

Native predators limit invasion of benthic invertebrate communities in Bodega Harbor, California, USA

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ABSTRACT: Consumption by native predators is an important means by which assemblages repel invasion by non-native species. This resistance may be compromised as the diversity and abundance of species at upper trophic levels continues to decline globally. We investigated whether consumptive biotic resistance by mobile benthic fauna could explain compositional differences between a highly invaded fouling community and a nearby rocky subtidal community in Bodega Bay, California, USA. Surveys revealed little overlap in the sessile and mobile invertebrate communities of the 2 habitats, with the fouling community dominated by non-native tunicates and bryozoans. Through a series of predation experiments, we established that many mobile species, particularly sea stars, crabs, and chitons, consume settlers and adults of non-native sessile invertebrates, and we observed these mobile species to be more abundant and diverse at the rocky subtidal site in field surveys. In a field experiment, we found that transplanted non-native sessile invertebrates (both settlers and adults) survived at the rocky subtidal site when cages excluded benthic predators but showed reduced survivorship when these predators were allowed access. Our results suggest that variation in the intensity of predation by native mobile consumers likely contributes to the dominance of non-native sessile invertebrates in the fouling community and the relative absence of these species from the rocky subtidal. Benthic marine invaders are often more abundant on floating anthropogenic structures than on the adjacent benthos. Our results suggest that one possible explanation may be the more abundant and diverse community of native consumers present in benthic rocky habitats.

KEY WORDS: Non-native species · Biotic resistance · Predation · Fouling communities · Ascidiarians

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INTRODUCTION

The consumption of non-native species by native consumers is an important means by which communities resist invasion and limit the spread of introduced species into new areas (Levine et al. 2004, Kimbro et al. 2013). Although other factors including abiotic conditions (Moyle & Light 1996, Holway et al. 2002, Dethier & Hacker 2005), propagule supply (Lockwood et al. 2005, von Holle & Simberloff 2005,

Simberloff 2009), and competition with native species (Elton 1958, Levine 2000, Stachowicz et al. 2002) also constrain the establishment of non-native species, understanding the role that predators play in biotic resistance is important in light of human impacts on predator diversity and abundance (Duffy 2003, Byrnes et al. 2007). Such changes may compromise the ability of communities to resist invasion, particularly as introductions continue to increase at predominantly lower trophic levels and extinctions

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occur disproportionately at higher trophic levels (Byrnes et al. 2007).

In marine environments, inland bays, harbors, and estuaries are typically much more invaded than open coast environments (Whitlatch & Osman 2000, Wasson et al. 2005, Preisler et al. 2009, Ruiz et al. 2009, Cheng & Hovel 2010). Within coastal waters, benthic communities on artificial structures, such as seawalls, pilings, and floating docks (pontoons), are often more heavily invaded than analogous communities in adjacent natural rocky habitats (Glasby et al. 2007, Ruiz et al. 2009, Bulleri & Chapman 2010, Simkanin et al. 2012). Although the proximity of estuarine and artificial habitats to sources of non-native propagules has certainly played a role in non-native species establishment within these communities (Cohen & Carlton 1998, Ruiz et al. 2000), recent studies have found that consumptive biotic resistance by native predators can limit the spread of particular invaders into suitable nearby habitats (Dumont et al. 2011a,b, Forrest et al. 2013, Simkanin et al. 2013). Benthic predators can exhibit strong top-down control of sessile invertebrate community composition (Keough & Downes 1982, Hunt & Scheibling 1997, Osman & Whitlatch 2004), and these predators are typically less abundant on artificial structures that lack structural complexity or are physically separated from the benthos, such as floating docks (Chapman 2003, Dumont et al. 2011a). Artificial structures may thereby provide a refuge from predation allowing for the establishment and persistence of non-native species within these habitats.

On the Pacific coast of North America, non-native sessile invertebrates are relatively uncommon in rocky subtidal communities (Preisler et al. 2009) but very common in the fouling communities on floating docks (Lambert & Lambert 2003, Sorte & Stachowicz 2011). In this study, we investigated whether consumptive biotic resistance by mobile benthic fauna contributes to community differences between a highly invaded fouling community and a nearby rocky subtidal community in Bodega Bay, California, USA. We addressed the influence of biotic resistance by quantifying (1) differences in the abundance and diversity of sessile invertebrates and mobile consumers at both study locations, (2) predation by mobile consumers on both juvenile and adult sessile invertebrates from the fouling community, and (3) survivorship of juvenile and adult sessile invertebrates from the fouling community at the rocky subtidal location when predators were either allowed or excluded.

MATERIALS AND METHODS

Study sites

Bodega Harbor is a shallow bay on the California coastline, protected at its entrance by 2 parallel man-made jetties (breakwaters) extending outward from the bay's narrow inlet. Our study examined the composition of 2 benthic invertebrate communities within Bodega Harbor: the fouling community on the concrete floating docks of the Spud Point Marina (38.3295°N, 123.0570°W, hereafter referred to as the dock habitat), and the rocky subtidal community on the shallow boulders of the southern Bodega Harbor jetty (protected side, proximal to shore; 38.3049°N, 123.0534°W, hereafter referred to as the jetty habitat). The 2 sites are separated by ~2.7 km, and both provide suitable habitat for marine invertebrates. Since the floating docks rise and fall with the tide and are never exposed to air, they are also subtidal. Although the jetty habitat is also a man-made structure, the sessile and mobile benthic community there is more similar to natural rocky subtidal communities than to harbor fouling communities (J. Byrnes pers. obs.). Although not formally measured, currents experienced by divers were stronger at the jetty than the dock, and the benthic communities studied at the jetty were at greater depth than those on the dock.

Both study sites host diverse communities of tunicates, bryozoans, sponges, anemones, algae, polychaetes, echinoderms, crabs, limpets, chitons, and other invertebrates. The docks have high abundances of non-native tunicates and bryozoans (Nydham & Stachowicz 2007, Sorte & Stachowicz 2011). The docks are not in direct contact with the benthos, and the benthic habitat beneath the docks is soft sediment, potentially making the docks less accessible to mobile benthic consumers characteristic of hard substrata. All laboratory work and experiments were performed at nearby Bodega Marine Laboratory. All statistical analyses were done in R version 3.2.2 (R Core Team 2015).

