

Predator effects on fouling community development

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ABSTRACT: Predation by small consumers has a demonstrable effect on the recruitment and development of sessile invertebrate (fouling) communities. However, few data are available to assess the degree to which different micropredators are functionally equivalent, and whether initial effects on recruitment translate into lasting effects on adult communities. In the present study, we used field surveys and manipulative experiments to examine the effect of 2 molluscan predators on both the recruitment of sessile invertebrates and the ultimate community development under continuous predation pressure for 12 mo. The mossy chiton *Mopalia muscosa* dramatically reduced recruits of some species and increased those of others, but ultimately total adult cover of all species was reduced by over half relative to predator-free controls. The file limpet *Lottia limatula* had minimal effects on recruitment, slightly reducing recruitment of some colonial ascidians. However, limpets had no effect on the total cover of invertebrates, instead altering species composition by slightly delaying overall successional trajectories. Field surveys suggested that both predators have measurable effects on community cover, as the abundance of each predator was positively correlated with an increase in free space. Plots with both chitons and limpets had nearly 4 times the open space of no-predator plots, and 2 times the open space of plots with limpets only. Therefore, both field surveys and experimental manipulations highlight the substantial impact of micropredators in determining the composition of this fouling community.

KEY WORDS: Predation · Fouling community · Succession · Recruitment

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INTRODUCTION

Fouling communities are composed primarily of sessile filter-feeding invertebrates and mobile epifauna such as ascidians, bryozoans, hydroids, sponges, barnacles, and other crustaceans that live on docks, pilings, and natural rock substrates worldwide. These communities often support numerous non-native species, and, given their proximity to commercial shipping ports, they are likely establishment sites for new invaders before they spread to the open coast. Thus, the factors that regulate community composition and resource availability in these systems are critical for understanding the invasion process. A broad range of biotic (competition, predation, larval supply) and abiotic (ocean proximity, hydrodynamics, temperature,

salinity) factors have been suggested to contribute to the development of particular fouling communities. For example, numerous studies have debated the importance of predation on early post-settlement larval survival (Stoner 1990, Osman et al. 1992, Osman & Whitlatch 1995), on early community development (Connell 2001), and on the adult community (Sutherland 1974, Karlson 1978, Keough & Butler 1979, Vance 1988).

Predators, especially large mobile fish, crabs, and sea urchins can shift community composition from early fast-growing, competitively superior species to slower growing, but predator-resistant groups (Sutherland 1974, Karlson 1978, Stoner 1990). Other studies have found that even when predation by mobile predators appears high, this has a minimal effect on

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species composition (e.g. Keough & Butler 1979, Vance 1988, Connell 2001), either because predators are non-selective or because other processes dominate.

While large predators can impact fouling assemblages, these communities also often host a diverse array of smaller predators, including small crabs and snails that may consume early post-settlement life-history stages of fouling invertebrates. In New England, small gastropods (micropredators) can dramatically alter the magnitude of recruitment and alter species composition from ascidians to bryozoans by selectively consuming juvenile ascidians (Osman & Whitlatch 1995). When multiple species of snails are present, they can reduce total cover and increase bare space availability, whereas individual species may simply alter species composition or even have no effect (Stachowicz & Whitlatch 2005). However, these studies generally lasted only a few weeks to several months, and it is not clear whether these effects on early life-history stages cause persistent changes in adult community composition. Given the variation in the outcome of exclusion experiments with large mobile predators, it is clear that intense consumption need not lead to long-term effects on community composition (e.g. Connell 2001). While separate studies have addressed the effects of micro-predation on recruits and the adult community, few studies have explicitly examined the link between initial predation on recruits and the subsequent composition of the adult community.

In the present study we addressed the impacts of 2 abundant predatory mollusks on both the immediate post-settlement survival of fouling recruits and the development of the fouling community of Bodega Bay, California, under sustained predation pressure for 12 mo. Specifically we asked: (1) How is the density of potential predators related to the availability of unoccupied space in the field? (2) What are the short-term effects of these predators on settlement and early post-settlement survival? (3) What are the consequences of chronic, continuous predation in the context of seasonal variation in the abundance and composition of larval settlement for fouling community development? (4) How do intra- and inter-annual variation in the recruitment patterns of fouling organisms affect the strength of predation pressure on fouling community development?

