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Revisiting competition in a classic model system using formal links between theory and data

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Abstract. Formal links between theory and data are a critical goal for ecology. However, while our current understanding of competition provides the foundation for solving many derived ecological problems, this understanding is fractured because competition theory and data are rarely unified. Conclusions from seminal studies in space-limited benthic marine systems, in particular, have been very influential for our general understanding of competition, but rely on traditional empirical methods with limited inferential power and compatibility with theory. Here we explicitly link mathematical theory with experimental field data to provide a more sophisticated understanding of competition in this classic model system. In contrast to predictions from conceptual models, our estimates of competition coefficients show that a dominant space competitor can be equally affected by interspecific competition with a poor competitor (traditionally defined) as it is by intraspecific competition. More generally, the often-invoked competitive hierarchies and intransitivities in this system might be usefully revisited using more sophisticated empirical and analytical approaches.

Key words: *competition; response surface; Ricker model; sessile benthic marine invertebrates.*

INTRODUCTION

Competition is only one of many important processes affecting the distribution and abundance of species but it is a central element of some of the most challenging problems in ecology such as understanding species coexistence. Unfortunately, many arguments about the role of competition in population and community dynamics continue because of logical contradictions in conceptual theory (Chesson and Huntly 1997, Freckleton et al. 2009), and the use of empirical approaches that have limited inferential power (Freckleton and Watkinson 2000, Inouye 2001, Damgaard 2008). If further progress is to be made, more sophisticated empirical and analytical approaches should be applied and, ideally, unified.

Further progress in understanding competition will be made when competition theory is formally linked to data (e.g., Levine and HilleRisLambers 2009). Surprisingly however, formal links between competition theory and data are extremely rare (Inouye 2001, Freckleton et al. 2009). This rarity is because traditional empirical approaches cannot be used to estimate competition parameters in units appropriate to mathematical theory (Inouye 1999). For example, common experimental designs such as neighborhood-removal experiments, and substitutive and additive experimental designs (Damgaard 1998, Gibson et al. 1999, Jolliffe 2000), largely restrict inference to estimating the magnitude of competition in terms of simple effect sizes. Furthermore, while density-independent, neighborhood-removal experiments focus on competitive effects on individuals, much competition theory focuses on competitive outcomes among populations (e.g., Lotka-Volterra models). Additive and substitutive designs do investigate competition over a range of densities; additive designs hold the density of a focal species constant while varying the density of the competitor, while substitutive designs manipulate the proportion of competitors at a single, fixed total density (see Inouye [2001] for details). However, inferences from both these designs are restricted to the intrinsically limited densities at which the experiment occurs. This is a major problem because competitor densities vary widely in nature and competitive effects can be nonlinear functions of density (Law and Watkinson 1987, Damgaard 2008). These features of real communities restrict the parameter space over which inference can be made thereby adding an extra layer of contingency to the results of traditional competition experiments.

Response-surface experiments are a powerful alternative that have several advantages over traditional approaches for studying competition (Inouye 2001, Damgaard 2008). Response-surface designs require manipulating competing species across a range of density combinations such that each species occurs at both different densities and relative abundances (Appendix A: Fig. A1). Such a design replicates the

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experience of species in real communities where species densities and relative abundances can take a wide range of values in space and time. Another major advantage of this approach is that data generated can be fit to nonlinear, theoretical models of competition (Inouye 2001). While rarely done, this allows simultaneous estimation of intra- and interspecific competition coefficients and density-independent rates of increase: the population-level parameters that are directly relevant to population dynamic outcomes (Damgaard 1998). Despite the significant advantages of response surface designs over traditional methods, and compelling recommendations for their use (Inouye 2001, Damgaard 2008), their use in the field is highly limited.

Nowhere are more sophisticated approaches to studying competition likely to be more important and useful than in benthic marine environments. This is because early studies of competition in these systems include seminal contributions on which a large portion of our current understanding of the role and context-dependent importance of competition is based (Connell 1978, Sutherland 1981, Paine 1984, Connell and Keough 1985). For example, early studies of competition in these communities provide the empirical foundation for demonstrating opportunities for coexistence as a consequence of intransitive competition (Buss 1980, 1986, Frean and Abraham 2001, Laird and Schamp 2006, Rojas-Echenique and Allesina 2011).

