esa

ECOSPHERE

Intraspecific diversity in prey body size influences survivorship by conferring resistance to predation

PAUL E. GRIBBEN [1,2,†] MELANIE J. BISHOP,[3] WAYNE A. O'CONNOR,[4] DANIEL J. BRADLEY,[5] AND A. RANDALL HUGHES [6]

[1]*Centre for Marine Science and Innovation, School of Earth, Environmental and Biological Sciences, University of New South Wales, Sydney, New South Wales 2052 Australia*
[2]*Sydney Institute of Marine Science, 19 Chowder Bay Road, Mosman, New South Wales 2088 Australia*
[3]*Department of Biological Sciences, Macquarie University, Sydney, New South Wales 2109 Australia*
[4]*NSW Department of Primary Industries, Nelson Bay, New South Wales 2315 Australia*
[5]*School of Life Sciences, University of Technology, Sydney, New South Wales 2007 Australia*
[6]*Northeastern University Marine Science Centre, 430 Nahant Raod, Nahant, Massachusetts 01908 USA*

Citation: Gribben, P. E., M. J., Bishop, W. A., O'connor, D. J., Bradleyand A. R., Hughes. 2020. Intraspecific diversity in prey body size influences survivorship by conferring resistance to predation. Ecosphere 11(4):e03106. 10.1002/ecs2.3106

Abstract. Intraspecific diversity can have as strong an effect on communities and ecosystems as more well-studied effects of species diversity. Intraspecific variation in prey body size may have particularly strong effects on populations by influencing the outcome of predator–prey interactions, but this has received little attention. We tested the hypotheses that (1) body size of the Sydney Rock Oyster, *Sacosstrea glomerata*, influences predation risk; (2) increasing intraspecific variation in body size of the oyster will enhance total survivorship; (3) oyster size phenotypes will differ in the magnitude of survivorship benefits they incur from association with other phenotypes; and (4) size-specific survivorship benefits of associating with other body sizes will vary with predator access. In a fully factorial field experiment, we manipulated the diversity of *S. glomerata* oyster body sizes (1–3 size classes per treatment) and predator access to prey (small vs. large mesh cages). Oyster total and individual phenotype survivorship was documented over an 8-week period. Overall, the relationship between diversity in *S. glomerata* body size and survivorship was positive and was related to changes in density of individual body sizes when grown in mixtures. In fact, no phenotype had lower percent survivorship in mixtures than in monoculture. Nevertheless, individual phenotypes displayed differing responses to predator access treatments and phenotype mixing that reflected differences in the types of predators (e.g., shell drilling or removing) to which they were most susceptible. In general, the greatest survivorship benefits of phenotype mixing were seen in treatments where the most disparate (i.e., small, large) size classes were mixed. Our study adds to growing evidence of the importance of intraspecific diversity in mediating key population processes such as predation. Importantly, different oyster phenotypes benefit from increasing phenotypic diversity depending on the predators that can access the oysters, suggesting that flexible complementarity among oyster phenotypes may be a useful tool for increasing the resistance and resilience of oysters in a range of environments which vary in their predator composition. These results will help to inform strategies for enhancing survivorship of species transplants in restoration projects.

Key words: intraspecific; oyster; phenotypic diversity; predation; survivorship.

Received 21 October 2019; revised 14 January 2020; accepted 24 January 2020; final version received 2 March 2020. Corresponding Editor: Hunter S. Lenihan.

† E-mail: p.gribben@unsw.edu.au

Introduction

Understanding how diversity controls the stability, resilience, and functioning of ecosystems is a central theme of ecology (Hooper et al. 2005, Stachowicz et al. 2007, Cardinale et al. 2012). Early research focused on relationships between biodiversity and ecosystem properties (Tilman 1996, Schläpfer and Schmid 1999). More recently, studies demonstrate that intraspecific diversity (phenotypic and/or genotypic diversity within species) also influences communities and ecosystem function (Price 1987, Whitham et al. 2006, Duffy 2010, Bolnick et al. 2011). The effects of intraspecific diversity may be particularly important for habitat-forming species such as plants, macro-algae, corals, and shellfish which, by creating structurally complex habitats that support diverse and productive food webs, are of disproportionate importance to the structure and integrity of ecosystems. Indeed, intraspecific diversity of habitat-forming species can enhance the stability of populations and promote resistance and resilience to environmental perturbations (Hughes and Stachowicz 2004, Whitham et al. 2006, Hughes et al. 2008). Such effects of intraspecific diversity on communities and on ecosystem processes can be of comparable magnitude to those of species presence and diversity (Cook-Patton et al. 2011, Des Roches et al. 2017). Yet, human disturbances are leading to demonstrable, and in some cases dramatic, reductions in intraspecific diversity in habitat-forming specier (Primack 2014).

Body size is a key trait influencing the relationship between an organism and its environment, and within species, body size is often correlated to organismal performance and fitness (Werner and Gilliam 1984, Woodward et al. 2005, Peacor et al. 2007, Marshall et al. 2018). In particular, the body size of predators and of their prey can have dramatic effects on the strength and outcome of predator–prey interactions (Werner and Gilliam 1984, Yang and Rudolf 2010, Asquith and Vonesh 2012). Given the key role of body size in influencing species interactions, intraspecific diversity in body size (e.g., the number of size classes of a species) could also affect community processes. To date, most experimental tests of the effects of body size diversity have focused on predators. For instance, in one experimental test, predator body size diversity increased total prey consumption (Toscano and Griffen 2012). However, diversity in predator body size can also increase cannibalism within the predator species, weakening average impacts on prey (Griffin and Silliman 2018). Whether prey body size diversity strengthens or weakens trophic linkages remains untested, although the dampening effects of interspecific variation in prey species diversity on consumption (e.g., Hillebrand and Cardinale 2004, Edwards et al. 2010) suggest that intraspecific variation in prey body size may also reduce consumer effects.

Intraspecific variation in prey body size influences predator consumption of prey in several ways. If predators prefer a particular size class of prey, then the presence of another size class may provide an associational refuge from predation for prey size classes. Alternatively, if predators are attracted to a patch containing a certain size class, this may increase the risk of predation of adjacent, less preferred prey items. If rates of predation on individual phenotypes are determined by their density, populations comprised of small numbers of each of multiple size classes may be less susceptible to predation than those comprised of larger numbers of a single size class, as less dense prey may be more difficult to locate. Alternatively, predation risk may be unrelated to prey phenotypic diversity if one predator type consumes all available size classes of prey (e.g., Toscano and Griffen 2012) or if predators are only capable of consuming a particular size class (O'Connor and Newman 2001).

Oysters are economically and ecologically important habitat-forming species that have experienced widespread declines worldwide (Beck et al. 2011). Recent studies indicate that intraspecific variation in oysters can influence population processes. For example, recruitment of eastern oysters, *Crassostrea virginica*, was higher to mixtures of adults from three populations compared to adults of a single population (Smee et al. 2013). In another study, the probability of Sydney rock oyster, *Saccostrea glomerata*, colonization was greater for genetically rich than genetically poor pools of larvae (Hedge et al. 2014). In addition, cohort diversity and genetic relatedness in juvenile oysters influenced

growth, survival, and subsequent recruitment in the absence of predation, and survivorship in the presence of high predation (Hanley et al. 2016). Although the specific mechanisms contributing to these effects are unknown, it is possible that variation in body size may contribute to effects of oyster intraspecific diversity on juvenile survival. Predation can be a key component of juvenile oyster mortality, with vulnerability to predation often inversely related to oyster body size (Newell et al. 2000, Johnson and Smee 2012). However, the relationship between oyster body size, or some other unmeasured trait correlated with body size (e.g., shell strength), and vulnerability also depends on the functional feeding modes (drilling vs. crushing predators) and the size of the predators present (Eggleston 1990, Rindone and Eggleston 2011). Thus, the potential for intraspecific diversity in oyster body size to influence survivorship in the presence of predation remains an open question.

