Faster Is Not Always Better: Selection on Growth Rate Fluctuates across Life History and Environments.

Author(s): Keyne Monro and Dustin J. Marshall
Source: *The American Naturalist*, Vol. 183, No. 6 (June 2014), pp. 798-809
Published by: The University of Chicago Press for The American Society of Naturalists
Stable URL: http://www.jstor.org/stable/10.1086/676006
Accessed: 07/10/2015 00:08

Faster Is Not Always Better: Selection on Growth Rate Fluctuates across Life History and Environments

Keyne Monro* and Dustin J. Marshall

School of Biological Sciences, University of Queensland, Brisbane, Queensland 4072, Australia; and School of Biological Sciences, Monash University, Clayton, Victoria 3800, Australia

Submitted July 30, 2013; Accepted January 3, 2014; Electronically published April 23, 2014

Online enhancements: appendixes. *Dryad data:* http://dx.doi.org/10.5061/dryad.30vn6.

abstract: Growth rate is increasingly recognized as a key life-history trait that may affect fitness directly rather than evolve as a by-product of selection on size or age. An ongoing challenge is to explain the abundant levels of phenotypic and genetic variation in growth rates often seen in natural populations, despite what is expected to be consistently strong selection on this trait. Such a paradox suggests limits to how contemporary growth rates evolve. We explored limits arising from variation in selection, based on selection differentials for age-specific growth rates expressed under different ecological conditions. We present results from a field experiment that measured growth rates and reproductive output in wild individuals of a colonial marine invertebrate (*Hippopodina iririkiensis*), replicated within and across the natural range of succession in its local community. Colony growth rates varied phenotypically throughout this range, but not all such variation was available for selection, nor was it always targeted by selection as expected. While the maintenance of both phenotypic and genetic variation in growth rate is often attributed to costs of growing rapidly, our study highlights the potential for fluctuating selection pressures throughout the life history and across environments to play an important role in this process.

Keywords: competition, individual fitness, age-specific growth, life-history evolution, succession.

Introduction

An organism's optimal life history maximizes lifetime reproduction by maximizing age-specific fecundity and survival (Roff 1992; Stearns 1992). For many organisms, however, fecundity and the risk of mortality depend as much on size as age per se, although the two may often covary (Werner and Caswell 1977; Hughes and Connell 1987; Ebenman and Persson 1988; Hanzawa and Kalisz 1993). Since size at any given age is the sum of growth increments during earlier life-history stages, growth rate (the ontogenetic change in size per unit time) defines the relationship between size and age and itself plays an important role in life-history evolution. Consequently, growth rates have been studied in many taxa, yet reviews of this literature (Arendt 1997; Dmitriew 2011) cite an ongoing issue. Selection on growth rates is expected to be consistently strong, given the fitness benefits of large adult size. However, natural populations typically harbor abundant levels of phenotypic and genetic variation in this trait that are expected to be depleted if it has undergone adaptive evolution (Turelli and Barton 2004; Walsh and Blows 2009). Such a paradox implies that our understanding of the evolutionary forces that act on growth rates and maintain their variability in nature is incomplete.

Growth rates are highly labile and closely tied to ecological conditions (Rose et al. 2009; Stinchcombe et al. 2010; Dmitriew 2011). A major framework for understanding their evolution has therefore emphasized the conditions of stress (factors that limit growth, such as resource availability or temperature) and disturbance (rates of damage or mortality) in which different growth rates should be adaptive (Grime and Hunt 1975; Case 1978; Arendt 1997). Low-stress environments, for example, are predicted to select for accelerated growth that gives individuals a size advantage over competitors. As stress increases or resources become limiting, however, individuals may benefit from growing more slowly—presumably because doing so improves environmental tolerance or the efficiency of resource use (Weis et al. 2000; Kimball et al. 2013). Accelerated growth is also predicted to be favored in disturbed, ephemeral, or seasonal environments where individuals have limited time to reach maturation or other developmental milestones (Blanckenhorn and Demont 2004) but to become less important as time constraints ease. Empirical evidence suggests that growth rates often diverge between species or populations in line with these predictions (Arendt 1997; Nylin and Gotthard 1998; Dmitriew 2011). However, the persistence of variable growth

* Corresponding author; e-mail: keyne.monro@monash.edu.

Am. Nat. 2014. Vol. 183, pp. 798–809.
DOI: 10.1086/676006

rates within populations also suggests that selection may just as often fail to target them as predicted or to produce the predicted response, signaling potential limits to its efficacy.