Community composition

We surveyed sessile invertebrate community composition at both the dock and jetty during June and July 2007. At the docks, we recorded the percent cover of all sessile invertebrates, algae, and bare (unoccupied) space within quadrats (25 × 25 cm) placed vertically on the sides of the floating docks, just below the water line. Five evenly spaced quadrats

per slip (3 on the main walkway and 1 on each finger pier) were surveyed in each of 16 south-facing slips, for a total of 80 quadrats. Total percent cover sometimes exceeded 100% because of species layering. We likewise recorded percent cover of sessile invertebrates, algae, and bare space from photographs of 13 quadrats (25 × 25 cm) placed haphazardly on vertical rock surfaces of the jetty between 5 and 8 m depth. For each species with >3% mean cover and for bare space, we compared percent cover between the dock and jetty using a Mann-Whitney *U*-test because of the unbalanced sampling design and heteroskedasticity in the data. The native/non-native status of each species was determined from Cohen & Carlton (1995) and Sorte & Stachowicz (2011).

We surveyed mobile consumer species at both the dock and jetty during July 2008. Using SCUBA, we quantified all mobile invertebrates and fish within 8 randomly positioned band transects (8 × 1 m). Fish were typically small mesopredators (<10 cm) and were not identified to species. We also counted all small mobile invertebrates (e.g. chitons and limpets) within 2 quadrats (25 × 25 cm) per band transect placed at the beginning and end of each transect (the 2 quadrats were averaged for analysis). We used both transect and quadrat methods, as small highly cryptic species (e.g. limpets and chitons at the jetty) were more likely to be observed in quadrats, whereas larger consumers (e.g. sea stars) and less dense consumers (e.g. chitons at the dock) were more likely to be observed in the band transects. Along the docks, band transects were positioned along the vertical sides of individual slips and included the lip of the underside of the dock in order to include species that preferentially used that habitat (e.g. *Pugettia producta*). At the jetty, band transects were surveyed along the vertical faces of boulders. For each of 5 major taxonomic categories (crabs, echinoderms, limpets, chitons, and fish), we compared the abundance of mobile consumers between the dock and the jetty using a generalized linear model with a Poisson error and log link function (O'Hara & Kotze 2010). We analyzed data from the band transects and quadrats separately for each category. We also noted any mobile species observed in the sessile community survey quadrats, as well as during other visits to the study sites.

Predation on sessile invertebrates

Since the composition of benthic invertebrate communities can be subject to strong consumer control (Osman & Whitlatch 1998, 2004), we hypothesized

that differences in mobile community composition among sites contributes to differences in sessile community composition. To test this hypothesis, we conducted a series of experiments to determine the effect of mobile consumers on the survival of common sessile invertebrates from the dock fouling community. We used mobile consumers observed at the jetty, as well as consumers observed at the dock.

Field predation on sessile invertebrate recruits

To determine the effect of 4 mobile molluscs on the recruitment of sessile invertebrates at the dock, we placed either no consumer or one adult individual of either *Lottia limatula* (limpet, 25–30 mm length), *Mopalia muscosa* (chiton, 26–37 mm), *Mopalia lignosa* (chiton, 28–47 mm), or *Tonicella lineata* (chiton, 23–27 mm) onto roughened, gray 10 × 10 cm PVC plates enclosed within plastic mesh cages (10 × 10 × 10 cm, 1 cm mesh size; n = 8). The caged plates were then suspended on racks at the dock for 2 wk during July 2007, oriented downward at ~1 m depth, to allow for colonization by tunicates and bryozoans. The consumer species used in this experiment were selected because they were among the most abundant invertebrate consumers found at the jetty and the dock and because preliminary trials indicated that they would survive and remain contained within the cages for the duration of the study. At the end of the experiment, we identified and counted the number of sessile recruits on each plate using a dissecting microscope. In this experiment and all experiments that follow, plates placed at the dock were colonized primarily by tunicates (*Botrylloides violaceus*, *Diplosoma listerianum*, *Distaplia occidentalis*, *Didemnum vexillum*) and the bryozoan *Watersipora subtorquata*. To determine the effect of consumers on settlers, we used a 1-way ANOVA with consumer treatment as a factor and the final number of settlers as the response variable. For pairwise comparisons, we used Dunnett's post-hoc test to compare each consumer treatment to the control (no consumer) treatment.

Lab predation on sessile invertebrate recruits

In the laboratory, we tested how invertebrate settlers were affected by another set of consumers from the dock and jetty, which were either too large or too small to be tested within the field cages. We first generated plates covered in newly settled sessile

invertebrates by deploying roughened, gray 10 × 10 cm PVC plates on racks at the dock for 3 wk, oriented downward at ~1 m depth, to allow for colonization by tunicates and bryozoans. We identified and counted all settlers on each plate in the lab using a dissecting microscope. We affixed each plate to the lid of a perforated plastic container (15 × 15 × 8 cm), such that the plate was oriented downward within the container when it was closed. We submerged containers in flowing seawater. Into each container, we placed either no consumer (n = 6) or 1 of the following 6 consumer species: *Pachygrapsus crassipes* (crab; 1 ind., n = 6), *Strongylocentrotus purpuratus* (urchin; 1 ind., n = 6), *Patiria miniata* (sea star; 1 ind., n = 6), *Pugettia richii* (crab; 1 ind., n = 6), *Lottia ochraceus* (limpet; 4 ind., n = 5), or *Lacuna marmorata* (snail; 4 ind., n = 5). All consumers used were full-sized adults. Since the crabs (*Pachygrapsus crassipes* and *Pugettia richii*) had difficulty climbing the smooth container walls to access the plate, the containers containing crabs were inverted halfway through the experiment. After 3 d of exposure to the consumers, we removed the plates and identified and counted the remaining settlers. To determine the effect of consumers on settlers, we used a 1-way ANCOVA with consumer treatment as a factor, the initial number of settlers (which ranged from 17 to 212) as a covariate, and the change in number of settlers (final – initial) as the response variable. For pairwise comparisons, we used Dunnett's post-hoc test on least square (LS) means to compare each consumer treatment to the control (no consumer) treatment.

