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Genetic diversity increases population productivity in a sessile marine invertebrate

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Abstract. Reductions in genetic diversity can have widespread ecological consequences: populations with higher genetic diversity are more stable, productive and resistant to disturbance or disease than populations with lower genetic diversity. These ecological effects of genetic diversity differ from the more familiar evolutionary consequences of depleting genetic diversity, because ecological effects manifest within a single generation. If common, genetic diversity effects have the potential to change the way we view and manage populations, but our understanding of these effects is far from complete, and the role of genetic diversity in sexually reproducing animals remains unclear. Here, we examined the effects of genetic diversity in a sexually reproducing marine invertebrate in the field. We manipulated the genetic diversity of experimental populations and then measured individual survival, growth, and fecundity, as well as the size of offspring produced by individuals in high and low genetic diversity populations. Overall, we found greater genetic diversity increased performance across all metrics, and that complementarity effects drove the increased productivity of our high-diversity populations. Our results show that differences in genetic diversity among populations can have pervasive effects on population productivity within remarkably short periods of time.

Key words: biodiversity–ecosystem function; complementarity; genetic diversity; marine invertebrate; productivity.

Introduction

Biodiversity and ecosystem function are linked: species-rich communities tend to have greater productivity and recover better from disturbance than species-poor communities (Loreau et al. 2001, Stachowicz et al. 2007, Cardinale et al. 2011). Human-mediated species extinctions therefore carry a twofold cost: first, the loss of species diversity, and second, the potential loss of ecosystem function and a diminished resilience (Hilborn et al. 2003, Cardinale 2011). Human activities also reduce genetic diversity within species, either deliberately (through selective breeding [Zhu et al. 2000]) or inadvertently (through habitat destruction or harvesting [Hauser et al. 2002]), and losses of genetic diversity can have similar ecological effects at the population level to those that losses of species diversity have at the community level (Hughes et al. 2008). Populations with higher genetic diversity tend to have greater productivity (Crutsinger et al. 2006, Mattila and Seeley 2007), recovery from disturbance (Hughes and Stachowicz 2004, Reusch et al. 2005, Phillips and Hickey 2010), as well as resistance to disease (Zhu et al. 2000, Altermatt and Ebert 2008), and invasion (Crutsinger et al. 2008). Importantly, these studies show that the ecological effects of genetic diversity can drive changes in the properties of populations within a single generation. Thus, reducing genetic diversity in natural populations, not only reduces the evolutionary potential of populations (Lande 1988, Franklin and Frankham 1998, Stockwell et al. 2003), human-driven reductions in genetic diversity could also have immediate, yet largely overlooked, negative impacts on population productivity. Given the extent of human impacts on genetic diversity (Hauser et al. 2002, Coltman et al. 2003), we urgently need to understand the ecological consequences of declining genetic diversity, but gaps in our knowledge remain.

Our understanding of the ecological effects of genetic diversity comes largely from studies of clonal vascular plants, in which researchers compare the performance of single-genotype populations to multi-genotype populations (Hughes et al. 2008). Single-genotype populations are the extreme case of low genetic diversity: every individual in the population is genetically identical. The lowest level of genetic diversity that is possible in outcrossing, sexually reproducing organisms is among full siblings, which share, on average, only half of their genes. Thus, the relative difference in genetic diversity between single-genotype monocultures (in asexual organisms) and polycultures is larger than the difference between full-sibling monocultures (in sexual organisms) and polycultures. Therefore, our ability to generalize the results of studies on asexually reproducing organisms to sexually reproducing organisms is limited, because the more subtle differences in genetic diversity between

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monocultures and polycultures in sexual organisms may not generate significant differences in performance. Furthermore, since the majority of studies have focused on clonal vascular plants, more studies examining genetic diversity effects in animals (e.g., Pakkasmaa and Aikio 2003, Gamfeldt et al. 2005, Gamfeldt and Källström 2007, Agashe 2009) are required to test the ubiquity of genetic diversity effects in nature.

