Invasive ecosystem engineer selects for different phenotypes of an associated native species

JEFFREY T. WRIGHT,[1,5] PAUL E. GRIBBEN,[2] JAMES E. BYERS,[3] AND KEYNE MONRO[4]

[1]*National Centre for Marine Conservation and Resource Sustainability, Australian Maritime College, University of Tasmania, P.O. Box 986, Launceston 7250 Australia*
[2]*Plant Functional Biology and Climate Change Cluster and, School of the Environment, University of Technology, NSW 2007 Australia*
[3]*Odum School of Ecology, University of Georgia, Athens, Georgia 30602 USA*
[4]*School of Biological Sciences, The University of Queensland, Queensland 4072 Australia*

Abstract. Invasive habitat-forming ecosystem engineers modify the abiotic environment and thus represent a major perturbation to many ecosystems. Because native species often persist in these invaded habitats but have no shared history with the ecosystem engineer, the engineer may impose novel selective pressure on native species. In this study, we used a phenotypic selection framework to determine whether an invasive habitat-forming ecosystem engineer (the seaweed *Caulerpa taxifolia*) selects for different phenotypes of a common co-occurring native species (the bivalve *Anadara trapezia*). Compared to unvegetated habitat, *Caulerpa* habitat has lower water flow, lower dissolved oxygen, and sediments are more silty and anoxic. We determined the performance consequences of variation in key functional traits that may be affected by these abiotic changes (shell morphology, gill mass, and palp mass) for *Anadara* transplanted into *Caulerpa* and unvegetated habitat. Both linear and nonlinear performance gradients in *Anadara* differed between habitats, and these gradients were stronger in *Caulerpa* compared to unvegetated sediment. Moreover, in *Caulerpa* alternate phenotypes performed well, and these phenotypes were different from the dominant phenotype in unvegetated sediment. By demonstrating that phenotype–performance gradients differ between habitats, we have highlighted a role for *Caulerpa* as an agent of selection on native species.

Key words: bivalve; ecosystem engineers; hypoxia; invasive species; marine algae; performance; phenotypic selection; plasticity; selection gradient analysis.

INTRODUCTION

Invasive species represent a major threat to natural ecosystems and biodiversity (Vitousek et al. 1996, Mack et al. 2000). Where strong ecological impacts occur within the new region, invasive species are also likely to impart strong and novel selective pressure on native species (Strauss et al. 2006). For example, changes in adaptive traits have been documented in native insects in response to invasive host plants (Carroll et al. 2005), native mollusks in response to invasive predatory crabs (Trussell and Smith 2000), and native snakes in response to invasive toads as prey (Phillips and Shine 2005). The majority of examples of invasive species causing selection on native species involve direct, often trophic, interactions (predation, herbivory, and competition; Strauss et al. 2006). In contrast, little is known about how modification of the abiotic environment by invasive habitat-forming ecosystem-engineers (e.g., plants, seaweed, sessile invertebrates) influences the strength or direction of selection on native species.

Invasive habitat-forming ecosystem engineers modify important abiotic factors such as soil and sediment physicochemistry, water, light, and oxygen availability, and disturbance regimes (Crooks 2002, Levine et al. 2003). Despite these large changes to the abiotic environment, there are many examples of native species using and persisting in these new habitats, often at high densities (Crooks 2002, McKinnon et al. 2009). The use of highly modified invasive habitat by native species suggests selection may occur for phenotypes able to tolerate the new abiotic conditions.

Caulerpa taxifolia (Vahl) C. Agardh is an invasive habitat-forming seaweed that forms extensive, dense stands in previously unvegetated sediment. *Caulerpa* has strong engineering effects on the abiotic environment that might change selective regimes for native species. In *Caulerpa* beds, there is lower water flow, lower dissolved oxygen, sediments are more anoxic, silt content is higher, and there is greater abundance of large phytoplankton compared to unvegetated sediment (Gribben et al. 2009, McKinnon et al. 2009). The dominant native bivalve in this system, *Anadara trapezia* (Arcidae, Deshayes 1840) recruits into *Caulerpa* in high numbers (Gribben and Wright 2006). However, it suffers a number of negative effects in *Caulerpa* ranging

from reduced survivorship to sublethal effects on reproduction, shell morphology, and burrowing behavior (Wright and Gribben 2008, Gribben et al. 2009, Wright et al. 2010).