Lab predation on sessile invertebrate adults

To determine the effect of various consumers on adult sessile invertebrates common in the dock community, we conducted a consumer choice experiment in the laboratory in the summers of 2006 and 2007 using 2 solitary tunicate species, 4 colonial tunicate species, and 1 bryozoan species collected from the dock. Perforated, lidded plastic containers (44 × 30 × 19 cm) were submerged in flowing seawater, and into the bottom of each container we placed one *Ascidia ceratodes* individual, one *Ciona intestinalis* individual, one ~5 cm diameter circular cutout of a *Botrylloides violaceus*, *Botrylloides diegensis*, and *Didemnum vexillum* colony, one *Distaplia occidentalis* colony, and one ~5 cm diameter piece of *Watersipora subtorquata*. Two species we used were native (*Ascidia ceratodes* and

Distaplia occidentalis), one was cryptogenic (*Botrylloides diegensis*), and the remainder were non-native. No *Ciona intestinalis* were used in 2007 due to low availability. Into each container we then placed either no consumer or one individual of one of the following 7 consumers: *Patiria miniata* (n = 6 in 2006, 5 in 2007), *Pachygrapsus crassipes* (n = 5 in 2007), *Pugettia richii* (n = 5 in 2007), *Pugettia producta* (crab; n = 8 in 2006), *Loxorhynchus crispatus* (crab; n = 7 in 2006), *Scyra acutifrons* (crab; n = 8 in 2006), or *Strongylocentrotus purpuratus* (n = 8 in 2006, 5 in 2007). All consumers used were full-sized adults. We examined the condition of the sessile invertebrates and feeding behavior of the consumers daily for 6 d. At the end of the experiment, we scored each sessile invertebrate as either eaten or uneaten. Invertebrates were considered eaten if they were either entirely or partially consumed or if they were picked apart. Based on observations of the no-consumer treatments, we were able to visually distinguish consumed invertebrates from those that had died naturally and decayed. We tested whether each prey species was preferred or avoided using an adaptation of Roa's (1992) multivariate approach to the analysis of multiple choice feeding trials, since feeding on one choice within a container was potentially non-independent of feeding on other choices. Since our data was binary, we utilized a multivariate logistic regression approach (Wang et al. 2012) with consumer treatment as a predictor of whether a food item was eaten. Separate models were run for 2006 and 2007 given differences in offered prey items. To test whether each consumer preferred or avoided different prey species, we used Monte Carlo resampling techniques (Warton 2011) to correct for correlations in prey consumption within a container, and adjusted p-values to account for multiple comparisons (Wang et al. 2012). A coefficient of 0 indicated that a particular prey item was consumed but neither preferred nor avoided. Coefficients that were positive and different from 0 indicated strong preference for a prey item, while coefficients that were negative and different from 0 indicated strong avoidance.

Field transplant experiment

To further evaluate the hypothesis that predation contributes to the low abundance of dock-dwelling sessile invertebrates in the jetty habitat, we conducted a transplant experiment to compare dock

sessile invertebrate survival in caged vs. uncaged conditions. We suspended roughened, gray PVC plates (10 × 10 cm) from racks at the dock in June 2007, oriented downward at ~1 m depth, to allow for colonization by tunicates and bryozoans. After 5 wk, at which point many tunicate and bryozoan settlers (1–10 mm diameter) were visible on the plates, we collected, photographed, and randomly assigned plates to treatments. All plates were collected on the same day, stored overnight in flowing seawater, and redeployed to the field the following day. We returned one set of control plates to racks at the dock and transplanted the other sets to cinder blocks at the jetty, where they received treatments allowing for different levels of consumer access. Each plate was placed in one of 2 positions ('rack' or 'block') and was either enclosed within its own mesh cage (10 × 10 × 10 cm, 1 cm mesh size) or was left uncaged. The 'rack' plates were suspended, facing downward, from racks attached to the tops of the blocks and were thus less accessible to crawling predators such as sea stars and crabs and thus potentially more similar to dock conditions in terms of predator access. The racks attached to the top of the cinder blocks were identical in structure to those hung at the docks. The 'block' plates were attached vertically against the sides of the cinder blocks, mimicking the position of the communities we surveyed at the jetty. The cinder blocks were placed at the base of large boulders at a depth of 8 m, and each cinder block held 2 replicates of each treatment combination. One week after deployment, all plates (n = 8 per treatment) were retrieved and re-photographed. We identified and counted all invertebrate settlers in the initial and final photographs. To determine the effect of experimental treatments on settlers, we used a 1-way ANCOVA with treatment as a factor, the initial number of settlers (which ranged from 16 to 84) as a covariate, and the change in number of settlers (final – initial) as the response variable. We dropped the interaction term from the model after determining that slopes were homogeneous (ANCOVA, treatment × initial settlers, $F_{4,30} = 1.21$, $p = 0.33$). For pairwise comparisons, we used Dunnett's post-hoc test on LS means to compare each treatment to uncaged control plates returned to the dock.

We repeated this caging experiment in January 2008 using another set of plates that had been suspended at the dock since June 2007 and had developed full adult fouling communities over the course of 6 mo. We photographed all plates and then transplanted them to either the jetty, in the same 4 treatments as the settler transplant experiment

(rack/block; caged/uncaged), or to the dock (rack, caged/uncaged). While predation at the dock was still assumed to be minimal given that panels had been left uncaged for community development, we included a dock cage control in order to assess the effects of reductions in flow and physical abrasion due to caging on adult communities. After 6 wk, we retrieved and rephotographed all plates (n = 6 per treatment) and estimated the change in percent of occupied space over the course of the experiment using ImageJ (Rasband 1997). To determine the effect of experimental treatments on the cover of sessile adults, we used a 1-way ANCOVA with treatment as a factor, the initial percentage of occupied space (which ranged from 62 to 99 %) as a covariate, and the change in percent occupied space (final – initial) as the response variable. We dropped the interaction term from the model after determining that slopes were homogeneous (ANCOVA, treatment × initial cover, $F_{5,20} = 0.82$, $p = 0.55$). For pairwise comparisons, we used Dunnett's post-hoc test on LS means to compare each treatment to caged control plates returned to the dock. Inspection of residuals showed that the data did not violate assumptions of normality of error or linearity; hence, we did not apply any logit transformations. Four plates were excluded from analysis because they were physically damaged in the field.

RESULTS

Community composition

Our surveys and observations revealed little overlap of either the sessile or mobile communities between the dock and jetty. None of the species with >3 % mean cover were shared between sites (Fig. 1a,b). Species abundant at one site were absent or rare at the alternate site, with significantly lower cover at the alternate site ($p < 0.02$ for all species except *Didemnum vexillum*, $p = 0.24$). Of the 9 most abundant species found at the dock, 5 were non-native and 1 was cryptogenic, whereas all 6 of the most abundant species found at the jetty were native. The cover of bare space at the jetty was 49 % higher than the cover of bare space at the dock ($U = 312.5$, $p = 0.022$; Fig. 1c).

