1 **Effects of pulse vs. steady recruitment on sessile marine**
2 **communities.**

3 Michael A. Sams¹ and Michael J. Keough¹

4 ¹*Department of Zoology, University of Melbourne, Victoria 3010, Australia*

5
6 *Author Contributions: MAS and MJK conceived and designed experiments, analysed the data*
7 *and wrote the manuscript. MAS performed the experiments.*

8 **Abstract**

9 Variation in patterns of propagule establishment (recruitment) has important effects on
10 population dynamics and the structure of some communities. Most experimental studies have
11 varied recruitment by changing the nature of a single event early in community development, but
12 recruitment can also vary from steady rates of arrival to highly episodic ‘pulse’ events, causing
13 differences in the temporal spacing of individuals recruiting into patches. We examined whether
14 two different temporal patterns of recruitment of sessile invertebrates affected temperate marine
15 communities in southeastern Australia in two experiments that were run at different times at the
16 same site and that manipulated several different species. Target species entered communities as
17 either a single pulse of recruits within a two week period or steady input of the same total
18 number of recruits over a longer time period (five to six weeks). The pattern of recruitment had
19 variable effects on community structure. The colonial ascidian *Botryllus schlosseri* did not have
20 a strong influence on community structure whether it recruited in a single pulse or steadily. The
21 cover of *B. schlosseri* was higher when recruitment occurred as a single pulse. In a second
22 experiment, botryllid ascidians caused changes in the composition of communities when they
23 recruited steadily compared to when they did not recruit or didemnids recruited, but caused no
24 differences in communities when they recruited in a shorter pulse. In contrast recruitment
25 frequency of didemnid ascidians had little effect, though their presence/absence caused
26 community differences. Though we found that different temporal recruitment patterns can alter
27 community composition, the life history and ecology of particular taxa as well as differences in
28 environmental background processes are likely to influence the strength of these effects.

29 Key words: Recruitment frequency, community, bryozoan, ascidian

Introduction

For sessile organisms that reproduce with dispersive propagules (e.g. seeds, spores and larvae) the number and type of offspring establishing themselves in habitats is often highly variable in time and space. Such variation in patterns of propagule establishment (recruitment) can influence the abundance and distribution of juveniles and adults, and has a fundamental role in the dynamics of plant, algal and marine animal populations (Reed 1990, Caley et al. 1996, Turnbull et al. 1999, Connell and Green 2000, Underwood and Keough 2001, Wright and Steinberg 2001). Recruitment variation can also have important consequences for many communities, but much less is known about the role of recruitment on community dynamics (but see Bingham 1992, Forde and Raimondi 2004, Fukami et al. 2005, Myers and Harms 2009, Paine and Harms 2009, Sams and Keough *In Press*).

Most studies have examined variation in recruitment by manipulating or measuring differences in space (e.g. between patches or experimental units) in the size of single recruitment events or as surveys of density along gradients varying in average recruitment. Recruitment can, however, vary in more complex ways. It may be steady over time or occur as episodic ‘pulses’, with most species falling somewhere between these extremes, including algae (Reed 1990, Graham et al. 1997), terrestrial plants (Schupp 1990, Connell and Green 2000) and marine invertebrates (Yoshioka 1996, Witman et al. 2003, Pineda et al. 2006).

While little is known of how such temporal variations influence community dynamics, a small number of studies have suggested its importance for populations. Using a modelling approach Wiegman et al. (2004) found that populations of *Acacia raddiana* that only received episodic recruitment of seedlings were less stable than those that received both continuous and episodic recruitment over time. In subtidal beds of Giant Kelp, *Macrocystis pyrifera*, sites that received

continuous recruitment were associated with relatively stable adult canopy cover whilst those that received episodic recruitment had much greater fluctuations in adult canopy cover (Graham et al. 1997). Large pulse recruitment events are also major determinants of colony density and age-frequency distributions in gorgonian coral communities (Yoshioka 1996).

An important feature of episodic or pulse recruitment is that individuals arrive into patches close together in time. Consequently, they will be of similar age and initially experience higher densities of conspecific recruits. Where recruitment occurs more steadily over time, individuals experience greater separation in their timing of recruitment. There is likely to be a range of individual ages, and conspecific recruit densities may initially be lower but steadily increase as more recruits arrive. Such differences in the temporal distribution of propagules entering habitats could alter community dynamics by influencing density and age-dependent competitive and facilitative interactions, predation rates and the effects of environmental and demographic stochasticity. However, episodic or pulse recruitment events are typically associated with higher total numbers of individuals compared to continuous recruitment events (e.g., Yoshioka 1996, Graham et al. 1997). Few studies, including those mentioned above, have decoupled the effects of different temporal recruitment patterns from those of overall recruit number and density, site and/or time. It is not clear whether the effects of different temporal recruitment patterns might cause differences in communities simply because of the overall higher numbers and densities often associated with pulse recruitment events compared to steady events, or because of differences in the distribution of recruit arrival through time.

Here, we experimentally examined the effects of different temporal recruitment patterns of colonial ascidians on temperate subtidal marine communities dominated by sessile invertebrates. Our aim was to test whether differences in the distribution of recruitment through time associated

with different temporal recruitment patterns influences the composition of communities and/or populations of animals they comprise. In two separate experiments, we experimentally manipulated recruitment of three common colonial ascidian taxa so that they recruited into communities as either ‘pulse’ or ‘steady’ recruitment patterns, but kept the total number of individuals that arrived through time the same. We also compared these recruitment treatments to communities where target taxa did not recruit, to determine if any lack of differences between temporal recruitment patterns was because target species simply do not alter community structure, or if they do influence community structure, whether different temporal recruitment patterns have similar effects. We predicted that, where recruitment occurred as a single pulse, communities would have a different composition to those where the same total number of individuals recruited steadily, and that these communities would differ from those that received no recruitment of target species.

