



Environment-dependent variation in selection on life history across small spatial scales

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Variation in life-history traits is ubiquitous, even though genetic variation is thought to be depleted by selection. One potential mechanism for the maintenance of trait variation is spatially variable selection. We explored spatial variation in selection in the field for a colonial marine invertebrate that shows phenotypic differences across a depth gradient of only 3 m. Our analysis included life-history traits relating to module size, colony growth, and phenology. Directional selection on colony growth varied in strength across depths, while module size was under directional selection at one depth but not the other. Differences in selection may explain some of the observed phenotypic differentiation among depths for one trait but not another: instead, selection should actually erode the differences observed for this trait. Our results suggest selection is not acting alone to maintain trait variation within and across environments in this system.

KEY WORDS: Bryozoan, competition, growth, heterogeneous selection, natural selection, *Watersipora*.

Why is it that some organisms grow, reproduce, and die more quickly than others? We often expect life-history traits—which are often tightly linked to fitness—to experience strong selection. Yet phenotypic variation is ubiquitous. For example, the benefits of growing quickly seem obvious, yet many species show tremendous variation in growth rates (Maranon and Grubb 1993; Stinchcombe et al. 2010; Dmitriew 2011). Similarly, rates of senescence can vary significantly within species (Hughes and Reynolds 2005; Ricklefs 2008). There are many reasons why life-history traits that confer fitness advantages remain variable. For instance, even though traits under selection can display considerable phenotypic variation, limited genetic variation can inhibit trait variation from being effectively depleted by selection. Genetic constraints can also occur in higher dimensional space; despite abundant genetic variation in a single trait, evolution remains constrained if the vector of selection is not aligned with genetic variation in that dimension (Walsh and Blows 2009). Examining multiple life-history traits simultaneously is more likely to yield insights into the evolutionary maintenance of variation in life-history traits. Finally, variation in life-history traits can also be maintained by environmental variation. Most phenotypes are not consistently

advantageous, but confer advantages only under some environmental conditions. For example, harsh and unpredictable environments should favor earlier reproduction, whereas benign and stable environments may favor later reproduction (Stearns and Koella 1986). Phenotypic diversity in life-history traits can thus persist because of environment-driven variation in selection pressures over space and time (Kassen 2002). When environmental variation selects for different phenotypes, these can be accommodated by genetic differentiation or phenotypic plasticity. At larger spatial scales, selection regimes can vary dramatically across different environments, often co-occur with low gene flow, and promote genetic differentiation (Reznick et al. 1990; Cook 2003; Allison 2004). At smaller spatial scales, high gene flow between habitats can prevent local adaptation and favors phenotypic plasticity (Baythavong 2011).

We studied selection across habitats within a population of a colonial, marine bryozoan, *Watersipora subtorquata* (henceforth *Watersipora*) connected by migration along a continuous, steep environmental gradient: depth. Depth is a key driver of environmental variation in marine systems with systematic changes in temperature, light, food, and competition across a narrow range

(Cowie 2010). Moreover, depth is increasingly recognized as an environmental gradient that maintains genetic variation (Muths et al. 2006; Vonlanthen et al. 2009; Mokhtar-Jamaï et al. 2011), phenotypic variation (Vonlanthen et al. 2009), and potentially induces speciation (Hyde et al. 2008; Shum et al. 2014). We find differences (in both means and covariances) in key morphological and life-history traits across this depth gradient and determine whether differences in selection can explain these phenotypic patterns.

To estimate selection across habitats, we measured the relationship between five life-history related traits and colony lifetime reproductive success (by measuring cumulative fecundity) in 173 *Watersipora* individuals in the field. We also estimate and compare the distribution of these traits across habitats. We then analyzed these data in a multivariate selection framework (Lande and Arnold 1983). Our aim in this work was to derive field estimates of selection across habitats within a population, and infer whether this could be a driver of life-history variation.

Methods

STUDY SPECIES

Watersipora subtorquata is an encrusting, colonial bryozoan commonly found on subtidal hard substrates (rocky reefs, marinas) in temperate regions. A colony consists of hundreds to thousands of clonal, isomorphic modules called zooids, which filter-feed by extending tentacular crowns (lophophores). Each module has a digestive and reproductive system, connected to the colony by pores that extend to neighbors (Bobin 1977). The life cycle starts with a free-swimming, planktonic larva that settles permanently onto a hard surface within minutes and up to a few hours after spawning; dispersal between depths is therefore limited (cf. Marshall and Keough 2003). These settlers then metamorphose into the first feeding module, the ancestrula. Colonies grow by budding outward, with future modules generated by a meristematic growing edge surrounding the colony margin. Reproductive modules are usually found in the intermediate section of a colony and produce eggs that are fertilized internally by externally shed sperm. With increasing age, colony senescence manifests as the deterioration of the oldest modules at the center of the colony (see Fig. 1). Previous studies on this species have established that module size, colony senescence, and growing edge width are important life-history traits (Hart and Keough 2009; Marshall and Monro 2013).