The abundance and diversity of benthic mobile consumers (crabs, echinoderms, limpets, and chitons) differed between sites (Table 1, Fig. 2). In both the quadrat and transect surveys, crabs and echinoderms (particularly sea stars) were more abundant and

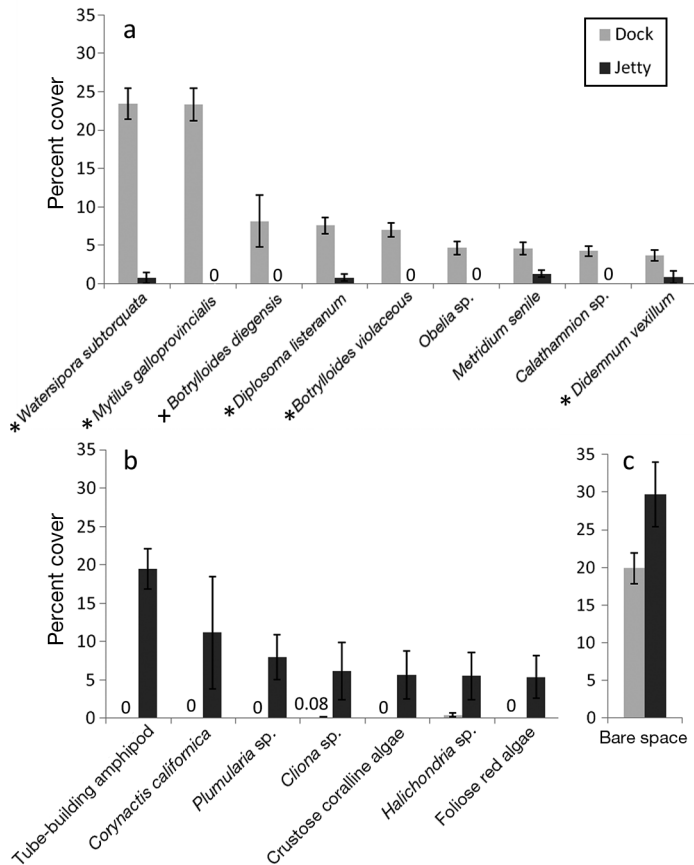


Fig. 1. Percent cover (mean \pm 1 SE), at both study locations, of the most common sessile invertebrate species ($>3\%$ cover) found at (a) the Spud Point dock and (b) the Bodega Harbor jetty. (c) Percent cover of bare space at the dock and jetty. The key applies to all panels. *: introduced species; +: cryptogenic species

diverse at the jetty and were rare or absent at the dock ($p < 0.01$ for all comparisons). The only echinoderms observed at the dock were sea urchins *Strongylocentrotus purpuratus*, which were at very low density. Chitons were also more abundant, but more cryptic, at the jetty, and thus were only observed in quadrat surveys at the jetty and only observed in the band transect surveys at the dock ($p < 0.001$ for both comparisons). Limpets, on the other hand, were more abundant and diverse at the dock ($p < 0.001$ for transect abundances, $p = 0.2$ for quadrat abundances). Only one limpet species (*Lottia ochraceus*) was observed at the jetty. Fish density did not differ between the 2 sites ($p = 0.9$); however, we observed many large fish (e.g. rockfish, cabezon) at the jetty that we did not observe at the dock, and these species were not captured in our transect surveys. All mobile consumers observed at both sites were native species.

Predation on sessile invertebrates

Field predation on sessile invertebrate recruits

The chitons *Mopalia muscosa* (found at the dock) and *Mopalia lignosa* (found at the jetty) reduced the number of settlers on plates suspended at the dock by 70 % relative to control plates with no consumers (ANOVA, $F_{4,35} = 36.1$, $p < 0.001$; Dunnett's test, $p < 0.001$; Fig. 3). The number of settlers on plates with the limpet *Lottia limatula* (found at the dock) and chiton *Tonicella lineata* (found at the jetty) did not detectably differ from the number on control plates (Dunnett's test, $p > 0.4$).

Lab predation on sessile invertebrate recruits

The change in number of settlers on each plate depended on both the consumer treatment and the initial number of settlers (ANCOVA, initial settlers \times consumer treatment, $F_{6,26} = 5.29$, $p = 0.001$). Allowing for unequal slopes and using LS means for comparison, the sea star *Patiria miniata*, crab *Pachygrapsus crassipes*, and urchin *Strongylocentrotus purpuratus* decreased the number of settlers on the plates relative to the control (ANCOVA, consumer treatment, $F_{6,26} = 19.5$, $p < 0.001$; Dunnett's test, $p < 0.001$, $p = 0.003$, $p = 0.016$ respectively; Fig. 4). The sea star *Patiria miniata* had the strongest effect on settler numbers, and this effect increased with the density of initial settlers (slope coefficient for initial settlers \times *Patiria miniata*, $t = 4.17$, $p < 0.001$). For the other consumer treatments, change in settler number did not differ with initial settler density (slope coefficients not different from 0, $p > 0.1$ for all). The crab *Pugettia richii*, limpet *Lottia ochraceus*, and snail *Lacuna marmorata* did not reduce the number of settlers (Dunnett's test, $p > 0.15$). Over the course of the experiment, the number of settlers increased in the control and in 2 of the consumer treatments, most likely because of the growth of settlers not previously visible under the microscope. Seawater was filtered prior to entering the experimental system and would not have contained propagules.

Lab predation on sessile invertebrate adults

Consumers from the jetty ate both a greater quantity and greater variety of sessile invertebrates than consumers from the dock (Fig. 5). The crab *Pachygrapsus crassipes* did not consume any of the species

presented, and the urchin *Strongylocentrotus purpuratus* consumed at least 1 *Botrylloides* species in only 3 of 13 total trials. In contrast, all sessile invertebrates were eaten by at least 1 consumer from the jetty, and with the exception of *Pugettia richii*, all consumers from the jetty ate at least 5 different species of the sessile invertebrates presented. *Pugettia producta*, which was present in both habitats, albeit very rare in the dock community, consumed 6 of the 7 species presented.