Materials and Methods

Study Site

Experiments were done subtidally from mid-November 2008 to late-August 2009 at Workshops Jetty, Williamstown, Australia (37°51'39.78"S, 144°54'34.17"E). Workshops Jetty is located in the northern end of Port Phillip Bay, a large shallow embayment in temperate southeastern Australia (for a more detailed description of the study site see Keough and Raimondi 1995, Sams and Keough 2007). Recruitment of larvae occurs primarily during the warm spring and summer months between November and March during which times the type, number and temporal pattern of species recruiting varies widely between days, weeks and months (Keough *unpublished data*). Overall, recruitment rates are consistently high at Williamstown relative to other sites in Port Phillip Bay, but this is highly variable through time and for different taxa.

99 **Methods**

100 To examine the effects of different temporal recruitment patterns on community structure we ran
101 two separate experiments at different times, where we manipulated the timing of recruitment of
102 different species of colonial ascidians onto individual Perspex settlement plates over a five
103 (Experiment 1) and six (Experiment 2) week period. Because recruitment at Williamstown
104 occurs mostly over the warmer summer months, recruitment manipulations of this length
105 represent a large portion of time during which our target species were recruiting. We ran
106 experiments at two different times and using different species/taxa to test the general importance
107 of different temporal recruitment patterns on community structure.

108 Both experiments followed the same general procedure. Perspex settlement plates (125 x 100
109 mm) were attached via 5 mm stainless steel bolts through the centre of each plate to weighted
110 PVC backing panels (600 x 600 mm) and suspended horizontally from pier pilings to a depth of
111 approximately 2.5 m below the low water mark. The plates were facing downwards, on the
112 undersides of the backing panels and were evenly spaced in a 4 x 4 array (though, to keep the
113 number of treatments even per panel not all available spaces were used – see below for details).
114 Treatments consisted of plates that received either:

- 115 • a single ‘pulse’ of recruits where all recruiting individuals of a single target species
116 arrived in the first two weeks of the experiment;
- 117 • a ‘steady’ input of recruits where the same total number of individuals of the same target
118 species recruited evenly for five (Experiment 1) or six (Experiment 2) weeks;
- 119 • no recruits of the target species.

120 Recruitment frequencies were manipulated by gardening newly-arrived recruits at the end of
121 every week. In order to garden assemblages, panels were removed from the water and submerged
122 in large tubs of seawater. Individuals were then haphazardly removed from plates with tweezers
123 or scraped off with small chisels to create desired recruitment patterns. The number of
124 individuals removed per plate varied greatly depending on the vagaries of recruitment, but up to
125 50 % of individuals were removed in pulse and steady recruitment treatments, and all individuals
126 were removed in no recruitment treatments. Only the recruitment patterns of target species were
127 manipulated and all other species were allowed to recruit in natural background densities from
128 the start of recruitment manipulations/panel deployment. We removed target individuals in “no
129 recruitment” treatments to help with interpreting any result in which there was no effects of
130 temporal recruitment patterns. The no recruitment treatment allowed us to determine whether
131 this was simply because the target species did not influence community structure at all (i.e. there
132 is no difference between plates with and without target species, regardless of temporal
133 recruitment patterns) or whether species can influence community structure but different
134 temporal recruitment patterns have similar effects on communities (i.e. where recruitment
135 frequency treatments do not differ from each other but both differ from no recruitment treatments,
136 or treatments that received different species recruitment in a similar way).

137 Recruitment is highly variable at our study site, and the taxa used in these experiments were
138 largely determined by availability at the time experiments were run. Due to this, we were unable
139 to use exactly the same species between the two experiments. However, the botryllid and
140 didemnid ascidians manipulated in these experiments are abundant as adults, important
141 contributors to community structure and share similar life histories. At Williamston, botryllid
142 and didemnid ascidians are some of the few species that recruit relatively steadily throughout the

summer recruitment seasons but also show increased ‘pulses’ of recruitment for short periods of time (from days up to one to three weeks), making them well suited to testing the effects of different temporal recruitment patterns. They are also commonly found in high abundance as recruits relative to other species during early community stages, and therefore potentially important influences on subsequent community development. The densities used in manipulations were chosen to reflect common natural recruitment densities measured over many recruitment seasons and are typical of medium to high recruitment levels for these species relative to this site (e.g., Johnston and Keough 2000, Holloway and Keough 2002, Keough unpublished data).

Experiment 1

Experiment 1 was run from early November 2008 until early July 2009. Only recruits of the colonial ascidian *Botryllus schlosseri* were manipulated over a five week period in this experiment, as no other species recruited in high enough densities for manipulation. Pulse recruitment treatments received approximately 25 individuals per plate in the first week and another 25 per plate in the second week for a total of 50 individuals per plate over a two week period. After this, any newly arriving individuals were removed from plates for the remaining three weeks of manipulations. Steady recruitment treatments received approximately 25 of the total individuals per plate in the first two weeks of recruitment and another 25 individuals per plate that accumulated over the next three week period for a total of 50 per plate individuals over a five week period. No recruitment treatments consisted of removing *B. schlosseri* recruits from plates during the entire manipulation period. In total there were ten replicates of each treatment plate. To keep the number of treatments and plates per panel even there were two replicates of

every treatment per panel spread across five panels and each panel had ten plates in total,
randomly placed in one of 16 available spaces (see above for details of panel design)