Given its strong engineering of the abiotic environment and the trait changes in *Anadara* in that habitat, we hypothesized that patterns of selection on key traits of *Anadara* would differ between *Caulerpa* and unvegetated sediment. To explore this hypothesis, we examined the performance consequences of variation in key traits among *Anadara* transplanted into these two habitats. Assuming that performance translates into fitness (Arnold 1983), any changes in the effects of traits on performance across habitats are likely to reflect divergent selection on *Anadara* phenotypes. The traits we examined were shell morphology (length and breadth), gill mass and palp mass, all of which we related to body size (biomass) as a performance trait correlated with important components of fitness in *Anadara* (e.g., fecundity and survival; Gribben and Wright 2006, Wright and Gribben 2008). In bivalves, shell morphology influences burrowing behavior and vulnerability to predation (Whitlow et al. 2003); gills function in respiration and the collection and initial sorting of food and sediment particles; while palps are primarily involved in sorting food and sediment particles (Shumway et al. 1983, Drent et al. 2004). Thus, the abiotic differences between *Caulerpa* and unvegetated sediment may influence selection on *Anadara* shell morphology, gills, and palps between habitats.

To test our hypothesis, we used phenotypic selection analyses. These analyses provide statistical estimates of fitness functions by regressing components of fitness (or performance) associated with particular trait values onto the range of all values observed in a given population. These functions may be linear or nonlinear in form, and describe the pattern and strength of phenotypic selection within generations in that population (Lande and Arnold 1983, Blows and Brooks 2003, Kingsolver and Pfennig 2007). Because we only measured performance as a proxy for fitness, we describe performance gradients on traits rather than selection gradients per se. Nonetheless, a key step in understanding how selection acts on traits is to determine trait–performance relationships (i.e., performance gradients; Arnold 1983). Specifically, we fitted multiple regression models of body size on trait values of *Anadara* recruits transplanted into *Caulerpa* and unvegetated sediment, and compared models across habitats. We used first-order models to estimate linear or directional selection on traits, second-order models to estimate nonlinear selection on traits, and canonical analyses of nonlinear regression coefficients (Phillips and Arnold 1989, Blows and Brooks 2003) to help interpret the patterns of nonlinear multivariate selection acting on trait combinations in *Anadara* in *Caulerpa* and unvegetated sediment.

Materials and Methods

Study system

In southeastern Australia, *Caulerpa* occurs in 14 estuaries where it primarily invades unvegetated sediment. *Anadara trapezia* is a dioecious, free-spawning species with a 10–12 day larval stage (Nell et al. 1994). *Anadara* grows up to 70 mm in shell length and occurs in 0–4 m water depth in sheltered mud, sand, seagrass, and now *Caulerpa* habitats (Wright et al. 2007). *Anadara* are suspension feeders and switch from being epifaunal as post-recruitment juveniles (Gribben and Wright 2006) to infaunal as they grow and typically occur fully or partially burrowed (~80%) in the sediment (Wright et al. 2010).

Our experiment was conducted in Sponge Bay, Lake Conjola (35°15′44.3″ S, 150°26′47.8″ E), a temporary barrier estuary approximately 210 km south of Sydney, Australia. At the beginning of our experiment there were intermingling patches of *Caulerpa* and unvegetated sediment and large populations of *Anadara* in both unvegetated sediment and *Caulerpa* (Wright et al. 2007). Seagrass was uncommon at our site with only a handful of small patches of *Halophila ovalis* and *Zostera capricorni* in shallow zones.

Experimental design

In February 2006, 60 male and female *Anadara* were collected from unvegetated sediment in Lake Macquarie (33.086° S, 151.662° E). *Anadara* recruits originating from this broodstock were produced using standard bivalve culture techniques (Nell et al. 1994). In May 2006, at 3 months of age, recruits were transported to our study site and added to mesh cages (standard scallop lantern nets 30 × 30 cm, 1 mm^2 mesh size; $n = 10$ cages/habitat). We added 40 *Anadara*/cage (shell length [anterior-posterior axis]; 12.43 ± 0.14 mm [mean ± SE]) and cages were placed into *Caulerpa* and unvegetated sediment at 1.5–2.0 m depth for 17 months. We had to cage recruits because they are mobile. Thus, the potential selective effects of predators on *Anadara* traits could not be examined (see Gribben and Wright [2006] and Byers et al. [2010] for habitat-dependent predation on *Anadara* recruits and adults). However, caging recruits allowed us to isolate the effects of the abiotic environment as a selective agent. We kept *Caulerpa* from unvegetated areas around each cage by hand-picking it every 4–6 weeks. After 17 months, shell length and breadth (dorsal-ventral axis perpendicular to the umbo) of each surviving *Anadara* were measured. Gills, palps, and the remaining tissue were removed from shells and all were blotted dry with a paper towel to remove excess water and weighed. Mortality in cages during the experiment resulted in a sample size of $N = 133$ in unvegetated sediment and $N = 77$ in *Caulerpa*.