LIFE-HISTORY TRAITS

The patterns of growth, reproduction, and death in *Watersipora* are similar to those of other sessile modular organisms, such as plants, fungi and other colonial marine invertebrates (Thomas 2004; Hughes 2005; Winston 2010). We studied a broad spectrum

of traits that reflect the flow of resources throughout a colony and are predicted to influence its reproductive success. In brief, the onset of senescence reflects the beginning of colony deterioration, the growing edge width reflects a colony's ability for future growth, and module size reflects the investment into each module within a colony. Functional analogues in plants are found in the onset of leaf senescence, the number of meristems, and leaf size at various ages (further discussion in the Supporting Information).

EXPERIMENTAL DESIGN

To collect and monitor *Watersipora* colonies, we deployed pre-roughened PVC settlement plates located at Blairgowrie Yacht Squadron, Australia (38°21'20.16" S, 144°46'22.82" E). Because we wanted to measure selection in different depths, we mounted plates upside down on to 60 cm × 60 cm panels, half of which were deployed at 1 m depth ("shallow"), the other half at 4 m depth ("deep"). We have previously shown that *Watersipora* is abundant across this depth range, that depth induces changes in habitat quality, and that dispersal between depths is frequent (Lange and Marshall 2016). The panels were stacked, with each shallow panel connected to a deep panel by a stainless steel cable. There were six stacks, carrying a total of 12 panels and 192 plates (16 plates per panel).

Once deployed, we photographed plates every four weeks to track settlement times and the onset of senescence of individual colonies. Colonies that arrived later than four weeks postdeployment were not included in the analysis. After 16 weeks in the field, we retrieved all plates from the field and brought them to Monash University Clayton for standardized photographs. We then redeployed panels and retrieved and photographed again after six more weeks. The extended gap between the last two measurements was because we avoided exposing our animals to increased heat stress during a heat wave. During the study, colonies experienced more intense interspecific competition and heat fluctuations in the shallow than deep (Lange pers. obs.).

Using photographs, we measured growing edge width (week 16), module sizes (week 16), and fecundity (cumulative, from counting brooded eggs) (see Fig. 1). Note that the duration of our field study approached the natural lifespan of *Watersipora* at this field site. Although it is likely that our cumulative fecundity underestimated true lifetime reproductive output, other studies on this species suggest that snapshots of fecundity are good approximations of relative differences in reproductive output within populations, with little indication of trade-offs between early and late reproduction (Marshall and Monro 2013).

STATISTICAL ANALYSIS

We estimated phenotypic correlations between traits that, when present, will cause selection to have both direct and indirect effects on trait distributions (Lande and Arnold 1983). Indeed,

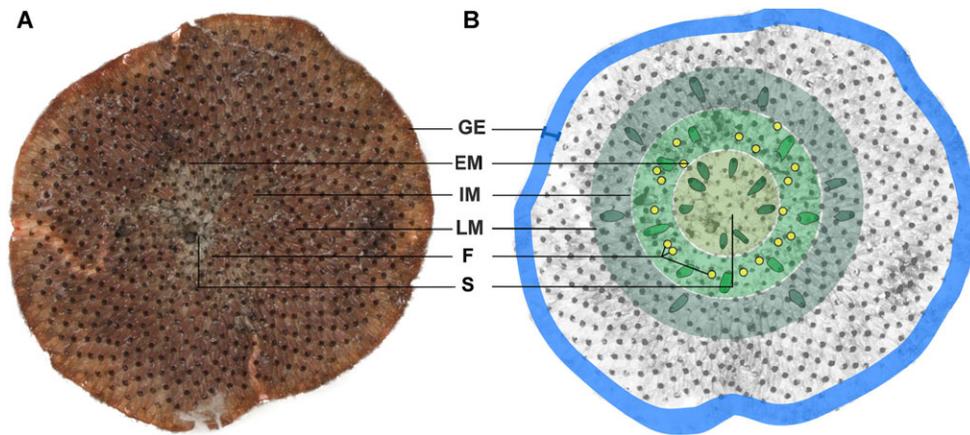


Figure 1. Traits analyzed in *Watersipora* colonies. (A) Original image. (B) Schematic version with traits highlighted in different colors. GE: growing edge width, measured as the width of the meristematic outer margin where new modules are budded; EM: early module size (eight randomly chosen modules within the 0.079 cm² circular area marking the oldest, central area); IM: intermediate module size (modules in the following 0.5 cm² area); LM: late module size (modules in the following 1 cm² area) F: fecundity, measured as the number of brooded eggs (found in the intermediate section); S: area of senesced modules (visible as translucent tissue near the colony center).