Of the various reasons why selection may be ineffective (see Barton and Partridge 2000), the most obvious is a lack of suitable variation. There can be no opportunity for selection without variation in individual fitness (e.g., differential survival or reproduction), and the intensity of selection that can act on other phenotypic traits depends on the extent to which they covary with fitness (Crow 1958; Arnold and Wade 1984). Selection for higher fitness, for instance, may not necessarily yield a faster growth rate if much of the latter's phenotypic variation simply reflects the accumulation of deleterious or neutral variants in a complex trait with large mutational target size (Houle 1998). Even when suitable phenotypic variation is available for single traits, selection may be limited in what it can achieve (and in its speed) if traits are correlated in ways that restrict their variation to just a few multivariate combinations that do not necessarily vary in the direction of higher fitness (Walsh and Blows 2009).

Further complicating selection on growth rates is their potential to be correlated not only with other traits (Mangel and Stamps 2001) but also throughout the life history (Kingsolver et al. 2012). Growth rates tend to decline with increasing size and age due to the rising costs of maintaining existing biomass or the diversion of fixed resources to other vital functions such as reproduction (West et al. 2001; Rose et al. 2009). Since individuals can differ in the timing, magnitude, and speed of this decline, another framework for understanding the evolution of growth rates has focused on phenotypic or genetic covariation among age-specific values (Kirkpatrick and Lofsvold 1992; Badyaev and Martin 2000), which may restrict variation in the direction of selection in much the same manner as correlations among disparate traits. Age-specific variation in size or growth is often interpreted in the context of compensatory (catch-up) responses to periods of resource limitation, which are presumed to be adaptive (Mangel and Munch 2005). However, studies that explicitly test the fitness consequences of ontogenetic variation in growth rate remain rare (but see Kingsolver et al. 2012).

Selection on growth rates may also be ineffective if it fluctuates in time or space (Barton and Partridge 2000; Merilä et al. 2001; Bell 2010), as may often result from changes in local ecological conditions (Schluter 2009). Spatially variable selection may slow or prevent local adaptation if there is substantial gene flow (via adult, larval, or gamete dispersal) between populations where different growth rates are favored (Hendry et al. 2001; Garant et al. 2007). Localized patterns of phenotypic and genetic variation in growth rates may then persist if those populations remain stable in size and contribute equally to the next generation (Christiansen 1975; Bell 2010). Likewise, variation in growth rates may persist if selection varies temporally (e.g., during ontogeny) to the point that its net intensity within a generation is minimal (Schluter et al. 1991; Siepielski et al. 2009; Dmitriew 2011). Of course, selection pressures can vary temporally and spatially at once (Kalisz 1986) and target traits that are not only correlated within environments but across environments also (Stinchcombe et al. 2010). For instance, growth rates that confer high fitness in some conditions may confer relatively low fitness when conditions change, allowing selection pressures at one time or place to have correlated effects at others (assuming that phenotypic variation in growth rate has a heritable component). This is necessarily a complex scenario but perhaps the most realistic of all.

Collectively, these considerations imply that the contemporary evolution of growth rate in natural populations depends on selection pressures that can fluctuate during ontogeny and with ecological conditions that vary in time or space. Understanding such pressures ideally requires that growth dynamics be followed through an organism's life history (Arendt 1997), that they be related to a relevant measure of fitness, and that this be done under a range of ecological conditions likely to be encountered in nature. These requirements have rarely been met (Dmitriew 2011). Here we estimate phenotypic variation and selection differentials for age-specific growth rates in wild individuals of a colonial marine invertebrate (the encrusting bryozoan, *Hippopodina iririkiensis*; Tilbrook 1999), replicated clonally and transplanted into experimentally manipulated communities at different stages of succession. The hard-substrate environments inhabited by this species typically comprise mosaics of small clearings renewed constantly by disturbance and surrounded by communities at various such stages (Sutherland and Karlson 1977; Connell and Keough 1985). We asked whether faster growth rates at different ages are positively correlated with fitness (in terms of reproductive output, measured as colony-wide fecundity at onset of senescence) and to what extent selection on growth rates varies with the changing ecological conditions that accompany succession.

Methods

Study Organism and Site

Hippopodina iririkiensis (named by genus hereafter) is widespread in the tropics, growing on submerged surfaces as sheetlike colonies of modular subunits (zooids). The primary module is a feeding zooid (feeding organ, gut, and hermaphroditic gonads enclosed in calcified walls) that can become functionally female in ontogeny. Sperm

are shed into the water column, but fertilization is internal, with each maternal zooid transferring fertilized oocytes one by one into an external brood chamber on its surface. There an embryo is brooded singly for ~2 weeks until it is released as a free-swimming larva that settles to start a new colony and a new embryo enters the vacant brood chamber. A maternal zooid may brood several successive embryos over its lifetime (Ström 1977; Ostrovsky 2013), which is probably ~4 weeks, based on studies of similar taxa (Hughes 2005; Hart and Keough 2009). Like many colonial taxa, *Hippopodina* can be propagated clonally by fragmentation, and its life-history schedule, including onsets of reproduction and senescence, is tied closely to colony size as well as age (Hughes 2005; K. Monro, personal observation). *Hippopodina* is common at our field site (Manly Boat Harbour, Queensland, Australia), where submerged surfaces host diverse epifaunal communities of bryozoans, ascidians, tube worms, and associated species.