Linear and nonlinear performance gradients in Caulerpa *and unvegetated sediment*

Because these *Anadara* were not yet reproductive we could not estimate fecundity. Hence, we chose the total biomass (wet mass of shell and tissue) of *Anadara* as a key measure of performance. Generally in bivalves, body size is an important measure of performance that correlates with fecundity (Byers 2005) and biomass of pre-reproductive *Anadara* is likely to be a good predictor of adult biomass. Prior to analysis, we calculated relative performance as the mass of each individual divided by the mean mass in each habitat (*Caulerpa* and unvegetated sediment; see Lande and Arnold 1983 for details on processing data for selection analyses), and log-transformed all traits except performance (see Stanton and Thiede 2005) to improve normality before converting them to units of standard deviation (SD).

We then fitted first- and second-order multiple regressions of relative performance on the trait values of *Anadara* in each habitat to estimate their linear (denoted by the vector β) and nonlinear (denoted by the matrix γ) performance gradients. (Lande and Arnold 1983). Preliminary inspection of variance inflation factors indicated that these gradients were not compromised by multicollinearity. The significance of gradients was tested using randomization tests (Stanton and Thiede 2005). Briefly, we re-estimated all gradients from models in which relative performance was randomized across trait values, and used Monte Carlo simulations (using the PopTools add-in for Excel; Hood 2008) to compare real and randomized gradients over 10 000 permutations. We then fitted thin-plate splines to visualize performance gradients on individual traits using R 2.9.0 (R Development Core Team 2009).

We used a sequential model-building approach (Draper and John 1988) to compare linear (β) and nonlinear (γ) performance gradients between habitats. First, to compare linear gradients between habitats, we fitted an analysis of covariance (ANCOVA) of relative performance on all traits with habitat as a categorical variable (model 1), and compared this model to one that included all trait × habitat interactions (model 2). The test statistic (as for each subsequent comparison) was a partial *F*, which takes into account the amount of unexplained (residual) variance and number of estimated parameters by which models differ (Draper and John 1988). Next, to test whether inclusion of nonlinear gradients significantly improved model fit, we compared model 2 to one that included all second-order terms (i.e., squares and cross-products of original traits; model 3). Last, to compare nonlinear gradients between habitats, we compared model 3 to a final model that included all second-order trait × habitat interactions.

We also conducted a canonical analysis (or eigenanalysis) of each γ matrix. This analysis rotates a given γ to set all correlational gradients (i.e., below-diagonal elements) to zero, leaving only nonlinear gradients on canonical axes (eigenvectors of γ, termed $\mathbf{m}_i$, which remain in units of standard deviation). These are linear combinations of the original traits (where traits with coordinated effects on fitness, or in our case, performance, load strongly on the same axes) on which curvature is strongest (Phillips and Arnold 1989, Blows and Brooks 2003). The strength and form of curvature on each axis is inferred from the magnitude and sign of its eigenvalue (λ_i), with positive values indicating concave curvature and negative values indicating convex curvature. As for individual traits, such patterns of curvature in trait combinations may be interpreted as disruptive and stabilizing selection, respectively, if they span obvious inflexion points (see Kingsolver and Pfennig 2007).

The significance of loadings of original traits on eigenvectors was tested using the method of Peres-Neto et al. (2003; their method 6). Briefly, we drew 1000 bootstrapped samples from the data and conducted an eigenanalysis of each, calculating *P* values as the proportions of bootstrapped loadings that were ≤ 0 for real loadings that were positive, or ≥ 0 for real loadings that were negative. We tested the significance of all eigenvalues using the method of Bisgaard and Ankenman (1996). Last, to visualize performance gradients on canonical axes, we fitted thin-plate splines to these composite traits in R 2.9.0.

Results

Anadara trapezia transplanted to unvegetated sediment had a greater biomass, longer, broader shells and heavier gills and palps compared to *Anadara* transplanted to *Caulerpa* (unpaired *t* tests, df = 208, $P < 0.001$ for all traits; Appendix).