Experiment 2

Experiment 2 was run from early January 2009 to late August 2009. Recruitment of both
didemnids and botryllids (*Botryllus schlosseri* and *Botrylloides leachii*) were manipulated in this
experiment. The exact identity of “didemnids” in this study is unclear but probably consist of one
or two morphologically very similar species in the Family Didemnidae belonging to *Didemnum*
and/or *Trididemnum*, that cannot be reliably told apart in the field or from photos (but not
including the easily distinguished *Diplosoma listerianum*, also in the Family Didemnidae). Both
B. schlosseri and *B. leachii* are easily identified from early colony stages onwards but were used
as one treatment because their very early recruits (usually consisting of one to a few zooids) were
difficult to tell apart in the field without removing plates from the water for an extended time.
Recruitment treatments received either didemnids or botryllids but total numbers were kept the
same between them. Pulse recruitment treatments received 15 individuals per plate in the first
week, and the another 15 per plate in the second week for a total of 30 individuals per plate over
two weeks. After this any newly arriving individuals were removed from plates. Steady
recruitment treatments received 15 individuals per plate in the first two weeks of recruitment and
another 15 individuals per plate that accumulated over the next four week period of recruitment
for a total of 30 individuals per plate over six weeks. No recruitment treatments consisted of
removing either botryllids or didemnids recruits throughout the entire manipulation period. In
total, there were eight replicates of each treatment. To keep the number of treatments and plates
per panel even there were there were two replicates of every treatment per panel, spread across

187 four panels, and each panel had 12 plates in total randomly placed in one of 16 available spaces
188 (see above for details of panel set-up).

189 **Sampling**

190 After manipulations of recruitment we followed community development by photographing all
191 plates monthly for three months and then again after six months. Sampling was done using a
192 standardised camera set up (Canon G9 with 12.1 megapixel resolution in a WP-DC21
193 underwater housing) with a framer to ensure that all photos were taken at the same distance and
194 orientation. All photos were taken whilst plates were submerged in large tubs at the surface of
195 Workshops Jetty, Williamstown.

196 To determine the structure of communities on each plate we estimated % cover (henceforth
197 referred to as cover for simplicity) of species by identifying the taxa beneath 200 points placed
198 randomly over photos of plates. Points analysis was performed using the program CPCe (Kohler
199 and Gill 2006).

200 **Data Analysis**

201 The experimental design for Experiment 1 consisted of three factors, Recruitment (fixed with
202 three levels: pulse recruitment, steady recruitment and no recruitment), Time (fixed with four
203 levels: one month, two months, three months and six months) and Plate (random with ten levels,
204 nested within Recruitment). Recruitment and Time were crossed factors.

205 The experimental design for Experiment 2 consisted of four factors: Species (fixed with two
206 levels: botryllid and didemnid ascidians), Recruitment (fixed with three levels: pulse recruitment,
207 steady recruitment and no recruitment), Time (fixed with four levels: one month, two months,

three months and six months) and Plate (random with eight levels, nested within Species x Recruitment). Species, Recruitment, and Time were fully crossed.

To test for the effects of differences in recruit type and frequency on overall community structure we analysed percent cover data as a partly-nested PERMANOVA with the PERMANOVA add on for Primer 6 (Anderson 2008) for each experiment using the models outlined above, using 9999 permutations, followed by PERMANOVA pairwise comparisons if significant differences were detected amongst treatments.

To determine which species were likely to be driving community level patterns (i.e. to determine which species had significant differences between treatments that reflected the results of PERMANOVA), as well as to detect any effects on individual species that may not have caused large changes in community composition we ran the equivalent univariate partly-nested ANOVA model on each individual species/taxa in the software package SYSTAT. We ran the same statistical models as outlined above for each experiment on each individual species present in communities. We have only presented the result of univariate analysis for the major space-occupying species in each experiment and those species that showed significant differences in cover between treatments.

Principal co-ordinates ordination (PCO) based on the Bray-Curtis dissimilarity matrix of % cover of taxa were also used to visualize differences in overall community structure through time for both experiments. To increase the clarity of PCO plots we have only shown a single object representing the distances among centroids sampled on the basis of the Bray-Curtis measure of % cover of taxa for each treatment at each time. This is considered one of the most suitable visual complements to PERMANOVA output (Anderson 2008).

The plates were by necessity deployed on panels. This was done for logistical reasons, and the panels were of no biological interest. Replicate plates were well separated from each other, and, in some cases, were closer to plates on other panels than to plates on the same panel. We did include Panels as an additional effect in analyses, but, across the large number of analyses, Panel effects were uncommon. Even when present, they did not alter the interpretation of the data, so for simplicity, we have presented analyses in which Panels are omitted.

Results

Experiment 1

Sessile communities in Experiment 1 were initially dominated by a variety of bryozoans (*Watersipora subtorquata*, *Bugula dentata* and *Bugula stolonifera*), colonial ascidians (*Botryllus schlosseri*, didemnids and *Diplosoma listerianum*) and jellyfish polyps of *Cyanea capillata*, but changed substantially over time until eventually becoming dominated by the bryozoan *Bugula dentata*, a unknown species of yellow sponge and tube building amphipods at six months.

Different temporal recruitment patterns of *Botryllus schlosseri* had little effect on the overall structure of communities or on most individual taxa, including a range of major space occupiers in Experiment 1 (Figure 1a and 2, Table 1, Appendix A Figure A1).

While different recruitment patterns of *Botryllus schlosseri* did not result in strong differences in overall community structure they did influence the amount of space subsequently occupied by *B. schlosseri* and didemnid ascidians at different stages of community development. After one month *B. schlosseri* occupied 4 times more space on plates that received pulse recruitment of *B. schlosseri* than when there was steady recruitment of *B. schlosseri* or no *B. schlosseri* recruits (Figure 2; Table 1). These differences did not persist and cover of *B. schlosseri* had declined

dramatically in two month communities, remaining low and similar between treatments up to six months. Didemnids had a higher cover on plates that received recruitment of *B. schlosseri* than on plates that had *B. schlosseri* recruits removed both two and three months after manipulations (Figure 2; Table 1). However there was not a strong difference in cover of didemnids between plates the received pulse or steady recruitment of *B. schlosseri*. The amount of free space available was relatively consistent throughout Experiment 1 and approximately 25-30 % of space was free between different treatments from one to six months (Figure 2).