In this study, we used a field experiment to test the interactive effects of intraspecific diversity in oyster size (holding oyster age and genetic diversity constant) and of predator access (manipulated via the use of cages with different mesh sizes) on the survivorship and predation mortality of the native *S. glomerata*. Specifically, we tested the hypotheses that (1) body size of the *S. glomerata*, influences predation risk; (2) increasing intraspecific variation of oyster body size would enhance total survivorship; (3) oyster size phenotypes would differ in the magnitude of survivorship benefits they incur from association with other phenotypes; and (4) size-specific survivorship benefits of associating with other body sizes would vary with predator access. We also included controls to account for the effects of changes in density of individual phenotypes when grown in combination with other phenotypes. Including density controls allowed us to tease apart potential mechanisms for the patterns observed in our experiment.

Materials and Methods

Study species and system

The Sydney rock oyster, *S. glomerata*, is common along the east Australian coast, extending from the border between New South Wales and Victoria in the south, to northern Queensland (Lamprell and Healy 1998). The oyster once formed large reefs that supported biodiverse communities but historic overharvesting coupled with more recent disease and pollution has rendered these functionally extinct (Beck et al. 2011). Wild oysters are now largely restricted to non-reef-forming populations on rocky shores, mangroves, and artificial structures (e.g., Bishop et al. 2012, Hughes et al. 2014, McAfee et al. 2016, Scanes et al. 2016). Additionally, the oyster continues to form the basis of a significant aquaculture industry, supported since the 1990s by a breeding program targeting fast growth and disease resistance (O'Connor and Dove 2009). The breeding program now has more than 380 single pair-mated family lines, across and within which there is substantial phenotypic variation with respect to size.

We utilized 10-month-old oysters, spawned under the breeding program at the Port Stephens Fisheries Institute (PSFI) in January 2015 and subsequently grown out on nearby oyster leases, to establish three phenotypic treatments with respect to size. The phenotypes were small (mean size ± SE; 18.88 ± 0.17 mm shell length), medium (32.23 ± 0.21 mm shell length), and large (39.04 ± 0.32 mm shell length), with each phenotype receiving at least 100 oysters from each of the same 16 family lines to produce treatments of comparable genetic diversity. We only considered body size as our grouping variable as it correlates with many other morphological variables. We used juvenile oysters as they are highly vulnerable to mortality from biotic sources (Newell et al. 2000). Oysters were manipulated on concrete tiles that were deployed at a mid-intertidal elevation along the eastern shoreline of Chowder Bay, Sydney Harbour, Australia (33°50′19.80″ S, 151°15′16.50″ E). This shoreline is characterized by a rock revetment of sandstone boulders, with suitable environmental conditions to support a wild *S. glomerata* population.

Effects of oyster diversity on survivorship

Oyster phenotypic diversity (three levels; 1, 2, or 3 size classes/tile) and predator access (two levels: small mesh cages and large mesh cages) were manipulated in a fully orthogonal experiment on concrete tiles, measuring 30 cm (length) × 30 cm (width) × 4 cm (height). The large mesh was 2.5 cm in diameter and allowed

access to oysters by most invertebrates and smaller fish, such as *Tetractenos* spp., but excluded large fish. The small mesh was 1.5 cm in diameter and excluded all fin fish predators but was small enough to allow access by predatory gastropods such as *Tenguella marginalba*, stylochid flatworms, and some crabs (Connell and Anderson 1999). In total, we had 14 treatments: small and large mesh cages containing small, medium, and large oysters on their own, all pairwise combinations, and all three phenotypes together. There were five replicates per treatment, giving a total of 70 tiles. Although we did not include cage controls, previous studies conducted under similar environmental conditions have not found artifacts of cages of similar mesh sizes (Connell and Anderson 1999). In addition, observations of our two cage types in the field suggested that our smallest mesh size did not enhance shading of tile surfaces compared to the larger mesh, possibly because the small mesh was still quite open and the mesh itself was thin (0.5 mm thick). We could not use a small mesh size to exclude all predators as this would have introduced environmental artifacts. Each tile received a total of 24 oysters, within the range of natural densities on rocky shorelines (Krassoi et al. 2008). Hence, the density of a given size class varied from 24 on the tiles with a single phenotype, 12 on the tiles with two phenotypes, and eight on the tiles with three phenotypes. To explore the role of changes in size class density as a mechanism for observed patterns in survivorship between monoculture and mixed body size tiles, we also included density controls in which monocultures of small, medium, and large oysters were added to plates at 12 and eight oysters per tile ($n = 5$ tiles per treatment). Density controls were used for small mesh cages only due to a shortage of oysters of each size class.

Oysters were glued to concrete tiles using a two-part epoxy adhesive (Megapoxy HT, Permatech, Wangara, Australia). Oysters were glued in haphazard positions on tiles but maintained a 3-cm margin with no oysters around each plate. For tiles receiving mixed body sizes, body sizes were further haphazardly interspersed. The tiles were left overnight for the glue to set, and to monitor any oyster mortality that may have occurred in the establishment of the treatments. No oysters died from this process, consistent with previous observations that this adhesive does not influence survivorship of *S. glomerata* (McAfee et al. 2017) and successful use of this method in other oyster predation studies (Kimbro et al. 2014, Hughes et al. 2017). Prior to caging of tiles, each was photographed (with a scale bar included) to determine the initial size of all oysters and the position on each tile of the various size classes. We used maximum shell length along the anterior–posterior axis as our measure of body size, as it is a standard way to measure oyster size and is highly correlated with other measures of body size (e.g., biomass; Hanley et al. 2016, Hughes et al. 2017). Tiles were then enclosed within a box cage consisting of stainless steel mesh of the assigned size. The tiles were not affixed to the mesh cage but sat on the bottom of it. The mesh extended 10 cm above the surface of the tile. Mesh was secured on the underside of the tile with cable ties.

Tiles were placed in Chowder Bay at the mid-intertidal elevation at which oysters naturally occur on 17 November 2015. Tiles were interspersed with respect to treatment, separated by at least 0.5 m and wedged between boulders to minimize flipping by waves. The tiles were sampled at 1 week and after 8 weeks (15 January 2016). At 1 week, three tiles were flipped by wave action but no damage to oysters or cages was observed, so these were righted and secured in new positions between boulders. No other flipping or damage to tiles was recorded at the end of the experiment. Although we surveyed the number of predatory molluscs on each plate on both sampling occasions, these data do not accurately reflect the entire predator community, which includes subtidal species not present during our intertidal sampling events, and intertidal predators that may retreat to refuges from desiccation at low tide, so these results are not presented here. Instead, the effects of different types of predators were inferred from shell damage observed to dead oysters (Peterson 1982, Kimbro et al. 2009). At the end of the study, dead oysters were recorded as drilled, crushed, valve removed, or intact (two valves present and undamaged). In no instance were both valves of an oyster missing. Drill holes were attributed to predation by naticid or muricid gastropods and crushed valves or valve removal to crab or fish predation (see Bishop et al. 2005, 2008). Although

undamaged, drilled, and crushed dead oysters may naturally lose their top valve over time, obscuring the source of damage, the results of a pilot study indicated that this takes longer than the duration of our study. Of 12 oysters that were experimentally killed so that they were dead but with two intact valves, all retained two valves over a 7-week period.

Statistical analyses

Our overall approach was to analyze total survival of oysters on tiles and then determine how the mortality of oysters that were predated in different ways contributed to those patterns.