MATERIALS AND METHODS

Study location. We chose to conduct this experiment at Spud Point Marina, Bodega Harbor, California (38° N, 123° W). This site supports a diverse community of sessile filter-feeding species, characteristic of protected harbors in northern California. We focused on

the dominant species, which include several colonial ascidians (*Botrylloides diegensis*, *Botrylloides violaceus*, *Botryllus schlosseri*, *Didemnum* sp., *Diplosoma listerianum*, *Distaplia occidentalis*), solitary ascidians (*Ascidia ceratodes*, *Ciona intestinalis*), encrusting bryozoans (*Schizoporella unicornis*, *Watersipora subtorquata*), and arborescent bryozoans (*Bugula californica*, *Bugula neritina*). In addition, the community contains several bivalves (*Hinnites giganteus*, *Mytilus galloprovincialis*), cnidarians (*Metridium senile*, *Obelia longissima*), polychaete worms (*Eudistylia polymorpha*, *Myxicola infundibulum*), and a sponge (*Haliclona permolis*). Numerous mobile predators and grazers also live on these docks, including crustaceans (*Pachygrapsus crassipes*, *Pugettia producta*), mollusks (*Lottia limatula*, *Mopalia muscosa*), and a scale worm (*Halosydna brevisetosa*).

Field survey. We assessed the potential for predators to affect fouling community biomass through a survey in which we recorded the percent of open (unoccupied) space, as well as the number and species identity of predators in 350 quadrats of 25 × 25 cm. Quadrats were randomly located among the 5 main docks of the marina, with 'dock' retained as a blocking factor in the analysis. Chitons *Mopalia muscosa* and limpets *Lottia limatula* were the most abundant potential predators of sessile invertebrates in these surveys; thus, we focus on these species in the rest of the paper. Both have been observed to either consume sessile invertebrates or, at least, bulldoze juveniles off the surface while grazing on algae (Morris et al. 1980).

Recruitment and community development. We assessed community development on 100 cm² (10 × 10 cm) PVC plates, with surfaces sanded to simulate the rough surface of a fouling dock and to promote settlement. Preliminary experiments found no differences in settlement rates among several different substrate types (R. C. Coates unpubl. data). Plates were suspended from the dock in blocks and randomly assigned to one of the following treatments: 1 *Mopalia muscosa* (the mossy chiton), 1 large (1.27 to 3.3 cm) *Lottia limatula* (the file limpet), 2 small (<1.269 cm) *L. limatula*, or no predator on each plate. We separately assessed the effects of small and large limpets because they had a bimodal size distribution (M. Nydam & J. Stachowicz pers. obs) suggesting the presence of 2 distinct groups. We enclosed either 1 large or 2 small limpets into each treatment to equalize the area of the plate covered by the predator's shell among all 3-predator inclusion treatments. The area covered by 1 large or 2 small limpets was roughly equivalent to that covered by a single chiton.

We then completely enclosed each plate in a 10 × 10 × 10 cm cage made from 1 × 1 cm Vexar mesh and attached both the cage and the plate to a PVC pipe

suspended off the dock. These mesh cages enclosed chitons and limpets and excluded crab and fish, while allowing larvae to settle on the plates. Cages were scrubbed frequently to remove animals growing directly on the cage that might have impeded water flow or invertebrate settlement. We also included 8 plates without cages to test for the combined effects of mobile predators like fishes and large crabs and the cage itself. Sixteen racks of 4 plates each (chiton treatment, small limpet treatment, large limpet treatment, no predator treatment) were deployed 0.5 m below the water surface, with the sanded surfaces of the plates facing downward. We placed the racks at 3 m intervals along a dock at Spud Point Marina on 17 June 2003. Plates were checked several times a week for the first 3.5 mo and biweekly for the remainder of the experiment to ensure that treatments remained intact. We replaced any dead predators with new predators of a similar size. All plates were photographed monthly thereafter with a digital camera. We determined percent cover of each species in the digital photograph by measuring the area of the plate covered by each species with an image analysis program (NIH Image J). As we quantified each visible layer of fouling cover, the total percent cover was occasionally >100% due to multiple layers. The experiment was concluded 1 yr after deployment.

Eight days after deployment of the racks, we counted the recruits and identified each to species level using a dissecting microscope. We used a combination of guidebooks from other regions and spawning experiments with local adults to identify the juvenile organisms (M. Nydam & J. Stachowicz unpubl. data, photos of all settlers and adults available at <http://convoluta.ucdavis.edu/gallery>). We then redeployed plates in the field. We performed an identical experiment in August 2002, although these plates were not redeployed after the recruits were counted and identified.

During the time the experiment was deployed (and for the previous year), recruitment onto separate but identical PVC plates was recorded every 2 wk to assess background levels of recruitment throughout the duration of the experiment. We collected the plates every 2 wk, counted and identified the recruits, and cleaned and redeployed the plates. All statistical analyses were conducted using SAS 9.1 (SAS Institute).