Sampling of Succession

To generate communities representing the range of successional environments at our field site, we bolted 0.01-m^2 polyvinyl chloride (PVC) plates to the undersides of 0.25-m^2 panels submerged below floating docks. We deployed 80 plates on five panels at our site initially and a replicate array 8 weeks later. Plates were roughened to encourage settlement of propagules from the water column, with subsequent communities developing naturally. After another 6 weeks, all 160 plates were brought to the laboratory, supplemented by another 80 plates that had been immersed for ~2 days but were largely free of epifauna. At this point, communities founded at different times had minimal coverage of bare space after developing for <1 week, ~50% coverage after developing for 6 weeks, and ~100% coverage after developing for 14 weeks. They were therefore composed of an early successional environment, with residents yet to establish; a midsuccessional environment, with residents established but unlikely to interact strongly given the space available; and a late-successional environment, with resident interactions likely to be strong enough for competitive exclusion to occur.

Sampling of Focal Colonies

To sample focal colonies of *Hippopodina*, we let larvae from wild colonies settle naturally onto sheets of roughened acetate that had been fixed to the undersides of PVC panels submerged below floating docks. Panels were spaced well apart initially to sample a broad cross-section of the local population. After ~2 weeks of settlement, we cleared sheets of all settlers other than *Hippopodina*, consolidated panels to minimize environmental variation, and removed new invaders for ~2 months thereafter to give focal colonies ample space to grow. We then brought 20 colonies, each ~6 cm across, on their acetate to the laboratory for manipulation. Since the limited dispersal of *Hippopodina* larvae (Eitan 1972; K. Monro, personal observation) means that neighboring colonies might be siblings, we took care to choose nonneighboring colonies from different acetate sheets. None was reproductive at this point.

Sampling of Colony Growth and Fecundity throughout Succession

In the laboratory, we cut 12 radial fragments (clonal replicates) from each focal colony, ensuring that they were consistent in size (<1 cm^2), shape, and amount of growing margin. We transplanted each replicate (by gluing its acetate base) into a patch of similar size and shape cleared on each plate, assigning four replicates per colony to each successional environment. Plates were photographed to record the initial size and position of the single replicate glued to each before being returned to the field. There plates were bolted to 40 panels in a split-plot design, with two plates per environment (a within-plot effect) on each of two panels per focal colony (both of which were between-plot effects). Preliminary tests of initial fragment size detected no variation at any level in this design that could have confounded our results (all $P \geq .22$). We submerged panels below floating docks and tended to them weekly, removing the buildup of invaders from early successional plates to hold them in this state. Every 8–9 days, we photographed replicates in situ to score their sizes (cm^2 of area) nondestructively via image processing in ImageJ (http://rsb.info.nih.gov/ij). By the study's end, sizes were scored after 9, 17, 25, and 33 days of growth in the field.

After 6 weeks, clonal replicates were reproductive (with onset of reproduction at ~4 weeks) and had started to senesce, evident in the die-off of central zooids. We calculated the absolute fecundity of each replicate as its total body size multiplied by the mean density of zooids carrying brood chambers in three 1-cm^2 sections of body tissue sampled along its radius. We added 1 to densities beforehand to retain the few replicates in which no brood chambers were sampled and ln-transformed data afterward for normality. Since our calculations of fecundity assumed that all replicates had a constant number of zooids per unit area of body size and may therefore have been biased by variation in the size of constituent zooids, we corrected for such bias using the regression procedure described in appendix A. Regression residuals, representing the absolute fecundity of clonal replicates corrected for zooid size, were used as fitness measures in subsequent analyses. Since several offspring may pass through a brood chamber before the maternal zooid senesces (Ström 1977) and colony-wide

senescence starts at reproductive maturity, these measures are more than static estimates of fecundity and should correlate well with lifetime reproduction. Four replicates, each from a unique experimental combination, died before this point.

Statistical Analyses

Our final approach had two stages. The first of these stages modeled among-colony variation in age-specific growth rates and fecundity within successional environments to explore how growth rates during ontogeny in each environment are targeted by selection. The second stage modeled among-colony variation in age-specific growth rates across environments, exploring whether selection on growth in one environment may have correlated effects on growth in others. Data are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.30vn6 (Monro and Marshall 2014). The steps that led us to take this two-stage approach are outlined below and in appendix A.