There were strong positive linear gradients of performance on *Anadara* shell length and breadth in unvegetated sediment, and on shell length, gill mass, and palp mass in *Caulerpa* (Fig. 1, Appendix). Overall, linear gradients differed between habitats (partial $F_{4, 200} = 3.72$; $P < 0.01$), which appeared largely due to the stronger impacts of gill and palp mass on performance in *Caulerpa* compared to unvegetated sediment (Fig. 1C and D). There were significant positive nonlinear gradients of performance on gill mass in unvegetated sediment and on shell length in *Caulerpa* (Appendix), indicating concave relationships with performance. This pattern was especially pronounced for gill mass in unvegetated sediment (Fig. 1). There was also a negative correlational gradient on shell length and gill mass in *Caulerpa* (Appendix) suggesting a performance cost of such integration. Nonlinear performance gradients explained a significant amount of variation in clam phenotypes across habitats (partial $F_{10, 190} = 5.76$; $P < 0.01$), and also differed significantly between them (partial $F_{10, 180} = 2.73$; $P < 0.01$).

Canonical analyses of γ identified significantly positive gradients of performance (indicating concave curvature) on two eigenvectors ($\mathbf{m}_1$ and $\mathbf{m}_2$) in each habitat (Table 1). Thus, all relevant details about the
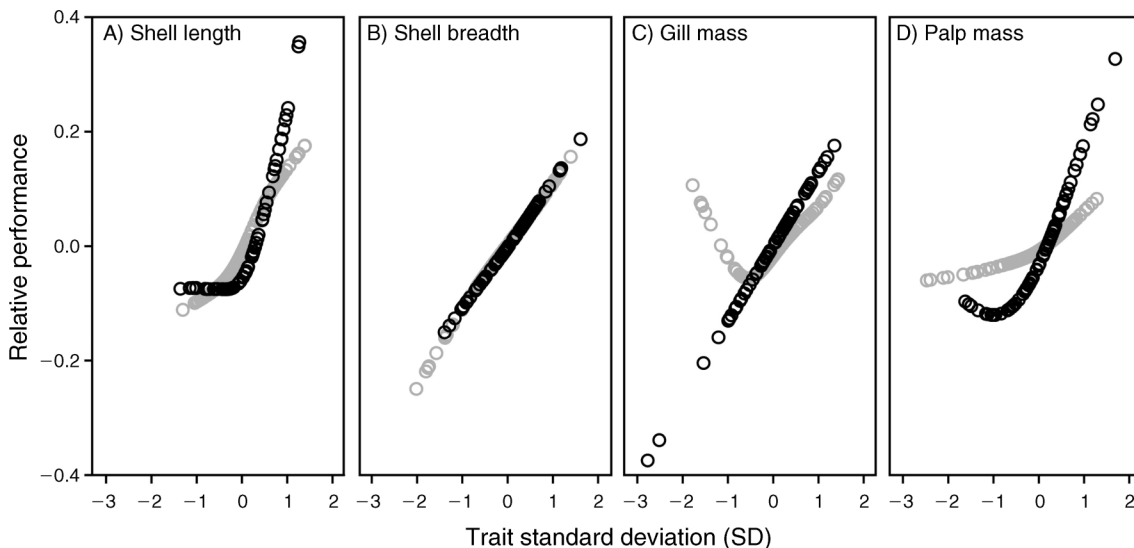
FIG. 1. Spline visualizations of linear (β) and nonlinear (γ) performance gradients on (A) shell length, (B) shell breadth, (C) gill mass and, (D) palp mass of *Anadara trapezia* transplanted to unvegetated sediment (gray circles) and to *Caulerpa taxifolia* (black circles).

nonlinear gradients in each γ can be described by a single performance surface with each pair of eigenvectors as axes (Fig. 2). Each performance surface is roughly a shallow bowl, skewed along the dominant axis ($\mathbf{m}_1$). For clams in unvegetated sediment, $\mathbf{m}_1$ had a significantly positive loading for gill mass and a significantly negative loading for palp mass, while $\mathbf{m}_2$ had a significantly negative loading for shell breadth (Table 1). As peak performance in unvegetated sediment is associated with low values of $\mathbf{m}_1$ and high values of $\mathbf{m}_2$ (Fig. 2A), clams near this peak have phenotypes with relatively large palps with small gills, and narrow shells.