RESULTS

Field survey

Chiton *Mopalia muscosa* density ranged from 0 to 2 ind. per 625 cm² (mean = 0.156) and limpets *Lottia limatula* ranged from 0 to 21 ind. per 625 cm²

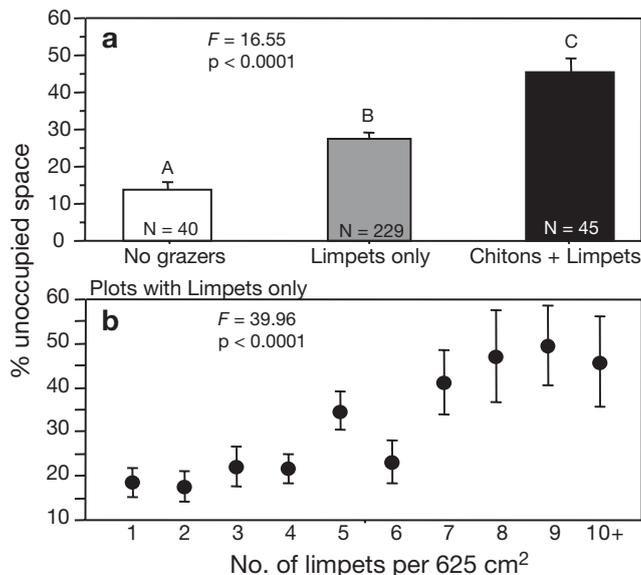


Fig. 1. *Mopalia muscosa* and *Lottia limatula*. (a) Percentage (+SE) of unoccupied space in plots with no grazers, with limpets only, and with chitons and limpets. (b) Percentage (\pm SE) of unoccupied space as a function of the number of limpets. Bars with different letters in (a) are significantly different from one another

(mean = 3.943). Thus, our limpet experimental treatments were within the range of observed natural density. While our chiton experimental treatments were higher than observed natural density, effects of chitons on the docks were localized due to their limited mobility (M. Nydam & J. Stachowicz pers. obs.). Therefore, chitons in our experimental treatments were expected to have similar effects to chitons on the docks in the areas where they occur. Nearly all plots with chitons also had limpets, so we could not rigorously separate the effects of individual species from our survey. However, grazer type and abundance clearly influenced the amount of unoccupied space (ANOVA $F = 16.55$, $p < 0.0001$). Plots with chitons and limpets had almost double the bare space of those with only limpets (Fig. 1a; ANOVA with Tukey HSD [honestly significant differences], $p < 0.05$), even though they did not differ in limpet density (t -test, $p = 0.19$), suggesting a strong effect of chitons. However, cover of open space in plots with limpets, but no chitons, was nearly double that of plots with no grazers (Fig. 1a; $p < 0.05$, Tukey HSD), suggesting limpets still may have an effect on total invertebrate cover, at least when chitons are absent. Among plots with at least 1 limpet but no chitons, there was significant positive linear correlation between limpet density and the percentage of unoccupied space (F value = 39.96, $df = 336$, $p < 0.0001$, multiple linear regression with percentage of unoccupied space logit-transformed). In fact, among plots with 7 or more

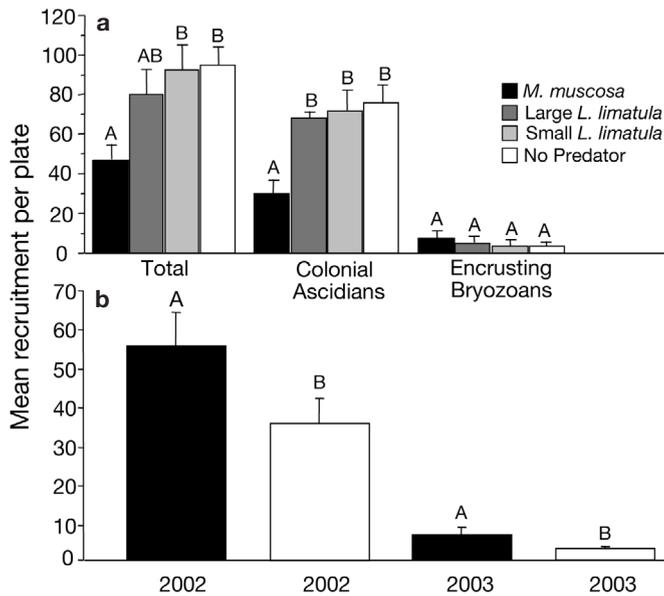


Fig. 2. *Mopalia muscosa* and *Lottia limatula*. (a) Recruitment of fouling organisms (+SE) after 8 d by morphological fouling group, averaged over all experimental plates in each treatment. Bars with different letters are significantly different from one another (ANOVA Tukey HSD test, $p < 0.05$). (b) Mean recruitment of the dominant encrusting bryozoan *Watersipora subtorquata* on *M. muscosa* and no-predator plates in the 2002 and 2003 predation experiments. Shading key applies to both (a) and (b)

limpets, about 50% of the plots consisted of bare space—a similar percentage to that in plots with chitons (compare Fig. 1b and the right column of Fig. 1a).