Benthic marine invertebrate assemblages have been important for competition research because competition has been considered a fundamentally simple and easily observable interaction in these systems (Buss 1990). Indeed, the advantages of the system for studying competition have, and should continue to provide formidable opportunities for general ecological understanding (e.g., Stachowicz et al. 1999). However, the impression of simplicity has also often resulted in simple assessments of competition, with a focus on interactions among individuals and the assumed primacy of competition for a single limiting resource (space) via obvious mechanisms (interference via overgrowth). In contrast, very little is known about the population-level consequences of competition, or the aggregate effects of multiple limiting resources and multiple competitive mechanisms. Furthermore, while the ratio of intra- to interspecific effects is fundamental to competitive coexistence (Chesson 2000), studies of competition among sessile invertebrates (and more generally, Siepielski and McPeek [2010]) rarely estimate intraspecific effects to "ground truth" the strength of interspecific effects. Indeed, how competition changes across a range of conspecific and heterospecific densities has, to our knowledge, not been assessed in this system. These critical information gaps have important implications given that model systems such as these are relied upon theoretically and empirically to solve derived ecological problems.

Here we begin to redress these issues and apply one framework for doing so. We assess competitive population dynamics in the field between two species of benthic invertebrates that are prominent members of this classic model system. We take a deliberately and explicitly phenomenological approach to quantify the aggregate effects of competition as well as density independent processes on population dynamics. Importantly, we make no assumptions about mechanisms of competition, nor are such assumptions necessary for our approach. In a rare example of this approach more generally, and a first for this system, we use data generated from a response surface experiment to parameterize a common mathematical model of competition to quantify the nature of the interactions between these species and to formally estimate density independent rates of increase and intra- and interspecific competition coefficients.

MATERIALS AND METHODS

Focal species and scope of the study

We quantitatively describe competition between a cohort of genetic individuals (i.e., colonies) of two common species of benthic marine bryozoans, *Watersipora subtorquata* and *Bugula neritina* (henceforth *Watersipora* and *Bugula*) in Queensland, Australia. *Watersipora* is an encrusting bryozoan that grows horizontally across the substratum and has large requirements for space whereas *Bugula* is an arborescent bryozoan with a small attachment to the substratum and therefore a small requirement for space (Hart and Marshall 2012). Traditional conceptual models of competition in these assemblages would predict that the dominant competitor for space, *Watersipora*, should outcompete *Bugula* through overgrowth (Jackson 1977, McKinney and Jackson 1991), and we have observed individuals of *Watersipora* overgrowing individuals of *Bugula* at our field site. We quantify competitive dynamics between the benthic stages of these species in early successional assemblages where these species are dominant. Competition among non-feeding planktonic larvae is unlikely, but we do not consider competition between settling larvae and adults however, and this is an important caveat to our results. The potential for population growth of our study species is defined in terms of production of larvae. Additional important details of the life histories of our study species and the community dynamics at our field site are provided in Appendix A.

Experimental methods

We assessed competition by manipulating the densities of both species according to a factorial, response surface experimental design (Inouye 2001). We used standard methods to collect recruits for the experiment that were less than five days old, and to manipulate recruit densities (Hart and Marshall 2009, 2012). The recruits should reflect natural size variation of recruits to bare space in these habitats. We attached recruits of each species haphazardly on 60 mm diameter (28.27 cm^2), plastic Petri dishes according to 15 different density combinations that covered a range of densities of both species that occur naturally in the field (0, 3, 6, and 12 individuals of both species in all possible combinations; Appendix A: Fig. A1). We replicated each density combination five times such that one full set of density combinations (i.e., 15 different Petri dishes with recruits attached) was attached to one of five different, PVC backing panels (400 × 400 × 6 mm) using small pieces of hook-and-loop fastener. Each backing panel was suspended from floating pontoons at 1 m depth, with Petri dishes facedown to prevent sedimentation and UV exposure. Competition occurred in the field where other biotic (e.g., settlement and growth of other species, predation) and abiotic factors (e.g., disturbance, water flow) were allowed to vary naturally.