Data Processing and General Modeling Procedures. Using the change in size of each clonal replicate from one sampling date (d_1) to the next (d_2), we calculated its relative growth rate (RGR, in $cm^2 \cdot cm^{-2} \cdot d^{-1}$) at a given age as $(\ln \text{size}_2 - \ln \text{size}_1)/(d_2 - d_1)$, equal to the slope of ln size against time for each interval (fig. 1; see also Hoffmann and Poorter 2002). Since our goal was to infer selection on growth rates based on associations with fecundity, we divided each replicate's RGR at a given age by the standard deviation of values for the same age and environment and then divided each replicate's absolute fecundity by the mean value per environment to convert fecundity to a relative scale. Thus scaled, the among-colony covariances between RGRs and fecundity are standardized selection differentials, estimating the intensity of selection on age-specific growth rates throughout succession while accounting for differences in phenotypic variance (Arnold and Wade 1984).

Data were analyzed in multivariate linear mixed models, fitted with restricted maximum likelihood in the MIXED procedure of SAS, version 9.3 (SAS Institute, Cary, NC). All models had trait (composed of four age-specific RGRs, plus fecundity where specified), environment (composed of early, mid-, and late successions), and trait × environment as fixed effects and estimated the among-colony variances and covariances of traits within and across environments based on the random deviations of focal colonies from the fixed population means (Littell et al. 2006). All models also had heterogeneous errors estimating the residual variances and covariances of traits among clonal replicates. Models had different random effects at the level of panel, as specified below (such effects were nonsignificant in final models and are reported in app. C; apps. B and C are available online). We tested fixed effects using *F*-tests or *t*-tests (in the case of pairwise contrasts, which were adjusted for multiple testing) with Satterthwaite's degrees of freedom (Littell et al. 2006). We tested random effects using likelihood ratio tests (LRTs), which were one-tailed for variances, two-tailed for covariances, and adjusted for multiple testing (Benjamini and Hochberg 1995; Fry 2004).

We fitted models using unconstrained covariance structures to start with, estimating all random effects uniquely (Littell et al. 2006). We then took each set of estimates at the colony level (collectively, the covariance matrix of among-colony variation) and used factor-analytic modeling to test whether it was less than full rank—that is, whether it had fewer independently varying dimensions (or trait combinations) than unique traits, signaling redundancy in those traits due to either lack of variance or to high multicollinearity (Pease and Bull 1988). We anticipated the latter especially, since traits were scored repeatedly on clonal replicates and successive RGRs shared a size term (but in a way that is expected to bias their correlation downward; Chayes 1949). The procedure is analogous to conducting a principal components (PCs) analysis on the desired matrix within the hypothesis-testing framework of the mixed model (for details, see Hine and Blows 2006). Here it involved fitting a series of models that we constrained to estimate the colony-level matrix in reduced-rank form with a dimension less at a time and using LRTs to find when dropping a dimension significantly reduced model fit. As with any PC analysis, the dimensions of each reduced-rank matrix supported by our tests were represented by the eigenvalues and the loadings of its PCs. The former describe how much of the among-colony variation in our original traits is explained by each dimension, while the latter describe trait contributions to each dimension and are interpretable as correlations after appropriate scaling (Legendre and Legendre 2012).

Modeling Experiment-Wide Variation in Age-Specific Growth Rates and Fecundity. We originally fitted a model to all 15 trait × environment combinations scored in our experiment, estimating an experiment-wide matrix of among-colony variation within and across environments (traits were also modeled as random at the level of panel; model results are reported in app. B). Factor-analytic modeling supported a reduced-rank matrix with five dimensions (table B1), represented as PCs in table B2 and visualized as correlation biplots in fig. B1. These biplots suggested that correlations among age-specific growth rates and fecundity varied in strength and sign throughout succession but were generally strongest within environ-

