Limiting resources in sessile systems: food enhances diversity and growth of suspension feeders despite available space

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Abstract. Much of our understanding of competition comes from observations in sessile systems, such as rainforests and marine invertebrate communities. In terrestrial systems, sessile species often compete for multiple limiting resources (i.e., space, light, and nutrients), but in marine systems, space is viewed as the primary or sole limiting resource. Competition theory, on the other hand, suggests that competition for a single limiting resource is unlikely to maintain high species diversity, but manipulative tests of competition for other resources in marine benthic systems are exceedingly rare. Here, we manipulate the availability of food for a classic system, marine sessile invertebrate communities, and investigate the effects on species diversity, abundance, and composition during early succession as well as on the growth of bryozoan populations in the field. We found the number of species to be greater, available space to be lower, and the community composition to be different in assemblages subjected to increased food availability compared to controls. Similarly, laboratory-settled bryozoans deployed into the field grew more in the presence of enhanced food. Our results suggest that food can act as a limiting resource, affecting both diversity and abundance, even when bare space is still available in hard-substratum communities. Consequently, broadening the view of resource limitation beyond solely space may increase our understanding and predictability of marine sessile systems.

Key words: benthic systems; biodiversity; Bugula neritina; *coexistence; food availability; marine invertebrates; resource competition; sessile species; sessile systems; species diversity.*

INTRODUCTION

Competition theory in ecology is based on the relative use of resources by species as well as the role of abiotic factors influencing resource availability. There are two main modes of competition, interference competition and exploitative competition, both of which may be influenced by abiotic processes. Interference competition refers to the direct effects of one organism on another, while exploitative competition is the indirect effects whereby an organism reduces resource availability for other organisms (Birch 1957). Many theories on these two forms of competition, both traditional and contemporary, are derived from observations and manipulative experimentation on sessile species, mainly terrestrial plants and marine benthic invertebrates (Grime 1973, Tilman 1982, Schoener 1983). One fundamental characteristic of sessile organisms is that they are immobile and therefore commonly assumed to compete for space to live on in both terrestrial and aquatic systems (Connell 1961, Dayton 1971, Keough 1984). Resources are considered limiting if an insufficient supply limits the growth, abundance, or distribution of an organism or a

population of organisms in an ecosystem (Vance 1972, Smith and Smith 2005, Loreau 2010). Space, i.e., available substrata, is therefore considered a limiting resource in sessile communities. In terrestrial sessile systems, competition for space by plants is most often considered together with competition for other limiting resources, such as water, light, and nutrients (Schoener 1983). Consequently, the predominant view of competition in this system is exploitative and the prevalent equilibrium-based models predict that dominance is achieved by the organism that has the lowest resource requirements for maintaining a stable population (Tilman 1982). Similarly, coexistence theory based on terrestrial sessile systems predicts that, at equilibrium, the maximum number of coexisting species is equal to the number of limiting resources (Tilman 1982) and the community as a whole exploits the resources more efficiently than would either species alone, yielding higher total production (Loreau 2010). In marine systems, however, sessile invertebrates are considered to be limited primarily by space, while competition for other resources is considered to be minor or nonexistent (Dayton 1971, Levinton 1972, Schoener 1983, Sousa 2001, Stachowicz et al. 2002). Interestingly, the study of competition in studies of plants and sessile marine invertebrates followed similar trajectories, but has

progressed further in plants than in studies of sessile marine invertebrates.

Studies of both plant and sessile marine invertebrate communities first inferred competition for limiting resources from circumstantial and anecdotal observations. For example, in the 1970s, numerous studies showed that plant growth rates increased when competitors were removed and competition was, therefore, inferred (Abul-Fatih and Bazzaz 1979, Fowler 1981, Hils and Vankat 1982). In marine systems, direct competition for space was observed as species overgrew each other, causing reduced growth and mortality (Dayton 1971, Buss 1979). In plants, the resources under competition were only unequivocally identified when Tilman began a series of experiments that directly manipulated the availability of resources (see Tilman 1984). Through these manipulations, a multivariate view of resource competition in plants emerged that persists today (Harpole and Tilman 2007, Farrior et al. 2013, Ferguson et al. 2013). Meanwhile, in studies of sessile marine invertebrate competition, it was noted that competition for resources other than space, such as food and oxygen, could occur, but direct manipulations of these resources has never been done. Consequently, space as a limiting resource remains the dominant and textbook view of competition in this system (Witman and Dayton 2001).