Despite an increasing number of studies demonstrating that populations with greater genetic diversity are more stable and productive than populations with lesser genetic diversity, few have identified the processes that drive theses effects (Hughes et al. 2008). Broadly, these processes can be divided into two classes: selection and complementarity effects. While both processes can increase the performance of high-diversity populations, the way in which they operate and their ecological consequences differ (Loreau and Hector 2001, Fox 2005). When positive selection effects drive the benefits of diversity, the best-performing genotypes are overrepresented in polycultures because they are more likely to survive and reproduce; these few high-performing genotypes then contribute disproportionately more to the performance of the population (Loreau and Hector 2001). Greater genetic diversity simply increases the mathematical probability that these highly productive genotypes will be sampled in the population (Huston 1997, Tilman et al. 1997). Moreover, because only the best-performing genotypes survive and reproduce, genetic diversity will decrease in each subsequent generation, and so the positive effects of genetic diversity could be short lived or even cease if environmental conditions change. In contrast, complementarity effects are an emergent property of genetic diversity that arise as a consequence of facilitation or reduced competition for resources. When complementarity effects drive the benefits of diversity, the net performance of the entire population is enhanced. Very few field studies have identified the processes underlying the benefits of genetic diversity, limiting our ability to generalize about the nature and persistence of genetic diversity effects in wild populations.

In a field experiment, we explored the effects of genetic diversity on the lifetime performance of individuals in a sexually reproducing marine invertebrate, the bryozoan *Bugula neritina* (see Plate 1). We manipulated genetic diversity at the population level by creating populations founded by siblings or unrelated individuals. The sessile nature of this animal allowed us to measure the survival, growth, and fecundity of each individual in the field, as well as the size of offspring in the second generation. We also measured morphological variation in the structure of the feeding organs of individuals from different families to explore the potential mechanisms underlying our results. Our data suggest that even small differences in genetic diversity are sufficient to generate large differences in population productivity and that these benefits of genetic diversity are driven by complementarity effects.

Methods

Study species

Bugula neritina is an arborescent bryozoan, found in fouling communities worldwide. In this species, fertilization and embryogenesis occur internally. Mothers brood sexually produced offspring in modified zooids called ovicells for approximately one week, and during this period offspring are provisioned via a placenta-like system (Woollacott and Zimmer 1975). As *B. neritina* is hermaphroditic, self-fertilization is possible (see Maturo [1991] for laboratory results), however, the prevalence and consequences of selfing in wild *B. neritina* populations are unknown. Furthermore, in the congener *B. stolonifera*, Johnson (2010) showed that although self-fertilized offspring can develop into reproductively mature adults, adults produced by selfing are incapable of producing viable offspring. After brooding, mothers release swimming, non-feeding larvae that typically settle and metamorphose within hours (Keough 1989, Marshall and Keough 2003), limiting the potential for long-distance dispersal (Burgess and Marshall 2011*a*). Independent feeding on planktonic particles commences with the formation of the lophophore. *Bugula neritina* colonies grow by asexual budding of zooids. Zooids bifurcate at regular intervals to form branches and the number of bifurcations along the longest branch is a good estimate of individual size (Keough and Chernoff 1987). The adult stage is sessile, and reproduction occurs within a few weeks of metamorphosis, allowing us to measure the survival, growth, and fecundity of each individual in the field. In addition, larval size is a very good indicator of recruitment potential in this species (Marshall et al. 2003).

Experimental procedures

Experiments and collections were done at the Moreton Bay Boat Club, Moreton Bay, Australia (27°11′36.33″ S, 153°06′29.47″ E), between April and December of 2008. Temperatures and salinities in Moreton Bay range between 15–29°C and 16–32‰, respectively (S. C. Burgess, *unpublished data*; Burgess and Marshall 2011*b*). We collected mature individuals from floating pontoons at the field site. Each individual was collected from a different pontoon and each pontoon was separated by more than 20 m to minimize the likelihood of sampling related individuals (Keough 1984). In the laboratory, individuals were placed in dark, aerated aquaria for 48 hours before each individual was separated into its own beaker and induced to spawn by being exposed to bright light. We immediately placed spawned larvae into roughened petri dishes (90 mm diameter) that were filled with fresh seawater. Any larvae that had not attached to the petri dish within four hours in constant darkness at 20°C were discarded. If more than 10 larvae settled per dish, excess

settlers were selected at random and removed. All individuals transplanted to the field were one zooid in size.

As the larvae that were used in our experiments were fertilized in the field, only maternal identity was known. Thus, the offspring in monocultures were at least half siblings but may have been full siblings, and so we use the term "siblings" to describe these individuals. In polycultures, we assume that some, if not all, individuals were unrelated. However, even if some of the offspring in polycultures were related, the average relatedness within polycultures would increase, and therefore decrease the relative difference in genetic diversity between treatments, making ours a conservative test of genetic diversity effects. Similarly, relatedness in polycultures would increase if some of the mothers were siblings because their offspring would be cousins.