Experiment 2

Communities in Experiment 2 also changed substantially over six months. The colonial ascidian *Botrylloides leachii* and the bryozoan *Watersipora subtorquata* were initially the most abundant space occupiers, but decreased in abundance through time, while the colonial ascidian *Diplosoma listerianum* and other didemnid ascidians, as well as the arborescent bryozoan *Bugula stolonifera*, the sponge *Sycon* sp. and the barnacle *Amphibalanus variegatus* were the most abundant space occupiers at six months.

In contrast to Experiment 1, the overall composition of communities was influenced by a combination of different temporal recruitment patterns as well as the particular species manipulated (Figure 1b; Table 2, Appendix A Fig A2). Communities that received a steady input of botryllid recruits or had didemnids removed had a similar overall community structure but differed from those from which botryllids were removed and that initially received pulse and steady recruitment of didemnids. Communities that received pulse recruitment of botryllids did not differ from any other treatments and treatments that had botryllids removed did not differ from those that received didemnid recruits at both frequencies. Communities that received either pulse or steady recruitment of didemnids also did not differ from each other.

Differences in overall community structure were driven by differences in the abundance of the colonial ascidian *Botrylloides leachii*, which was influenced by the type of species recruiting, and the initial temporal pattern of botryllid recruitment (Figure 3; Table 2). Treatments that received a steady input of botryllids or had didemnids removed had a higher cover of *B. leachii* than those that had botryllids removed or received recruitment of didemnids at both frequencies but had a similar abundance to each other and communities that received pulse recruitment of botryllids. The cover of *B. leachii* on plates that received pulse recruitment of botryllids did not differ from any other treatment. The frequency with which recruits of botryllid and didemnid ascidians colonised plates during early community development did not influence the abundances of any other species other than *B. leachii* (Figure 3, Table 2, Appendix A Figure A2). Initially the amount of free space available was much lower in Experiment 1 than Experiment 2 with approximately 10 % free space at one month, but as communities aged more space became available increasing to approximately 30 % and 25 % at three and six months respectively.

Discussion

These experiments show that different temporal recruitment patterns of colonial ascidians can influence the dynamics of sessile epifaunal communities. The strength of their effects, however, differed between experiments that were run at different times, depended on the type of colonial ascidian manipulated and did not persist into later community stages.

In Experiment 1 different recruitment frequencies of *Botryllus schlosseri* had little effect on overall community structure at any time, and comparisons to no recruitment treatments suggest that the simple presence of *B. schlosseri* had no influence on communities. At Williamstown, *B. schlosseri* is relatively short lived and does not form large colonies compared to many other

species (Sams 2011, Sams and Keough *In Press*). Unlike many other colonial ascidians, which have the potential to grow indefinitely, *B. schlosseri* senesces after one or a few episodes of larval release which is determined by colony size, temperature and competition (Grosberg 1988, Chadwickfurman and Weissman 1995). Consequently colonies may be less likely to exert strong direct effects on community structure over time if individuals are not replaced by new recruits after they senesce. Alternatively, the freeing up of space occupied by *B. schlosseri* colonies after they senesce could also influence community structure by releasing other incumbent species from competition or providing space for larval recruitment (e.g. Sams and Keough *In Press*). However, colonies of *B. schlosseri* did not occupy high amounts of space in this community and the senescence of colonies appears to have had little effect.

In other study systems the presence of *B. schlosseri* colonies does influence larval settlement patterns and the abundance of adults of other species (Grosberg 1981, Osman et al. 1992, Osman and Whitlatch 1995a). Such effects were not observed in these experiments, suggesting that *B. schlosseri* may have weak interactions with other species recruiting at Williamstown, or that recruitment patterns were too low to exert strong effects (but see below). Consequently different temporal recruitment patterns of this species may exert little effect on overall community structure at this site. *B. schlosseri* can be a competitive dominant in some systems, but have weak effects on settlement and recruitment in others (Bullard et al. 2004, Osman and Whitlatch 2004, Sams 2011). Variations in temporal recruitment patterns may have a stronger influence on community structure in where *B. schlosseri* is more dominant, or recruits in higher numbers, but the strength of its influence on other species may vary under different environmental conditions

While different temporal patterns of recruitment did not have a strong effect on overall community structure, they did influence the abundance of *Botryllus schlosseri* during the early

321 stages of community development with colonies occupying more space in treatments that
322 received a pulse of recruits than in those that had steady recruitment. Such increases in cover due
323 to pulse recruitment may have important consequences for *B. schlosseri* populations, despite
324 having little effects on communities. *B. schlosseri* is sexually mature after five to six asexual
325 cycles in Atlantic populations and seven asexual cycles (49 days) in Pacific populations
326 (Grosberg 1988, Chadwickfurman and Weissman 1995). In Experiment 1 the higher percent
327 cover of *B. schlosseri* found on pulse recruitment treatments was driven by six large colonies
328 occurring on three plates, five of which were large and old enough to be capable of reproduction,
329 based on the aforementioned studies. Pulse recruitment may therefore confer an advantage to *B.*
330 *schlosseri* populations compared to steady recruitment by increasing the chances that more
331 colonies will grow large enough to reach age of reproduction and release larvae and may also
332 increase fertilisation success.