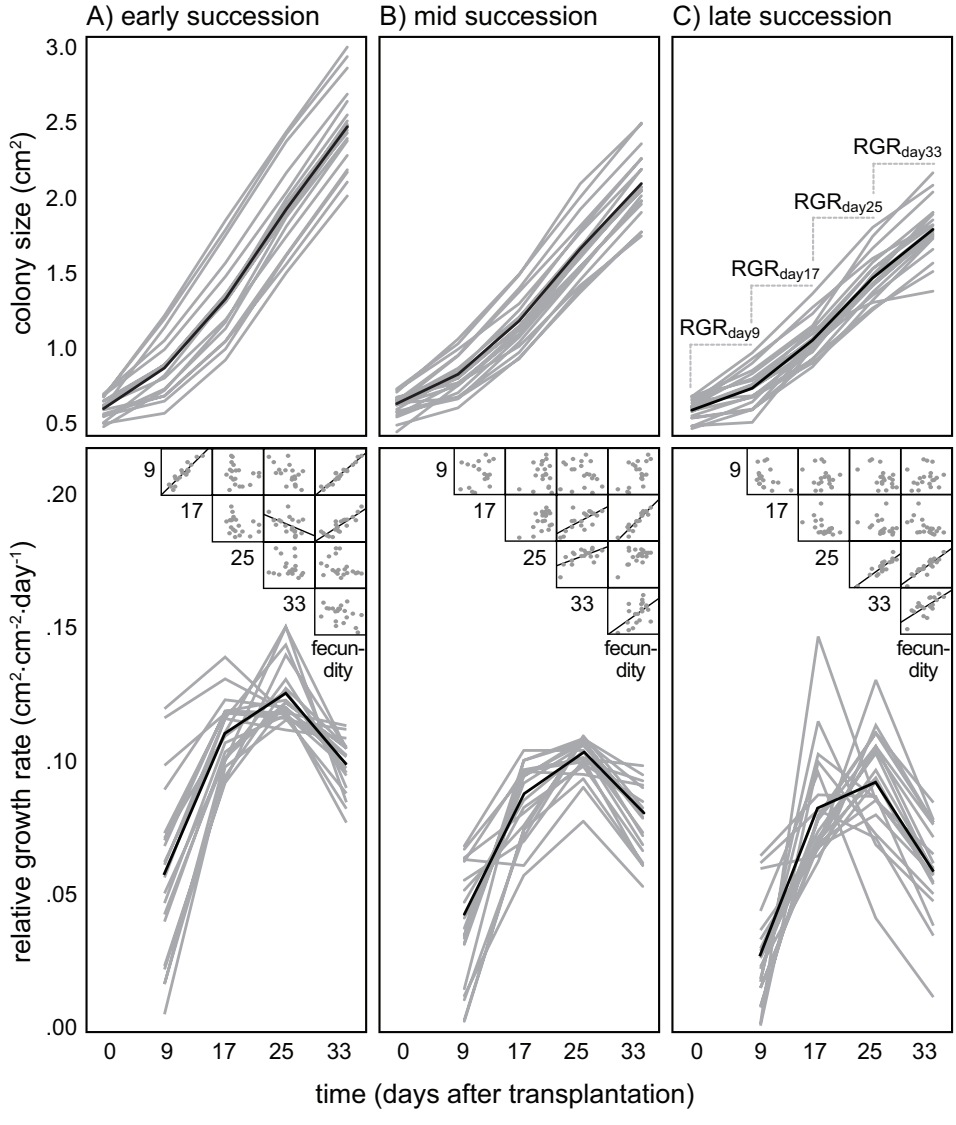


Figure 1: Growth dynamics of *Hippopodina* in different successional environments. Upper panels show temporal changes in ln-transformed colony size, included for illustration only. Lower panels show temporal changes in relative growth rates (RGRs, equal to the slopes of size increments shown in upper-panel *C*) that are the focus of our analyses. Gray lines are the predicted values of focal colonies, and black lines are the population means, extracted from models and expressed on the original measurement scale. Among-colony variation is described by the deviations of gray lines from black, while pairwise covariances of RGRs with each other and with fecundity are described by the inset plots of predicted values (fitted lines are shown for covariances that are significant or marginally so; see table C1).

ments or for the same age compared across environments. To distill each of these main patterns into a simpler, more accessible set of dimensions with fewer loadings on each, we finally chose to model them using the two-stage approach specified below.

Modeling Variation in Age-Specific Growth Rates and Fecundity within Environments. We respecified random effects at the colony level to estimate variation in age-specific growth rates and fecundity pooled across environments (the model above was otherwise unchanged) and then compared this model to one estimating such variation for early, mid-, and late successional environments separately (table C1). Since the latter model fit the data significantly better ($\chi^2_{30} = 119.2$, $P < .01$), we concluded that covariation between age-specific growth rates or between growth rates and fecundity (i.e., selection differentials) differed throughout succession and explored such patterns of co-

Table 1: Statistically supported dimensions (principal components [PCs]) of among-colony variation in the relative growth rates (RGR) and fecundity of *Hippopodina* at early succession, midsuccession, and late succession (with RGR measured at 9, 17, 25, and 33 days after transplantation into each environment)

	Early succession		Midsuccession		Late succession	
	PC1	PC2	PC1	PC2	PC1	PC2
RGR_{day9}	.77	.07	.63	−.73	.01	−.43
RGR_{day17}	.49	−.05	.57	.52	−.02	.90
RGR_{day25}	−.16	.93	.34	.10	.69	−.04
RGR_{day33}	−.36	−.35	.25	.41	.71	.08
Fecundity	.10	−.01	.30	.10	.14	−.04
Eigenvalue (% total variation)	.90 (76%)	.28 (24%)	.42 (60%)	.28 (40%)	.87 (65%)	.47 (35%)

Note: PCs (extracted from table C2) have an eigenvalue describing how much of the total variation in original traits is explained by that particular dimension and loadings describing the relative contribution of each original trait to that dimension.

variation further within environments. We did so within the framework of the full mixed model, taking the matrix of among-colony variation for each environment at a time and using factor-analytic modeling to find its rank (table C2).