We measured mortality, size (i.e., as a consequence of vegetative growth) and fecundity (embryo production) of all colonies after one, two, four, and seven weeks in the field. Our main response variable for parameterizing the competition model was per capita (i.e., per initial recruit density), species-specific, sexual reproductive output (i.e., embryo production) within each density combination over the duration of the experiment. For *Watersipora*, at each survey time we removed each Petri dish from the water and took a high-resolution digital photograph of all colonies. We then used image processing software (ImageJ; Rasband 1997–2008) to count well-developed embryos within each colony; embryos in *Watersipora* are visible as spherical pink structures behind zooid frontal walls (Hart and Keough 2009). We used the same images and software to measure colony size and mortality. Embryos in *Bugula* are brooded in specialized zooids called ovicells. Because it is difficult to count all ovicells, at each survey time we estimated fecundity by counting ovicells along the longest and shortest branch (to account for any gross asymmetry in colony morphology) of each colony. This estimate of fecundity is a good predictor of the reproductive capacity of an individual (Marshall et al. 2003). Size of *Bugula* colonies was estimated by averaging the number of bifurcations along the longest and shortest branches within a colony, and then converting these counts to zooid number using a standard relationship (Keough and Chernoff 1987).

Analytical methods

Our goals were to (1) describe competitive dynamics between a single cohort of genetic individuals of these species by specifying a theoretical, phenomenological competition model that describes the interactions; (2) estimate density-independent rates of increase and intra- and interspecific competition coefficients for each species; and (3) determine how changes in size and survival of individuals in response to competition may have contributed to the population-level outcomes. Additional details of our approach, analytical methods, and important assumptions are provided in Appendix A.

To describe competition between *Watersipora* and *Bugula* we fit our experimental data to a modified Ricker model (Ricker 1954, May 1974)

$$\frac{N_{t+1}}{N_t} = \lambda e^{-\alpha_{ii}N_i - \alpha_{ij}N_j}$$

where N_t is the initial density of recruits, N_{t+1} is the total reproductive output (embryo production) at the end of the experiment, λ is the density independent growth rate, N_i and N_j are initial conspecific and heterospecific densities, respectively, and α_{ii} and α_{ij} are the intra- and interspecific competition coefficients, respectively. We used the sum of our estimates of per capita fecundity at weeks one through seven as the response variable in our analyses. We fit the data to the model using nonlinear least-squares estimation. To determine the explanatory power of the parameters in our model, we compared full and reduced models with likelihood-ratio tests. Profile-likelihoods were used to calculate 95% confidence intervals on parameter estimates (Venables and Ripley 2002).

Final model fits were assessed using lack-of-fit tests where we used an approximate F test to compare the mean-squared deviations from the model fits to the pure error mean square calculated from a linear model that included separate terms for each density combination (Law and Watkinson 1987, Inouye 1999, Ritz and Streibig 2008). We also assessed the quality of the linear approximation assumption using estimates of intrinsic and parameter-effects curvature (Venables and Ripley 2002). To detect differences in the magnitude of intra- and interspecific effects, we used the delta method (Ritz and Streibig 2008) to calculate the difference between α_{ii} and α_{ij} (i.e., intra- and interspecific effects on a single focal species) and then compared this estimate to zero (i.e., a null hypothesis of no difference) using a one-sample location, two-way approximate Z test.

We assessed the effects of competition on colony size and colony survival to determine how these variables contributed to population-level outcomes. *Watersipora* survival was high (>84%) across all separate and combined densities of both *Watersipora* and *Bugula* (i.e., density combinations) so was not formally analyzed. We assessed survival of *Bugula* using a GLMM with binomial errors and a logit link. *Bugula* and *Watersipora* densities were fixed and backing panel was an additive, random term. Models were simplified using log-likelihood ratio tests (random terms were left in the model). We also assessed the effect of competitor density on average colony size of *Watersipora* after seven weeks using multiple-linear ANCOVA with backing panel included as a random effect and *Watersipora* and *Bugula* densities as covariates. We did not repeat this analysis for *Bugula* because of high levels of density-independent