333 The mechanism behind the higher survival and growth of colonies that arrived during pulse
334 recruitment is not entirely clear. During the first two weeks of recruitment manipulations, *B.*
335 *schlosseri* had higher densities in pulse recruitment treatments than steady recruitment, and a
336 greater number of individuals may have had a head start in growth in pulse treatments, compared
337 to individuals that arrived later under steady treatments. A higher number of individuals may
338 also have survived or avoided disturbance or predation in pulse treatments during this early
339 period, but we cannot say with certainty if such processes were important at this time. We did
340 not see strong evidence of predation or many predators active on plates when they were sampled,
341 and previous work at Williamstown has shown that predation occurs but can have little effect on
342 developing communities during early stages (Sams and Keough 2007). Workshops Jetty is

343 regularly exposed to high suspended sediments and flushing from nearby rivers and such
344 disturbances may be more common sources of mortality for species at this site.

345 The presence of *Botryllus schlosseri* recruits also had a positive effect on the abundance of
346 didemnids but this effect was not altered by different temporal recruitment patterns. The
347 mechanism behind this positive relationship is likely to be increased settlement or colony growth
348 of didemnids where *B. schlosseri* colonies are present. Didemnids may be able to use *B.*
349 *schlosseri* as a cue for settlement, but little is actually known about the settlement behaviour of
350 most didemnid larvae (but see Todd and Keough 1994) and Keough (1988) found no effect of
351 established botryllid colonies on 7-day recruitment of didemnids.

352 In contrast to Experiment 1, differences in temporal recruitment patterns of botryllids did had
353 complex effects on community structure in Experiment 2. Differences amongst treatments were
354 largely driven by the higher amount of space occupied by colonies of *Botrylloides leachii* on
355 steady recruitment treatments and no-didemnid treatments than on no botryllid and both
356 didemnid treatments. The higher cover of *B. leachii* colonies that occurred during steady
357 recruitment in Experiment 2 is likely to have been due to higher survival or growth of colonies,
358 which are most likely driven by different early densities between them and no-botryllid and
359 didemnid treatments. The fact that steady and pulse botryllid recruitment treatments did not
360 differ from each other suggests that the effects of different temporal recruitment patterns of this
361 species on communities are complex, and may be more obvious when compared to patches
362 where botryllids occur in lower abundances (e.g. no botryllid and didemnid recruitment
363 treatments).

364 While the effects of different temporal recruitment patterns on community structure were
365 complex, a strong pattern that did emerge from Experiment 2 was that the simple presence or
366 absence of both botryllid and didemnid recruits during the initial stages of community
367 development. Both botryllids and didemnids can occupy high amounts of space relative to most
368 other taxa and persisted in these abundances for at least the first three months of community
369 development after manipulations. They are likely to have influenced communities through
370 competition for space and effects on later arriving recruits. In this experiment, and more
371 generally at our study site, individual colonies of *Botrylloides leachii* appears to grow to larger
372 sizes than didemnids and can occupy more space. We have observed single colonies of
373 *Botrylloides leachii* large enough to cover a whole plate, while the largest didemnids we have
374 observed grow to approximately 5-6 cm in diameter. This may suggest that species level traits
375 such as colony size, competitive ability and/or levels of competition could be important for
376 determining whether different temporal recruitment patterns influence communities. Further
377 studies on the effects of temporal recruitment on a wide range of species with differing life
378 histories recruiting together under the same environmental conditions are required to confirm
379 this, however.

380 Although botryllid ascidians were manipulated in both experiments their effects on community
381 structure also differed. In Experiment 2 early recruits of *Botryllus schlosseri* and *Botrylloides*
382 *leachii* could not be told apart easily, but the majority of adult colonies found on plates were
383 individuals of *B. leachii* and they may have been the primary species present as recruits during
384 the manipulation period. Unlike individuals of *B. schlosseri*, which were manipulated in
385 Experiment 1 and only appear to persist in our study community for one to two months (e.g.
386 Sams 2011, Sams and Keough *In Press*), individuals of *B. leachii* persisted for much longer in

communities and occupied a much larger amount of space. Little information exists regarding the life history of *B. leachii*, particularly in comparison to *B. schlosseri*, but in communities at Williamstown, at least during these experiments, it appears to be longer lived and more competitively dominant than *B. schlosseri*, occupying more space and consequently more likely to influence community structure. However, because our experiments were run at different times it is difficult to tell whether these differences are caused by the intrinsic life-history of these particular species, or driven by environmental processes that differed between experiments.

In other systems, recruitment rates of botryllid and didemnid ascidians can be much higher than those observed at our study site (e.g., Hurlbut 1991, Osman and Whitlatch 1995b). Under higher recruitment rates the effects of pulse vs. steady recruitment may have greater potential to drive differences in communities, as space may become more limiting in a shorter time. In our study space was not limiting, and may explain why the effects of pulse vs. steady recruitment were not strong for *B. schlosseri* and didemnids. However, species did not recruit in a uniform spatial pattern in this experiment and competition for space between recruits that settled near each other was common (M. Sams. *pers obs*), and likely to be important even though space was not limiting. In another study site, we found that recruitment of *Botryllus schlosseri* over two weeks at much lower densities than those used in this experiment, and where space was similarly not limiting, had strong persistent effects on communities that lasted for at least six months (Sams and Keough *In Press*). In the same study we found that *B. schlosseri* had short term effects on communities at Williamstown at similar densities used in this study. This coupled with the findings that *B. leachii* had different effects on communities as a result temporal recruitment patters, suggests that even at the densities of recruitment used in this study, and without limiting

space, pulse and steady recruitment of particular species may influence community composition differently.