Modeling Variation in Age-Specific Growth Rates across Environments. To explore whether selection on colony growth in one successional environment may have correlated effects on growth in others, we respecified random effects at the colony level to estimate variation in age-specific growth rates across environments for each age separately (table C3). The model also had environments (not traits, as in previous models) specified as random effects at the level of panel. As above, we took the matrix of among-colony variation for each age at a time and used factor-analytic modeling to find its rank (table C4). This approach offers a novel way of exploring cross-environment correlations across more than two environments simultaneously (for details, see Smith et al. 2001; Meyer 2009).

Results

Hippopodina's mean response to succession (fig. 1, black lines) differed among traits ($F_{\text{trait} \times \text{environment}\ (8, 27)} = 105.1$, $P < .01$). Within environments, colony growth rates rose until 25 days after transplantation (though not significantly so beyond 17 days in early and late succession: all $P \geq .17$) and then fell with the onset of reproduction. Across environments, growth rates remained similar at 9 days after transplantation, then declined throughout succession for every age sampled thereafter (except for RGR at 25 days from early to midsuccession: $P = .75$).

Variation in Age-Specific Growth Rates and Fecundity within Environments

Within each successional environment, age-specific growth rates and fecundity varied significantly among focal colonies (fig. 1, gray lines) based on unconstrained estimates of among-colony variation (table C1). Factor-analytic modeling of this variation gave statistical support for two dimensions out of a possible five (table C2), implying that the variation was concentrated in just two independently varying trait combinations per environment. Within each environment, only the largest of the PCs representing these dimensions was closely correlated with fecundity and therefore relevant to selection (<3% of the total variance in fecundity was ever explained by the second PC; table 1; fig. 2).

At early succession, PC1 (explaining 76% of the total variation in our traits) had strong positive correlations with fecundity and RGRs at days 9 and 17 but a weak correlation with RGR at day 25 and a more negative correlation with RGR at day 33. At midsuccession, PC1 (explaining 60% of the total variation) was positively correlated with all traits. At late succession, however, PC1 (explaining 65% of the total variation) had strong positive correlations with fecundity and RGRs at days 25 and 33 but weak correlations with RGRs at days 9 and 17. Consistent with selection differentials in table C1, these results imply that selection on growth rates in *Hippopodina* fluctuates with colony age and according to the local environment, favoring faster growth earlier in the life history at early succession but progressively later in the life history later on in succession. The remaining variation explained by PC2 described negative correlations between RGRs at days 25 and 33 at early succession, between RGR at day 9 and all subsequent RGRs at midsuccession, and between RGRs at days 9 and 17 in late succession but was barely associated with fecundity in any case (fig. 2).