Challenges to the view that space is the primary, or sole, limiting resource in sessile marine invertebrate systems are becoming more common because noncontact competition can be intense among sessile species, despite the presence of free space (e.g., Myers 1990, Côté et al. 1994, Dalby 1995, Lohse 2002, Marshall and Keough 2003, Clark and Johnston 2009, Hart and Marshall 2013). Recent studies have shown that manipulations of flow velocity and the direction of currents can affect the growth of sessile species as well as the diversity of hard-substratum assemblages, regardless of available space (Lohse 2002, Palardy and Witman 2011, 2014). Furthermore, numerous studies have shown that reduced growth occurs when population densities increase, even when free space is abundant (Dalby 1995, Marshall and Keough 2003, Hart and Marshall 2013) Clearly then, density dependence can occur in this system even when space is available, but manipulations of the resources under competition have not been done, and so the resources under competition (e.g., food or oxygen) have not been tested. In the absence of such manipulations, the mechanisms that are driving the effects of interest remain unclear. For example, reduced growth rates at higher densities could be driven by allelopathic effects rather than resource limitation. Similarly, the effects of increased flow could be driven by the increased delivery of recruits rather than resource limitation (Palardy and Witman 2014). As such, our understanding of competition in this classic system remains incomplete because of the absence of direct manipulations of resource availability.

In this study, we manipulated the availability of planktonic food in a filter-feeding marine invertebrate community during early succession and examined its effects on assembly. We also tested the effects of food on laboratory-settled, field-deployed populations of a bryozoan at different densities to determine whether the effects interacted with consumer density.

MATERIALS AND METHODS

Experimental design

The study was carried out at the Royal Brighton Yacht Club, Melbourne, Australia (37°54′19.08″ S, 144°58′51.94″ E), which has 240 berths, an area of 200 × 400 m, and is 3–4 m deep. The sessile communities in the marina are dominated by the tunicates, *Pyura stolinifera* and *Ascidiella aspersa*; the mussel, *Mytilus eduli*; as well as the tube worms, *Sabellastarte australiensis* and *Sabella spallanzani*. Common epibionts include the encrusting polychaetes, *Ficopomatus enigmaticus*, *Hydroides elegans*, and *Pomatocerus taeniata*; the encrusting bryozoan, *Watersipora subtorquata*; and arborescent bryozoans from the *Bugula* genus.

We modified an existing experimental approach that uses dental plaster blocks as slow-dissolving medium for releasing heavy metals (e.g., copper), which has very localized effects immediately surrounding the block (Johnston and Webb 2000). We used this approach, but mixed plaster blocks that contained planktonic food rather than heavy metals. The four different treatments of food availability in this study were labeled "green," "mix," "orange," and "control." The control consisted solely of Gyprock dental plaster (CSR, North Ryde BC, Australia) and provided no food for our organisms. The treatments green, mix, and orange were mixtures of food sources. Each food block had a volume of 30 mL and the ratio of dental plaster was 100 parts plaster to 70 parts water, by mass, as per the manufacturer's instructions. Treatment green consisted of the food source Reef Phytoplankton (Seachem, Madison, Georgia, USA), containing several species of phytoplankton (*Thalassiosira weissflogii*, *Isochrysis* sp., and *Nannochloropsis* sp.), ranging in size from 1 to 20 μm, concentration is $1.8 \times 10^3 \pm 5.4 \times 10^1$ cells/mL ($n = 10$ samples counted; mean ± SE). Treatment orange consisted of the food source NutraPlus Reef Feed (Nutra-Kol, Mullaloo, Australia), containing both microalgae and rotifers (*Brachionus plicatilis*, *Dunaliella salina*, and *Nannochloropsis* sp.) ranging in size from 3 to 200 μm, concentration is $2.9 \times 10^4 \pm 3.2 \times 10^3$ cells/mL ($n = 10$ samples counted; mean ± SE). Treatment mix consisted of 50% of each food type. The size ranges of the planktonic species in our food treatments is within the range of preference in particle size of the sessile species in our experimental communities (Okamura 1984, Lesser et al. 1992). In order to achieve appropriate hardening of the dental plaster for treatment orange, food blocks were mixed with 50% water and 50% NutraPlus Reef Feed. All food blocks were replaced