Influence of phenotype diversity and predation risk on oyster survivorship

We used a two-factor generalized linear model (GLM) to determine the effects of size class diversity and predator access on the total proportion of oysters surviving on tiles. The model used a binomial error structure with a logit link. Because we had three of the single size class treatments, three of the two size class treatments, and only a single three size class treatment, we included each treatment in the model (i.e., there were seven levels of phenotypic diversity treatments). Pairwise post hoc tests using least significant difference adjustments for multiple comparisons were used to determine differences among diversity treatments (i.e., 1 vs. 2 vs. 3 size class). These were done among diversity treatments within predator access treatments, and between predator access treatments for individual diversity treatments because of a predator access × diversity treatment interaction.

We then determined how size class diversity and predation access influenced the survivorship of individual size class. That is, we determined the percent survivorship of small, medium, and large oysters when grown on their own versus with one or more of the other size class. Following this, for the small mesh cages, the effects of oyster density on survivorship were determined by comparing survivorship when in monoculture at different densities (i.e., 24, 12, and eight oysters per tile), and then comparing treatments at equivalent densities. Data were analyzed using one-factor GLMs, with pairwise post hoc tests (as described above) used to determined differences among density treatments when grown in monoculture.

Influence of predation risk and oyster phenotype on oyster predation

We used the same models described above to determine the effect of size class diversity on each of the percent of shells with removed valves or drilled shells. We did not run a separate analysis on crushed oysters as this was only observed for 4% of all oysters (see *Results*). Similarly, dead oysters with both valves present and undamaged were not analyzed separately because these could have died from predation (e.g., Stylochid flatworms; O'Connor and Newman 2001) or non-predatory sources of mortality (e.g., disease, heat stress). In fact, the total percent of dead oysters with valves found intact (i.e., those that potentially suffered from natural mortality) as a function of all oysters deployed was only 4.9% and was consistent across phenotypes. All analyses were conducted in SPSS (SPSS, Version 25.0, IBM, Armonk, New York, USA).

Results

Influence of phenotype diversity and predator access on total survivorship

After two months, survivorship on individual tiles ranged from 0% to 100%. Mean percent (± SE) survivorship was lowest for monocultures of small oysters grown in small mesh cages (3.33 ± 1.56) and highest for the mixtures of medium and large oysters in the small mesh cages (37.50 ± 14.07) and the mixtures of small and large oysters in large mesh cages (38.33 ± 16.16; Fig. 1A,B).

Oyster survivorship was strongly dependent on interactions between predator access and diversity treatments (Wald $\chi^2 = 53.764$, df = 6, $P < 0.001$; Fig. 1A,B). For the small mesh cages, survivorship was generally greater for multi- than single-phenotype treatments and, among monocultures, increased with increasing oyster size (Fig. 1A). For monocultures enclosed in the large mesh cages, survivorship was greater for the medium than the small or large oysters (Fig. 1B). Whether survivorship was greater in monocultures or mixtures in large mesh cages was, however, variable and dependent on the composition of mixtures (Fig. 1B). When

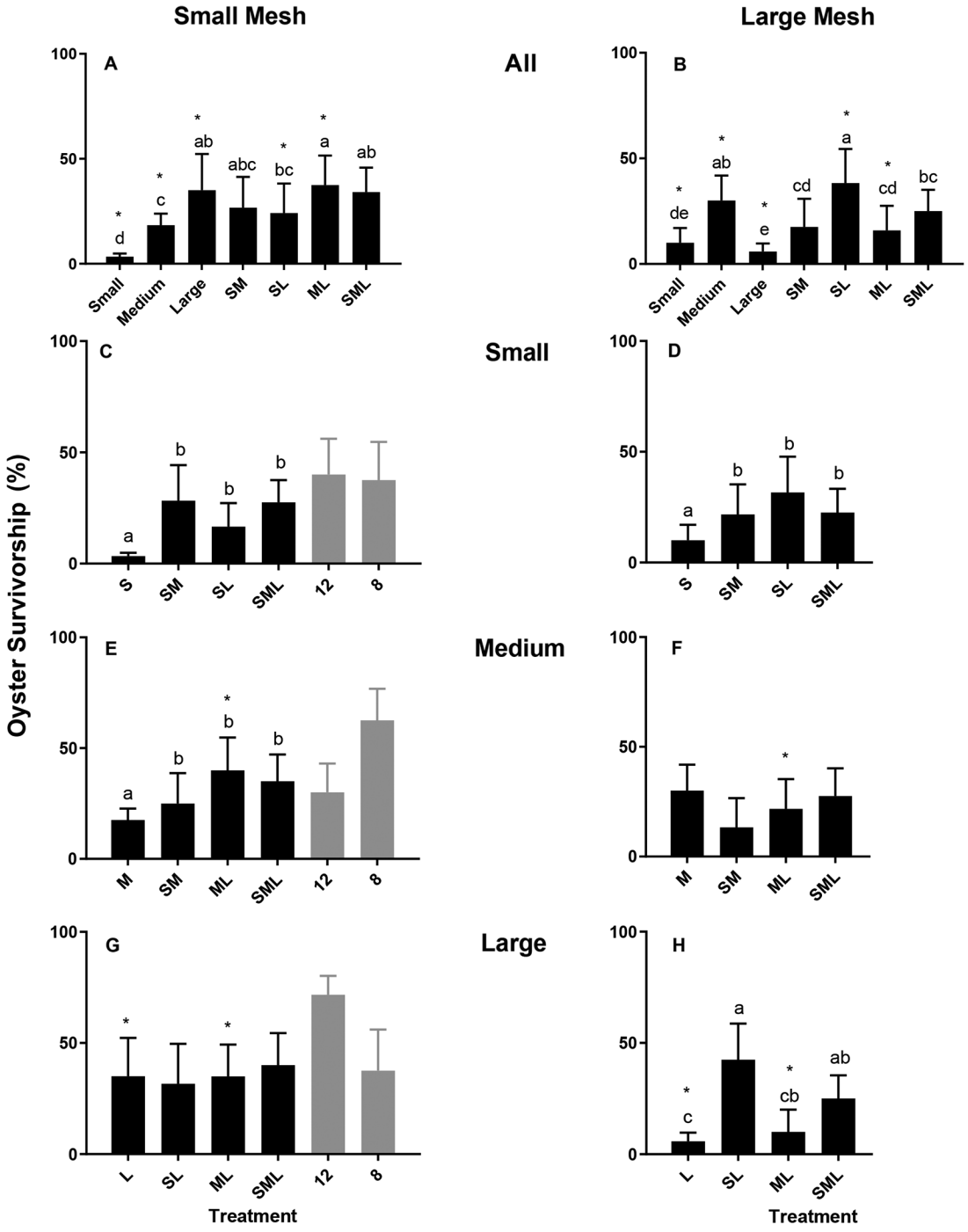

Fig. 1. Survivorship (mean + SE) of all phenotypes (A, B), and small (C, D), medium (D, F), and large oysters (G, H) when grown on tiles with monocultures or mixtures of phenotypes. Tiles were enclosed with small (1.5 cm; left panel) or large (2.5 cm; right panel) mesh cages. $N = 5$ replicates per treatment. Letters indicate significant differences among diversity treatments within predator access treatments; asterisks indicate significant differences in individual diversity treatments between predator access treatments. Gray bars are survivorship of density controls for individual phenotypes grown on tiles in monoculture at 12 and 8 oysters per tile in small mesh cages only.

diversity treatments were compared across predator access treatments, small and medium oyster monocultures displayed greater survivorship in large than small mesh cages, but large oysters displayed the reverse pattern. For the mixed diversity treatments, the direction of differences between predator access treatments depended on the combination of phenotypes: The small and large combination had greater survivorship in large than small mesh cages, but the opposite pattern was observed for the large oyster monoculture and the medium and large combination.