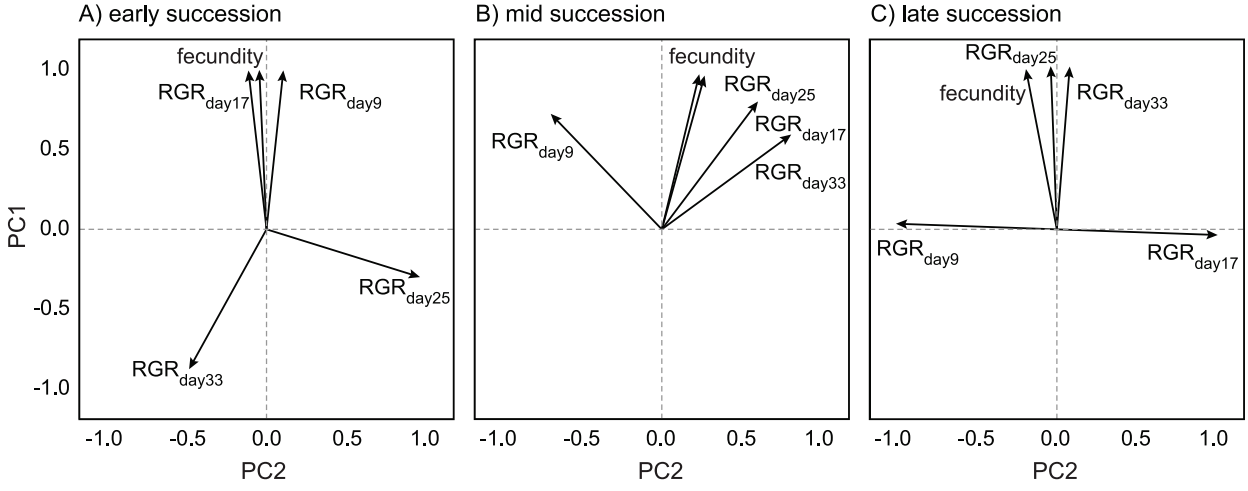


Figure 2: Correlation biplots displaying the supported dimensions (principal components [PCs], PC1 and PC2) of among-colony variation in the relative growth rates and fecundity of *Hippopodina* at early succession (*A*), midsuccession (*B*), and late succession (*C*; with growth rate measured at 9, 17, 25, and 33 days after transplantation into each environment). Arrows are based on loadings in table 1, scaled so that the angles between them describe intertrait correlations (angles of 0°, 90°, and 180° indicate correlations of 1, 0, and −1, respectively); the angles formed with plot axes describe trait correlations with PCs; and the squared values of arrowhead coordinates describe how much trait variation is associated with each PC. In the case of fecundity, at least 97% of variation within each successional environment is associated with PC1.

Variation in Age-Specific Growth Rates across Environments

Across successional environments, correlations between age-specific growth rates were all significantly positive at day 9, based on unconstrained estimates of among-colony variation (table C3). At this age, therefore, fast-growing colonies in one environment also grew similarly fast throughout succession. For subsequent ages, such correlations were often large but not significant in isolation. Factor-analytic modeling of among-colony variation across environments for each age supported two independent dimensions at day 9 but only one dimension for each age thereafter (table C4).

At day 9, PC1 (explaining 85% of its total variation) described positive correlations across all environments, while PC2 described a negative correlation between early succession and both of the later environments but explained relatively little of the variation at this age (table 2). For subsequent ages, the PC for day 17 primarily described a negative correlation across the mid- and late successional environments, while the PCs for days 25 and 33 described positive (but occasionally weak) correlations across all environments (table 2). Note, however, that the relatively small eigenvalues of these PCs suggest limited overall variation in cross-environment correlations beyond day 9. Overall, these results imply that cross-environment correlations in age-specific growth rates may sometimes reinforce selection within particular environments (with RGR at day 9 covarying positively across the early and midsuccessional environments, which both favored faster growth at this age) but often show little potential to translate direct selection on growth in one environment into correlated effects on growth in others.

Discussion

The benefits of large size and the little obvious advantage to increasing size slowly have long been used to argue that organismal growth rates should be targeted by natural selection (Arendt 1997; Mangel and Stamps 2001; Dmitriew 2011). In terms of microevolutionary theory, this translates into an expectation of phenotypic covariance between growth rates and fitness (Arnold and Wade 1984). The tendency for selection, if effective, to deplete among-individual variation as populations evolve adaptively in response (Barrett and Schluter 2008; Walsh and Blows 2009) underlies the further expectation that growth rates should be largely invariant (Dmitriew 2011).

Against these expectations, we detected significant variation in the age-specific growth rates of *Hippopodina* colonies assayed throughout a range of successional environments. We also detected significant variation in reproductive output in each environment, as well as positive covariation between colony growth rates and reproduction, although this covariation differed according to colony age and in response to the changing ecological conditions that accom-

Table 2: Statistically supported dimensions (principal components [PCs]) of among-colony variation across successional environments in the relative growth rates (RGR) of *Hippopodina* at 9, 17, 25, and 33 days after transplantation into each environment

	RGR_{day9}		RGR_{day17}	RGR_{day25}	RGR_{day33}
	PC1	PC2	PC1	PC1	PC1
Early succession	.54	.82	.003	.98	.89
Midsuccession	.55	−.51	−.26	.06	.34
Late succession	.63	−.26	.97	.15	.30
Eigenvalue (% of total variation)	1.30 (85%)	.23 (15%)	.49 (100%)	.30 (100%)	.49 (100%)

Note: PCs (extracted from table C4) have an eigenvalue describing how much of the total trait variation throughout succession is explained by that particular dimension and loadings describing the relative contribution of each successional environment to that dimension.

pany succession (Sutherland and Karlson 1977; Connell and Keough 1985). Thus, our study population of *Hippopodina* shows ample opportunity for selection, in terms of variation in reproductive output that constitutes a major component of individual fitness (Arnold and Wade 1984), and selection often targets colony growth rates as expected. However, it does so inconsistently throughout an individual's life history and is modified in intensity (and to some extent direction, reversing sign across environments at the final age sampled before colonies started to senesce) by the succession process—specifically by 2–3 months of community development. Since *Hippopodina*'s generation time was ~2 months during our study, this leaves little scope for evolutionary responses from one generation to the next to be finer grained than successional change, even if heritable variation to support them was abundant (Bell 2010). Rather, selection on growth rate fluctuates with intrinsic and extrinsic conditions that may change too fast—to the point that net selection is effectively nil when integrated across the life history or environments—for populations to track them adaptively. In acting to constrain adaptation, such fluctuating selection pressures may help explain the persistence of variation in targeted traits, such as growth rates, in natural populations (Barton and Partridge 2000; Merilä et al. 2001; Siepielski et al. 2009; Bell 2010).