FIG. 1. Experimental design of (A) settlement plates with food cages (green) on a PVC panel, (B) laboratory-settled *Bugula neritina* with food cages (mix) on a PVC panel, and (C) food block (control) with dismantled food cage.
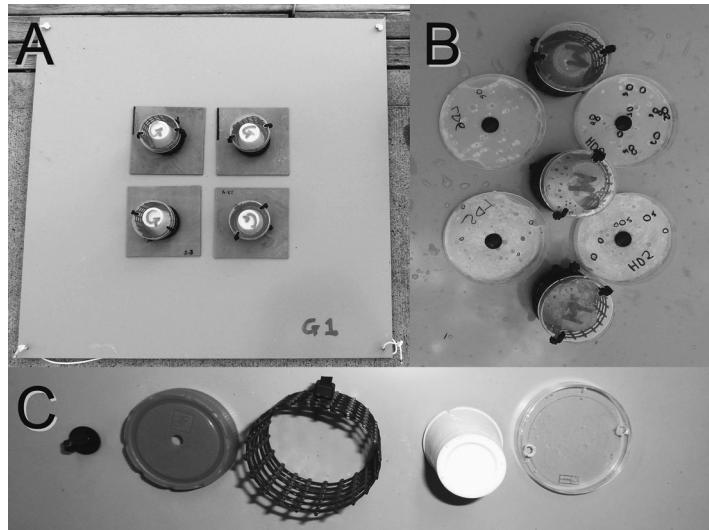
after two weeks in the field. The initial masses of food blocks were 52.36 ± 2.42, 55.43 ± 1.13, 59.54 ± 0.85, and 56.30 ± 1.11 g ($n = 12$ blocks), compared to 0.030 ± 0.030, 0.053 ± 0.036, 1.28 ± 0.39, and 1.63 ± 0.38 g after two weeks in the field for treatments control, green, mix, and orange, respectively. As such, we released an average of $5.3 \times 10^4 \pm 1.6 \times 10^3$, $4.6 \times 10^5 \pm 4.9 \times 10^4$, and $4.3 \times 10^5 \pm 4.8 \times 10^4$ cells into the area immediately surrounding the blocks for the green, mix, and orange treatment, respectively.

For the community experiment, PVC plates ($100 \times 100 \times 6$ mm) were fastened in groups of four on PVC panels ($550 \times 550 \times 8$ mm) and equipped with a small cage containing a block of food, either green, mix, orange, or control (Fig. 1). Each PVC panel contained four settlement plates with the same food treatment and three panels were assigned to each food treatment, with a total of 12 panels and 48 plates being deployed in the field. The food cages were made from plastic garden mesh (mesh size 10×10 mm) shaped in a cylinder form with a PVC lid (with an outer diameter of 50 mm) in the bottom and a Petri dish as a lid (outer diameter 55 mm) on the top. The area of a plate occupied by a food cage was omitted from the calculations of free space in the analyses. The panels were put at a depth of 1.5 m. After four weeks in the field, the plates were brought back to the laboratory in cooler boxes filled with seawater. Each plate was photographed at high resolution (5184×3456 pixels, 18 megapixels) with a CANON 600D (Canon, Melville, New York, USA) for species identification and quantification using the program Coral Point Count (CPCe v. 4.1; Kohler and Gill 2006).

For the density experiment, the number of laboratory-settled bryozoan, *Bugula neritina*, was a continuous variable in the design and varied randomly between four and 30 individuals per experimental unit. Adult colonies of *B. neritina* were collected in the field and conditioned in darkness overnight in a constant temperature room

(17°C), whereafter a light was positioned to shine on the colonies in order to induce spawning. The released larvae of *B. neritina* were collected individually with a plastic pipette and transferred to Petri dishes (outer diameter 95 mm). The Petri dishes were transported to the marina in a cooler box filled with sea water and attached to PVC panels ($550 \times 550 \times 8$ mm), which in turn were attached to an attenuator at a depth of 1.5 m. Four Petri dishes with a random density of *B. neritina* individuals were attached to each PVC panel. Unlike the setup for the settlement plates, the cages with food blocks were positioned three in a row between two pairs of Petri dishes (Fig. 1). This way each Petri dish was equidistantly adjacent to two food blocks. The growth of *B. neritina* was quantified in the field by counting the bifurcations of each individual (Keough and Chernoff 1987) and the number of surviving individuals per Petri dish was counted.