Percent survivorship of individual phenotypes

The effects of phenotypic diversity and predator access treatments on survivorship varied among individual phenotypes (Fig. 1C–H; Table 1). Yet, important patterns were apparent. For example, survivorship of small oysters was greater in mixed- than single-phenotype treatments for both predator access treatments (Fig. 1C,D; Table 1). A similar pattern occurred for medium oysters in small mesh cages, but survivorship did not differ among the diversity treatments in the large mesh cages (Fig. 1E,F; Table 1). For large oysters, the opposite pattern occurred to that for medium oysters: Survivorship was equivalent among diversity treatments in the small mesh cages, yet in the large mesh cages was significantly greater in mixtures containing small oysters than treatments without these (Fig. 1G,H; Table 1). There were limited effects of predator access treatment on individual phenotypes, but both medium and large oysters had lower survivorship in the large than small mesh cage when grown together, as did the monoculture of large oysters (asterisks in Fig. 1C–H).

For all phenotypes in the small mesh cages, survivorship was higher on density controls (tiles with eight or 12 oysters) compared to monocultures at full densities (i.e., tiles with 24 oysters) except for the large phenotype, for which there was no difference in survivorship between tiles with 24 or eight oysters (Fig. 1; Appendix S1: Table S1). However, for each phenotype, survivorship of oysters on density controls was either equal to or higher, but never lower, than on mixtures containing the equivalent density of the same phenotype (Fig. 1; Appendix S1: Table S1).

Influence of predation risk and oyster phenotype on oyster predation

Overall, only 5% of all shells were found dead with intact valves (i.e., shells representative of

Table 1. Univariate generalized linear models examining the effect of predator access and oyster diversity treatments on the survivorship, and mortality due to different factors, of individual oyster phenotypes.

	Survivorship			Valve removed			Drilled		
Oyster size	Wald $\chi2$	df	P	Wald $\chi2$	df	P	Wald $\chi2$	df	P
Small									
Access	0.626	1	0.429	0.011	1	0.915	1.758	1	0.185
Diversity	26.113	3	**<0.001**	13.002	3	**0.005**	4.656	3	0.199
A × D	7.214	3	0.065	8.700	3	**0.034**	19.605	3	**<0.001**
Small mesh				20.794	3	**<0.001**	14.564	3	**<0.001**
Large mesh				1.147	3	0.766	10.646	3	**<0.014**
Medium									
Access	2.304	1	0.129	1.121	1	0.290	1.784	1	0.182
Diversity	6.082	3	0.108	1.033	3	0.793	5.019	3	0.170
A × D	12.457	3	**0.006**	12.154	3	**0.007**	6.854	3	0.077
Small mesh	11.736	3	**0.008**	2.761	3	0.430	4659.96	3	**<0.001**
Large mesh	6.224	3	0.101	9.700		**0.021**			
Large									
Access	16.794	1	**<0.001**	2.956	1	0.086	48.411	1	**<0.001**
Diversity	18.352	3	**<0.001**	10.963	3	**0.188**	6.357	3	0.095
A × D	23.220	3	**<0.001**	4.785	3	0.188	18.985	3	**<0.001**
Small mesh	0.732	3	0.866				5.289	3	**<0.001**
Large mesh	33.268	3	**<0.001**				26.927		

Bold value indicates statistically significant *P-values*.

natural mortality) suggesting that patterns in oyster survivorship largely reflect different rates of predation among treatments. Of the remaining dead oysters, which were considered preyed upon, 59% had their top valve missing (n = 394) and 37% had drill holes present (n = 252) were crushed. Among monocultures, the percent of dead oysters with missing top valves decreased with size from 72% for small to 53% for medium and 48% for large. By contrast, the percent of dead oysters that had been drilled increased with size, from 24% for small to 44% for medium and 48% for large. Thus, small oysters were three times more likely to have their top valves missing than be drilled. Medium and large oysters were, by contrast, almost equally as likely to have their valve missing as be drilled.

Differences in valve loss between predator access treatments were only apparent for monocultures of small or medium oysters and in both instances were in the direction of fewer missing valves in large than small mesh cages (Fig. 2). In the small mesh cages, small oysters displayed more missing valves when in monoculture than in mixtures (Fig. 2A,B; Table 1). In the large mesh cages, medium oysters displayed the reverse pattern of fewer missing valves when in monoculture than in mixtures (Fig. 2C; Table 1). For large oysters, missing valves were higher when in monoculture or in mixtures with medium oysters across both predator access treatments (Fig. 2D,E, Table 1).

Overall, there were few differences in the percentage of oysters drilled between small and large mesh cages (Fig. 3). Where differences between predator access treatments in drilling were apparent (i.e., for small or large oysters in monoculture, and for medium/large oyster mixtures), these were in the direction of a greater percentage of oysters drilled in the large mesh cages (Fig. 3). Whereas in the small mesh cages there were few differences in drilling between monocultures and mixtures or among mixture treatments, in the large mesh cages, small and large oysters experienced greater drilling when in monocultures than in mixtures.

Discussion

We found support for all four of our predictions. Firstly, vulnerability to predation varied with oyster body size, or with traits correlated with body size (e.g., shell strength) that were not explicitly examined here. Second, the relationship between intraspecific diversity in *S. glomerata* body size and survivorship was generally positive. In fact, there was not a single instance where one of the three size classes experienced lower percent survivorship as a mixture than as a monoculture, suggesting an associational refuge of mixtures (Barbosa et al. 2009). Third, the magnitude of these benefits did vary by size. Fourth, the phenotypes that benefitted most from being present in mixtures as opposed to monocultures varied depending on predator access (i.e., caging treatment). Overall, our results are consistent with predictions that intraspecific variation in offspring body size can serve as a bet-hedging strategy in unpredictable environments, increasing the likelihood that some offspring survive in the current conditions (Marshall et al. 2018). Nevertheless, though we focused on variation in body size within a single cohort of oysters, similar effects of size variation are likely in species with overlapping cohorts (Asquith and Vonesh 2012). Although we cannot speak to the relative importance of trait vs. genetic variation in driving the effects of intraspecific diversity, our results support studies showing that metrics that incorporate information on functional trait variance (e.g., genetic relatedness, phenotypic dissimilarity, functional trait diversity) can be a strong predictor of ecological performance (Ellers et al. 2011, Stachowicz et al. 2013, Hughes 2014).

Body size is known to affect susceptibility to predation in plants and animals, though no single size is universally optimal (e.g., larger individuals can be more of less susceptible to predation, depending on the source; Reznick et al. 2015, Marshall et al. 2018). Variation in survivorship in our study, in part, reflected variation in sources of predation among oyster phenotypes. Indeed, our shell forensics suggest some size selection of different phenotypes by predators was occurring. For example, mortality by drilling predators increased with increasing oyster body size. Most likely, the mulberry whelk, *T. marginalba,* was the key predator responsible for oyster drilling at our site, as it was often observed on our plates and is a common predator of invertebrates in intertidal rocky shores in New South Wales (Edgar 2000). However, other

