We have not shown error bars around mean values as they do not represent error terms used to compare groups within factors of interest in partly-nested ANOVAs

total space, there was still an effect of recruitment treatments that varied over time, indicated by a significant R × T interaction for total space. In the first month of community development, *C. seurati* colonies covered 3 to 4 times more total space on plates that initially received *C. seurati* recruitment treatments than on those that received other recruitment treatments (Fig. 6, Table 1). Again, these differences did not persist into 5 and 8 mo communities, and *C. seurati* occupied very little total space at these times.

DISCUSSION

This experiment shows that both the presence of resident adults and initial patterns of individual species' recruitment can influence the structure and development of a temperate fouling community and have complex effects on individual taxa. However, in this particular study the presence of established *Pyura dalbyi* did not alter the effects of different recruitment patterns at the community level (i.e. there were not strong P × R or P × R × T interactions).

While the effects of *P. dalbyi* were longer lived, the effects of initial recruitment pattern did not persist into older communities.

Effects of established *Pyura dalbyi*

The main effect of *Pyura dalbyi* on community structure was to reduce the cover of a range of taxa where it was present (e.g. *Amphibalanus variegatus*, *Balanus trigonus*, *Cyanea capillata* and *Diplosoma listerianum*). A likely mechanism for this was through the reduction of primary space available for the recruitment and growth of species. For example, *Cyanea capillata* had a much higher abundance where there was no *P. dalbyi* across total space, but its % cover did not differ when we examined primary space only (suggesting that *C. capillata* do not use *P. dalbyi* tunics), although this did not result in a local concentration on primary space (also see Holst & Jarms 2007). At a study site adjacent to ours, *Pyura 'stolonifera'* (now *P. dalbyi*) growing on jetty pilings was found to reduce the growth rates of nearby conspecifics without direct contact, poten-

tially through the consumption of food or reduction of food supply via the baffling of currents (Dalby 1995). *P. dalbyi* may also have reduced the growth and/or survivorship of some taxa in our study through similar mechanisms. *P. dalbyi* may also have caused a reduction in the recruitment of these taxa by preying on larvae. The congeneric ascidian *Pyura haustor* can consume ascidian tadpoles and barnacle nauplii and cyprids (Bingham & Walters 1989). However, the presence of solitary ascidians has been found to have little effect on recruitment of invertebrates onto nearby space, despite feeding on the larvae of a range of species (Young 1989). The larvae of some species have been shown to avoid settling near large space-occupying competitors or established recruits, which can also influence recruitment patterns and the distribution of recruits (Grosberg 1981, Gaines et al. 1985, Todd & Keough 1994, Osman & Whitlatch 1995a), although little is known about the specific effects of *P. dalbyi* on larval settlement preferences. *P. dalbyi* had a positive effect on some species (*B. dentata* and didemnids), which had higher cover on primary space adjacent to established *P. dalbyi*, and may result from increased larval settlement, higher colony growth, a higher concentration of colonies on more limiting primary space or a combination of these effects (Osman et al. 1989, Osman & Whitlatch 1995b).

We chose *Pyura dalbyi* for this experiment because it is a large and abundant space-occupying sessile animal found in our study area. For logistical reasons, we only used a fixed density of 2 adult *P. dalbyi*, but densities can range from isolated individuals to dense aggregation of dozens of individuals found on a range of natural and artificial substrates including rocky reef, sand and jetty piles (Dalby 1997). *P. dalbyi* colonize steadily for much of the year but rarely dominate settlement events (Dalby 1994). As individuals become established, they grow steadily for several years to cover primary space leaving only secondary space available for colonization. At higher densities, established solitary ascidians such as *P. dalbyi* may alter flow, food availability and limit available primary space more dramatically than at low densities, while providing more secondary space on tunics for recruitment of other species to occur (Dalby 1995, Osman & Whitlatch 1995a,b, Claar et al. 2011). Consequently, different densities and ages of *P. dalbyi* may have different effects on community composition and how it is influenced by recruitment, although further work is required to determine the direction and nature of any of these effects.

Effects of initial recruitment treatments

Community responses to different initial recruitment treatments were associated with highly variable differences in the amount of space occupied by a small number of taxa. The higher amount of space of *Conopeum seurati* colonies on plates inoculated with *C. seurati* during the early stages of experiments was mostly due to the growth of colonies planted in recruitment treatments. However, the presence of low abundances of *C. seurati* colonies on other recruitment treatments demonstrates that natural larval recruitment of *C. seurati* occurred during the early stages of experiment and may also have contributed to higher abundances of *C. seurati* colonies. On *C. seurati* recruitment treatments where *Pyura dalbyi* was present, the higher cover of *C. seurati* colonies may be simply be due to greater crowding of a similar number of planted colonies onto less primary space. There may have been some enhanced larval recruitment of new *C. seurati* individuals on *C. seurati* recruitment treatments where *P. dalbyi* was present. However, there were no statistically significant differences in the cover of *C. seurati* between other recruitment treatments with or without *P. dalbyi*, which suggests that *P. dalbyi* on its own did not greatly enhance larval recruitment of *C. seurati.*

Compared to other recruitment treatments, barnacles add greater complexity to the surfaces of settlement plates and can create refuges that enhance larval settlement and post-settlement survival of a range of taxa, including didemnids and *Bugula neritina* (Walters & Wethey 1996). Barnacle recruitment treatments may have driven the higher abundances of didemnids and *B. neritina* observed in this experiment through similar mechanisms.