Some prey species appeared to be avoided by particular consumers: *Loxorhynchus crispatus* and *Scyra acutifrons* each consumed many species, but both avoided *Ciona intestinalis*. On the other hand, *Pugettia producta* frequently consumed *C. intestinalis* but avoided *Distaplia occidentalis* (see Table S1 in the Supplement for statistical analysis; www.int-res.com/articles/suppl/m545p161_supp.pdf). Thus, when considered together as an assemblage,

Table 1. Mobile consumer species observed at the Spud Point dock and Bodega Harbor jetty

Species	Dock	Jetty
Crabs		
<i>Cancer jordanii</i>		×
<i>Cancer productus</i>		×
<i>Loxorhynchus crispatus</i>		×
<i>Pachygrapsus crassipies</i>	×	
<i>Pagurus</i> sp.		×
<i>Pugettia producta</i>	×	×
<i>Pugettia richii</i>		×
<i>Scyra acutifrons</i>		×
Echinoderms		
<i>Dermasterias imbricata</i>		×
<i>Patiria miniata</i>		×
<i>Pisaster brevispinus</i>		×
<i>Pisaster giganteus</i>		×
<i>Pisaster ochraceus</i>		×
<i>Pycnopodia helianthoides</i>		×
<i>Strongylocentrotus purpuratus</i>	×	
Limpets		
<i>Lottia digitalis</i>	×	
<i>Lottia limatula</i>	×	
<i>Lottia ochraceus</i>		×
<i>Lottia pelta</i>	×	
<i>Lottia scabra</i>	×	
<i>Tectura scutum</i>	×	
Chitons		
<i>Leptochiton</i> sp.	×	
<i>Mopalia muscosa</i>	×	
<i>Mopalia lignosa</i>		×
<i>Tonicella lineata</i>		×
<i>Tonicella lokii</i>		×
<i>Tonicella</i> sp.	×	
Other molluscs		
<i>Hemissenda crassicornis</i>	×	×
<i>Lacuna marmorata</i>		×

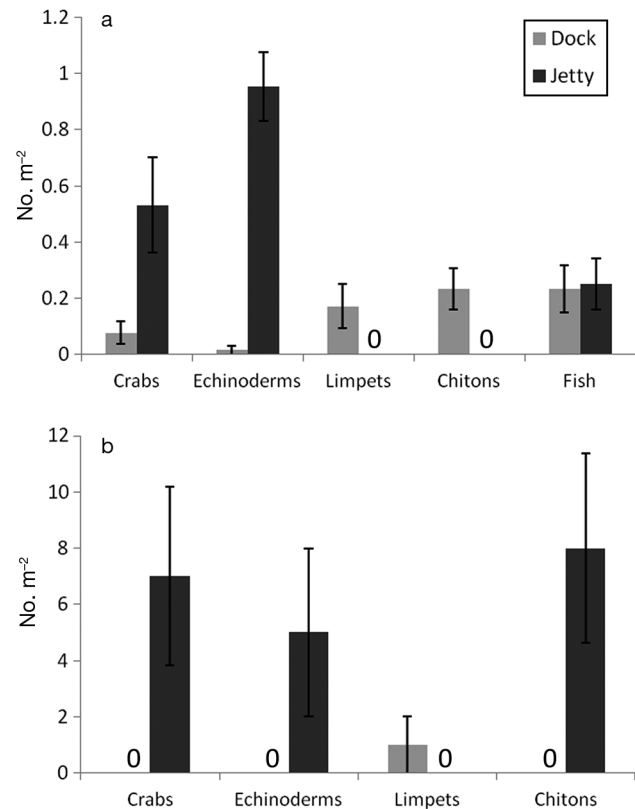


Fig. 2. Densities (mean \pm 1 SE) of mobile consumers found in (a) band transect and (b) quadrat surveys at the Spud Point dock and Bodega Harbor jetty

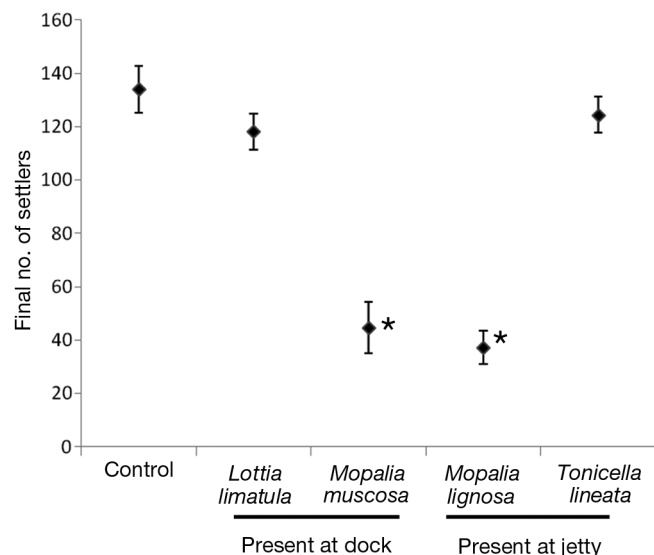


Fig. 3. Number of settlers (mean \pm 1 SE) present on settlement plates suspended from the Spud Point dock at the conclusion of the 2 wk field predation experiment. Plates were caged and enclosed with either no consumer (control) or 1 consumer (n = 8). *: different from no-consumer control at the p \leq 0.05 level

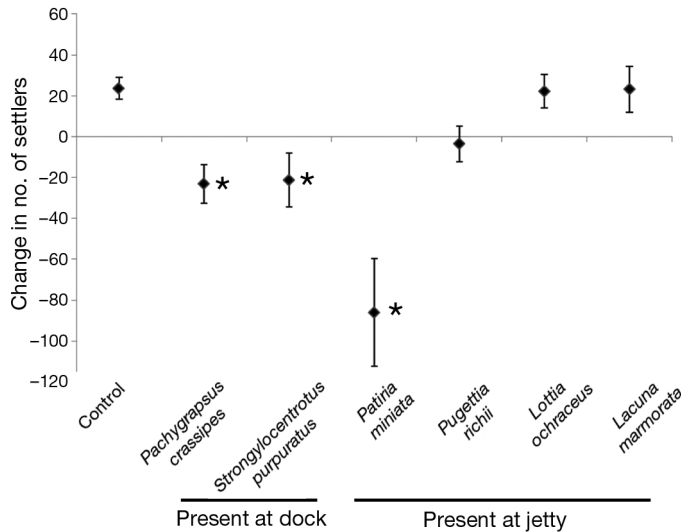


Fig. 4. Change in number of settlers (mean \pm 1 SE) on settlement plates exposed to various consumers for 3 d in the laboratory ($n = 5-6$). *: different from no-consumer control at the $p \leq 0.05$ level

the predator fauna at the jetty has the potential to consume any of the tested species.