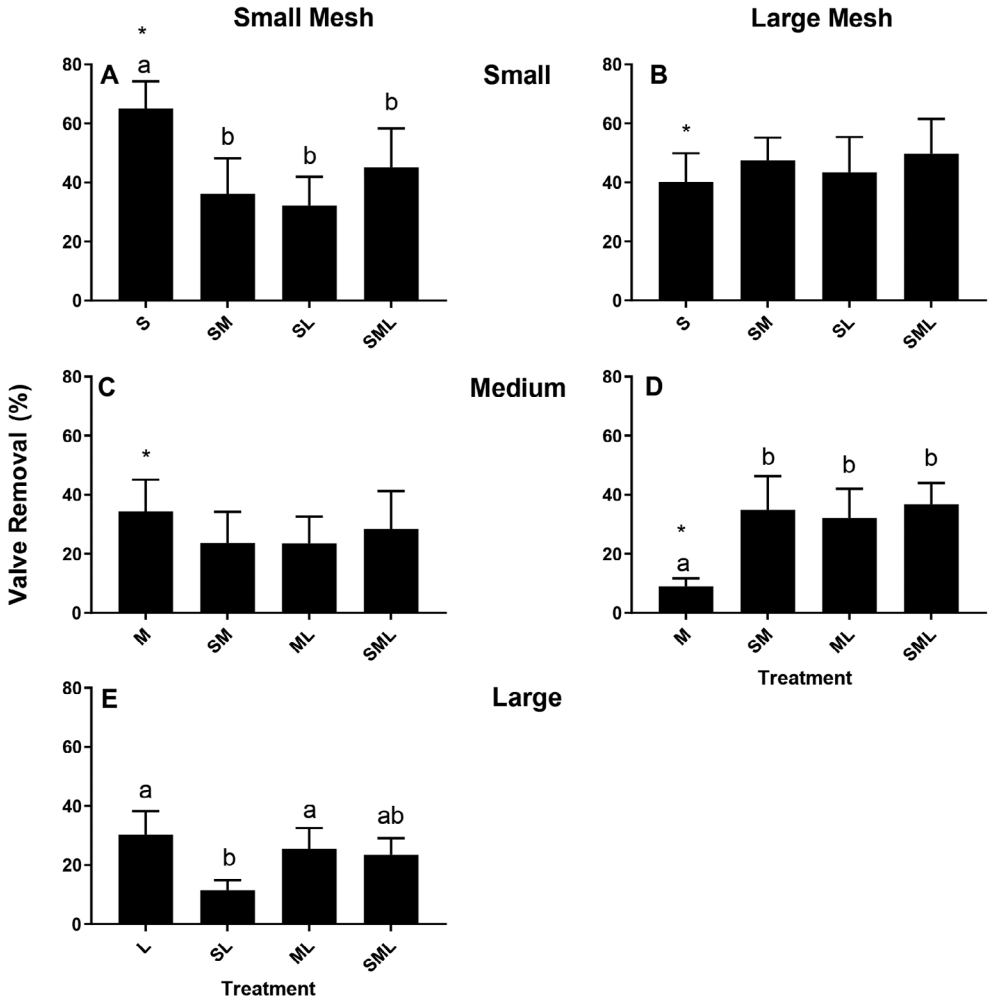

Fig. 2. Small (A, B), medium (C, D), and large oysters (E) with valves missing (mean + SE) when grown on tiles with monocultures or mixtures of phenotypes. For large oysters (E), there was no significant effect of predator access treatment so results are pooled across predator access treatments. Tiles were enclosed with small (1.5 cm; left panel) or large (2.5 cm; right panel) mesh cages. $N = 5$ replicates per treatment. Letters indicate significant differences among diversity treatments within predator access treatments; asterisks indicate significant differences in individual diversity treatments between predator access treatments.

muricid gastropods (e.g., oyster drill, *Bedeva hanleyi* and the white rock shell, *Dicathais orbita*) could have contributed. One possible explanation for why oyster mortality from drilling predators increased with oyster body size is because smaller oysters do not provide enough calories to justify the energetic expense of drilling through shell. Mortality associated with missing valves showed the opposite pattern to that caused by drilling, decreasing with increasing body size. Most likely, small crabs or predators capable of valve removal preferred small oysters because the shells were easiest to remove. It is unlikely that valve removal was caused by natural mortality or predators such as flatworms (O'Connor and Newman 2001), because these leave both valves intact. Our pilot study indicated that valve disarticulation following death did not occur within the time frame of our study, such that loss of the top valve following other sources of mortality is also unlikely.

Juvenile oysters are susceptible to mortality from both biotic (e.g., predation and disease; O'Connor and Newman 2001, Spiers et al. 2014)

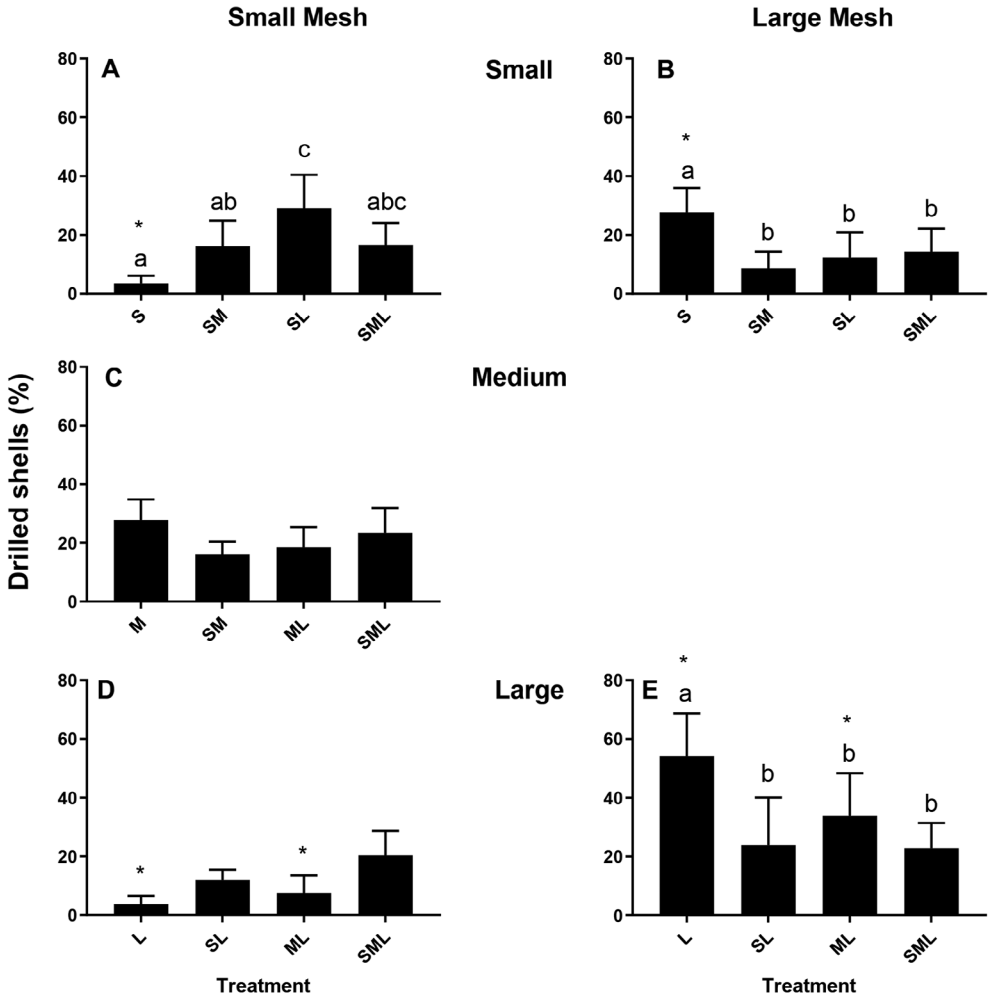

Fig. 3. Small (A, B), medium (C), and large oysters (D, E) with drilled shells (mean + SE) when grown on tiles with monocultures or mixtures of phenotypes. For medium oysters (C), there was no significant effect of predator access treatment so results are pooled across predator access treatments. In all other instances, $N = 5$ replicates per treatment. Tiles were enclosed with small (1.5 cm; left panel) or large (2.5 cm; right panel) mesh cages. Letters indicate significant differences among diversity treatments within predator access treatments; asterisks indicate significant differences in individual diversity treatments between predator access treatments.

and abiotic sources (e.g., temperature and salinity fluctuations; Nell and Holliday 1988, Dove and O'Connor 2007). Thus, the positive effects of increased body size diversity may have also occurred through other means such as reduced competition for resources or buffering of environmental conditions of one phenotype for another. For example, evidence from frogs and sessile invertebrates provides support for food resource partitioning among different-sized siblings such that diversity in size positively influences overall performance (Martin and Pfennig 2010, Cameron et al. 2017). Within aggregations of organisms, the amount of unoccupied space (determined by a combination of body size and density) can be a key determinant of temperature, and hence, organismal survival (Lathlean et al. 2012) and particular phenotypes can provide a disproportionate role in buffering thermal extremes experienced by adjacent organisms (McAfee et al. 2018). Although we lacked cage controls that excluded all predators and provided direct estimates of natural mortality, only 5% of all shells were found dead with intact

valves (i.e., shells representative of natural mortality) suggesting that our findings are due to different rates of predation among our treatment combinations, rather than these alternative explanations.