Statistical analyses

Data on the species diversity and available space (free substratum) of the experimental assemblages of the settlement plates was statistically analyzed using a two-way analysis of variance (ANOVA) using Statistica v. 6.0 (Statsoft, Tulsa, Oklahoma, USA) with the food availability treatment as a fixed factor with four levels, and panel as a nested random factor with three levels. The same factorial design was used for the multivariate analyses with permutational multivariate analysis of variance (PERMANOVA) using the PRIMER software package (PRIMER-E, Plymouth, UK). Data on the total biomass and average colony biomass of laboratory-settled *B. neritina* in the field was statistically analyzed using a three-way analysis of covariance (ANCOVA), with food availability treatment as a fixed factor with four levels, panel as a nested random factor with three levels, and initial density used as a covariate. Prior to all statistical analyses, data were tested for

TABLE 1. Abundance of sessile invertebrate and algal species present in the experimental assemblages subjected to different treatments of food availability.

Species	Control	Green	Mix	Orange
			Treatment	
Chlorophyceae				
Ulva sp.	0	0	0.16 ± 0.16	0
Cnidaria				
Hydroidae sp.	0	0	0.80 ± 0.37	0
Annelida				
Serpulidae sp.	39.86 ± 3.29	37.66 ± 2.30	43.11 ± 3.29	33.65 ± 2.21
Crustacea				
Balanus sp.	16.26 ± 2.54	19.55 ± 1.86	9.29 ± 1.08	14.90 ± 2.83
Elminius sp.	4.55 ± 0.71	5.45 ± 1.08	2.72 ± 0.60	4.57 ± 1.20
Corophium sp.	0.87 ± 0.38	1.12 ± 0.44	2.24 ± 0.78	2.16 ± 1.23
Mollusca				
Anomia sp.	0.17 ± 0.17	0.16 ± 0.16	0	0
Bryozoa				
Bugula flabellata	0.87 ± 0.67	1.92 ± 0.63	0.96 ± 0.37	0.24 ± 0.24
Bugula neritina	0	2.08 ± 0.73	1.92 ± 0.47	1.44 ± 0.31
Bugula stolinifera	0.70 ± 0.67	0.16 ± 0.16	2.88 ± 1.31	2.88 ± 0.96
Watersipora subtorquata	0.70 ± 0.37	0.16 ± 0.16	0.32 ± 0.22	0
Chordata				
Botryllidae sp.	9.44 ± 1.89	11.38 ± 1.19	16.19 ± 2.42	20.67 ± 2.05
Ciona intestinalis	0.17 ± 0.17	0.96 ± 0.37	0	1.68 ± 0.57
Didemnidae sp.	1.75 ± 0.52	1.60 ± 0.57	1.44 ± 0.42	2.88 ± 1.09
Diplosoma listernium	5.24 ± 1.19	5.13 ± 0.80	9.13 ± 1.91	6.49 ± 1.40
Pyura stolinifera	0.52 ± 0.26	2.56 ± 0.96	1.12 ± 0.37	0.48 ± 0.31

Note: Values are means and SE.

homogeneity of variances with Cochran's C and the degrees of freedom for the nested factor panel were reduced by one, due to a lost panel in the field (Quinn and Keough 2002). Furthermore, the covariate ranges in the ANCOVA analyses followed the criteria outlined in Quinn and Keough (2002). The abundance data for the multivariate analyses was transformed to the fourth root, in order to avoid bias by the greater influence of abundant species (Clark and Warwick 1994). Post hoc tests of differences among means were analyzed using the Student-Neuman-Keuls test (SNK), a stepwise approach with low type I error rate, for the ANOVA (Quinn and Keough 2002). In order to visualize patterns of the multivariate tests, as well as identify differences in individual species' responses, canonical analysis of principal coordinates (CAP; Anderson and Willis 2003) was used as a constrained ordination procedure on appropriate terms found to be significant using PERMANOVA.