Both native and non-native species appeared equally susceptible to predation by jetty consumers. The native tunicate *Ascidia ceratodes* was consumed by all consumers from the jetty, and the native tunicate *Distaplia occidentalis* was consumed by 2 consumers from the jetty. The cryptogenic species *Botrylloides diegensis* was consumed very similarly to its non-native congener *Botrylloides violaceus*.

Field transplant experiment

In the summer caging experiment using invertebrate settlers, uncaged plates attached vertically to cinder blocks at the jetty (the position that would be most accessible to benthic mobile consumers), showed the greatest decline in number of settlers, and the change in settler number was significantly

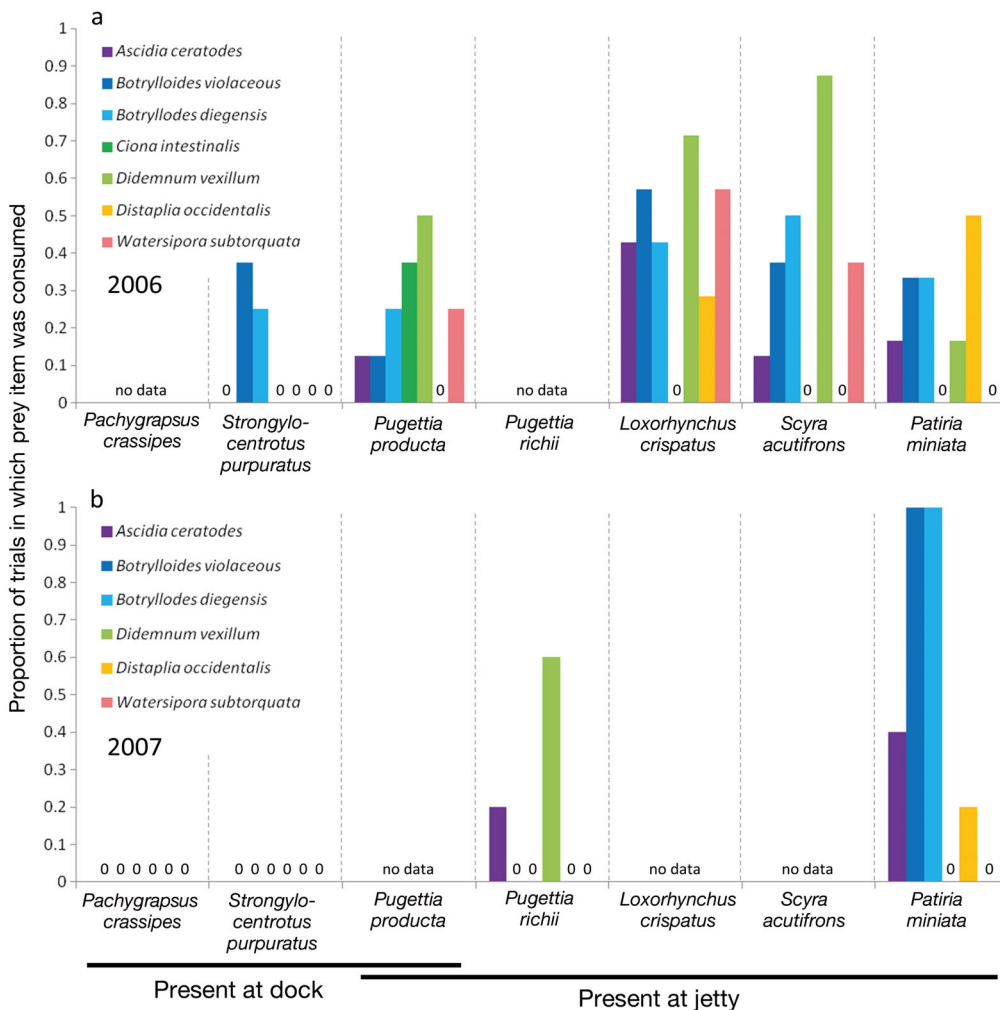


Fig. 5. The proportion of trials in (a) 2006 and (b) 2007 in which adult sessile invertebrates presented to various consumers in the lab were eaten by those consumers

different from that in the control treatment (ANCOVA, treatment $F_{4,34} = 5.34$, $p = 0.002$; Dunnett's test, $p = 0.003$; Fig. 6). Over the course of the experiment, the number of settlers on plates returned to the dock increased, reflecting additional settlement. The change in number of settlers on the other plates at the jetty (caged plates, and uncaged plates on rack) did not differ from that of the control (Dunnett's test, $p > 0.2$).

In the winter experiment using established adult communities, plates at the dock and caged plates at the jetty showed little change in occupied space, but uncaged plates at the jetty showed reductions in cover. In the treatment with greatest predator access (uncaged plates attached vertically to cinder blocks) occupied space decreased by 35 percentage points on average (ANCOVA, treatment, $F_{5,25} = 2.77$, $p = 0.040$; Dunnett's test, $p = 0.032$; Fig. 7). Occupied space on uncaged plates suspended from racks decreased by 24 percentage points on average, but this was not different from the observed change in control plates returned to the dock (Dunnett's test, $p = 0.157$). Change in occupied space did not differ between caged plates at the jetty and caged plates at the dock, or between caged and uncaged plates at the dock (Dunnett's test, $p > 0.9$ for all comparisons).

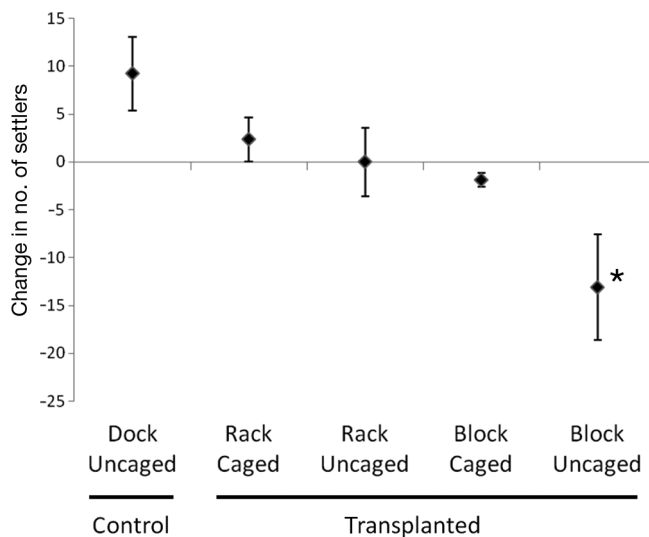


Fig. 6. Change in number of settlers (mean \pm 1 SE) on settlement plates transplanted from the Spud Point dock to the Bodega Harbor jetty. Settler communities were allowed to develop on plates at the dock for 5 wk prior to transplantation. Control plates were returned uncaged to the dock. Transplanted plates were either hung from racks (Rack) or placed vertically on the sides of blocks (Block), and were either caged or uncaged ($n = 8$ per treatment combination).