Although the small mesh did not appear to completely prevent common predators from accessing oysters, patterns of predation nevertheless varied between predator access treatments. Interactions between oyster phenotypes and cage mesh size highlight the potential importance of predator and prey body sizes in influencing predator–prey interactions (e.g., Sinclair et al. 2003). For small oysters, similarly high numbers of oysters with missing valves in each of the predator access treatments suggest predators had equal access to them in both cage types. In small mesh cages, survivorship of medium oysters in monoculture was lower than that of large oysters, suggesting small mesh cages offered large oysters a size refuge from predation. The small mesh cages may provide small mesopredators a refuge from higher order predators and hence allow them to attain higher abundances, resulting in the greater mortality of medium compared to large oysters in this caging treatment (Lavender et al. 2014). In addition, the larger mesh size may also allow access by other larger predators, such as toadfish, *Tetractenos* spp. and/or bream (Nell 1993, Anderson and Connell 1999). Alternatively, smaller predators may not be able to consume larger prey items and/or the rate of prey consumption may increase with predator size (see Moran 1985).

The positive effects of increasing intraspecific diversity are often attributed to selection effects or complementarity among phenotypes (Loreau and Hector 2001), without accounting for changes in density across diversity treatments (Byrnes and Stachowicz 2009). For example, prey at lower densities in mixtures may be harder to locate (visually or tactilely) by predators (an associational refuge; Barbosa et al. 2009). Indeed, rates of predation by *T. marginalba* on other prey species can decrease with decreasing prey density, following a type II functional response (Moran 1985). Our density controls strongly suggest that, for oysters in the small mesh cages, the positive effects of increasing oyster phenotype diversity on survivorship were due to reduced densities of individual phenotypes on mixed tiles. Indeed, reduced predation by crabs on bivalves occurring in lower compared higher density patches has been demonstrated (Micheli 1997). In some instances, density controls had higher survivorship compared to oysters at the same density but grown with another phenotype, suggestive of negative frequency dependence. This could be either be due to the spill over of predators attracted to the co-occurring phenotype or the increased abundance of oysters (twice or three times as many) on mixed phenotype tiles relative to the density controls, regardless of the density of individual phenotypes present. Alternatively, the oysters on the density controls may have experienced less competition due to the lower total number of oysters on tiles compared to oysters in the caged treatments. However, as all oysters were relatively small and were not in contact with other oysters on tiles, competition for resources (e.g., space and food) was likely low. Regardless, while being in mixed cultures generally has positive density-related effects, being in mixed culture can also reduce survivorship relative to being at low densities on your own (i.e., associational susceptibility; Barbosa et al. 2009). Although we did not have density controls for the large mesh size cages, given we observed similar positive effects of oyster phenotypic diversity in both cage types we suggest the mechanisms are likely similar. It is unclear how these results might translate to natural populations that include adult cohorts, and in which size differences among individuals may play a more important role in determining structural complexity and the amount of free space—key determinants of predator effects (Warfe and Barmuta 2006, Humphries et al. 2011).

Compared to our study, weaker effects of intraspecific diversity on survivorship in the presence of predation occurred for the eastern oyster, *Crassostrea virginica* (Hanley et al. 2016). Unlike our study in which we manipulated phenotypic diversity, Hanley et al. (2016) manipulated juvenile cohort richness (the number of cohorts from six different parental broodstocks). Weaker effects of increasing cohort diversity for *C. virginica* may have occurred if the different cohorts did not differ consistently in phenotypic traits that influence survivorship (e.g., body size). However, caution should be applied in the interpretation of our results given that we could

not determine the genotypes present within each of the phenotypes on the tiles, and some scope remains for within family genetic diversity and other phenotypic variations. Although every effort was made to draw phenotypes from across family lines so that each was of similar genetic diversity, it is possible that results could still be confounded by the over-representation of one or two family lines on individual tiles. Indeed, this may have contributed to the high variation observed among tiles for some treatments. Alternatively, differences between studies in the effect of intraspecific variation in mediating predation may reflect among-site variation in other environmental conditions (biotic and/or abiotic; Hanley et al. 2016). The positive effects of genetic diversity can increase with environmental stress (Hughes and Stachowicz 2004, 2011, Reusch et al. 2005, Hughes et al. 2008), and positive effects of phenotypic diversity may similarly vary across environmental gradients.

Understanding which predators consume which phenotypes under different environmental settings will be important for reconciling some of our experimental results, and also for informing rehabilitation efforts endangered species, including oysters (Beck et al. 2011, Grabowski et al. 2012). However, survivorship is only one necessary component for developing successful long-term restoration strategies; these also depend upon factors such as the availability of substrate for colonization, a supply of larvae and successful recruitment. Increasing intraspecific diversity can also have positive effects on recruitment, including for oysters (Smee et al. 2013, Hanley et al. 2016), possibly because more phenotypically diverse assemblages provide a broader range of settlement cues (Smee et al. 2013). It is unclear whether the same or different phenotypic traits underpin positive effects of intraspecific diversity on survivorship as recruitment. If different, then successful restoration may only be achievable through increasing intraspecific variation in multiple traits.

Our study adds to growing evidence of the importance of intraspecific diversity, and diversity more generally (Edwards et al. 2010), for consumer–resource interactions in regulating key population processes (Hughes and Stachowicz 2004, Post et al. 2008, Abdala-Roberts et al. 2015). In our case, increasing prey phenotype diversity increased survivorship of the oyster *S. glomerata*, in part, through mediating predation. Importantly, our results highlight that absolute differences in size need not be large in order to observe benefits of body size diversity. These results complement studies, primarily from plants, showing that intraspecific diversity in resources can dampen consumer effects (Hughes and Stachowicz 2004, Abdala-Roberts et al. 2015). In addition, they suggest a potential mechanism (i.e., via changes in density) underlying relationships between phenotypic dissimilarity and population biomass and size (Ellers et al. 2011). Our results further indicate that the positive effects of increasing intraspecific variation are strongest on the most susceptible phenotypes, consistent with an associational refuge mechanism that is mediated in part by changes in density (Barbosa et al. 2009). Finally, the different mortality experienced by different phenotypes across predator access treatments suggests that consumer size and/or size diversity is likely also important for mediating predator/prey interactions in this system, as in others (Post et al. 2008, Rudolf 2012, Rudolf and Rasmussen 2013, Atkins et al. 2015).

Acknowledgments

The work was supported by the Australian Research Council Future Fellowships to PEG (FT140100322), a National Science Foundation Biological Oceanography grant (OCE-1652320) to ARH, and an Australian Research Council Discovery Grant to MJB and WPO (DP150101363). The authors thank Sofie Voerman and Francisco Martínez-Baena for assistance with fieldwork. We also thank staff at NSWDPI for producing and sorting oysters. PEG, ARH, and MJB conceived the ideas and designed methodology; WAO reared juvenile oysters; PEG, MJB, and DJB set up the experiment; DJB collected the data; PEG analyzed the data; and PEG led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Literature Cited

Abdala-Roberts, L., J. C. Berny-MieryTerán, X. Moreira, A. Durán-Yáñez, and F. Tut-Pech. 2015. Effects of pepper (*Capsicum chinense*) genotypic diversity on insect herbivores. Agricultural and Forest Entomology 17:433–438.

Anderson, M. J., and S. D. Connell. 1999. Predation by fish on intertidal oysters. Marine Ecology Progress Series 187:203–211.