Experiment 1: Does genetic diversity affect performance in B. neritina *populations?*

We created experimental populations with two levels of genetic diversity at the scale of petri dishes: low genetic diversity monocultures (10 individuals with the same mother) and high genetic diversity polycultures (10 individuals, each with a different mother). The experiment was replicated across nine panels, and three experimental runs (two panels in run one, three panels in run two, and four panels in run three). Each panel represented a unique genetic unit comprising 10 different maternal families, and consisted of 10 low-diversity treatments (monocultures) and one high-diversity treatment (polyculture). All maternal families represented in monocultures were represented in the corresponding polyculture.

To deploy recruits into the field, we attached the petri dishes to PVC panels ($550 \times 550 \times 6$ mm) with stainless steel bolts. We suspended panels 1 m below the water surface with the dishes facing downward to mimic the orientation of wild individuals at this site. After two, four, and six weeks in the field, we measured the survival (number of individuals remaining in each petri dish) and size (number of bifurcations) of the remaining individuals. After six weeks in the field, >75% of individuals had reached reproductive maturity, and a species-rich fouling community had colonized most of the free space on each petri dish. Therefore, after six weeks, we terminated the field component of the experiment and returned all the dishes to the laboratory. In the laboratory, we measured fecundity (the number of ovicells per individual), and induced focal individuals to spawn so we could measure offspring size in the second generation (we used the same methods as above to induce spawning). We then preserved all larvae in 10% buffered formaldehyde solution (preservation does not affect larval size in this species [Marshall et al. 2003]). To estimate larval size, first, we photographed five randomly selected larvae in the same orientation under a compound microscope then we measured larval cross-sectional area (a good estimate of offspring performance in this species; [Marshall et al. 2003]) with Image Pro Express version 5.1 image analysis software (Media Cybernetics, Bethesda, Maryland, USA). To measure biomass, we dried and then weighed each individual to the nearest milligram.

For survival and growth analyses, repeated-measures ANOVAs were performed, where the mean survival (measured as a proportion) and mean size of individuals in each treatment on each panel were the response variables. Separate mixed-model ANOVAs were done for the mean fecundity (log-transformed) and mean larval size of individuals in each treatment. Larval size was measured only in runs 2 and 3. We also analyzed differences in fecundity accounting for differences in individual size among treatments (see *Results*) by first converting measurements of individual size (number of bifurcations) after six weeks in the field to estimates of the number of zooids with the formula described in Keough and Chernoff (1987), then dividing the number of ovicells by the estimated number of zooids to calculate the number of ovicells per zooid for each individual. Traditional ANCOVA analyses, where size is included as a covariate in the model, were not appropriate because differences in size among treatments resulted in nonoverlapping covariate ranges. Diversity was a fixed factor with two levels (monoculture and polyculture), while run and panel nested with run were random factors. Time was a fixed repeated factor. Random factors were removed from the analysis if $P > 0.25$ (Quinn and Keough 2002). Although diversity $\times$ run interactions were nonsignificant in all analyses, the degrees of freedom for the correct hypothesis tests will differ depending on whether diversity $\times$ run interactions are retained in the model. Data met homogeneity of variance and normality assumptions of ANOVA on the transformed scale.

For the population-level traits, population biomass and offspring production, we used the resampling method of Johnson et al. (2006), to examine whether additive (i.e., selection) or nonadditive (i.e., complementarity) effects drove the observed differences in productivity between monocultures and polycultures. Sampling only occurred within a panel, as families were unique to each panel. The probability of including an individual's trait value was weighted by the family's probability of survival in monoculture. We then used a mixed-model ANOVA to identify the processes (additive or nonadditive) driving increases in population biomass and offspring production. Here, data set was a fixed factor with two levels (observed and expected), while run and panel(run) were random factors. For each population-level trait, the response was the mean of the expected polycultures and the observed polyculture value for each panel. Expected data sets were generated in R (version 2.10.1; R Development Core Team 2009), but all analyses were done in SYSTAT (version 11; Systat Software, Chicago, Illinois, USA).