*: different from control at the $p \leq 0.05$ level

In both the settler and adult transplant experiments, we observed sea stars and other small consumers nearby the blocks, but not on the racks, when we visited the transplanted plates prior to removal and at the time of removal.

While our experiment lacked a formal partial-cage control, several contrasts suggest that cage artifacts were negligible. We found no difference in adult survival between caged plates at the jetty, caged plates at the dock, and uncaged plates at the dock. There was also no difference in settler survival between caged and uncaged rack plates at the jetty, which were suspended above the bottom and thus subject to limited predator access. While some sedimentation was observed at the jetty, and sand burial damaged 4 of the transplanted adult plates, both caged and uncaged plates were equally affected.

DISCUSSION

Our results suggest that predation by native consumers contributes to the virtual absence of non-native sessile invertebrates at the subtidal boulders of the Bodega Harbor jetty compared to the dominance of these species on the floating docks at Spud Point Marina. Our lab studies demonstrated that

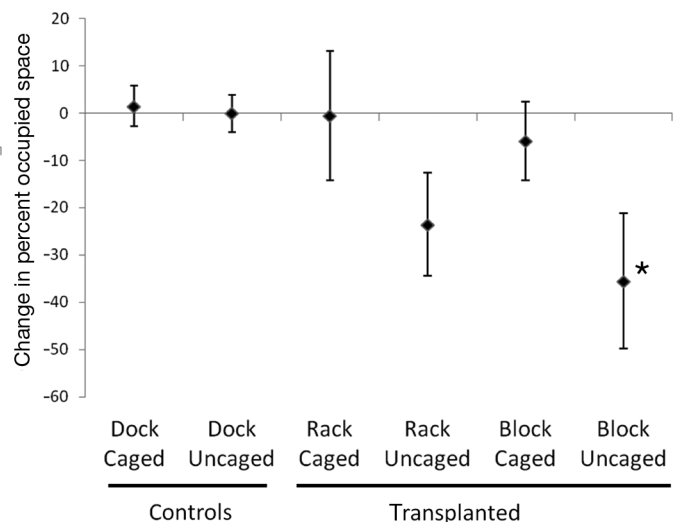


Fig. 7. Change in percent occupied space (mean \pm 1 SE) on settlement plates transplanted from the Spud Point dock to the Bodega Harbor jetty. Adult communities were allowed to develop on plates at dock for 6 mo prior to transplantation. Control plates were returned to the dock. Transplanted plates were either hung from racks (Rack) or placed vertically on the sides of blocks (Block), and were either caged or uncaged ($n = 4-6$ per treatment combination).

*: different from control at the $p \leq 0.05$ level

many mobile species, particularly sea stars, crabs, and chitons, consume settlers and adults of non-native sessile invertebrates, and we observed these mobile species to be more abundant, and their assemblage more diverse, at the jetty in field surveys. When benthic consumers at the jetty were able to access uncaged experimental plates of dock-abundant organisms, survivorship of transplanted sessile invertebrates (both settlers and adults) was reduced considerably. Low settler mortality on uncaged plates on racks, which were less accessible to benthic consumers, further supports the role of this predator guild. Low mortality of sessile invertebrates on caged transplanted plates further suggests that predation pressure, but not differences in environmental conditions, is a contributing factor limiting these species to floating docks in Bodega Harbor.

The species we found to consume settlers and/or adults of non-native sessile invertebrates included: the chitons *Mopalia muscosa* and *Mopalia lignosa*; the crabs *Pachygrapsus crassipes*, *Loxorhynchus crispatus*, *Scyra acutifrons*, *Pugettia producta*, and *Pugettia richii*; the urchin *Strongylocentrotus purpuratus*; and the sea star *Patiria miniata*. Similarly, other studies have found that *Mopalia muscosa*, *Pachygrapsus crassipes*, and *Strongylocentrotus purpuratus* decreased recruitment and/or cover on caged panels at the dock site (Nydam & Stachowicz 2007, Byrnes & Stachowicz 2009). Epelbaum et al. (2009) found that other species of strongylocentrotid sea urchins (*Strongylocentrotus droebachiensis* and *S. franciscanus*) and some species we observed but did not use in our predation trials (*Dermasterias imbricata*, *Cancer productus*, and *Hermisenda crassicornis*) consumed non-native tunicates including *Botrylloides violaceus* and *Didemnum vexillum*. The non-native mussel *Mytilus galloprovincialis*, which was the second most abundant species on the docks, but which we did not include in our predation trials, is also known to be eaten by cancrid crabs and *Pisaster ochraceus* (Shinen et al. 2009). We found that native predators consistently consumed native as well as non-native ascidians, and native ascidians observed at the dock were also rare at the jetty. Thus, the resistance to invasion imparted by native predators may stem from the fact that most of these non-native species belong to a functional group that they already readily consume.

Although some of the mobile species we found to consume non-native tunicates in our experiments (*Mopalia muscosa*, *Pachygrapsus crassipes*, *Pugettia producta*, *Strongylocentrotus purpuratus*) were found at the dock and have the potential to affect the fouling community, the abundance of chitons, crabs,

and echinoderms overall was much higher at the jetty than at the dock (Fig. 2), suggesting a much higher total impact of these species in the jetty habitat. In our predation experiments and other experiments (Nydam & Stachowicz 2007, Byrnes & Stachowicz 2009), the consumer densities used were much higher than those in the field, and the impact of the dock predators at natural densities is likely minimal.