finding many phenotypic correlations among our focal traits (Supporting Information), we explored selection on them using the multiple regression approach of Lande and Arnold (1983), which generates standardized estimates of selection gradients that can be compared across species (cf. Kingsolver et al. 2001). In short, these gradients are produced by regressing standardized phenotypic traits against relative fitness to estimate only the direct effects of selection. We also calculated selection differentials, which estimate total (direct + indirect) selection acting on traits.

Data were analyzed in SAS, version 9.3 (SAS Institute, Cary, NC) using ML estimation in PROC MIXED. Our baseline model included backing panel as a random factor and separate error variances per depth based on model diagnostics (error variance due to differences among replicate colonies was 1.43 ± 0.19 at 1 m depth and 0.39 ± 0.08 at 4 m depth). First, we compared traits and fitness across depths using log-likelihood ratio tests. Next, we estimated selection gradients for all traits and compared selection across depths. To estimate directional selection gradients (B), we added traits as fixed, linear effects, mean-centered, and standardized to unit variance within environments (depth). The response variable was relative fitness (obtained by dividing by mean fitness within environments). Quadratic and correlational terms were subsequently added to estimate quadratic and correlational selection gradients (γ). Coefficients of quadratic gradients and their standard errors were doubled to provide the appropriate estimates without altering *P*-values (Stinchcombe et al. 2008). To test for differences in selection across environments, we used log-likelihood ratio tests to compare multiple regression models that included trait-by-depth interactions (estimating different gradients for each depth) with reduced models that omitted these

interactions (constraining gradients to be equal across depths), as advocated by Chenoweth and Blows (2005). We calculated selection differentials from univariate regressions of each standardized trait against relative fitness within each depth.

Results

Deeper waters offered a higher quality environment to *Watersipora*, in that colonies at the greater depth had a nearly fourfold higher reproductive output than colonies at the shallower depth (GLMM: $N = 173$, estimate = 0.2760, $t = 3.959$, $P < 0.001$; median \pm SE 1 m = 15.5 ± 4.91 ; 4 m = 67.0 ± 13.41). We also detected phenotypic differentiation across environments in our measured traits (Fig. 2; see trait means and SDs in Table S2). All zooid size measures were on average larger and the onset of senescence earlier in the shallow, whereas growing edges were wider in the deep.

Our selection analysis revealed that directional selection gradients differed between environments (LRT = 24.78, $df = 5$, $P < 0.01$). Wider growing edges were favored in both environments, but the strength of selection on growing margin was steeper in the deep environment. Small modules later in colony development (“late module size”) were favored in the shallow, and selection on all other module sizes was relaxed. Both shallow and deep waters favored a relatively early onset of senescence, while early and intermediate module sizes were selectively neutral in both environments (Table 1). The effects of all traits on cumulative fecundity within depths are shown in Fig. 2. Adding quadratic and correlational gradients did not improve model fit (LRT = 15.34, $df = 15$, $P = 0.43$), nor did adding their interactions with depth (LRT = 20.38, $df = 15$, $P = 0.16$).