Experiment 2: Partitioning selection and complementarity effects

Resampling methods test whether nonadditive effects influenced the increased performance in polyculture, but the relative contribution of selection and complementarity effects remains unknown. Therefore, we designed a second experiment to examine the relative contribution of selection and complementarity using additive partitioning. Mature individuals were collected and induced to spawn as above, but rather than allowing larvae to settle directly onto the petri dishes, the larvae were instead settled onto acetate sheets (0.25 mm thickness). We then cut out approximately 10×10 mm pieces of acetate with only one recruit attached, and created our two treatments (monocultures and polycultures) by gluing the acetate and attached recruits to petri dishes. In each treatment, the 10 recruits were dispersed at random within each petri dish. By manually attaching recruits, we could follow the maternal origin of each recruit in the polyculture treatment. Dishes were transplanted to the field as above, and survival and size assayed at two weeks. In experiment 2, the response was the performance of each family in monoculture and polyculture, which we calculated by multiplying size by survival. Because the number of bifurcations is a good estimate of biomass in our population (J. D. Aguirre, *unpublished data*), performance is a good estimate of population biomass. The experiment was carried out in two runs and there were four panels in run one and five panels in run two.

In experiment 2, we used additive partitioning to determine the relative contribution of dominance, trait-dependent complementarity (TDC), and trait-independent complementarity effects to differences in performance among monocultures and polycultures (Loreau and Hector 2001, Fox 2005). Hereafter, we will refer to trait-independent complementarity simply as complementarity sensu Loreau and Hector (2001). A t test then determines whether the effects of dominance, TDC, and complementarity differ significantly from zero.

Experiment 3: Morphological variation in lophophore structure

The lophophore is the organ used to capture planktonic food particles and transfer food to the mouth, thus morphological variation in the structure of the feeding organs may underlie the benefits of diversity we found in experiments 1 and 2. In experiment 3, we created 17 monocultures with five individuals per petri dish and no polycultures. We used the same methods as in experiment 1 to spawn mature individuals, settle larvae, and transplant recruits to the field. All families were transferred to the field simultaneously, and all petri dishes where attached to the same backing panel. After two weeks in the field, we returned individuals to the laboratory. Individuals were between two and four bifurcations in size. To measure the area of the lophophore at the crown, the number of tentacles that make up the lophophore, as well as the area of the mouth, we carefully removed individuals from their petri dishes by cutting the ancestrula and stolons with a scalpel. Cutting colonies in this way does not affect feeding activity (Okamura 1984). We then laid three individuals from each family horizontally on a petri dish filled with unfiltered sea water. Individuals commenced feeding almost immediately. We then photographed each individual with a camera mounted on a dissecting microscope. For each individual, we haphazardly selected three to seven fully extended lophophores, in an orientation parallel to the camera, then measured lophophore crown area, tentacle number as well as mouth area with Image Pro Express version 5.1 image analysis software. We used separate ANOVAs for each lophophore trait (lophophore crown area, tentacle number and mouth area) to examine if variation was greater among families than within families. Family and individual nested within family were the factors included in the models. Data for lophophore crown area and tentacle number were log transformed and conformed to assumptions of ANOVA on the transformed scale. Analyses were done in SYSTAT (version 11).

Results

Experiment 1: Does genetic diversity affect performance in B. neritina *populations?*

After six weeks in the field, individuals in high-diversity populations (polycultures) had higher survival than individuals in low-diversity populations (monocultures) (Fig. 1A). In this experiment, there was a significant time $\times$ diversity interaction in the repeated-measures analysis (repeated-measures ANOVA: time $\times$ diversity $F_{2,16} = 7.880$, $P = 0.011$); hence, data were analyzed separately for each sampling interval and the results compared among analyses. Differences in survival were only significant after 6 weeks in the field (at two weeks, $F_{1,8} = 0.387$, $P = 0.551$; at four weeks, $F_{1,8} = 3.382$, $P = 0.103$; at six weeks, $F_{1,8} = 8.018$, $P = 0.022$), but the trend was qualitatively similar across time periods: individuals in polycultures were more likely to survive than individuals in monocultures (Fig. 1A).