RESULTS

We found a total of 16 sessile species and/or genera in our experimental assemblages from a range of such different taxonomic groups as tunicates, bryozoans, barnacles, bivalves, amphipods, hydroids, polychaetes, and macroalgae (Table 1). There was a significant effect of food availability on species richness and free space in the experimental assemblages (Table 2). Post hoc analyses revealed that all treatments of increased food

TABLE 2. Analysis of variance (ANOVA) on effects of food availability on species richness and free space; permutational analysis of variance (PERMANOVA) on effects of food availability on community composition of marine sessile invertebrate assemblages; and analysis of covariance (ANCOVA) on effects of food availability and initial density on total biomass and average colony biomass of *Bugula neritina* in the field.

| Variables	df	MS	F	P
Richness				
Food	3	7.91	5.62	0.028
Panel(Food)	7	1.41	1.24	0.308
Error	32	1.13		
Cover				
Food	3	80.19	5.54	0.029
Panel(Food)	7	14.47	0.83	0.568
Error	32	17.36		
Multivariate				
Food	3	1139.90	2.25	0.021
Panel(Food)	7	506.27	1.62	0.019
Error	32	312.49		
Total biomass				
Density	1	4.324	81.62	0.000
Food	3	0.014	0.03	0.994
Density × Food	3	0.388	7.32	0.001
Panel(Food)	8	0.554	10.46	0.000
Error	31	0.053		
Average biomass				
Density	1	0.063	35.35	0.000
Food	3	0.013	0.78	0.539
Density × Food	3	0.006	3.46	0.028
Panel(Food)	8	0.017	9.34	0.000
Error	31	0.002		
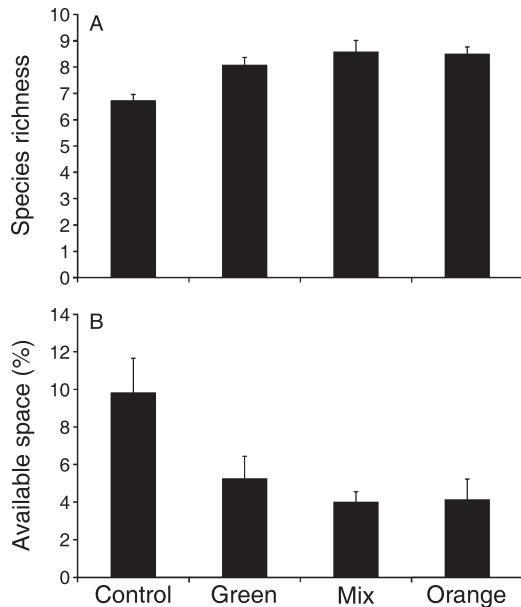
FIG. 2. Effects of increased food availability on (A) species richness and (B) amount of free space in natural sessile invertebrate assemblages. Values are means; error bars indicate SE.

availability were different from the control (SNK$_{Food}$, control $\neq$ green = mix = orange; SNK$_{Space}$, control $\neq$ green = mix = orange; $\alpha = 0.05$) showing higher species richness (Fig. 2A) and lower amounts of free space (Fig. 2B) compared to control. Similarly, the multivariate analysis showed that food availability significantly affected the composition of the experimental assemblages (Table 2), and post hoc analysis showed differences between control and mix, as well as between control and orange (post hoc analysis, control $\neq$ mix; control $\neq$ orange; control = green; green = mix = orange; $\alpha = 0.05$). Further graphical examination using CAP reflected the post hoc tests, with more apparent separation between control and mix as well as between control and orange than among other groups (Fig. 3). Individual species also showed dissimilar responses to the different treatments of food availability, and the responses of *B. neritina*, *Ciona intestinalis*, *Balanus* sp., and *Corophium* sp. were also reflected by their abundances in different treatments (Fig. 3, Table 1). In the density manipulation experiment, there was a significant interaction between food availability and the initial density of settlers on the total biomass as well as average colony biomass of laboratory-settled *B. neritina* in the field (Table 2). The total biomass of *B. neritina* in each population was greater in presence of food relative to controls, and the increase in biomass was greater for assemblages with higher initial density (Fig. 4A). The average size of individual colonies decreased with density, but average size was higher in the food treatments relative to controls (Fig. 4B).