Effects of predators on recruitment

Chitons *Mopalia muscosa* exerted the largest effect of any of the predator treatments on the fouling recruits after 8 d. The no-predator plates contained twice the total recruitment present on chiton plates. Colonial ascidian recruitment, comprising ~79% of the total recruitment, was 2.5 times greater on no-predator plates than on *M. muscosa* plates (Fig. 2a; $p < 0.05$, ANOVA Tukey HSD test). Chitons did not appear to distinguish strongly among colonial ascidian species. *Botrylloides violaceus* decreased by 43%, *Distaplia occidentalis* decreased by 48%, and *Diplosoma listerianum* by 65% (differences were not significantly different from one another; $p > 0.05$, ANOVA Tukey HSD test). Solitary ascidian and arborescent bryozoan recruitment after 8 d was insufficient for analysis, so we were unable to conclude anything about predator effects on early post-settlement mortality of these species (but see the subsection 'Longer-term effects of predators on community development' below).

Encrusting bryozoans (mainly *Watersipora subtorquata*) were more abundant on chiton plates than on any of the other treatments after 8 d, although not significantly (Fig. 2a). A previous experiment in August 2002 did find significantly higher *W. subtorquata* recruitment on *Mopalia muscosa* plates (Fig. 2b; $p < 0.048$, t -test). Recruitment of *W. subtorquata* was twice as high in August to November 2002 as in August to November 2003 (Fig. 2b). Thus, the lack of a significant result in 2003 could be due to a relatively lower power caused by reduced larval supply.

Diplosoma listerianum abundance was marginally lower in both limpet plates relative to those without predators (–29%), although this difference was not statistically significant ($p > 0.05$, ANOVA Tukey HSD). No other group's recruitment was even marginally affected by limpets.

Longer-term effects of predators on community development

All treatments increased in the percent cover of organisms throughout the experiment, but treatments rapidly diverged in both total cover and species composition within just a few months (Time \times Treatment interaction, $F = 1.46$, $df = 587$, $p = 0.0484$, repeated measures auto-regressive ANOVA). The invertebrate community on plates with chitons differed quantitatively from all other treatments after just 2 mo, with consistently lower percent cover (20 to 40% for chitons versus 70 to 105% for all others; Fig. 3). Specifically, the total cover of invertebrates in chiton communities differed significantly from no-predator treatments in Months 2 to 7, 9, and 10, from large limpet treatments in Months 3 to 10, and from small limpet treatments in Months 2 to 7, and 10 ($p < 0.05$, repeated measures

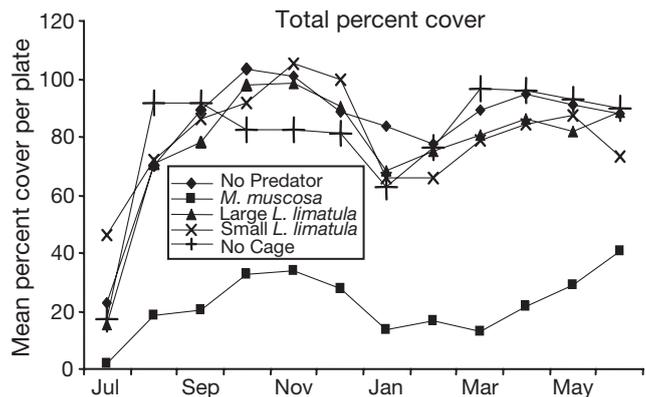


Fig. 3. *Mopalia muscosa* and *Lottia limatula*. Total percent cover by treatment, averaged over all experimental plates within a treatment