Since our study is limited to 2 sites within one harbor, our scope of inference is also limited, but the patterns we document are consistent with observations reported from other harbors along the Pacific coast of North America, and our results are consistent with other findings on biotic resistance in benthic invertebrate communities. Predation by benthic consumers has been found to limit the spread of non-native sessile invertebrates, including *Ciona intestinalis* (Dumont et al. 2011a, Collin & Johnson 2014), *Bugula neritina* (Dumont et al. 2011b), *Didemnum vexillum* (Forrest et al. 2013), and *Botrylloides violaceus* (Simkanin et al. 2013), from suspended (or otherwise less accessible) artificial structures to nearby rocky habitats. On the Atlantic coast of North America, predation on recruits by small snails was found to exclude tunicates from open coast habitats (Osman & Whitlatch 1995, 2004). Our results provide another possible example of resistance to invasion by diverse and abundant native consumers at the whole-community level and may help explain why Pacific coast rocky subtidal communities are relatively free of introduced species in spite of heavy invasion on artificial structures such as floating docks.

Although our results demonstrate the importance of benthic predators in controlling community composition, there are a number of other drivers that could play an additional role. Dispersal limitation could contribute to observed community differences, given the distance between the study sites (~2.7 km) and the short larval duration of many non-native tunicates (Fletcher et al. 2013). Initial colonization of Bodega Harbor by non-native species is likely to occur at docks because arrival of boats with reproductive adults attached provides a ready source of recruits (Clarke Murray et al. 2011). In our transplant experiment, additional recruitment of tunicate and bryozoan settlers on plates returned to the dock, but not on those at the jetty, suggests that overall recruitment of these species is higher at the dock. However, many non-native species have been present in the area for over a decade (Cohen & Carlton 1995) and were present in low numbers at the jetty in our surveys, yet these species have not been able to achieve similar cover as they have on the docks.

Combined with the failure of exposed transplants to survive, this suggests that the local biotic or abiotic environment is likely limiting spread.

The 2 sites, although in the same harbor, differ slightly in environmental conditions (e.g. light, temperature, flow, and sand scour, all related to differences in depth and flow restriction), and additional work is needed to evaluate the effect of abiotic factors on community composition. While our study demonstrates the importance of predation, our transplant experiments were relatively short in duration because of the speed with which predators consumed transplanted individuals. While species may have survived in caged treatments at the jetty, effects of the abiotic environment on long-term survival and fecundity are not known. Cages may have buffered against some abiotic disturbance; however, the equivalent survival of settlers on caged and uncaged rack plates at the jetty suggests that caging effects were relatively minor compared to the effects of predation. In addition, sedimentation affected both caged and uncaged plates equally.

Competition with native sessile species is another possible alternative explanation for community differences; however, the greater percentage of bare space at the jetty than the dock, as well as the increase in open space in uncaged transplanted adult communities, suggest that competition for primary space is not likely to be excluding non-native species from the jetty (Stachowicz & Byrnes 2006).

Other predator guilds, such as fish, may also play a role in structuring communities at the jetty. There was no difference in fish abundance between sites in our field surveys; however, these surveys did not capture larger fish species, which we observed to be more abundant at the jetty. In addition, these surveys were done only in the daytime, and nocturnally active predators may have been underestimated or unobserved, particularly at the jetty, which is more structurally complex and may have more places for species to hide during the day. In the adult transplant experiment, uncaged plates on both the block and rack showed a reduction in cover, suggesting that pelagic consumers may be involved. Alternatively, the longer duration of the adult transplant experiment (6 vs. 1 wk) may have given benthic consumers more opportunity to find a way on to the rack plates.

Although predation gradients have been found to influence invasibility at local and regional scales (e.g. Osman & Whitlatch 2004, de Rivera et al. 2005, Cheng & Hovel 2010), variability in the colonization of subtidal habitats by non-native invertebrates at larger spatial scales (Simkanin et al. 2012) may like-

wise be driven by differences in predation pressure. Consumptive biotic resistance to invasion has been found to be greater at lower latitudes (Freestone et al. 2013, Kimbro et al. 2013), which are known to have more diverse predator communities (Hillebrand 2004). Biotic resistance may also vary among geographic regions that differ in predator diversity and abundance. For instance, on the Atlantic coast of North America, in Long Island Sound, the distribution of *Didemnum vexillum* is thought to be controlled by competitive interactions and the availability of open space rather than through direct predation (Osman & Whitlatch 2007, Janiak et al. 2013). Unusually for invasive tunicates, this species can also reach great abundances in deep water (Mercer et al. 2009). In New Zealand, however, *Didemnum vexillum* is prevented from invading natural rocky habitats by predation (Forrest et al. 2013), and there is evidence from our study and other studies that this species is consumed on the Pacific coast of North America (Epelbaum et al. 2009). In Bodega Harbor, *Didemnum vexillum* was not dominant at either of our study sites and did not differ significantly in cover between sites, perhaps suggesting that competition with other non-native tunicates limits establishment on docks, but predation limits establishment in rocky subtidal.

Although the Pacific coast has more total invasions than the Atlantic coast (Ruiz et al. 2000, Preisler et al. 2009), we hypothesize that the Atlantic coast has lower resistance to invasion in nearshore environments outside of floating artificial structures because of a more depauperate predator fauna. In New England, non-native tunicates such as *Botrylloides violaceus* and *Didemnum vexillum* can be abundant in shallow subtidal and low intertidal habitats (Harris & Tyrrell 2001, Bullard et al. 2007, Valentine et al. 2007, Miller & Etter 2008) but are rarely seen in equivalent habitats on the Pacific coast (Wasson et al. 2005, Pister 2009). The possibility that this could reflect geographic differences in consumptive biotic resistance warrants additional investigation.

In summary, we add to the evidence that an abundant, diverse predator fauna in benthic habitats that is lacking on docks and marinas contributes to the greater abundance of non-native species on floating artificial substratum. The loss of consumers from rocky subtidal communities may compromise their ability to resist invasion. Conversely, cultivating a diverse predator fauna on docks has the potential to reduce the establishment and proliferation of introduced species on these structures. However, the factors determining the distribution and abundance of these predators is not clear and may preclude their establishment.

Acknowledgements. This research was supported by NSF REU grant #DBI-04-53251 from the National Science Foundation to S. L. Williams. Field assistance for subtidal surveys and experimental deployment was provided by K. Aquilino, A. Chaudoin, and K. Hultgren. Comments and suggestions from 3 anonymous reviewers and the editor (R. Osman) improved the manuscript. This publication is a contribution of the Bodega Marine Laboratory, University of California, Davis.

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Editorial responsibility: Richard Osman,
Edgewater, Maryland, USA

Submitted: August 10, 2015; Accepted: January 12, 2016
Proofs received from author(s): February 26, 2016