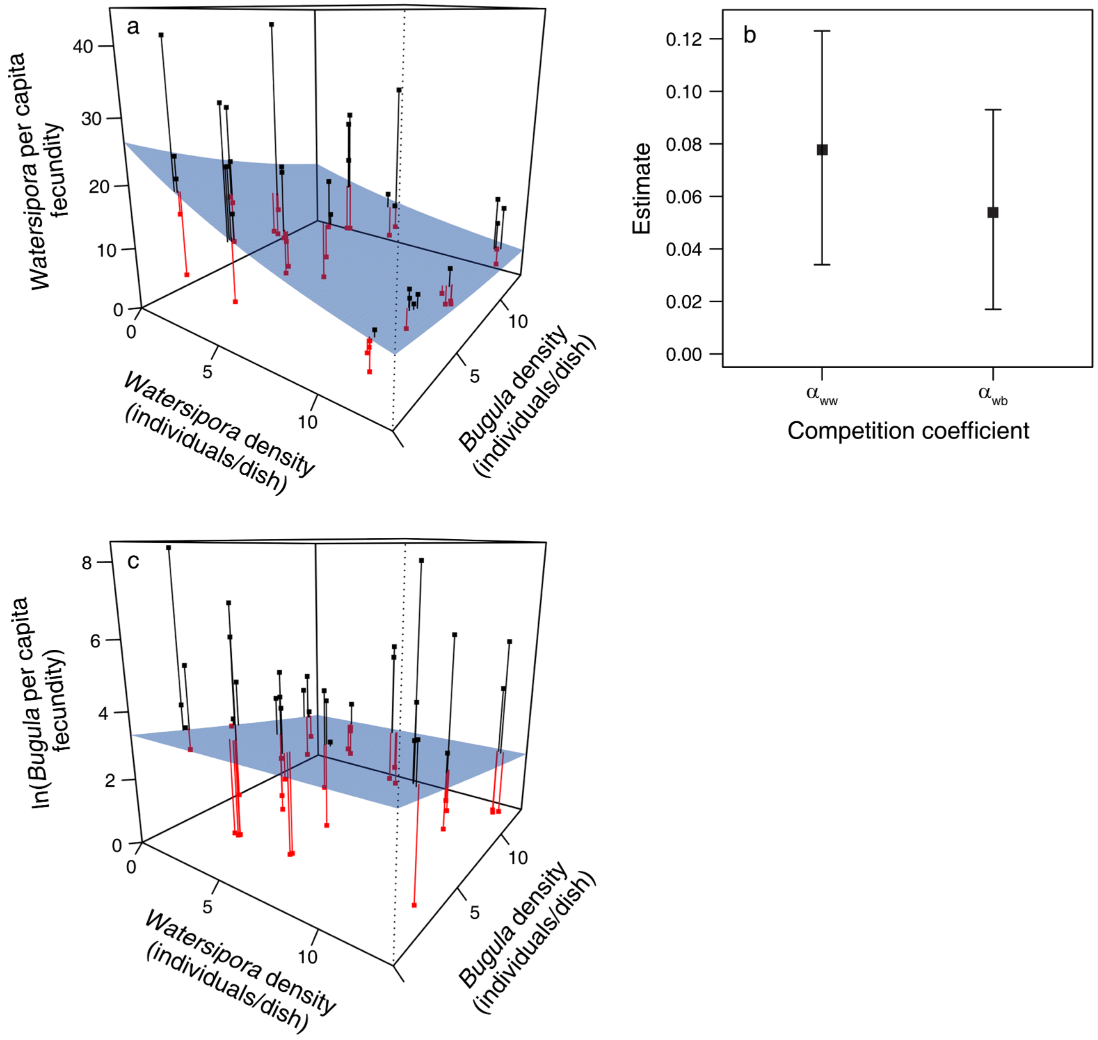

FIG. 1. Competitive population dynamics of *Watersipora subtorquata* and *Bugula neritina*. (a) Population-level effects of intra- and interspecific competition in *Watersipora*. (b) Estimates and 95% profile likelihood confidence intervals of the intra- and interspecific competition coefficients for *Watersipora*. The subscripts on α on the x-axis indicate species identity: w, *Watersipora*; and b, *Bugula*. (c) Population-level effects of intra- and interspecific competition in *Bugula*. In panels (a) and (c), points are observed values, and the surface is the predicted relationship from the fitted competition model. Actual estimates, including estimates of λ and model diagnostics, are provided in Appendix B.

mortality in this species across all density combinations. Analyses were done in R, version 2.13.0 (R Development Core Team 2011).