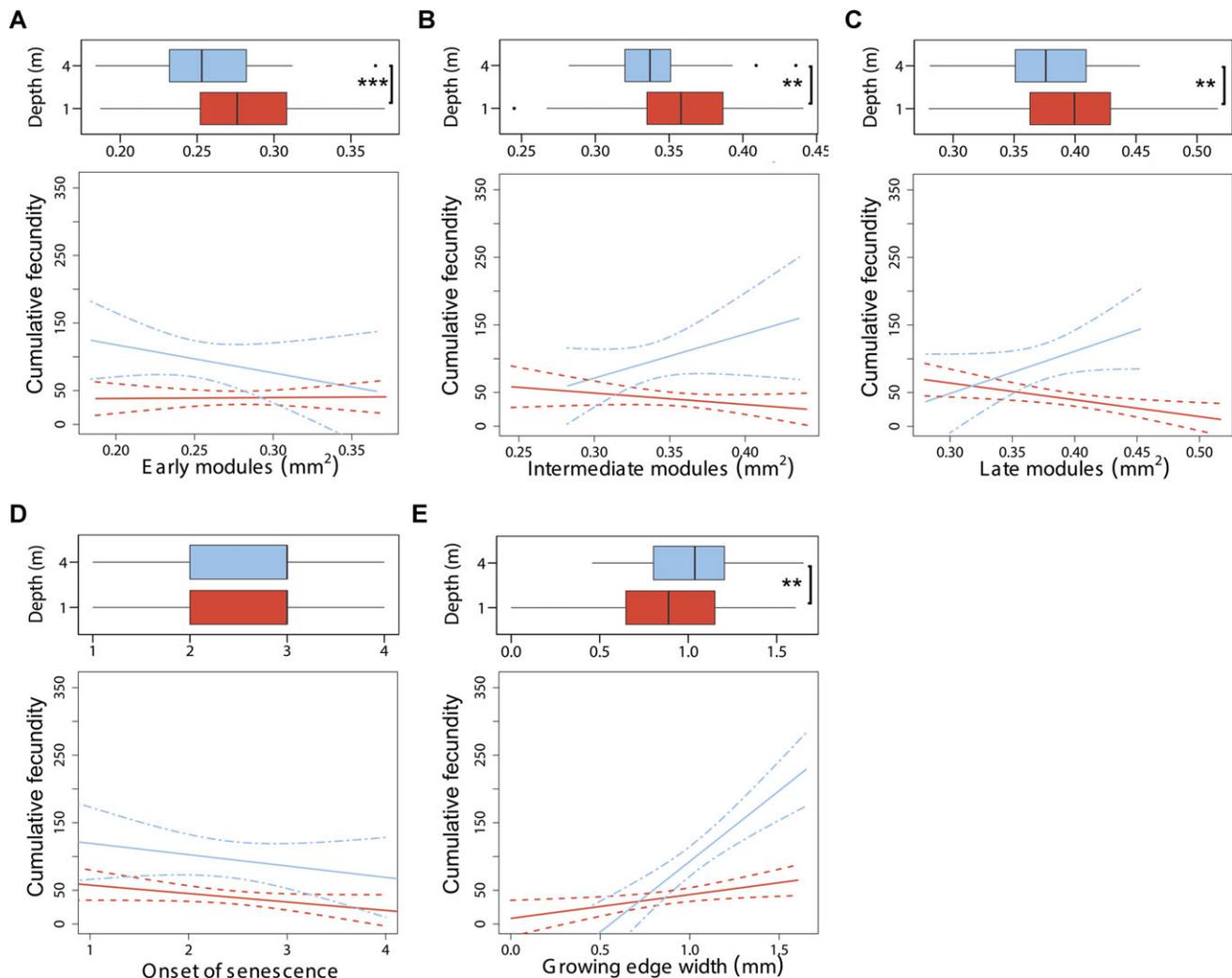


Figure 2. Trait distributions within environments (box plots) and the effects of measured traits (A–C: module size measures, D: onset of senescence, E: growing edge width) on cumulative fecundity (absolute fitness). Red/dark boxplots and red/dark dashed lines indicate the shallow environment; blue/light boxplots and blue/light dashed lines indicate the deep environment. Asterisks on box plots indicate significant differences between environments (one, two, and three asterisks denote P -values of < 0.05 , < 0.01 , and < 0.001 , respectively). Solid lines are fitted (univariate) regression lines and dashed lines are 95% confidence intervals.

Discussion

Here in *Watersipora* colonies, trait means, correlations among traits, and mean fitness (in terms of reproductive output) all differed between habitats separated by only a few meters. The deeper habitat was conducive to higher fitness, as deeper colonies had four times the reproductive output of shallower colonies. We conclude that the deep was a higher quality habitat for *Watersipora*. Selection on life-history traits also varied between depths. In the deep habitat, selection for greater investment in meristematic tissue that generates future growth was particularly strong, and selection on module size was relaxed, broadly favoring a fast-growing “opportunistic” phenotype. In the shallow habitat, in contrast, colonies were exposed to increasing intra- and interspecific competition from dense communities. As competition

intensified, small, densely packed modules were favored later in the colony lifecycle (Fig. 2C) and selection on meristematic tissue was weaker relative to the deeper habitat (Fig. 2E). Overall, this favored a “thrifty” phenotype in the shallower habitat (Hales and Barker 1992; Wells 2007) that likely requires fewer resources and filter-feeds more efficiently by having more modules per unit area.