DISCUSSION

In this study, we found empirical evidence for food as a limiting resource for sessile marine invertebrates regardless of available substratum. The number of species was greater, available space was lower, and the community composition was different in assemblages subjected to increased food availability compared to control, but there were no differences among types of food for either the uni- or multivariate analyses. There
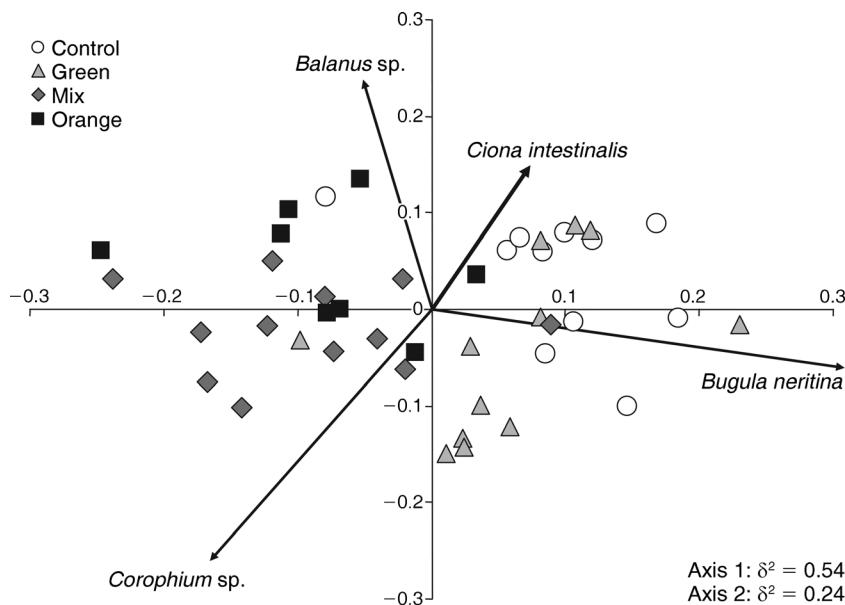

FIG. 3. Constrained canonical analysis of principal coordinates (CAP) plot on Bray-Curtis similarity comparing sessile assemblages among treatments of food availability (open circles show control, solid triangles show green, solid diamonds show mix, and solid squares show orange). Values shown for δ^2 are the squared canonical correlation coefficients.
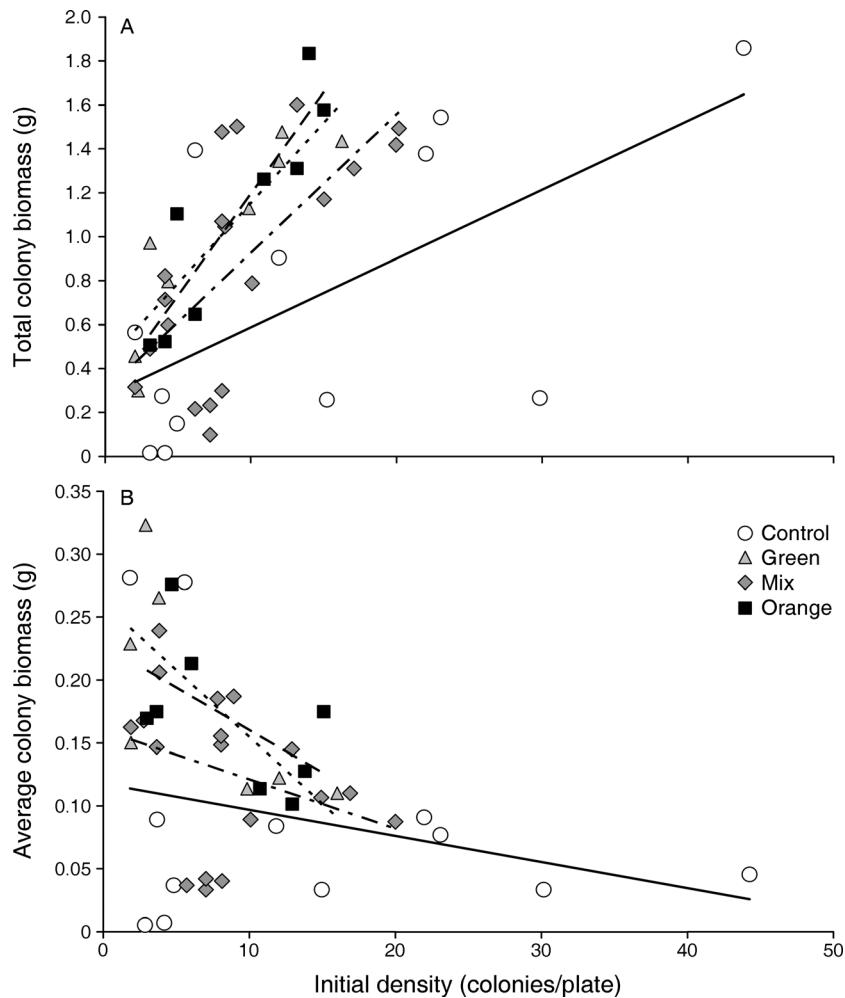
FIG. 4. Effects of increased food availability (open circles and solid line show control, solid triangles and dotted line show green, solid diamonds and dashed line show mix, and solid squares and dot-dashed line show orange) and initial density (covariate) on (A) total biomass and (B) average colony biomass of laboratory-settled *Bugula neritina* in the field.