RESULTS

Model fitting and parameter estimates

The Ricker model adequately described competition between *Watersipora* and *Bugula* (Fig. 1, Appendix B). Residual plots indicated good model fits and lack-of-fit tests were nonsignificant for both species (*Watersipora* $F_{9,48} = 0.437$, $P = 0.908$; *Bugula* $F_{9,48} = 0.972$, $P = 0.474$). Linear approximation assumptions were somewhat high for both species (*Watersipora* parameter effects 0.50, intrinsic effects 0.05; *Bugula* parameter effects 2.24, intrinsic effects 0.05; values >0.3 are generally considered high). Inspection of plots of the profile-t functions for each parameter can be used to determine the direction in which the linear approximation may be misleading (Venables and Ripley 2002: section 8.5). High values of parameter effects curvature were associated with estimates of λ, although the effects were minor for *Watersipora*. For *Bugula*, the model ultimately simplified to a linear, constants-only model so this assumption did not apply.

Watersipora and *Bugula* had significant negative effects on *Watersipora* population growth (Fig. 1, Appendix B; λ $F_{1,57} = 213.8$, $P < 0.001$; α_{ww} $F_{1,57} = 12.9$, $P < 0.001$; α_{wb} $F_{1,57} = 8.6$, $P = 0.005$). There was no difference between the strength of intra- and interspecific competition on *Watersipora* ($z = 0.823$, P

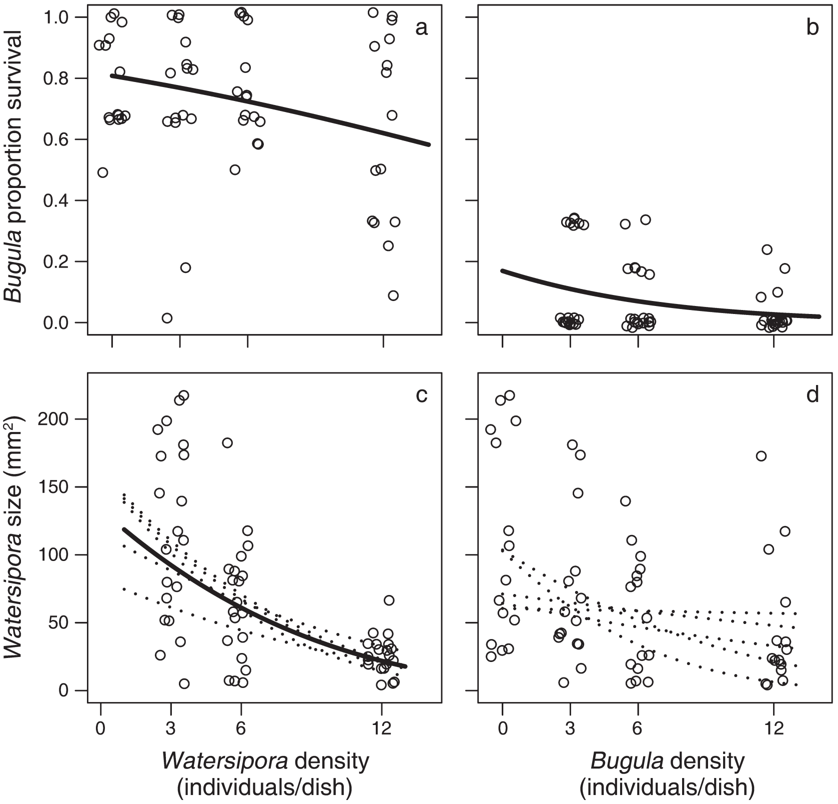

FIG. 2. The effect of competition on (a, b) survival in *Bugula* and (c, d) size in *Watersipora*. Panels (a) and (b) show effects of competition on mortality of *Bugula* as a consequence of *Watersipora* density at week one, and *Bugula* density at week seven, respectively. Panels (c) and (d) show the effect of *Watersipora* and *Bugula*, respectively, on per capita final colony size. Circles are observed values, solid lines are predicted values from model fits, and dashed lines in panels (c) and (d) indicate results for individual backing panels. No main effect of density is shown in panel (d) because of a significant density × backing panel interaction (Appedix C).