Our detection of selection for small modules in low-quality, highly competitive environments, and for greater investment in growth in high-quality environments, parallels findings in plants and other modular organisms. Heterogeneous selection along environmental gradients is common (see Kingsolver 2001) and resource availability is considered to be a key driver of selection on growth and module size (Grime and Hunt 1975; Grime 1977;

Table 1. Standardized directional selection differentials (S) from univariate regressions, directional selection gradients (β) from a multiple regression with linear terms only, and quadratic and correlational selection gradients (γ) from a full quadratic regression of traits (onset of senescence, growing edge width and module size at early, intermediate, and late stages of the colony lifecycle) on reproductive output at different depths.

1 m	$S \pm SE$	$\beta \pm SE$	$\gamma \pm SE$					
			Onset	Growing Edge	Early Modules	intermediate Modules	Late Modules	
Onset of senescence	-0.22 ± 0.12	-0.26 ± 0.12	-0.12 ± 0.22					
Growing edge width (mm)	0.30 ± 0.12	$0.39^{**} \pm 0.12$	0.13 ± 0.12	0.14 ± 0.18				
Early modules (mm ²)	0.01 ± 0.13	0.08 ± 0.13	-0.19 ± 0.13	0.11 ± 0.15	0.14 ± 0.24			
Int. modules (mm ²)	-0.16 ± 0.13	0.00 ± 0.16	-0.04 ± 0.19	-0.26 ± 0.16	0.09 ± 0.20	-0.04 ± 0.34		
Late modules (mm ²)	$-0.33^* \pm 0.12$	-0.28 ± 0.12	0.09 ± 0.15	-0.15 ± 0.16	-0.25 ± 0.21	0.06 ± 0.27		-0.06 ± 0.26
N = 116								
4 m								
Onset of senescence	-0.18 ± 0.14	-0.21 ± 0.09	-0.42 ± 0.24					
Growing edge width	$0.62^{***} \pm 0.11$	$0.55^{***} \pm 0.11$	-0.09 ± 0.11	$0.64^{**} \pm 0.20$				
Early modules (mm ²)	-0.15 ± 0.14	-0.14 ± 0.1	-0.01 ± 0.10	-0.18 ± 0.17	0.30 ± 0.18			
Int. modules (mm ²)	0.21 ± 0.14	0.07 ± 0.11	-0.09 ± 0.12	0.00 ± 0.16	0.17 ± 0.14	-0.10 ± 0.20		
Late modules (mm ²)	0.25 ± 0.14	0.05 ± 0.1	0.08 ± 0.11	0.00 ± 0.17	0.20 ± 0.15	-0.05 ± 0.17		-0.20 ± 0.24
N = 57								

P -values < 0.05 are in bold; P -values < 0.01 and < 0.001 are indicated by two and three asterisks, respectively.

Ackerly et al. 2002; Westoby et al. 2002). Photosynthetic modular organisms, such as plants and seaweeds, are often selected to escape low resource conditions via elongation responses (algae: Monro et al. 2007; plants: Lovett Doust 1981; Dudley and Schmitt 1996; Weinig 2000). Low resource conditions may, however, become unavoidable. Moreover, many modular organisms, including *Watersipora*, lack the capacity for elongation. Such circumstances may therefore favor other strategies of tolerance and persistence, including building robust modules, resource conservation through slow growth, or reproduction at small size (plants: Iwasa and Cohen 1989; Westoby et al. 2002; Bonser and Aarssen 2009; Kunstler et al. 2016, but see Stanton et al. 2000; bryozoans: Pratt 2004). Conversely, more favorable conditions, characterized by low competition or low shading, favor strategies that pre-empt space and secure high-quality, uncolonized habitat (Lovett Doust 1981; Westoby et al. 2002). Accordingly, long leaves, high growth rates, and densely spaced modules often confer a selective advantage in high-quality environments (Lotz et al. 1990; Stanton et al. 2000, 2004; Monro et al. 2007). Consistent with this idea, we found that investment in meristematic tissue that allows individuals to better pre-empt space was favored in both environments, but significantly more so in the deeper habitat where environmental quality was higher (and competition lower).

An earlier onset of senescence was equally favored in both environments (Fig. 2D). This may seem counterintuitive at first, because partial senescence decreases the number of active, resource-acquiring modules. Phenomenologically, senescence and mortality depend strongly on environmental fluctuations and have characteristically greater susceptibility to environmental stress with advancing age (Roach 2001; Roach et al. 2009).