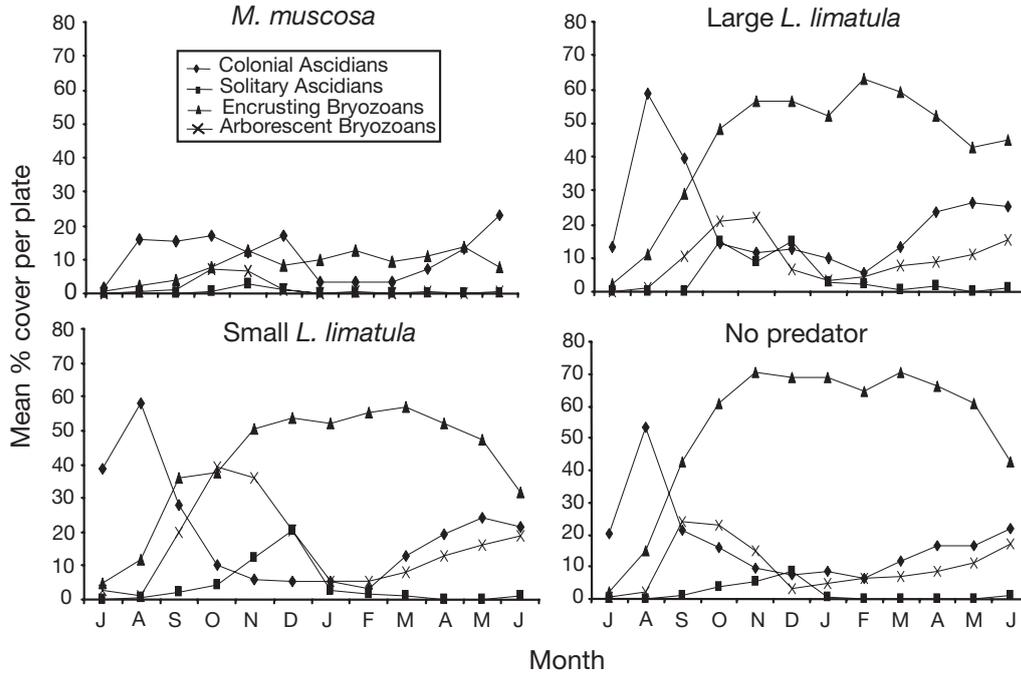


Fig. 4. *Mopalia muscosa* and *Lottia limatula*. Percent cover by morphological fouling group, averaged over all experimental plates within a treatment

auto-regressive ANOVA with Bonferroni correction for multiple testing and percent cover logit-transformed). Limpet treatments differed from the no-predator treatments mainly in the species composition, rather than the total cover. For ease of interpretation, we present effects of predators on species composition by first describing the pattern of community development on no-predator plates. We then use this as a reference state with which to compare each predator treatment. We present results with sessile invertebrates split into 4 main morphological groups (colonial and solitary ascidians, encrusting and arborescent bryozoans) for ease of comparison (Fig. 4). No-predator treatments were initially dominated by colonial ascidians (*Diplosoma listerianum*, *Botryllus schlosseri*, *Botrylloides diegensis*, and *Botrylloides violaceus*; maximum total cover 53%), but these were replaced by arborescent bryozoans and then encrusting bryozoans; solitary ascidians were mostly absent from these communities. The colonial ascidian cover only increased again in the spring, as the encrusting and arborescent bryozoan cover declined (Fig. 4), despite the fact that recruitment of colonial ascidians to independently deployed bare plates was present throughout fall (Fig. 5). Solitary ascidians (primarily *Ascidia ceratodes*) recruited during the late fall (Fig. 5), but never reached >10% cover on no-predator plates throughout the early winter (Fig. 4). When present, the percent cover of *A. ceratodes* declined dramatically after 6 mo, coincident with winter rains. Communities on the panels without cages developed similarly to the no-predator plates

(Fig. 3); thus, it seems likely that cage artifacts and effects of mobile predators are inconsequential in our study system, although it is possible that they perfectly counteract each other.

Chitons *Mopalia muscosa*

Maximum total sessile invertebrate cover reached only 41% on chiton plates, compared with 103% cover on no-predator plates (Fig. 3). Reductions in cover occurred for all groups. The slight increase in colonial ascidian cover on chiton plates at the end of the experiment was due to a few replicates in which the chiton died and was not replaced immediately, leading to a short-term increase. Colonial ascidians were 50 to 70% lower than no-predator plates, and were significantly different from no-predator plates after 2, 3, 8, 10, and 11 mo ($p < 0.0012$, $p < 0.0012$, $p = 0.0132$, $p = 0.0168$ and $p = 0.01312$, respectively, repeated measures auto-regressive ANOVA with Bonferroni correction for multiple testing and percent colonial ascidian cover logit-transformed). Solitary ascidians were very rare on *M. muscosa* plates (3% cover, no different from no-predator controls; analysis as for colonial ascidians, above). Encrusting bryozoan percent cover was significantly lower in every month on *M. muscosa* plates than on no-predator plates (Fig. 4; $p < 0.0012$, analysis as for colonial ascidians, above), this despite the fact that initial recruitment of encrusting bryozoans was highest in this treatment (Fig. 2a,b). Arborescent bryozoan cover on the *M. muscosa* plates was as much as 3