Variation in temporal recruitment patterns has only been shown to influence communities in a small number of studies (Yoshioka 1996, Graham et al. 1997). These studies have either only examined communities with relatively low diversity or only examined populations (from which community effects can be inferred), and did not explicitly separate the effects of total density from effects of different distribution of recruit arrival associated with different temporal recruitment patterns. This study demonstrates that variation in the distribution of recruiting individuals over time associated with ‘pulse’ or ‘steady’ recruitment patterns can influence the dynamics of diverse communities and populations of sessile animals, but that these effects vary in strength between species and times and can be complex. The findings of this study may also have broader implications for a range of other systems that rely on recruitment via dispersive propagules, particularly where recruiting species have stronger interactions with other species or much higher recruitment rates than those in this study. In many systems pulses and steady recruitment can occur at different times of the season, during different stages of community development and multiple pulses may occur in a series rather than just a single pulse. The timing and number of pulses and steady recruitment events is likely to be important for community dynamics, though dependent on species and environment. These kinds of temporal recruitment patterns are also likely to be highly variable in many plant, algal and animal communities and may have a similarly complex influence on their dynamics.

Acknowledgments

We thank Paul Carnell for his assistance with field work. We also thank Richard Osman and John Witman for helpful comments on the PhD thesis chapter that generated this manuscript.

This research was supported by grants from the Australian Research Council awarded to Michael J Keough and a Holsworth Wildlife Research Endowment awarded to Michael Sams.

References

Anderson, M. J., Gorley R.N. and Clarke KR, editor. 2008. Permanova+ for Primer: Guide to software and statistical methods. PRIMER-E, Plymouth UK.

Bingham, B. L. 1992. Life histories in an epifaunal community - coupling of adult and larval processes. *Ecology* **73**:2244-2259.

Bullard, S. G., R. B. Whitlatch, and R. W. Osman. 2004. Checking the landing zone: Do invertebrate larvae avoid settling near superior spatial competitors? *Marine Ecology-Progress Series* **280**:239-247.

Caley, M. J., M. H. Carr, M. A. Hixon, T. P. Hughes, G. P. Jones, and B. A. Menge. 1996. Recruitment and the local dynamics of open marine populations. *Annual Review of Ecology and Systematics* **27**:477-500.

Chadwickfurman, N. E. and I. L. Weissman. 1995. Life-histories and senescence of *Botryllus-schlosseri* (Chordata, Ascidiacea) in Monterey Bay. *Biological Bulletin* **189**:36-41.

Connell, J. H. and P. T. Green. 2000. Seedling dynamics over thirty-two years in a tropical rain forest tree. *Ecology* **81**:568-584.

Forde, S. E. and P. T. Raimondi. 2004. An experimental test of the effects of variation in recruitment intensity on intertidal community composition. *Journal of Experimental Marine Biology and Ecology* **301**:1-14.

Fukami, T., T. M. Bezemer, S. R. Mortimer, and W. H. van der Putten. 2005. Species divergence and trait convergence in experimental plant community assembly. *Ecology Letters* **8**:1283-1290.

455 Graham, M. H., C. Harrold, S. Lisin, K. Light, J. M. Watanabe, and M. S. Foster. 1997.
 456 Population dynamics of giant kelp *Macrocystis pyrifera* along a wave exposure gradient.
 457 Marine Ecology-Progress Series **148**:269-279.

458 Grosberg, R. K. 1981. Competitive ability influences habitat choice in marine-invertebrates.
 459 Nature **290**:700-702.

460 Grosberg, R. K. 1988. Life-history variation within a population of the colonial ascidian
 461 *Botryllus-schlosseri* .1. The genetic and environmental-control of seasonal-variation.
 462 Evolution **42**:900-920.

463 Holloway, M. G. and M. J. Keough. 2002. An introduced polychaete affects recruitment and
 464 larval abundance of sessile invertebrates. Ecological Applications **12**:1803-1823.

465 Hurlbut, C. J. 1991. The effects of larval abundance, settlement and juvenile mortality on the
 466 depth distribution of a colonial ascidian. Journal of Experimental Marine Biology and
 467 Ecology **150**:183-202.

468 Johnston, E. L. and M. J. Keough. 2000. Field assessment of effects of timing and frequency of
 469 copper pulses on settlement of sessile marine invertebrates. Marine Biology **137**:1017-
 470 1029.

471 Keough, M. J. and P. T. Raimondi. 1995. Responses of settling invertebrate larvae to bioorganic
 472 films - effects of different types of films. Journal of Experimental Marine Biology and
 473 Ecology **185**:235-253.

474 Kohler, K. E. and S. M. Gill. 2006. Coral Point Count with Excel extensions (CPCe): A Visual
 475 Basic program for the determination of coral and substrate coverage using random point
 476 count methodology. Computers & Geosciences **32**:1259-1269.

477 Myers, J. A. and K. E. Harms. 2009. Seed arrival, ecological filters, and plant species richness: a
 478 meta-analysis. *Ecology Letters* **12**:1250-1260.

479 Osman, R. W. and R. B. Whitlatch. 1995a. The influence of resident adults on larval settlement -
 480 experiments with 4 species of ascidians. *Journal of Experimental Marine Biology and*
 481 *Ecology* **190**:199-220.

482 Osman, R. W. and R. B. Whitlatch. 1995b. The influence of resident adults on recruitment - a
 483 comparison to settlement. *Journal of Experimental Marine Biology and Ecology* **190**:169-
 484 198.

485 Osman, R. W. and R. B. Whitlatch. 2004. The control of the development of a marine benthic
 486 community by predation on recruits. *Journal of Experimental Marine Biology and*
 487 *Ecology* **311**:117-145.