Although senescence is a common feature of modular organisms (McKinney and Jackson 1991; Roach and Carey 2014), its selective advantages remain poorly explored (but see Marshall and Monro 2013). Theoretically, partial senescence (or module senescence) can benefit the genet when module ageing or self-shading renders old or badly positioned modules useless and favors building new modules (Ackerly 1999; Kikuzawa and Ackerly 1999). We speculate that a relatively early onset of senescence may be selected for if it accelerates growth or reproduction.

Our incentive was to infer whether heterogeneous selection along an environmental gradient can maintain life-history variation. This does not seem to be the case for *Watersipora*. Despite phenotypic differentiation across environments for most of our focal traits, the patterns of selection were not always conducive to maintain this differentiation. For example, we found that late module size was larger in the shallow habitat but our analyses suggest that selection should reduce module size in that habitat to make it more similar to that of the deep habitat. Although there was no difference in the direction of selection on the width of the growing edge between habitats, selection for larger growing edges was much stronger in the deep habitat relative to the shallow. It is unclear whether this difference in the strength of selection between habitats alone is sufficient to explain why growing edges were generally larger in the deeper habitat.

Although genetic differentiation between our study habitats seems unlikely given the limited dispersal of *Watersipora* larvae, it is noteworthy that most mathematical models for the maintenance of quantitative genetic variation under heterogeneous selection require different trait optima for genetic variation to be maintained (Slatkin 1978; Barton 1999; Geroldinger and Bürger

2015). However, differences in the strength (but not sign) of directional selection—as we detected here—appear to be common in field estimates of selection (Kingsolver et al. 2001; Siepielski et al. 2013). Initial modeling efforts (M. Morrissey, pers. comm.) indicate that differences in the strength of directional selection alone are insufficient to maintain quantitative genetic variation across environments that are connected by migration. We therefore conclude that the observed patterns of phenotypic differentiation between our two environments (which are likely connected by gene flow) are a consequence of phenotypic plasticity. Given the observed patterns of selection acting on *Watersipora* colonies at different depths, this plasticity seems to be adaptive for growing edge size but not for module size. Hence, selection may not always be effective at maintaining adaptive trait differentiation over relatively small spatial scales.

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The authors declare that there is no conflict of interest.