Asquith, C. M., and J. R. Vonesh. 2012. Effects of size and size structure on predation and inter-cohort competition in red-eyed treefrog tadpoles. Oecologia 170:629–639.

Atkins, R. L., J. N. Griffin, C. Angelini, M. I. O'Connor, and B. R. Silliman. 2015. Consumer–plant interaction strength: importance of body size, density and metabolic biomass. Oikos 124:1274–1281.

Barbosa, P., J. Hines, I. Kaplan, H. Martinson, A. Szczepaniec, and Z. Szendrei. 2009. Associational resistance and associational susceptibility: having right or wrong neighbors. Annual Review of Ecology, Evolution, and Systematics 40:1–20.

Beck, M. W., et al. 2011. Oyster reefs at risk and recommendations for conservation, restoration, and management. BioScience 61:107–116.

Bishop, M. J., J. E. Byers, B. J. Marcek, and P. E. Gribben. 2012. Density-dependent facilitation cascades determine epifaunal community structure in temperate Australian mangroves. Ecology 93:1388–1401.

Bishop, M. J., M. R. Cole, S. L. Taylor, E. M. Wilkie, and B. P. Kelaher. 2008. Size-specific predation by dominant consumers maintains a 'trophic cul-de-sac'. Marine Ecology Progress Series 354:75–83.

Bishop, M. J., J. A. Rivera, E. A. Irlandi, W. G. Jr Ambrose, and C. H. Peterson. 2005. Spatio-temporal patterns in the mortality of bay scallop recruits in North Carolina: investigation of a life history anomaly. Journal of Experimental Marine Biology and Ecology 315:127–146.

Bolnick, D. I., P. Amarasekare, M. S. Araújo, R. Bürger, J. M. Levine, M. Novak, V. H. Rudolf, S. J. Schreiber, M. C. Urban, and D. A. Vasseur. 2011. Why intraspecific trait variation matters in community ecology. Trends in Ecology & Evolution 26:183–192.

Byrnes, J. E., and J. J. Stachowicz. 2009. The consequences of consumer diversity loss: different answers from different experimental designs. Ecology 90:2879–2888.

Cameron, H., K. Monro, and D. J. Marshall. 2017. Should mothers provision their offspring equally? A manipulative field test. Ecology Letters 20:1025–1033.

Cardinale, B. J., et al. 2012. Biodiversity loss and its impact on humanity. Nature 486:59–67.

Connell, S., and M. Anderson. 1999. Predation by fish on assemblages of intertidal epibiota: effects of predator size and patch size. Journal of Experimental Marine Biology and Ecology 241:15–29.

Cook-Patton, S. C., S. H. McArt, A. L. Parachnowitsch, J. S. Thaler, and A. A. Agrawal. 2011. A direct comparison of the consequences of plant genotypic and species diversity on communities and ecosystem function. Ecology 92:915–923.

Des Roches, S., D. M. Post, N. E. Turley, J. K. Bailey, A. P. Hendry, M. T. Kinnison, J. A. Schweitzer, and E. P. Palkovacs. 2017. The ecological importance of intraspecific variation. Nature Ecology & Evolution.

Dove, M. C., and W. O'Connor. 2007. Salinity and temperature tolerance of Sydney rock oysters *Saccostrea glomerata* during early ontogeny. Journal of Shellfish Research 26:939–948.

Duffy, M. A. 2010. Ecological consequences of intraspecific variation in lake Daphnia. Freshwater Biology 55:995–1004.

Edgar, G. J. 2000. Australian marine life: the plants and animals of temperate waters. Reed New Holland, Sydney, New South Wales, Australia.

Edwards, K. F., K. M. Aquilino, R. J. Best, K. L. Sellheim, and J. J. Stachowicz. 2010. Prey diversity is associated with weaker consumer effects in a meta-analysis of benthic marine experiments. Ecology Letters 13:194–201.

Eggleston, D. B. 1990. Foraging behavior of the blue crab, *Callinectes sapidus*, on juvenile oysters, *Crassostrea virginica*: effects of prey density and size. Bulletin of Marine Science 46:62–82.

Ellers, J., S. Rog, C. Braam, and M. P. Berg. 2011. Genotypic richness and phenotypic dissimilarity enhance population performance. Ecology 92:1605–1615.

Grabowski, J. H., R. D. Brumbaugh, R. F. Conrad, A. G. Keeler, J. J. Opaluch, C. H. Peterson, M. F. Piehler, S. P. Powers, and A. R. Smyth. 2012. Economic valuation of ecosystem services provided by oyster reefs. BioScience 62:900–909.

Griffin, J. N., and B. R. Silliman. 2018. Predator size-structure and species identity determine cascading effects in a coastal ecosystem. Ecology and Evolution 8:12435–12442.

Hanley, T. C., A. R. Hughes, B. Williams, H. Garland, and D. L. Kimbro. 2016. Effects of intraspecific diversity on survivorship, growth, and recruitment of the eastern oyster across sites. Ecology 97:1518–1529.

Hedge, L. H., B. Leung, W. A. O'Connor, and E. L. Johnston. 2014. The interacting effects of diversity and propagule pressure on early colonization and population size. Journal of Animal Ecology 83:168–175.

Hillebrand, H., and B. J. Cardinale. 2004. Consumer effects decline with prey diversity. Ecology Letters 7:192–201.

Hooper, D. U., et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs 75:3–35.

Hughes, A. R. 2014. Genotypic diversity and trait variance interact to affect marsh plant performance. Journal of Ecology 102:651–658.

Hughes, A. R., P. E. Gribben, D. L. Kimbro, and M. J. Bishop. 2014. Additive and site-specific effects of two foundation species on invertebrate community structure. Marine Ecology Progress Series 508:129–138.

Hughes, A. R., T. C. Hanley, J. E. Byers, J. H. Grabowski, J. C. Malek, M. F. Piehler, and D. L. Kimbro. 2017. Genetic by environmental variation but no local adaptation in oysters (*Crassostrea virginica*). Ecology and Evolution 7:697–709.

Hughes, A. R., B. D. Inouye, M. T. J. Johnson, N. Underwood, and M. Vellend. 2008. Ecological consequences of genetic diversity. Ecology Letters 11:609–623.

Hughes, A. R., and J. J. Stachowicz. 2004. Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. Proceedings of the National Academy of Sciences of the United States of America 101:8998–9002.

Hughes, A. R., and J. J. Stachowicz. 2011. Seagrass genotypic diversity increases disturbance response via complementarity and dominance. Journal of Ecology 99:445–453.

Humphries, A. T., M. K. La Peyre, and G. A. Decossas. 2011. The effect of structural complexity, prey density, and "predator-free space" on prey survivorship at created oyster reef mesocosms. PLOS ONE 6:e28339.

Johnson, K. D., and D. L. Smee. 2012. Size matters for risk assessment and resource allocation in bivalves. Marine Ecology Progress Series 462:103–110.

Kimbro, D. L., J. E. Byers, J. H. Grabowski, A. R. Hughes, and M. F. Piehler. 2014. The biogeography of trophic cascades on US oyster reefs. Ecology Letters 17:845–854.

Kimbro, D., E. Grosholz, A. Baukus, N. Nesbitt, N. Travis, S. Attoe, and C. Coleman-Hulbert. 2009. Invasive species cause large-scale loss of native California oyster habitat by disrupting trophic cascades. Oecologia 160:563–575.

Krassoi, F. R., K. R. Brown, M. J. Bishop, B. P. Kelaher, and S. Summerhayes. 2008. Condition-specific competition allows coexistence of competitively superior exotic oysters with native oysters. Journal of Animal Ecology 77:5–15.

Lamprell, K., and J. Healy. 1998. Bivalves of Australia. Backhuys Publishers, Leiden, The Netherlands.