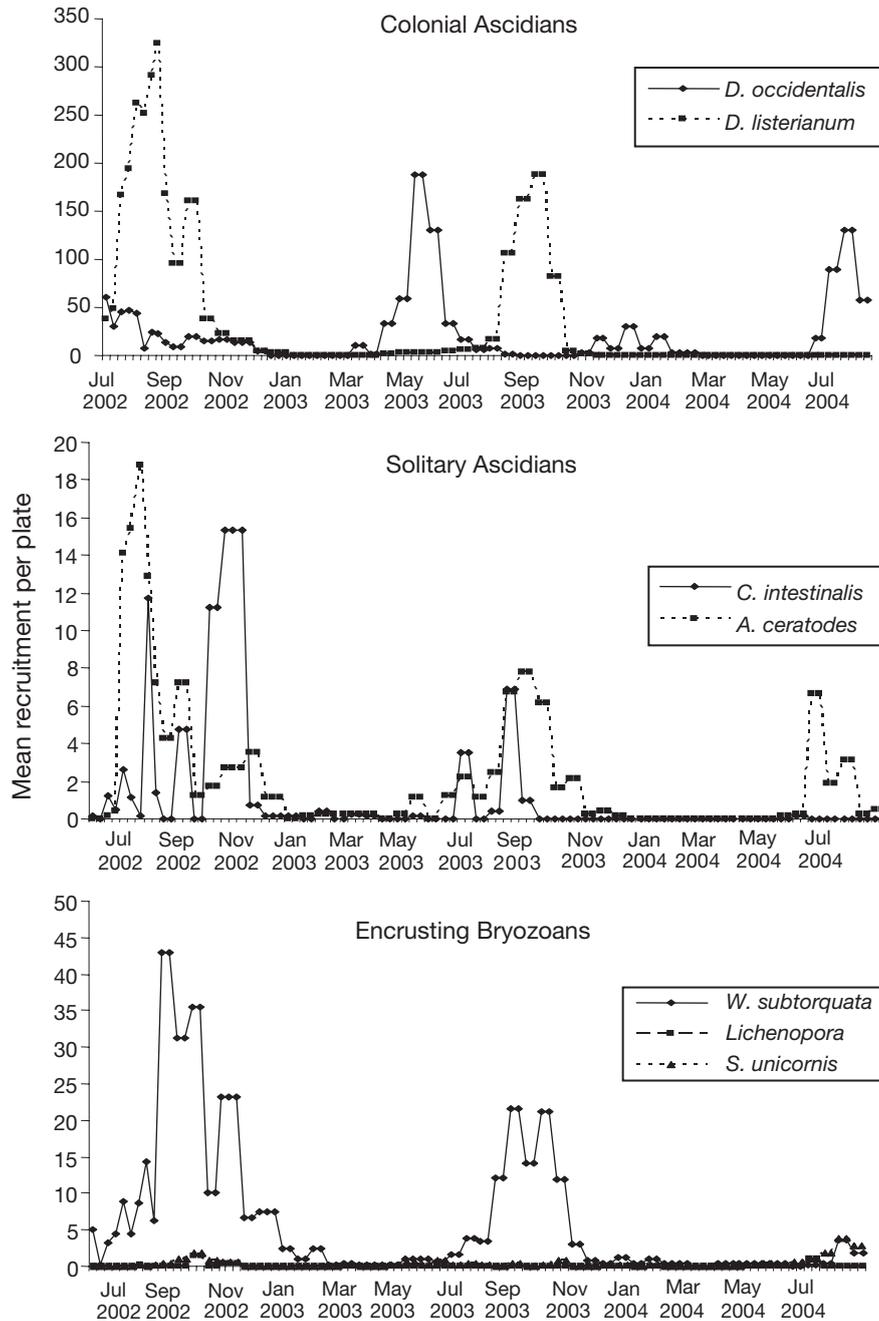


Fig. 5. Mean recruitment by morphological fouling group (colonial ascidians—*Diplosoma occidentalis*, *D. listerianum*; solitary ascidians—*Ciona intestinalis*, *Ascidia ceratodes*; encrusting bryozoans—*Watersipora subtorquata*, *Lichenopora*, *Schizoporella unicornis*) over a 2 yr period, averaged over 4 plates

times lower than on the no-predator plates (Fig. 4; $p < 0.05$ for Months 2, 3, 4, and 12).