DATA ARCHIVING

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LITERATURE CITED

- Ackerly, D. 1999. Self-shading, carbon gain and leaf dynamics: a test of alternative optimality models. *Oecologia* 119:300–310.
- Ackerly, D., C. Knight, S. Weiss, K. Barton, and K. Starmer. 2002. Leaf size, specific leaf area and microhabitat distribution of chaparral woody plants: contrasting patterns in species level and community level analyses. *Oecologia* 130:449–457.
- Allison, A. C. 2004. Two lessons from the interface of genetics and medicine. *Genetics* 166:1591–1599.
- Barton, N. H. 1999. Clines in polygenic traits. *Genet. Res.* 74:223–236.
- Baythavong, B. S. 2011. Linking the spatial scale of environmental variation and the evolution of phenotypic plasticity: selection favors adaptive plasticity in fine-grained environments. *Am. Nat.* 178:75–87.
- Bobin, G. 1977. Interzoocelial communications and the funicular system. Pp. 307–333 in R.M. Woollacott and R.L. Zimmer, eds. *Biology of Bryozoans*. Academic Press, New York.
- Bonsler, S. P., and L. W. Aarssen. 2009. Interpreting reproductive allometry: individual strategies of allocation explain size-dependent reproduction in plant populations. *Perspect. Plant Ecol. Evol. Syst.* 11:31–40.
- Chenoweth, S. F., and M. W. Blows. 2005. Contrasting mutual sexual selection on homologous signal traits in *Drosophila serrata*. *Am. Nat.* 165:281–289.
- Cook, Laurence M. 2003. The rise and fall of the Carbonaria form of the peppered moth. *Q. Rev. Biol.* 78:399–417.
- Cowie, P. R. 2010. Biofouling patterns with depth. Pp. 87–99 in Dürr, Simone and Jeremy C. Thomason, eds. *Biofouling*. Wiley-Blackwell, Oxford, UK.
- Dmitriew, C. M. 2011. The evolution of growth trajectories: what limits growth rate? *Biol. Rev.* 86:97–116.
- Dudley, S. A., and J. Schmitt. 1996. Testing the adaptive plasticity hypothesis: density-dependent selection on manipulated stem length in *Impatiens capensis*. *Am. Nat.* 147:445–465.
- Geroldinger, L., and R. Bürger. 2015. Clines in quantitative traits: the role of migration patterns and selection scenarios. *Theor. Popul. Biol.* 99:43–66.
- Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.* 111:1169–1194.
- Grime, J. P., and R. Hunt. 1975. Relative growth-rate: its range and adaptive significance in a local flora. *J. Ecol.* 63:393–422.
- Hales, C. N., and D. J. P. Barker. 1992. Type 2 (non-insulin-dependent) diabetes mellitus: the thrifty phenotype hypothesis. *Diabetologia* 35:595–601.
- Hart, S. P., and M. J. Keough. 2009. Does size predict demographic fate? Modular demography and constraints on growth determine response to decreases in size. *Ecology* 90:1670–1678.
- Hughes, K. A., and R. M. Reynolds. 2005. Evolutionary and mechanistic theories of aging. *Annu. Rev. Entomol.* 50:421–445.
- Hughes, R. N. 2005. Lessons in modularity: the evolutionary ecology of colonial invertebrates. *Sci. Mar.* 69:169–179.
- Hyde, J. R., C. A. Kimbrell, J. E. Budrick, E. A. Lynn, and R. D. Vetter. 2008. Cryptic speciation in the vermilion rockfish (*Sebastes miniatus*) and the role of bathymetry in the speciation process. *Mol. Ecol.* 17:1122–1136.
- Iwasa, Y., and D. Cohen. 1989. Optimal growth schedule of a perennial plant. *Am. Nat.* 133:480–505.
- Kassen, R. 2002. The experimental evolution of specialists, generalists, and the maintenance of diversity. *J. Evol. Biol.* 15:173–190.
- Kikuzawa, K., and D. Ackerly. 1999. Significance of leaf longevity in plants. *Plant Species Biol.* 14:39–45.
- Kingsolver, J. G., H. E. Hoekstra, J. M. Hoekstra, D. Berrigan, S. N. Vignieri, C. E. Hill, A. Hoang, P. Gibert, and P. Beerli. 2001. The strength of phenotypic selection in natural populations. *Am. Nat.* 157:245–261.
- Kunstler, G., D. Falster, D. A. Coomes, F. Hui, R. M. Kooyman, D. C. Laughlin, L. Poorter, M. Vanderwel, G. Vieilledent, and S. J. Wright. 2016. Plant functional traits have globally consistent effects on competition. *Nature* 529:204–207.
- Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. *Evolution* 37:1210–1226.
- Lange, R., and D. J. Marshall. 2016. Relative contributions of offspring quality and environmental quality to adult field performance. *Oikos* 125:210–217.
- Lotz, L. A. P., H. Olf, and P. H. Vantenderen. 1990. Within-population variability in morphology and life-history of *Plantago-major* L. ssp. *pleiosperma* Pilger in relation to environmental heterogeneity. *Oecologia* 84:404–410.
- Lovett Doust, L. 1981. Population dynamics and local specialization in a clonal perennial (*Ranunculus repens*): I. The dynamics of ramets in contrasting habitats. *J. Ecol.* 69:743–755.
- Maranon, T., and P. J. Grubb. 1993. Physiological basis and ecological significance of the seed size and relative growth rate relationship in Mediterranean annuals. *Funct. Ecol.* 7:591–599.
- Marshall, D. J., and M. J. Keough. 2003. Variation in the dispersal potential of non-feeding invertebrate larvae: the desperate larva hypothesis and larval size. *Mar. Ecol. Prog. Ser.* 255:145–153.
- Marshall, D. J., and K. Monro. 2013. Interspecific competition alters nonlinear selection on offspring size in the field. *Evolution* 67:328–337.