was a significant interaction between food availability and initial density of laboratory-settled bryozoans in the field, showing an increase in total biomass that could be sustained in the presence of additional food. Hence, the effects of food availability on both recruitment of species and growth of established species in hard-substratum communities show that food can be a limiting resource during early succession in marine sessile systems.

Our findings mirror studies on multiple limiting resources in other systems (Tilman 1982, Farrior et al. 2013) and provide definitive proof for food-mediated competition in marine systems, as previously suggested by circumstantial evidence for many of the species in our experimental communities. For instance, the bryozoan, *Bugula stolinifera*, can affect the food-capturing capacity (i.e., number of latex beads) of colonies downstream in laboratory experiments (Okamura 1984) and the tunicate, *Botrylloides leachii*, has lower growth rates on settlement plates with competitors, despite a cleared

zone around the colonies to avoid space competition (Myers 1990). Noncontact intraspecific competition has also been reported in the tunicate, *Pyura stolonifera* (Dalby 1995), where individuals inside aggregations were smaller and lighter compared to outside aggregations, and Côté et al. (1994) observed decreased growth in high density assemblages with live scallops, *Placopecten magellanicus*, compared to those where nonliving scallops were added to occupy space but not compete for food resources. Similarly, the direction and velocity of currents have been shown to affect both the growth and diversity of sessile species assemblages regardless of available space (Lohse 2002, Palardy and Witman 2011, 2014). However, observed differences among communities experiencing different flow in the studies of Palardy and Whitman (2011, 2014) were solely attributed to propagule supply, while food supply was not considered and might have been an important driver of benthic diversity. Furthermore, the diminished growth rate of arborescent bryozoans (e.g., *Bugula* sp.) in the presence

of higher conspecific densities shown in this paper and many others (Allen et al. 2008, Hart et al. 2012, Hart and Marshall 2013) shows that when the population density approaches carrying capacity, growth rates decline even when free space is available. Consequently, these laboratory and field experiments convincingly show that resources other than space can be limiting in marine sessile systems, and our results show that food is one such resource.

Predictions of competition theory on community responses in biodiversity, unlike production (i.e., growth), to additions of limiting resources is not straightforward. On one hand, if the number of coexisting species equals the amount of limiting resources at equilibrium (Tilman 1982), additions of a resource in large amounts may make it non-limiting and therefore ultimately decrease diversity (Harpole and Tilman 2007). However, resource additions may also increase the carrying capacity of a community while still being limiting. For instance, the increase in available substrata through disturbance is a classic example in space-limited sessile systems (Sousa 2001). In such cases, both production and diversity, through recruitment, may initially increase (i.e., prior to established equilibrium), whereas strong interference competition over large timescales will likely result in competitive exclusion despite the added space. Similarly, in oxygen limited communities, where space is not limiting, oxygen additions have the potential to initially increase diversity as settlers are no longer prevented from establishment by hypoxia (Ferguson et al. 2013). In systems limited by food, additions of food may increase the carrying capacity of the community before it becomes non-limiting, which would lead to increase in both diversity and growth. However, in marine benthic systems, the effects of food limitation is likely stronger at early successional stages before all substrata is depleted, and space becomes limiting in accordance with Liebig's law of the minimum (Smith and Smith 2005). Nonetheless, noncontact competition for food in assemblages during early succession will determine initial community composition and therefore also long-term community trajectories.