488 Osman, R. W., R. B. Whitlatch, and R. J. Malatesta. 1992. Potential role of micropredators in
 489 determining recruitment into a marine community. *Marine Ecology-Progress Series*
 490 **83**:35-43.

491 Paine, C. E. T. and K. E. Harms. 2009. Quantifying the effects of seed arrival and environmental
 492 conditions on tropical seedling community structure. *Oecologia* **160**:139-150.

493 Pineda, J., V. Starczak, and T. A. Stueckle. 2006. Timing of successful settlement: demonstration
 494 of a recruitment window in the barnacle *Semibalanus balanoides*. *Marine Ecology-*
 495 *Progress Series* **320**:233-237.

496 Reed, D. C. 1990. The effects of variable settlement and early competition on patterns of kelp
 497 recruitment. *Ecology* **71**:776-787.

498 Sams, M. A. 2011. Effects of variable recruitment on the structure and development of marine
 499 sessile communities. PhD. University of Melbourne, Melbourne.

500 Sams, M. A. and M. J. Keough. 2007. Predation during early post-settlement varies in
 501 importance for shaping marine sessile communities. *Marine Ecology-Progress Series*
 502 **348**:85-101.

503 Sams, M. A. and M. J. Keough. *In Press*. Contrasting effects of variable recruitment on marine
 504 sessile communities. *Ecology*.

505 Schupp, E. W. 1990. Annual variation in seedfall, postdispersal predation, and recruitment of a
 506 neotropical tree. *Ecology* **71**:504-515.

507 Todd, C. D. and M. J. Keough. 1994. Larval settlement in hard substratum epifaunal
 508 assemblages - a manipulative field-study of the effects of substratum filming and the
 509 presence of incumbents. *Journal of Experimental Marine Biology and Ecology* **181**:159-
 510 187.

511 Turnbull, L. A., M. Rees, and M. J. Crawley. 1999. Seed mass and the competition/colonization
 512 trade-off: a sowing experiment. *Journal of Ecology* **87**:899-912.

513 Underwood, A. J. and M. J. Keough. 2001. Supply-side ecology: the nature and consequences of
 514 variations in recruitment of intertidal organisms. *in* M. D. G. Bertness, S.D.; Hay, M.E.,
 515 editor. *Marine Community Ecology*. Sinauer Associates, Sunderland, MA.

516 Wiegand, K., F. Jeltsch, and D. Ward. 2004. Minimum recruitment frequency in plants with
 517 episodic recruitment. *Oecologia* **141**:363-372.

518 Witman, J. D., S. J. Genovese, J. F. Bruno, J. W. McLaughlin, and B. I. Pavlin. 2003. Massive
 519 prey recruitment and the control of rocky subtidal communities on large spatial scales.
 520 *Ecological Monographs* **73**:441-462.

521 Wright, J. T. and P. D. Steinberg. 2001. Effect of variable recruitment and post-recruitment
 522 herbivory on local abundance of a marine alga. *Ecology* **82**:2200-2215.

523 Yoshioka, P. M. 1996. Variable recruitment and its effects on the population and community
524 structure of shallow-water gorgonians. Bulletin of Marine Science **59**:433-443.
525
526

Table 1. Results of partly-nested ANOVA comparing the most abundant taxa and partly-nested PERMANOVA comparing all taxa found on settlement plates exposed to pulse recruitment of *B. schlosseri*, steady recruitment of *B. schlosseri* or no recruitment of *B. schlosseri* for a 5 week period and sampled one month, two months, three months and six months after manipulations. Numbers underneath main factor headings are p-values, while values under MS (btwn) are the mean square error values between subjects (plates) and values under MS (within) are the mean square error values within subjects (plates) for each analysis. Where there were significant differences in the cover of taxa or the overall structure of communities between treatments results of pairwise post-hoc comparisons (Tukey's HSD) are shown below. Letters denote treatments types in each pairwise comparison and where there was an interaction with time semicolons separate each time plates were sampled in order from left to right (see key).

	Recruitment	Time	RXT	MS(btwn)	MS(wthn)
df	2	3	6	20	60
<i>Botryllus schlosseri</i>	0.000	0.001	0.010	1.427	1.638
Didemnids ascidians	0.039	0.002	0.082	21.821	7.264
<i>Diplosoma listerianum</i>	0.973	0.031	0.253	35.769	14.752
<i>Bugula dentata</i>	0.208	0.000	0.904	106.189	91.438
<i>Bugula stolonifera</i>	0.996	0.002	0.417	26.247	14.345
<i>Watersipora subtorquata</i>	0.529	0.000	0.621	87.185	44.203
<i>Cyanea cappilata</i>	0.442	0.000	0.342	40.845	19.881
<i>Sycon</i> sp.	0.381	0.175	0.096	3.312	2.054
Yellow sponge	0.979	0.000	0.937	5.359	2.585
Amphipod tubes	0.096	0.000	0.446	80.196	40.697
PERMANOVA	0.665	0.000	0.5386	574.8	601.27
<i>pairwise comparisons*</i>					
<i>Botryllus schlosseri</i>	BH>BS BH>NB BS=NB; BH=BS=NB; BH=BS=NB; BH=BS=NB				
Didemnid ascidians	BH>NB BH=BS BS=NB				

*BH=*B. schlosseri* pulse, BS = *B. schlosseri* steady, NB= No *B. schlosseri*

Table 2. Results of partly-nested ANOVA for the most abundant taxa found on settlement plates exposed to pulse recruitment of botryllids, steady recruitment of botryllids, no recruitment of botryllids, pulse recruitment of didemnids, steady recruitment of didemnids or no recruitment of didemnids for a 6 week period and sampled one month, two months, three months and six months after manipulations. Numbers underneath main factor headings are p-values, while values under MS (btwn) are the mean square error values between subjects (plates) and values under MS (within) are the mean square error values within subjects (plates) for each analysis. Where there were significant differences in the cover of taxa or the overall structure of communities between treatments results of pairwise post-hoc comparisons (Tukey's HSD) are shown below. Letters denote treatments types in each pairwise comparison and where there was an interaction with time semicolons separate each time period plates were sampled in order from left to right (see key).