- McKinney, F. K., and J. B. C. Jackson. 1991. Bryozoan evolution. Univ. of Chicago Press, Chicago and London.
- Mokhtar-Jamaï, K., M. Pascual, J. B. Ledoux, R. Coma, J. P. Féral, J. Garrabou, and D. Aurelle. 2011. From global to local genetic structuring in the red gorgonian *Paramuricea clavata*: the interplay between oceanographic conditions and limited larval dispersal. *Mol. Ecol.* 20:3291–3305.
- Monro, K., A. G. B. Poore, and R. Brooks. 2007. Multivariate selection shapes environment-dependent variation in the clonal morphology of a red seaweed. *Evol. Ecol.* 21:765–782.
- Muths, D., D. Davoult, F. Gentil, and D. Jollivet. 2006. Incomplete cryptic speciation between intertidal and subtidal morphs of *Acrocnida brachinata* (Echinodermata: Ophiuroidea) in the Northeast Atlantic. *Mol. Ecol.* 15:3303–3318.
- Pratt, M. C. 2004. Effect of zooid spacing on bryozoan feeding success: is competition or facilitation more important? *Biol. Bull.* 207:17–27.
- Reznick, D. A., H. Bryga, and J. A. Endler. 1990. Experimentally induced life-history evolution in a natural population. *Nature* 346:357–359.
- Ricklefs, R. E. 2008. The evolution of senescence from a comparative perspective. *Funct. Ecol.* 22:379–392.
- Roach, D. A. 2001. Environmental effects on age-dependent mortality: a test with a perennial plant species under natural and protected conditions. *Exp. Gerontol.* 36:687–694.
- Roach, D. A., and J. R. Carey. 2014. Population biology of aging in the wild. *Ann. Rev. Ecol. Evol. Syst.* 45:421–443.
- Roach, D. A., C. E. Ridley, and J. L. Dudycha. 2009. Longitudinal analysis of *Plantago*: age-by-environment interactions reveal aging. *Ecology* 90:1427–1433.
- Shum, P., C. Pampoulie, C. Sacchi, and S. Mariani. 2014. Divergence by depth in an oceanic fish. *Peer J.* 2:e525.
- Siepielski, A. M., K. M. Gotanda, M. B. Morrissey, S. E. Diamond, J. D. DiBattista, and S. M. Carlson. 2013. The spatial patterns of directional phenotypic selection. *Ecol. Lett.* 16:1382–1392.
- Slatkin, M. 1978. Spatial patterns in the distributions of polygenic characters. *J. Theor. Biol.* 70:213–228.
- Stanton, M. L., B. A. Roy, and D. A. Thiede. 2000. Evolution in stressful environments. I. Phenotypic variability, phenotypic selection, and response to selection in five distinct environmental stresses. *Evolution* 54:93–111.
- Stanton, M. L., D. Thiede, and B. Roy. 2004. Consequences of intraspecific competition and environmental variation for selection in the mustard *Sinapsis arvensis*: contrasting ecological and evolutionary perspectives. *Am. Nat.* 164:736–752.
- Stearns, S. C. and J. C. Koella. 1986. The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. *Evolution* 40:893–913.
- Stinchcombe, J. R., A. F. Agrawa, P. A. Hohenlohe, S. J. Arnold, and M. W. Blows. 2008. Estimating nonlinear selection gradients using quadratic regression coefficients: double or nothing? *Evolution* 62:2435–2440.
- Stinchcombe, J. R., R. Izem, M. S. Heschel, B. V. McGoey, and J. Schmitt. 2010. Across-environment genetic correlations and the frequency of selective environments shape the evolutionary dynamics of growth rate in *impatiens capensis*. *Evolution* 64:2887–2903.
- Thomas, H. 2004. Do green plants age, and if so, how? Pp. 145–171 in Thomas Nyström, and Heinz D. Osiewacz, eds. *Model systems in aging*. Springer, Springer Berlin Heidelberg.
- Vonlanthen, P., D. Roy, A. G. Hudson, C. R. Lurgiader, D. Bittner, and O. Seehausen. 2009. Divergence along a steep ecological gradient in lake whitefish (*Coregonus* sp.). *J. Evol. Biol.* 22:498–514.
- Walsh, B. and M. W. Blows. 2009. Abundant genetic variation + strong selection = multivariate genetic constraints: a geometric view of adaptation. *Ann. Rev. Ecol. Evol. Syst.* 40:41–59.
- Weinig, C. 2000. Differing selection in alternative competitive environments: shade-avoidance responses and germination timing. *Evolution* 54:124–136.
- Wells, J. C. K. 2007. The thrifty phenotype as an adaptive maternal effect. *Biol. Rev.* 82:143–172.
- Westoby, M., D. S. Falster, A. T. Moles, P. A. Vesk, and I. J. Wright. 2002. Plant ecological strategies: some leading dimensions of variation between species. *Annu. Rev. Ecol. Syst.* 33:125–159.
- Winston, J. E. 2010. Life in the colonies: learning the alien ways of colonial organisms. *Integr. Comp. Biol.* 50:919–933.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Table S1. Phenotypic correlation matrix between traits in each environment.

Table S2. Means and standard deviations of each trait within each environment.