For clams in *Caulerpa*, there were different patterns of trait loading: $\mathbf{m}_1$ had a significantly positive loading for shell length and a significantly negative loading for gill mass, while $\mathbf{m}_2$ had significantly positive loadings for both shell breadth and palp mass (Table 1). In addition, in *Caulerpa*, peak performance is associated with high

values of both $\mathbf{m}_1$ and $\mathbf{m}_2$ (Fig. 2B) corresponding to phenotypes with long shells with small gills, and broad shells with large palps. In *Caulerpa*, moreover, alternate phenotypes with short shells with large gills, and narrow shells with small palps also performed well (Fig. 2B). Concavity comes from a diminishing cost of moving to average phenotypes and the presence of an inflexion point along $\mathbf{m}_1$. That is, there is a benefit for more extreme phenotypes on $\mathbf{m}_1$. For example, clams with phenotypes located approximately one standard deviation below the $\mathbf{m}_1$ mean perform as well as clams located a standard deviation above this mean (Fig. 2B).

DISCUSSION

Our study shows that linear and nonlinear performance gradients in the native bivalve *Anadara trapezia* differed between habitats invaded by *Caulerpa taxifolia* compared to unvegetated sediment. In particular, selection on

TABLE 1. Performance gradients (λ_i) on eigenvectors of γ ($\mathbf{m}_i$) for *Anadara trapezia* transplanted to unvegetated sediment and to *Caulerpa taxifolia*.

| | Loading of original trait | | | | Gradient |
Eigenvector	Shell length	Shell breadth	Gill mass	Palp mass	λ_i
Unvegetated sediment					
$\mathbf{m}_1$	−0.431	−0.166	0.697*	−0.549*	0.118**
$\mathbf{m}_2$	0.356	−0.529*	0.533	0.556	0.064**
Caulerpa					
$\mathbf{m}_1$	0.845**	−0.236	−0.433**	0.205	0.362**
$\mathbf{m}_2$	−0.047	0.515*	0.032	0.855**	0.092**

Notes: Each vector is a combination of the original traits, whose contributions are described by their associated loadings (traits with coordinated effects on performance load strongly on the same axes; only vectors with significant gradients are presented). Eigenvectors of the same γ are independent (Blows 2007).

   * $P < 0.05$; ** $P < 0.01$.

Reports

Reports

A) Unvegetated sediment

B) *Caulerpa*

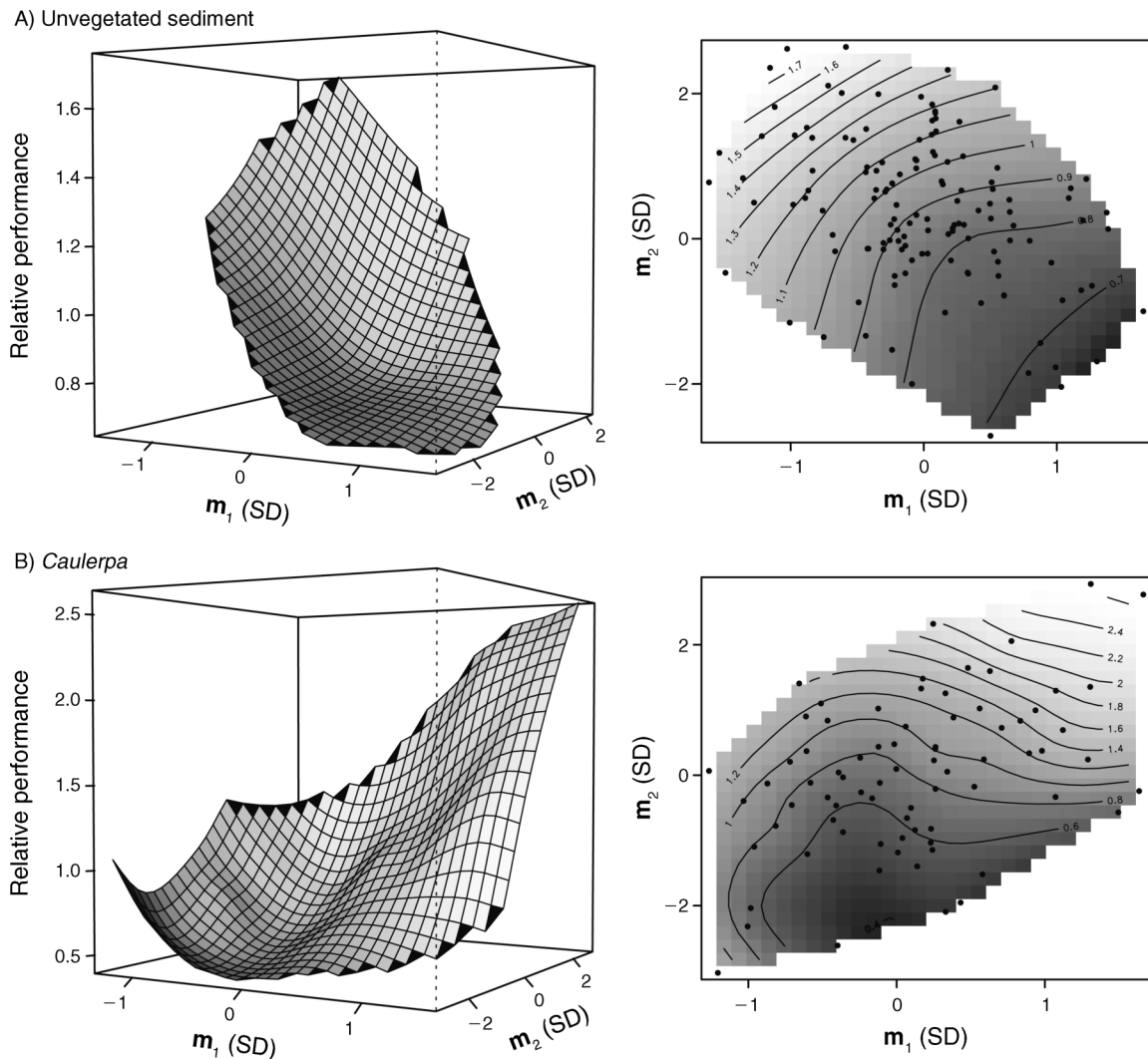Fig. 2. Spline visualizations of the two significant performance gradients on eigenvectors of γ (m_1 and m_2, in units of standard deviation) for *Anadara trapezia* transplanted to (A) unvegetated sediment and (B) to *Caulerpa taxifolia*. Relatively high-performing phenotypes can be determined by interpreting the loadings of original traits that contribute most to both axes from Table 1. The current mean phenotype is located at zero on each axis. Thus, negative values denote below-average phenotypes, and positive values denote above-average phenotypes. To aid interpretation, splines are presented as both three-dimensional surfaces (on the left) and as contour plots of these surfaces viewed from above (on the right, with dots showing values of individual clams with relative performance increasing from dark to light shading).