= 0.41; Fig. 1b, Appendix B). Competitive population dynamics of *Bugula* were best described by a constants-only model, including only a parameter (λ) for density-independent increase (Fig. 1, Appendix B; α_{bb} $F_{1,57} = 0.073$, $P = 0.788$; α_{bw} $F_{1,57} = 2.578$, $P = 0.114$).

The influence of colony survival and colony size on aggregate responses

Bugula population dynamics were dominated by high levels of mortality across all density combinations (Fig. 2a, b). *Watersipora* density negatively influenced early mortality of *Bugula* (effect of *Watersipora*, week 1, $\chi^2 = 9.73$, df = 1, $P = 0.002$; Fig. 2a) and there was a weak negative effect of *Bugula* on its own mortality by the end of the experiment (effect of *Bugula*, week 7, $\chi^2 = 7.98$, df = 2, $P = 0.019$; Fig. 2b). Universally high levels of mortality across density combinations suggest substantial density-independent mortality in *Bugula* (Fig. 2b).

Both *Watersipora* and *Bugula* had negative effects on average colony size in *Watersipora*. Effects of *Watersipora* were consistent across backing panels, whereas the strength of the effect of *Bugula* varied among backing panels (Fig. 2c, d, Appendix C). Because of high levels of mortality, it was only possible to assess the effect of competition on colony size in *Bugula* during the earlier weeks. There was a significant negative effect of *Watersipora* on average colony size of *Bugula* at week one, but no effect by week two (Appendix C).

DISCUSSION

Despite decades of research on competition in marine environments in general, and sessile invertebrate communities in particular, we are aware of no other studies that have directly parameterized theoretical models to describe competition among sessile marine organisms. Most studies of these organisms quantify competition as the "winner" of overgrowth interactions, and this approach has been used to rank species in competitive hierarchies (e.g., Buss and Jackson 1979, Russ 1982, Idjadi and Karlson 2007). According to a traditional approach, *Watersipora* should competitively exclude *Bugula* because while both species require space, encrusting species are assumed to compete more strongly for it. In contrast to this prediction, we show that population dynamics of *Watersipora* were strongly influenced by interspecific competition from *Bugula* (a poor competitor, traditionally defined) while the population dynamics of *Bugula* were dominated by density-independent dynamics. These results suggest the assumed primacy of competition for a single limiting resource (space) is insufficient to understand population-level competitive outcomes in this system. Consequently, the often-invoked competitive hierarchies and intransitivities in this system might be usefully revisited using more sophisticated empirical and analytical approaches.

Our approach allows for an empirically grounded overview of the consequences of competition for populations defined in terms in mathematical, population dynamic theory. We did our experiment in the field and deliberately bypassed mechanistic understanding, which allowed us to quantify the aggregate response of our study species to all mechanisms of competition. We also simultaneously estimated reciprocal competitive effects (i.e., effects of *Watersipora* on *Bugula* and vice versa) and calibrated these interspecific effects with estimates of intraspecific effects. Furthermore, our results put the effects of competition in the broader context of density independent effects on population dynamics (see also Grey 2011), which were particularly important for *Bugula*. Such an approach should be useful for understanding competitive population dynamics in a range of systems.

A Ricker model adequately described competition in our system. Our study is most similar to experiments done on plants, although these have not been done in the field (Firbank and Watkinson 1985, Law and Watkinson 1987, Bullock et al. 1994). Not surprisingly these studies describe diverse responses to competition, although a clear competitive dominant is often recognized. Other examples of response surface assessments of competition have also been done in fruit flies (Inouye 1999) and marine fishes (Forrester et al. 2006). Inouye (1999) demonstrated a competitive hierarchy among fruit flies and both these studies showed large differences between intra- and interspecific effects. In contrast, there was no clear competitive dominant in our study and for *Watersipora*, there was little difference in the response to intra- and interspecific competition (Fig. 1).