Individuals in polycultures were also significantly larger than individuals in monocultures (Fig. 1B). Again, there was a significant time $\times$ diversity interaction (repeated-measures ANOVA, time $\times$ diversity $F_{2,16} = 8.386$, $P = 0.006$). Individuals in polycultures were larger than individuals in monocultures at every sampling interval (at two weeks, $F_{1,8} = 26.200$, $P = 0.003$; at four weeks, $F_{1,8} = 17.923$, $P = 0.003$; at six weeks, $F_{1,8} = 44.928$, $P < 0.001$), but the magnitude of the difference in size between polycultures and monocultures differed among time periods. Converting the differences in the number of bifurcations into differences in zooid number (Keough and Chernoff 1987), individuals in polyculture had on average 110%, 300%, and

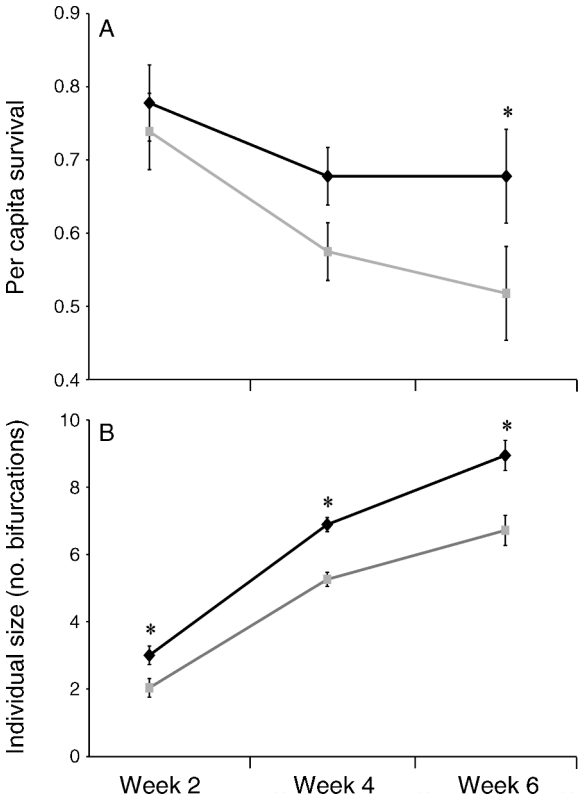

FIG. 1. (A) Individuals in high-diversity populations (black line and diamond symbols) had greater survival than individuals in low-diversity populations (gray line and square symbols) after six weeks in the field. (B) Individuals in high-diversity populations were significantly larger than individuals in low-diversity populations throughout the experiment. Survival represents the mean number of focal individuals remaining in each population at each sampling period. The mean number of bifurcations along the longest branch of each individual was used as an estimate of individual size. Means ± SE are shown. Asterisks denote groups that are significantly different ($P < 0.05$).

300% more zooids than individuals in monoculture after two, four, and six weeks, respectively.

Individuals in polycultures were, on average, 83% more fecund than individuals in monocultures ($F_{1,8} = 30.796$, $P < 0.001$; Fig. 2A). However, after accounting for differences in individual size there was no significant difference ($F_{1,2} = 0.322$, $P = 0.628$) in the ratio of ovicells per zooid among treatments, indicating that differences in fecundity were likely driven by differences in size among treatments rather than differences in per zooid fecundity. Individuals in polycultures also produced offspring that were on average 10% larger than offspring in monocultures ($F_{1,6} = 9.189$, $P = 0.023$; Fig. 2B).

A significant difference between the performances of the observed and expected polycultures indicated that the benefits of genetic diversity for population biomass ($F_{1,8} = 5.891$, $P = 0.041$) and total offspring production ($F_{1,8} = 7.612$, $P = 0.025$) were driven by positive nonadditive effects.

Experiment 2: Partitioning selection and complementarity effects

After two weeks in the field, the effect of diversity on performance was marginally significant and positive (mean biodiversity effect = 4.771, $t_8 = 1.659$, $P = 0.068$). Formal partitioning of the relative contribution of complementarity and selection effects showed that selection effects were significant and negative (mean dominance effect = −4.943, $t_8 = -2.662$, $P = 0.029$; mean trait-dependent complementarity effect = −2.367, $t_8 = -2.660$, $P = 0.029$), whereas complementarity effects were significant and positive (mean complementarity effect = 10.674, $t_8 = 2.405$, $P = 0.043$). These results suggest greater performance in polyculture was due to positive interactions among individuals (niche complementarity or facilitation), and not because of a greater likelihood of sampling, or selecting, the better performing individuals. Instead, negative dominance and trait-dependent complementarity effects suggest poorer performing families had relatively higher performance in polycultures than monocultures.