Anadara was stronger in *Caulerpa* (stronger gradients for individual traits and larger eigenvalues for trait combinations) and different phenotypes were favored in each habitat. Although our analyses describe gradients of performance within a single generation that may reflect both differential mortality and plasticity, they highlight important changes to *Anadara* shell morphology, gills, and palps following *Caulerpa* invasion.

In unvegetated sediment, strong linear performance gradients on shell length and breadth may drive increases in shell size in *Anadara*. While these linear gradients predict the change in the means of individual traits, adaptation is an inherently multivariate process.

Thus, selection will frequently act upon sets of functionally related traits, rather than individual traits in isolation, and nonlinear selection (affecting trait variances and covariances) can complicate the interpretation of selection on the means of individual traits (Lande and Arnold 1983, Phillips and Arnold 1989). Although the performance–phenotype relationship for *Anadara* in unvegetated sediment is concave, a single dominant phenotype with relatively large palps, small gills and narrow shells is likely to be favored there (Fig. 2B). Selection for a phenotype with large palps may be driven by the general need for *Anadara* to meet food uptake requirements and to sort food from sediment

(Shumway et al. 1983, Drent et al. 2004). Moreover, in unvegetated sediment selection may gradually eliminate *Anadara* phenotypes with relatively small palps and large gills as individuals with this trait combination performed poorly (Fig. 2A).

The strong linear performance gradient on *Anadara* shell length in *Caulerpa* suggests selection for increased size in that habitat too but in contrast to unvegetated sediment, there were also linear performance gradients for larger gills and palps. Canonical analysis of nonlinear performance gradients for *Anadara* in *Caulerpa*, revealed that *Anadara* phenotypes with the highest relative performance had large palps, small gills (similar to the dominant phenotype favored in unvegetated sediment), and long, broad shells. Although superficially, this suggests similar phenotypes perform best in both habitats, as eigenvectors of the same γ are independent (Blows 2007), performance depends on an allocation trade-off between gills and palps in unvegetated sediment, but on their interactions with shell morphology in *Caulerpa*. In *Caulerpa*, relatively large palps may be linked to having to increase the amount of sediment sorting due to the finer sediments (McKinnon et al. 2009) or more abundant, larger sized phytoplankton (Gribben et al. 2009) in that habitat. The deposit-feeding bivalve, *Macoma balthica*, has a higher palp : gill ratio with increasing mud content of sites (Drent et al. 2004). *Anadara* phenotypes with long, broad shells may be able to better pop-up above the hypoxic boundary layer beneath the *Caulerpa* canopy (Wright et al. 2010). Alternative phenotypes that also performed well in *Caulerpa* had relatively large gills that may enable a greater efficiency in gas exchange or enhance particle sorting in the low-flow, low-dissolved-oxygen water under *Caulerpa* (Gribben et al. 2009, Wright et al. 2010). Different phenotypes with high relative performance may occur if existing (pre-invasion) *Anadara* phenotypes are not well adapted to *Caulerpa*. Under this scenario, selection may favor individuals at the tails of the phenotypic distribution (away from the average phenotype). Alternatively, different phenotypes with high performance may be related to the patchiness in the biomass of *Caulerpa*. Water column dissolved oxygen and sediment anoxia are correlated with *Caulerpa* biomass (P. E. Gribben, *unpublished data*). Phenotypes with large gills may be favored at high *Caulerpa* densities where the concentration of dissolved oxygen is low, whereas phenotypes with large shells and palps may be favored at low *Caulerpa* densities, where selection on gills may be weaker.