Lathlean, J. A., D. J. Ayre, and T. E. Minchinton. 2012. Using infrared imagery to test for quadrat-level temperature variation and effects on the early life history of a rocky-shore barnacle. Limnology and Oceanography 57:1279–1291.

Lavender, J. T., K. A. Dafforn, and E. L. Johnston. 2014. Meso-predators: a confounding variable in consumer exclusion studies. Journal of Experimental Marine Biology and Ecology 456:26–33.

Loreau, M., and A. Hector. 2001. Partitioning selection and complementarity in biodiversity experiments. Nature 412:72–76.

Marshall, D. J., A. K. Pettersen, and H. Cameron. 2018. A global synthesis of offspring size variation, its eco-evolutionary causes and consequences. Functional Ecology 32:1436–1446.

Martin, R. A., and D. W. Pfennig. 2010. Maternal investment influences expression of resource polymorphism in amphibians: implications for the evolution of novel resource-use phenotypes. PLOS ONE 5:e9117.

McAfee, D., M. J. Bishop, T. N. Yu, and G. A. Williams. 2018. Structural traits dictate abiotic stress amelioration by intertidal oysters. Functional Ecology 32:2666–2677.

McAfee, D., V. J. Cole, and M. J. Bishop. 2016. Latitudinal gradients in ecosystem engineering by oysters vary across habitats. Ecology 97:929–939.

McAfee, D., W. A. O'Connor, and M. J. Bishop. 2017. Fast-growing oysters show reduced capacity to provide a thermal refuge to intertidal biodiversity at high temperatures. Journal of Animal Ecology 86:1352–1362.

Micheli, F. 1997. Effects of predator foraging behavior on patterns of prey mortality in marine soft bottoms. Ecological Monographs 67:203–224.

Moran, M. 1985. Effects of prey density, prey size and predator size on rates of feeding by an intertidal predatory gastropod *Morula marginalba* Blainville (Muricidae), on several species of prey. Journal of Experimental Marine Biology and Ecology 90:97–105.

Nell, J. A. 1993. Farming the Sydney rock oyster (*Saccostrea commercialis*) in Australia. Reviews in Fisheries Science 1:97–120.

Nell, J. A., and J. E. Holliday. 1988. Effects of salinity on the growth and survival of Sydney rock oyster (*Saccostrea commercialis*) and Pacific oyster (*Crassostrea gigas*) larvae and spat. Aquaculture 68:39–44.

Newell, R. I. E., G. S. Jr Alspach, V. S. Kennedy, and D. Jacobs. 2000. Mortality of newly metamorphosed eastern oysters (*Crassostrea virginica*) in mesohaline Chesapeake Bay. Marine Biology 136:665–676.

O'Connor, W., and L. Newman. 2001. Predatory behaviour and halotolerance of stylochid flatworms, Imogine mcgrathi, from Port Stephens. New South Wales, Australia. Hydrobiology 459:157–163.

O'Connor, W. A., and M. C. Dove. 2009. The changing face of oyster culture in New South Wales, Australia. Journal of Shellfish Research 28:803–811.

O'Connor, W., and L. Newman. 2001. Halotolerance of the oyster predator, *Imogine mcgrathi*, a stylochid flatworm from Port Stephens, New South Wales, Australia. Hydrobiologia 459:157–163.

Peacor, S. D., L. Schiesari, and E. E. Werner. 2007. Mechanisms of nonlethal predator effect on cohort size variation: ecological and evolutionary implications. Ecology 88:1536–1547.

Peterson, C. H. 1982. Clam predation by whelks (*Busycon* spp.): experimental tests of the importance of prey size, prey density, and seagrass cover. Marine Biology 66:159–170.

Post, D. M., E. P. Palkovacs, E. G. Schielke, and S. I. Dodson. 2008. Intraspecific variation in a predator affects community structure and cascading trophic interactions. Ecology 89:2019–2032.

Price, T. 1987. Diet variation in a population of Darwin's finches. Ecology 68:1015–1028.

Primack, R. B. 2014. Essentials of conservation biology. Sixth edition. Sinauer Associates, Sunderland, Massachusetts, USA.

Reusch, T. B. H., A. Ehlers, A. Hammerli, and B. Worm. 2005. Ecosystem recovery after climatic extremes enhanced by genotypic diversity. Proceedings of the National Academy of Sciences of the United States of America 102:2826–2831.

Reznick, D., H. Callahan, and R. Llauredo. 2015. Maternal effects on offspring quality in poeciliid fishes1. American Zoologist 36:147–156.

Rindone, R. R., and D. B. Eggleston. 2011. Predator–prey dynamics between recently established stone crabs (*Menippe* spp.) and oyster prey (*Crassostrea virginica*). Journal of Experimental Marine Biology and Ecology 407:216–225.

Rudolf, V. H. 2012. Seasonal shifts in predator body size diversity and trophic interactions in size-structured predator–prey systems. Journal of Animal Ecology 81:524–532.

Rudolf, V. H., and N. L. Rasmussen. 2013. Ontogenetic functional diversity: Size structure of a keystone predator drives functioning of a complex ecosystem. Ecology 94:1046–1056.

Scanes, E., E. L. Johnston, V. J. Cole, W. A. O'Connor, L. M. Parker, and P. M. Ross. 2016. Quantifying abundance and distribution of native and invasive oysters in an urbanised estuary. Aquatic Invasions 11:425–436.

Schläpfer, F., and B. Schmid. 1999. Ecosystem effects of biodiversity: a classification of hypotheses and exploration of empirical results. Ecological Applications 9:893–912.

Sinclair, A. R. E., S. Mduma, and J. S. Brashares. 2003. Patterns of predation in a diverse predator-prey system. Nature 425:288–290.

Smee, D. L., R. D. Overath, K. D. Johnson, and J. A. Sanchez. 2013. Intraspecific variation influences natural settlement of eastern oysters. Oecologia 173:947–953.

Spiers, Z. B., M. Gabor, S. A. Fell, R. B. Carnegie, M. Dove, W. O. Connor, J. Frances, J. Go, I. B. Marsh, and C. Jenkins. 2014. Longitudinal study of winter mortality disease in Sydney rock oysters *Saccostrea glomerata*. Diseases of Aquatic Organisms 110:151–164.

Stachowicz, J. J., J. F. Bruno, and J. E. Duffy. 2007. Understanding the effects of marine biodiversity on communities and ecosystems. Annual Review of Ecology Evolution and Systematics 38:739–766.

Stachowicz, J. J., S. J. Kamel, A. R. Hughes, and R. K. Grosberg. 2013. Genetic relatedness influences plant biomass accumulation in eelgrass (*Zostera marina*). American Naturalist 181:715–724.

Tilman, D. 1996. Biodiversity: population versus ecosystem stability. Ecology 77:350–363.

Toscano, B. J., and B. D. Griffen. 2012. Predatory crab size diversity and bivalve consumption in oyster reefs. Marine Ecology Progress Series 445:65–74.

Warfe, D. M., and L. A. Barmuta. 2006. Habitat structural complexity mediates food web dynamics in a freshwater macrophyte community. Oecologia 150:141–154.

Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology and Systematics 15:393–425.

Whitham, T. G., et al. 2006. A framework for community and ecosystem genetics: from genes to ecosystems. Nature Reviews Genetics 7:510–523.

Woodward, G., B. Ebenman, M. Emmerson, J. M. Montoya, J. M. Olesen, A. Valido, and P. H. Warren. 2005. Body size in ecological networks. Trends in Ecology & Evolution 20:402–409.

Yang, L. H., and V. H. W. Rudolf. 2010. Phenology, ontogeny, and the effects of climate change on the timing of species interactions. Ecology Letters 13:1–10.

Data Availability

Data associated with this manuscript are deposited with National Science Foundation Biological and Chemical Oceanography Data Management Office (BCO-DMO) at https://doi.org/10.1575/1912/bco-dmo.804502.1