The strength of competition for food in marine benthic systems is likely to vary and it remains unclear as to whether our findings are broadly representative. We conducted our experiments in the southeast of Australia, in waters that are oligotrophic relative to many marine systems worldwide. Adding food to such an environment is likely to have a large impact on competition and, thereby, growth and diversity of assemblages. It is yet unclear what the response of similar food treatments would be of sessile assemblages in eutrophic systems. Presumably, effect sizes would be smaller in more eutrophic systems, such as the rich Californian waters, but this awaits further testing. Similar to food resources, oxygen limitation will vary among systems and may be more likely in warmer

systems (Ferguson et al. 2013). Both oxygen and food limitation will also depend on flow conditions, where low flow conditions deliver low amounts of resources and too high flow will hamper species resource capturing abilities (Okamura 1984). Therefore, the limitation of resources in the water column for sessile species can be caused by either a de facto shortage or by abiotic factors causing a reduction in species resource capture. Another factor that may influence the strength of competition and the resources for which communities compete is the successional stage of communities (Schoener 1983, Sousa 2001). Our experimental assemblages were relatively young and, as such, our results show that food limitation has strong effects on growth and diversity of primarily establishing communities. However, many of the species in our study, such as spirorbids and bryozoans, can complete their entire life cycles within the time scale of our experiment (Keough and Chernoff 1987). Therefore, the noncontact competition for food in young assemblages may not only determine early winners and losers in community assembly but also community trajectories beyond the short term. Consequently, we need further studies on the specific mechanism as well as studies on resource limitation from multiple systems, preferably manipulation experiments comparative among habitats, to assess the generality of food limitation. Nonetheless, it is clear that both food and oxygen can limit sessile species proliferation even when substrata for settlement are readily available in marine communities.

One interesting aspect of experiments on multiple limiting resources in sessile systems is the possibility of resource interactions, which may create complex resource spectra. Space as a resource may interact with food on species' performances, because amount of occupied substrata has been suggested to be a surrogate for amount of food acquisition (e.g., Buss and Jackson 1981). However, the roles of competition for food and space may be more complex than they appear initially. First, sessile species' food capturing capacity depend on, among other factors, current velocity and neighboring individuals, both con- and heterospecifics (Okamura 1984, 1985, 1988). Access to food can increase for upstream individuals when velocity is low, which may deplete planktonic food before it reaches individuals downstream (i.e., exploitative competition; Okamura 1984). Conversely, if the flow velocity is high, upstream individuals encountering the moving water column may not be able to use their feeding apparatus, while their bodies reduce the flow velocity enabling individuals downstream to feed more efficiently (i.e., facilitation; Okamura 1985). Second, the amount of substrata may be a poor proxy for food acquisition because encrusting species and arborescent (i.e., upright) species differ in number of feeding zooids per area of occupied substrata, which may lead to differences in competitive strategy (Vance 1984). More specifically, the interference-competitive ability of encrusting species, such as *Watersipora*

spp., is accompanied with large space requirements, whereas arborescent species, such as *Bugula* spp., require little substrata and show high resource use efficiency (Hart and Marshall 2012). Consequently, an individual's or a species' access to food sources in the water column may not accurately be estimated by amount of occupied substrata alone, especially for comparisons among species with different growth forms; the interaction between these limiting resources is more complex.

Recognizing that resources other than space can be limiting for sessile species in marine systems may provide new insights. First, it may reconcile discrepancies between observations of highly diverse marine sessile assemblages and contemporary coexistence theory suggesting that one limiting resource is not sufficient to explain such large species diversity (Tilman 1982, Farrior et al. 2013, Ferguson et al. 2013). Second, a larger range of limiting resources may more accurately determine species' niche space, which is an assumption for coexistence mechanisms such as spatiotemporal niche creation (Pacala and Rees 1998, Farrior et al. 2013) and niche dimensionality, which has recently been shown to be a useful predictor of species diversity (Harpole and Tilman 2007). Third, a more complex view of marine sessile systems may explain more complex patterns. Even though there are no guarantees a complex model is more powerful than a simple one, it has the potential to accurately predict a more diverse set of conditions (Zucchini 2000). Hence, patterns in diversity that are not reconcilable with competition solely for space, could potentially be understood to a higher degree if competition for other resources, such as food and oxygen, are taken into account. It is clear from many excellent empirical and theoretical studies (Dayton 1971, Keough 1984, Sousa 2001 and references therein) that competition for space is vital in hard-substratum communities, but our study shows that even more patterns in diversity and species distribution may be explained and predicted if we broaden our view of limiting resources in marine sessile systems.

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