Although we have documented differences in performance gradients in *Anadara* between *Caulerpa* and unvegetated sediment that appear linked to the abiotic changes caused by *Caulerpa*, because we had to cage *Anadara* we cannot rule out a selective role for predation. Predators can drive evolutionary change in shells of marine mollusks (Trussell and Smith 2000) and given that predation is high on *Anadara* recruits in unvegetated sediment (Gribben and Wright 2006) and on adults in both habitats (Byers et al. 2010), predators may impose selection on shell morphology in *Anadara*.

Caging *Anadara* also prohibited them from moving away from *Caulerpa* to unvegetated sediment. However, the large area of *Caulerpa* beds and their thick canopy appears to restrict movement of most *Anadara* out of *Caulerpa* (Gribben et al. 2009). We also do not know the underlying genetic variance of traits measured here and thus how strongly they are likely to respond to selection. Moreover, we do not know the relative importance of plasticity and differential mortality in explaining the observed changes in phenotype. Given *Anadara* populations are likely to be open with gene flow between them; selection for plasticity may be just as likely to occur as selection for locally adapted phenotypes.

Given the large influences invasive ecosystem engineers have on the abiotic environment and the frequent occurrence of native species in those habitats, phenotypic selection mediated by invader-driven changes to the abiotic environment may be common. Recent reviews highlight an important role for evolutionary responses in native species to invasive species (Cox 2004, Strauss et al. 2006) but ours is the first to link abiotic changes caused by an invasive ecosystem engineer to selection for different phenotypes of a native species. By demonstrating that the changes to traits and combinations of traits are linked to performance and, that these phenotype–performance gradients differ between habitats, we have highlighted how *Caulerpa* acts as an agent of phenotypic selection on *Anadara*. Moreover, because the impact of *Caulerpa* on *Anadara* occurs via modification of the abiotic environment, it does not involve a direct biotic interaction between species and thus the impact of the invader on the native species is indirect (mediated through the abiotic change the ecosystem engineer causes). A greater focus on how invasive ecosystem engineers indirectly impose trait changes on native species and the underlying genetic basis to any changes should enhance our understanding of invasive ecosystem engineers as agents of evolutionary change.

Literature Cited

Arnold, S. J. 1983. Morphology, performance, and fitness. American Zoologist 23:347–361.

Bisgaard, S., and B. Ankenman. 1996. Standard errors for the eigenvalues in second-order response surface models. Technometrics 38:238–246.

Blows, M. W. 2007. A tale of two matrices: multivariate approaches in evolutionary biology. Journal of Evolutionary Biology 20:1–8.

Blows, M. W., and R. Brooks. 2003. Measuring non-linear selection. American Naturalist 162:815–820.

Byers, J. E. 2005. Marine reserves enhance abundance but not competitive impacts of a harvested nonindigenous species. Ecology 86:487–500.

Byers, J. E., J. T. Wright, and P. E. Gribben. 2010. Variable direct and indirect effects of a habitat-modifying invasive species on mortality of native fauna. Ecology 91:1787–1798.

Reports

Carroll, S. P., J. E. Loye, H. Dingle, M. Mathieson, T. R. Famula, and M. P. Zalucki. 2005. And the beak shall inherit—evolution in response to invasion. Ecology Letters 8:944–951.

Cox, G. W. 2004. Alien species and evolution. Island Press, Washington, D.C., USA.

Crooks, J. A. 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. Oikos 97:153–166.