Acetate squares may have also provided positive settlement cues or slightly increased surface complexity by providing raised edges on plates that may have positively affected the abundance of *Bugula neritina* compared to *Conopeum seurati* recruitment and no recruitment treatments. In contrast, acetate may have provided a negative settlement cue or difficult surface for attachment or growth than barnacle recruitment treatments for *Amphibalanus variegatus* during early community stages. We do not know what the specific effects of acetate were on these species, although substratum effects can arise through a variety of mechanisms (Anderson & Underwood 1994). In these experiments, acetate was merely a convenient way to transfer a balanced number of recruits onto experimental treatments, rather than being of particular interest. Acetate treatments

were only included so that we could separate the effects of our live recruits from those of acetate or glue. Importantly, in this experiment the effects of acetate on other species were not widespread (only 2 out of 42 taxa showed differences due to acetate) and were distinguishable from any effects of live recruits.

Both the bryozoan *Conopeum seurati* and colonial ascidian *Diplosoma listerianum* were influenced by combined effects of *Pyura dalbyi* and recruitment treatments. In contrast to *C seurati, D. listerianum* had a higher cover on no initial recruitment treatments where *P. dalbyi* was absent than on no initial recruitment treatments where *P. dalbyi* was present, which may reflect either a positive settlement preference or increased survival on unoccupied space, or a negative settlement preference, larval predation or increased mortality on surfaces with *P. dalbyi* and initial recruits or acetate. Alternatively, this could reflect greater colony growth from lower spatial competition on surfaces where there were fewer established recruits and no adult *P. dalbyi* (e.g. Valdivia et al. 2005). In this experiment, the combined effects of the presence of *P. dalbyi* and recruitment on these species did not translate into changes in overall community composition, most likely because *C. seurati* did not persist for long in communities and *D. listerianum* did not occupy high amounts of space.

Differences across total and primary space

The effects of recruitment on didemnid ascidians and *Bugula neritina* also changed between total and primary space (in opposite directions), due to shifts in their distribution across the different types of space. This might suggest that established adults can alter recruitment effects in more subtle ways by changing amount of different substrate types available, but again these effects did not result in major community changes or direct interactions between *Pyura dalbyi* and initial recruitment.

Patterns of community development

In this experiment, differences between communities that arose due to different recruitment treatments did not persist beyond 5 mo, and there are some important attributes of our community that may reduce the persistence of such effects. Our study community converged on a similar structure as it aged, particularly on primary space. The results from this experiment alone might suggest that our study community

followed a predictable or deterministic pattern of community development that overrides initial recruitment effects (e.g. Dean & Hurd 1980, Mook 1981, Bram et al. 2005). However, in 4 of our previous experiments at this same study site, initial differences in recruitment of a variety of species were similarly found to cause early differences in community structure that did not persist into later community stages, but communities did not converge on a common structure either within or between experiments (Sams & Keough 2012a,b). Based on the results of the present study and our 4 previous experiments (Sams and Keough 2012a,b), there does not appear to be a generally predictable or deterministic pattern of community development in these communities, which reflects the findings of a range of studies of similar fouling communities in other parts of the world (Sutherland 1974, Osman 1977, Sutherland & Karlson 1977, Cifuentes et al. 2010). Unlike studies from other systems, the communities in the present study did not converge because they became dominated by one or 2 large, competitively superior species, but because they had a similar mixture of a variety of species. The lack of strong effect of initial recruitment in this experiment most likely arose from a combination of high propagule pressure over the duration of community development, a high diversity of propagules as well as variable and generally weak effects of initial recruits on species that subsequently colonised experimental surfaces (Sams & Keough 2012a). Any potential interactions between discrete initial recruitment and established adults may therefore be less likely to have strong persistent effects on our study community.

Life history of recruiting species

A species' lifespan may also play an important role in determining how long the effects of recruitment persist. The species that were available for recruitment manipulation in our experiment consisted of a fast-growing, short-lived bryozoan (*Conopeum seurati*), and barnacles that individually take up little space. Recruitment of these species may also be less likely to influence subsequent community structure compared to recruitment of larger, longer-lived species in our study community, though even short-lived species have the potential to alter community structure through direct and indirect interactions with longer-lived species (Menge 1995). Our study community contains many colonial species in high abundances that can become large, even problematic, space occupiers in other systems (e.g. *Diplosoma lis-*

terianum, didemnid asicidians, *Botrylloides leachii*); however, we rarely observe them dominating large amounts of space in communities at Williamstown, even on larger more continuous surfaces (Sams & Keough 2012a, M. J. Keough pers. obs.). The small, isolated patches of artificial habitat provided by settlement plates often support communities containing species that invest heavily in larval recruitment rather than asexual growth, and post-recruitment processes such as competition and facilitation can be less important compared to communities containing large, long-lived clonal species (Jackson 1977, Keough 1983, 1984, Glasby 1999). Consequently, we may have less likely observed strong interactions between established adults and different recruitment events compared to other habitats, though many processes controlling the distribution of animals are likely to be the same between these types of habitats and more natural habitats (Cole et al. 2005). In communities or recruitment events comprising longer-lived and larger colonial species, or species that have stronger competitive or facilitative interactions than those observed in this experiment, established adults and different recruitment patterns may have a stronger influence on community structure and have stronger combined effects, but this remains to be seen. The results of this experiment suggest that any combined effects of recruitment and established adults on individual taxa are likely to be complex and non-uniform between taxa, and may not always cause large changes in community composition.

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