	Species	Recruitment	Time	SXR	SXT	RXT	SXRXT	MS(btwn)	MS(wthn)
df	<i>1</i>	<i>2</i>	<i>3</i>	<i>2</i>	<i>3</i>	<i>3</i>	<i>6</i>	<i>41</i>	<i>123</i>
<i>Botrylloides leachii</i>	0.887	0.640	0.000	0.018	0.968	0.593	0.006	796.479	124.589
<i>Botryllus schlosseri</i>	0.560	0.756	0.001	0.384	0.738	0.920	0.171	6.144	5.511
Didemnid ascidians	0.558	0.055	0.000	0.395	0.604	0.296	0.195	51.154	11.242
<i>Diplosoma listerianum</i>	0.936	0.804	0.000	0.586	0.356	0.680	0.615	351.041	27.893
<i>Styela clava</i>	0.606	0.265	0.000	0.282	0.975	0.199	0.328	6.382	3.362
<i>Bugula stolonifera</i>	0.590	0.994	0.000	0.981	0.922	0.882	0.999	13.545	8.115
<i>Watersipora subtorquata</i>	0.494	0.146	0.000	0.059	0.462	0.257	0.739	214.249	131.204
<i>Amphibalanus variegatus</i>	0.893	0.744	0.000	0.404	0.929	0.452	0.276	14.278	2.779
<i>Cyanea capillata</i>	0.949	0.851	0.000	0.667	0.940	0.520	0.358	13.185	7.104
<i>Sycon</i> sp.	0.535	0.608	0.000	0.194	0.963	0.966	0.191	4.125	2.790
PERMANOVA	0.98	0.98	0.000	0.04	0.76	0.42	0.12	3058	696.7
pairwise comparisons									
<i>Botrylloides leachii</i>	BS>NB DS>ND DH>ND NB<ND BS=ND BH=NB=DH=DS								
PERMANOVA	BS≠NB BS≠DS BS≠DH BS=ND BS=BH BH=NB BH=ND BH=DH BH=DS DH≠ND								
	DH=DS DH=NB DS≠ND DS=NB ND≠ND								

*BH=Botryllids pulse, BS = Botryllids steady, NB= No Botryllids, DH= Didemnid pulse, DS=Didemnid Steady, ND = No didemnid

List of Figures

Figure 1. Principal co-ordinates ordination (PCO) of distances among centroids on the basis of the Bray-Curtis measures of percent cover of taxa colonising settlement plates from Experiment a) 1 and b) 2 at Williamstown, Australia in 2008-2009. In Experiment 1 communities were exposed to either a single episodic pulse of *Botryllus schlosseri* recruits, steady recruitment of *B. schlosseri*, or no recruitment of *B. schlosseri* over a 5 week period. In Experiment 2 communities were exposed to either a single episodic pulse of botryllid ascidian recruits, steady recruitment of botryllid ascidians, no recruitment of botryllid ascidians, a single episodic pulse of didemnid ascidian recruits, steady recruitment of didemnid ascidians, or no recruitment of didemnid ascidians. Both experiments were sampled at one, two, three and six months after manipulations . Centroids represent average distances between recruitment treatments at each time sampled within each experiment. For details of differences between treatments see pairwise comparisons for PERMANOVA in Table 1

Figure 2. Experiment 1: Percent cover of the colonial ascidians a) *Botryllus schlosseri* and b) didemnid ascidians, as well as two representative main space occupying taxa, c) the bryozoan *Bugula dentata* and d) amphipod tubes and e) free space on settlement plates exposed to either an episodic pulse of *B. schlosseri* recruits, steady recruitment of *B. schlosseri* or no recruitment of *B. schlosseri* sampled at one, two, three and six months after experimental manipulations. Asterisks denote times when there were differences in cover between treatments according to partly-nested ANOVA (see pair-wise comparisons on Table 1 for details). 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

Figure 3. Experiment 2: Percent cover of the main space occupying colonial ascidians a) *Botryllus schlosseri*, b) didemnid ascidians and c) *Botrylloides leachii* as well as a

577 representative major space occupier, d) the encrusting bryozoan *Watersipora subtorquata* and
578 e) free space on settlement plates exposed to either an episodic pulse of botryllid ascidian
579 recruits, steady recruitment of botryllid ascidians, no recruitment of botryllid ascidians, a
580 high pulse of didemnid ascidians, steady recruitment of didemnid ascidians or no recruitment
581 of didemnid ascidians and sampled at one, two, three and six months after experimental
582 manipulations. Asterisks denote times when there were differences in cover between
583 treatments according to partly-nested ANOVA (see pairwise comparisons on Table 2 for
584 details). We have not shown error bars around mean values as they do not represent error
585 terms used to compare groups within factors of interest in partly-nested ANOVAs

Figure 1

Figure 2

Figure 3

Minerva Access is the Institutional Repository of The University of Melbourne

Author/s:

Sams, MA;Keough, MJ

Title:

Effects of pulse versus steady recruitment on sessile marine communities

Date:

2012-09-01

Citation:

Sams, M. A. & Keough, M. J. (2012). Effects of pulse versus steady recruitment on sessile marine communities. *OECOLOGIA*, 170 (1), pp.209-219. <https://doi.org/10.1007/s00442-012-2284-1>.

Persistent Link:

<http://hdl.handle.net/11343/283105>