Draper, N. R., and J. A. John. 1988. Response surface designs for quantitative and qualitative variables. Technometrics 30:423–428.

Drent, J., P. C. Luttikhuizen, and T. Piersma. 2004. Morphological dynamics in the foraging apparatus of a deposit feeding marine bivalve: phenotypic plasticity and heritable effects. Functional Ecology 18:349–356.

Gribben, P. E., and J. T. Wright. 2006. Invasive seaweed enhances recruitment of a native bivalve: roles of refuge from predation and the habitat choice of recruits. Marine Ecology Progress Series 318:177–185.

Gribben, P. E., J. T. Wright, W. A. O'Connor, M. A. Doblin, B. Eyre, and P. D. Steinberg. 2009. Reduced performance of native infauna following recruitment to a habitat-forming invasive marine alga. Oecologia 158:733–745.

Hood, G. M. 2008. Poptools, version 3.0.6. http://www.cse.csiro.au/poptools

Kingsolver, J. G., and D. W. Pfennig. 2007. Patterns and power of phenotypic selection in nature. BioScience 57:561–572.

Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. Evolution 37:1210–1226.

Levine, J. M., M. Vila, C. M. D'Antonio, J. S. Dukes, K. Grigulis, and S. Lavorel. 2003. Mechanisms underlying the impacts of exotic plant invasions. Proceedings of the Royal Society B 270:775–781.

Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications 10:689–710.

McKinnon, J. G., P. E. Gribben, A. R. Davis, D. F. Jolley, and J. T. Wright. 2009. Differences in soft-sediment macrobenthic assemblages invaded by *Caulerpa taxifolia* compared to uninvaded habitats. Marine Ecology Progress Series 380:59–71.

Nell, J. A., W. A. O'Connor, M. P. Heasman, and L. J. Goard. 1994. Hatchery production for the venerid clam *Katelysia rhytiphora* (Lamy) and the Sydney cockle *Anadara trapezia* (Deshayes). Aquaculture 119:149–156.

Peres-Neto, P., D. A. Jackson, and K. M. Somers. 2003. Giving meaningful interpretation to ordination axes: assessing loading significance in principal component analyses. Ecology 84:2347–2363.

Phillips, B. L., and R. Shine. 2005. Adapting to an invasive species: toxic cane toads induce morphological change in Australian snakes. Proceedings of the National Academy of Sciences USA 101:17150–17155.

Phillips, P. C., and S. J. Arnold. 1989. Visualizing multivariate selection. Evolution 43:1209–1222.

R Development Core Team. 2009. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org

Shumway, S. E., T. M. Scott, and J. M. Shick. 1983. The effects of anoxia and hydrogen sulphide on survival, activity and metabolic rate in the coot clam, *Mulinia lateralis* (Say). Journal of Experimental Marine Biology and Ecology 71:135–146.

Stanton, M. L., and D. A. Thiede. 2005. Statistical convenience vs biological insight: consequences of data transformation for the analysis of fitness variation in heterogeneous environments. New Phytologist 166:319–338.

Strauss, S. Y., J. A. Lau, and S. P. Carroll. 2006. Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities? Trends in Ecology and Evolution 9:357–374.

Trussell, G. C., and L. D. Smith. 2000. Induced defenses in response to an invading crab predator: An explanation of historical and geographic phenotypic change. Proceedings of the National Academy of Sciences USA 97:2123–2127.

Vitousek, P. M., C. M. D'Antonio, L. L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. American Scientist 84:468–478.

Whitlow, W. L., N. A. Rice, and C. Sweeney. 2003. Native species vulnerability to introduced predators: testing an inducible defense and a refuge from predation. Biological Invasions 5:23–31.

Wright, J. T., J. E. Byers, L. P. Koukoumaftsis, P. J. Ralph, and P. E. Gribben. 2010. Native species behavior mitigates the impact of habitat-forming invasive seaweed. Oecologia 163:527–534.

Wright, J. T., and P. E. Gribben. 2008. Predicting the impact of an invasive seaweed on the fitness of native fauna. Journal of Applied Ecology 45:1540–1549.

Wright, J. T., L. A. McKenzie, and P. E. Gribben. 2007. A decline in the density and health of a native bivalve associated with *Caulerpa taxifolia* invasion. Marine and Freshwater Research 58:263–272.

SUPPLEMENTAL MATERIAL

Appendix

Tables showing trait values and performance gradients on traits of *Anadara trapezia* transplanted to unvegetated sediment and *Caulerpa taxifolia* (*Ecological Archives* E093-109-A1).

Reports