Limpets *Lottia limatula*

A single large limpet (>1.27 cm shell width) exerted weaker effects than 1 chiton, but marginally stronger

effects than 2 small limpets. Total sessile invertebrate percent cover on large limpet plates remained similar to that of small limpet and no-predator treatments throughout the experiment (Fig. 3), although the progression of the community through the successional stages described for the no-predator treatment did appear to proceed at a slower rate in the large limpet treatment than the other 2 (Fig. 4). There is also a trend

towards greater cover of solitary ascidians on both large (15%) and small limpet (21%) plates compared to no-predator plates (9%) at the solitary ascidian peak, but this trend is not significant (Fig. 4; $p > 0.05$, ANOVA Tukey HSD). Encrusting bryozoan cover never differed between limpet plates and controls ($p > 0.05$, repeated measures ANOVA).

Bi-weekly recruitment

Recruitment of all species showed a strongly seasonal pattern, with little recruitment during the winter and early spring months, and peaks ranging from spring (*Distaplia occidentalis*) to late summer (*Water-sipora subtorquata*) (Fig. 5). The colonial ascidians *Diplosoma listerianum* and *D. occidentalis* have strongly non-overlapping recruitment peaks, with the former peaking 3 mo after the latter (Fig. 5). Solitary ascidian recruitment was less predictable: *Ascidia ceratodes* peaked in August 2002 and 2003, whereas *Ciona intestinalis* peaked in November 2002 and August 2003 (Fig. 5). *W. subtorquata* was the dominant encrusting bryozoan on our recruitment plates and also on the docks. This species recruited from July to November of each year, with a peak in late August/early September (Fig. 5). Recruitment of arborescent bryozoan species (*Bugula californica* and *Bugula neritina*) peaked in September/October 2002, but was nearly non-existent in 2003 and 2004 (data not shown). The magnitude of recruitment for all groups was generally higher in 2002 than in 2003 or 2004 (Fig. 5).

DISCUSSION

Predators, particularly the chitons *Mopalia muscosa*, had a dramatic effect on the abundance and species composition of the communities that colonized our plates, while the no-predator plates in this experiment exhibited a successional trajectory commonly seen in other fouling community studies on substrates free of predators (Sutherland 1974, Osman 1977). Initially, colonial ascidians colonize bare substrate. Many of these colonial ascidians senesce after releasing larvae (Brunetti et al. 1988, Grosberg 1988), and encrusting and arborescent bryozoans, which initially recruit at lower densities (Figs. 2 & 5), eventually replace colonial ascidians as the dominant space holders. Eventually, the encrusting bryozoans plateau as dominants and the arborescent bryozoans decline. Solitary ascidians sometimes occur as alternative dominants depending on the seasonal timing of substrate deployment (Sutherland 1974).

In many fouling community studies predators accelerate succession by preferentially consuming poorly defended, but fast-growing early successional species that can suppress slower-growing recruits of later successional species (Osman et al. 1992). Chitons did alter the relative abundance of recruits in favor of late successional encrusting bryozoans (Fig. 2a,b), perhaps by increasing settlement space by preferentially consuming ascidian recruits. Other bryozoan larvae are known to actively avoid settling in areas with colonial ascidians to reduce the likelihood of overgrowth (Grosberg 1981). However, these effects did not translate into differences in the adult community, as final cover of chiton plates was low and dominated by fast-growing colonial ascidians. Because bryozoan growth is slower and recruitment lower, colonial ascidians were the only species to occur in this highly disturbed community, but most colonies remained small and individual colony mortality was high, effectively suppressing succession in an early state, rendering this environment a sink for most fouling species.

The year in which this experiment was conducted was a year of lower recruitment relative to the previous year (Figs. 2b & 5), and it is possible that different results would have been obtained in higher recruitment years, as the facilitative effect of chitons on bryozoan recruitment was stronger in 2002, when recruitment was higher. The degree and speed with which bryozoans reach a size refuge from chiton predation likely play a role in determining whether this is the case. Some work has found that bryozoan colonies can reach a refuge from molluscan predation as soon as they lay down their second zooid, which is more heavily calcified than the initial zooid (Osman & Whitlatch 2004). However, the chitons in our study were several orders of magnitude larger than the snails in that of Osman and Whitlatch, and may be less likely to be deterred by calcification in the zooid walls. In general, the low cover in communities with chitons is consistent with field surveys showing the presence of limpets, and especially chitons, is positively correlated with unoccupied space (Fig. 1). Our experimental results suggest that this effect is largely due to chitons, although by virtue of their high abundance, limpets may also have an effect, or there may be synergistic interactions between limpets and chitons that we could not assess. Survey data also support a strong effect of chitons, as plots with chitons had much lower invertebrate cover than those without chitons, despite having equal numbers of limpets (Fig. 1). However, because the abundance of the 2 predators was positively correlated in the field, we could not use the field surveys to assess the relative importance of the 2 predators at natural densities.