Competitive population dynamics of Watersipora

Bugula had effects on *Watersipora* population growth that were similar in magnitude to *Watersipora*'s effects on itself (Fig. 1). The effect of *Bugula* on *Watersipora* seemed to be at least partly mediated by decreases in size of *Watersipora* colonies with increasing *Bugula* density (Fig. 2d). This is a somewhat surprising result given the focus on interference competition for space as the primary mechanism of competition in these communities (e.g., Sebens 1982, Buss 1990, Muko et al. 2001). *Bugula* has only small requirements for space and so is unlikely to restrict the growth of *Watersipora* colonies through space pre-emption or overgrowth. Therefore, *Bugula* is likely to be a competitor of *Watersipora* through exploitation of shared resources such as food or oxygen. Because it is technically difficult to do so, exploitative competition has rarely been explored in these assemblages but deserves further attention. Regardless, the results of our experimental and analytical approach emphasize the usefulness of phenomenological approaches to quantifying competitive outcomes without assuming a particular mechanism of competition.

Intraspecific competition in *Watersipora* also appeared to be mediated by effects on average colony size. Higher densities of *Watersipora* reduced the average size of colonies (Fig. 2c), which are in turn, less likely to be reproductive and also have lower fecundity (Appendix D). This result is likely to be at least partially a consequence of direct competition for space and so conforms to the more traditional view of competition in these environments. Our results for *Watersipora* may be broadly applicable to sessile species that are space limited and whose population size structure is an important determinant of demography (Buss 1980). High densities of other encrusting competitors reduce space available for colony growth (and may also reduce other, space-independent resources), which will result in smaller colony sizes, higher mortality (Dunstan and Johnson 2004) and, consequently, lower population-level reproductive output. However, the nature of competition and the magnitude of competition coefficients will depend strongly on the species-specific relationship between individual size and fecundity (Hart and Keough 2009), as well as the specific mechanisms of competition operating among space-limited species.

The clear effects of high densities of both conspecifics and heterospecifics on *Watersipora* indicate the importance of recruitment densities for *Watersipora* population dynamics. We assessed competition from approximately the time of settlement through to seven weeks of community development. Individuals occurring in communities with high recruit densities are likely to have lower per capita contributions to subsequent generations. Recruitment rates are known to have strong effects on community assembly (Lockwood et al. 1997), invasion (Dunstan and Johnson 2004), and coexistence (Edwards and Stachowicz 2011). These effects occur largely as a consequence of changes in competitive dynamics such as those highlighted in our study.

Bugula *population dynamics*

In contrast to the results for *Watersipora*, *Bugula* population dynamics were dominated by density-independent dynamics. While there was some evidence for density-dependent mortality as a consequence of both intra- and interspecific competition (Fig. 2a, b), this did not translate to detectable effects on population growth. Indeed, high rates of mortality across all density combinations suggest density-independent mortality dominated *Bugula* dynamics. It is unclear what caused the high levels of mortality in *Bugula* during our experiment, although sudden die-offs have been regularly observed at our field sites over the last three years and high post-settlement mortality regularly occurs in this species (Keough and Chernoff 1987). While intraspecific competition in *Bugula* does occur (Allen et al. 2008), our results here suggest strong density-independent population dynamics can be important. The nature and strength of competition is known to be highly context dependent; current work is investigating variability in competitive dynamics in these assemblages (S. P. Hart and D. J. Marshall, *unpublished manuscript*).

A major advantage of parameterizing population dynamic models is that it can allow prediction of the outcome of competitive population dynamics (Damgaard 2008, Levine and HilleRisLambers 2009). This is not possible with our data but is an important goal. Our approach assesses competition among a single cohort of individuals and essentially assumes nonoverlapping generations, and so takes no account of competition between adults and new recruits from the plankton. *Watersipora*, for example, may affect recruitment of new individuals by pre-empting space (a negative competitive effect), or by providing secondary space for recruitment (a positive effect [Stachowicz and Byrnes 2006]); the net effect of these influences on the estimated competition coefficients is not clear but deserves attention. Improved estimates of lifetime reproductive success and quantitative estimates of planktonic mortality (Appendix A) are also required for better prediction. Nevertheless, our study is an important first step toward a better understanding of the population-level outcomes of competition in this system.

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SUPPLEMENTAL MATERIAL

Appendix A

Response surface design, study system and species, scope of the study, and details of analytical methods (*Ecological Archives* E093-192-A1).

Appendix B

Parameter estimates (*Ecological Archives* E093-192-A2).

Appendix C

Results of ANCOVA testing for effects of competition on colony size (*Ecological Archives* E093-192-A3).

Appendix D

Relationship between colony size and reproduction in *Watersipora subtorquata* (*Ecological Archives* E093-192-A4).