Experiment 3: Morphological variation in lophophore structure

The area of the mouth differed significantly more among individuals from different families than among individuals of the same family ($F_{16,34} = 2.532$, $P = 0.011$). Lophophore crown area (log-transformed) and tentacle

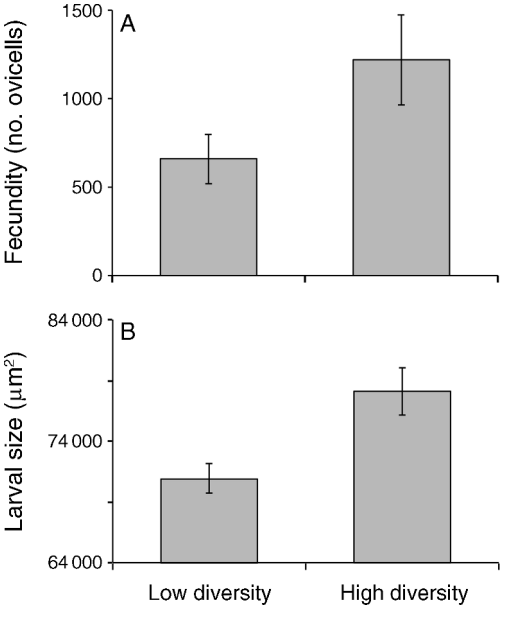

FIG. 2. (A) Individuals in high-diversity populations had significantly higher fecundity than individuals in low-diversity populations. (B) The size of offspring that were produced in high-diversity populations was significantly greater than in low-diversity populations. Fecundity is presented as the mean (±SE) number of ovicells per individual after six weeks in the field. Offspring size is represented as mean (±SE) larval cross-sectional area.

number (log-transformed) did not differ significantly among families ($F_{16,34} = 1.307$, $P = 0.249$ and $F_{16,34} = 1.512$, $P = 0.152$, respectively). We also found significant variation in mouth area, lophophore crown area, and tentacle number among individuals of the same family (mouth area, $F_{34,257} = 2.61$, $P < 0.001$; lophophore crown area, $F_{34,257} = 2.082$, $P = 0.001$; and tentacle number, $F_{34,257} = 1.873$, $P = 0.004$). Of the total variation in mouth area, 62% of the variation in mouth area was attributed to family identity, whereas only 8% of the total variation in mouth area could be attributed to individuals nested within families. This result should be interpreted with caution however, as there was some imbalance in terms of the number of lophophores (subsamples) we measured for each individual (Quinn and Keough 2002).

Discussion

Individuals in populations with greater genetic diversity had greater survival, growth, and fecundity than individuals in populations with lower genetic diversity. These positive effects of genetic diversity also crossed generations: individuals in polycultures produced larger offspring than individuals in monocultures. Therefore, despite the fact that the same families were represented in both polycultures and monocultures, their arrangement at small scales strongly affected performance.

The benefits of genetic diversity we observed in our first and second experiment were driven by nonadditive effects. Furthermore, in our second experiment, we found evidence for positive complementarity and negative selection effects (dominance and TDC). In published studies demonstrating benefits of genetic diversity using additive partitioning (Loreau and Hector 2001, Fox 2005), a pattern of positive complementarity and negative selection effects has emerged in most studies (e.g., Reusch et al. 2005, Hughes et al. 2010, Parker et al. 2010, Cook-Patton et al. 2011; but see Hughes and Stachowicz 2011). Positive complementarity and negative selection effects imply that while the overall increase in the performance of polycultures is driven by greater resource partitioning or facilitation, in many cases it is the poorest performing families in monoculture that benefit the most from increases in genetic diversity. Unfortunately, in comparison with studies of species diversity effects, which have uncovered the mechanisms underlying complementarity effects in some systems (e.g., Cardinale et al. 2002, Bracken and Stachowicz 2006), finding clear evidence for the mechanisms underlying genetic diversity effects remains a challenge (Appendix).