Rather than effectively halting succession, large and small limpets *Lottia limatula* appeared to mostly delay

it, but in ways that were not entirely predictable from their effects on short-term recruitment. Large limpets decreased colonial ascidian recruitment during the post-settlement experiment, yet colonial ascidians cover a slightly larger area on large limpet plates than on no-predator plates, although neither difference is statistically significant (Fig. 4). In contrast, smaller limpets caused both the arborescent bryozoans and the solitary ascidians to attain a higher percent cover and a longer period of abundance at the expense of encrusting bryozoans. But these predators had no effect on recruitment of any species in the 8 d experiment, so these longer-term differences are difficult to explain. Small limpets could have an effect on encrusting bryozoan recruitment that we missed in the 8 d experiment because recruitment of this group was so low. Reducing bryozoan recruitment could lead to lower bryozoan cover and greater survival of solitary ascidian recruits, which rose to ~20% cover in small limpet treatments compared to only ~8% in the no-predator communities (Fig. 4).

Solitary ascidian cover declined precipitously in all treatments in January, associated with a period of heavy rain. Similar die-offs of solitary ascidians in response to salinity stress associated with winter rains have been reported elsewhere in California (MacGinitie 1939, Lambert & Lambert 2003). We observed decomposing, but still attached, solitary ascidians on our plates at this time, suggesting that the cause of this die-off was indeed low salinity rather than predation. This suggests that the small limpet treatments may have become more rapidly or more completely dominated by solitary ascidians than other treatments in the absence of heavy rains. Solitary ascidians do persist in dense assemblages in deeper water (2 m below mean low water, M. Nydam & J. Stachowicz pers. obs.), where surface runoff is less likely to impact salinity, but we do not know the abundance or effect of limpets at this depth.

Field survey data suggest that limpets may play a larger role than expected from the results of our experiments (Fig. 1). This could be because our experiments used limpet densities near the middle of the range in the field (~6 per field quadrat = 1 large limpet per plate), whereas chiton densities in our experiment were at the upper limit of those encountered in the field. Limpets do appear to be more mobile than chitons, and this, combined with their abundance, may allow them to play an important role in consuming early post-settlement stages of fast-growing species, before they reach a size refuge (see Osman & Whitlatch 2004 for a discussion of size refuges). Such an effect may be relatively unimportant on a small plate, but may be more important at larger spatial scales. Finally, it is possible that the minor effects of limpets on colonial ascidians

that we observed in our experiment could interact with the larger effects of chitons discussed above, such that the 2 together may be more effective than either alone. Given that colonial ascidians remained the dominant space holders on chiton panels in our experiment, this is an intriguing possibility, but one that we cannot rigorously assess with our data.

The structure of a particular fouling community often depends, not only on the predation pressures, but on the composition of the larval supply that colonizes the substrate at a particular time (Sutherland 1974, Osman 1977, Sutherland & Karlson 1977, Hurlbut 1992). The experiment detailed above was deployed at a single time point, in July 2003. Although colonial ascidians were the dominant recruiting group at this time (Fig. 5), adults are often short lived and semelparous, so it is not surprising that they did not persist at high cover. Encrusting bryozoans (e.g. *Watersipora subtorquata*) were also recruiting well at the time the plates were deployed, so final dominance by *W. subtorquata* in non-chiton treatments may have had something to do with the timing of deployment. If the experiment were deployed in the fall, when solitary ascidians were recruiting most heavily, perhaps they would have become more dominant, although their intolerance of salinity stress would have made survival through the winter unlikely.

Conclusions

Molluscan predators affect the development of the Bodega Bay fouling community, both directly through consumption of recruits and bulldozing of established juvenile colonies and indirectly by mediating competitive interactions and preventing monopolization of space by superior competitors. These effects may have cascading effects throughout the local community. Later successional species like *Watersipora subtorquata*, and to a lesser extent *Ascidia ceratodes*, form a complex 3-dimensional habitat, which provides shelter for many mobile invertebrates and juvenile native fishes, such as the northern clingfish *Gobiesox maendricus* and the striped kelpfish *Gibbonsia metzi* (C. Coates & J. Stachowicz unpubl. data). *W. subtorquata* is also resistant to anti-fouling paint and may thus provide a safe site for the attachment of other potential fouling organisms on boat hulls and docks, potentially facilitating new invasions (Floerl et al. 2004). Indeed higher cover of *W. subtorquata* increased the number of sessile species present in a similar survey in Bodega Harbor (Stachowicz & Byrnes 2006). Thus, by decreasing the abundance of this important habitat forming species, grazing chitons may have profound impacts throughout the community.

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