In our third experiment, we found that families with the largest mouths had 31% more mouth area than families with the smallest mouths. Interestingly, differences in mouth area were not associated with changes in lophophore crown area, thus it appears that the overall shape of the lophophore changes from more triangular to more rectangular for families with smaller and larger mouths, respectively. The cilia that line the lophophores of bryozoans generate a feeding current that pumps water from the surrounding water column, through the center of the lophophore, toward the mouth. While the size of the mouth limits the size and number of particles that can be ingested, there is evidence that smaller particles are avoided in favor of larger particles (Okamura 1987, 1990). Additionally, the size of ingested particles, and the feeding behaviors adopted to capture particles, can differ depending on the velocity of the flow in the surrounding water column (Okamura 1987, 1990). Changing the shape of the lophophore may change the interaction between the feeding current and the surrounding water column, which could affect food particle velocity though the lophophore, and possibly the size and number of particles that are pumped, captured, or rejected (Winston 1978, Best and Thorpe 1983, Okamura 1987). The ecological relevance of these observations requires explicit examination; nevertheless, it is possible that variation in mouth area increases resource partitioning, or variation in mouth area changes the

Plate 1. Adult *Bugula neritina* showing the bifurcating growth pattern, zooids, ovicells, and feeding lophophores. Photo: J. D. Aguirre.

properties of the feeding current in a way that facilitates particle capture in polyculture.

Negative dominance and TDC effects indicate that improved performance in polycultures was greater for individuals from poorer performing families than for individuals from better performing families (Fox 2005). Importantly, dominance and TDC were both negative (Fox and Rauch 2009). Hence, it is possible that the feeding current of larger individuals facilitates feeding by smaller individuals because it increases the pumping of food particles from the surrounding water column. Alternatively, it may be that variation in mouth area was less in poorer performing monocultures, and thus the relative release from competition in polycultures was greater for poorer performing families, resulting in negative selection effects. These predictions require further testing, but nevertheless, in our study the properties of the population (e.g., its intrinsic rate of increase and carrying capacity) depended on genetic diversity, that is, the productivity of populations as an emergent property of genetic diversity.

In our first experiment, we found that individuals in polycultures not only had greater survival, growth, and fecundity than individuals in monocultures, but they also produced larger offspring. Several factors could explain the increase in offspring size we observed in polycultures. First, if paternity is determined by the proximity of the nearest conspecific male, individuals in monoculture are more likely to breed with siblings, and thus smaller offspring size in monoculture could have been a result of inbreeding. Evidence for distance-based paternity biasing in organisms such as *B. neritina* is mixed (Yund and McCartney 1994, Bishop et al. 2000, Johnson and Yund 2009), so we hesitate to speculate on the likelihood of inbreeding depression, but we note that such an effect is possible. However, studies have shown that paternity can determine maternal investment in offspring size (Hammerschmidt et al. 2011), and is possible that mothers allocated fewer resources to offspring in monocultures because the sperm belonged to close relatives. A second alternative explanation also relates to adaptive maternal effects: studies have shown that conspecific density has a positive effect on offspring size in *B. neritina*, and suggest that mothers at higher densities produce larger offspring to compensate for the greater likelihood that offspring will face a more competitive environment (Allen et al. 2008). We found that polycultures had greater survival than monocultures, thus it could be that higher densities induced mothers to produce larger offspring in polycultures. Last, if individuals in polycultures experienced lower competition for resources, it could be that individuals in polycultures produced larger offspring simply because they had more energetic resources available to invest in reproduction (Marshall and Keough 2004; but see the Appendix). While we cannot distinguish between these three competing hypotheses, larger *B. neritina* offspring survive, grow, and reproduce more than smaller offspring (Marshall et al. 2003), so any increase in offspring size is likely to have pervasive effects on population growth rates across generations.

Despite a dispersive larval phase, studies have found that marine larvae sometimes settle in sibling aggregations (Selkoe et al. 2006, Veliz et al. 2006, Buston et al. 2009). We found that aggregations of siblings had lower performance than aggregations of unrelated individuals and so we would predict that larvae in this species should avoid settling next to siblings in the field. Surprisingly, studies have shown that *B. neritina* larvae sometimes settle in closer proximity to siblings than unrelated individuals in the laboratory (Keough 1984) and, although this tendency varies among populations (Raimondi and Keough 1990), the adaptive significance of these behaviors remains unclear. There are a number of behavioral (Grosberg and Quinn 1986, Raimondi and Keough 1990, Gamfeldt et al. 2005), physical (Petersen and Svane 1995), and hydrodynamic (Selkoe et al. 2006, Veliz et al. 2006, Christie et al. 2010) factors that can generate variation in the likelihood of sibling interactions. Given our results, factors that generate variability in the likelihood of sibling aggregation at settlement may have important, possibly unanticipated, consequences for productivity in marine populations.

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Supplemental Material

Appendix

Laboratory test of resource consumption in monoculture and polyculture (*Ecological Archives* E093-098-A1).