Our analytical approach allowed growth rates to vary naturally through ontogeny, unlike traditional growth analyses based on linear regression, which treat growth rates as temporally constant (Paine et al. 2012). Other ways of modeling growth using nonlinear functions (e.g., von Bertalanffy or logistic growth curves; Rose et al. 2009; Stinchcombe et al. 2010) are gaining in popularity but still tend to subsume growth rates into single values that preclude exploring how selection on them may also vary ontogenetically. In our view, the so-called infinite-dimensional approach (centering on the principal components analysis of covariance matrices for traits scored at different times or ages; Kirkpatrick and Heckman 1989) offers the most elegant framework for exploring the selection and evolution of temporally varying growth dynamics (e.g., Kirkpatrick and Lofsvold 1992; see also Stinchcombe et al. 2012) but remains technically challenging to implement (Kuparinen and Björklund 2011). Our approach offers a simplified way of inferring selection on such dynamics and in doing so highlights its limited flexibility to shape those of *Hippopodina* colonies.

Within each successional environment, the mean trajectory of focal colonies displayed the classic pattern of declining growth rate with age and onset of reproduction (West et al. 2001; Rose et al. 2009), but colonies also varied significantly in growth rate at every age sampled. Superficially, this might suggest that selection has ample scope to optimize colony growth rates throughout ontogeny, but correlations among age-specific values restrict this variation to only a subset of underlying dimensions that can be targeted independently, thereby limiting the ways in which selection can potentially act. Such a lack of independent variation among age-specific growth rates has been reported for other taxa (e.g., Kirkpatrick and Lofsvold 1992; Badyaev and Martin 2000). Its further impact on *Hippopodina*, however, is to render substantial amounts of growth-rate variation unavailable to selection, since virtually all of the selection on colony growth rates within any environment was confined to a single dimension of ontogeny, which excluded more than a third of their variation from midsuccession onward. Only at midsuccession, moreover, did all of the age-specific growth rates sampled align (more or less) with the direction of selection, favoring their adaptive increase throughout ontogeny. At either successional extreme, selection favors faster growth either earlier in the life history (in the case of early succession) or later in the life history (in the case of late succession) but not across the life history as a whole. We can only speculate as to why this might be. *Hippopodina* tends to specialize in different successional environments (Monro and Marshall 2013), which our results here suggest might reflect individual variation in the expression, timing, and reproductive consequences of compensatory growth (e.g., Mangel and Munch 2005) as communities become

increasingly saturated (and increasingly limited in key resources, including food, space, and oxygen) during succession.

The implication that *Hippopodina* colonies gain a reproductive benefit from accelerating growth earlier in life at early succession but do so later on in life in later successional communities broadly supports conceptual models of how ecological conditions should modify selection on growth rates (Arendt 1997; Dmitriew 2011), though such models have not yet been tested against succession. For example, Grime and Hunt's (1975) scheme relating seedling growth rates to gradients of stress and disturbance predicts rapid growth early in ontogeny as an adaptation to low-stress conditions where resources are abundant, since an individual's success in that context depends on its ability over competitors to preempt resources and convert them to reproductive output (Aarssen and Keogh 2002). Alternatively, if such conditions coincide with disturbance, selection may favor faster-growing individuals because their accelerated life histories improve the odds of reaching maturation before mortality can occur. While growth rates of sessile marine taxa are typically discussed in relation to competitive ability (e.g., Sebens 1982; Petraitis 1995; Marshall et al. 2006), we consider the latter scenario to be equally plausible for *Hippopodina*, since the role of disturbance in constantly renewing the limiting resources of food, space, and oxygen in epifaunal communities (Connell and Keough 1985; Ferguson et al. 2013) means that conditions of resource abundance may often coincide with selection for rapid development. The fact that exposure to later successional environments saw *Hippopodina*'s reproductive output progressively decoupled from early growth also supports predictions that the benefits of preempting resources decline as resources become limiting (Grime and Hunt 1975; Arendt 1997), with more saturated communities instead selecting for accelerated colony growth closer to maturation.

Our study offered little evidence of direct fitness costs of rapid growth in *Hippopodina*. Such costs are often proposed to explain why growth rates often fail to be maximized within physical or physiological bounds (e.g., Mangel and Stamps 2001; Rose et al. 2009) but are rarely detected (Dmitriew 2011). Considering how selection targets age-specific growth rates of *Hippopodina* throughout ontogeny, the occasional negative association with reproductive output might imply that faster growth is costly at certain points in the life history (e.g., near maturation at early succession; see fig. 2*A*). Generally, however, such implied costs contributed little to the overall patterns of selection that we detected. Nor did we find colony growth rates to be correlated across successional environments in ways that opposed the selection pressures apparent within any single one. Rather, age-specific growth rates that conferred a selective advantage within adjacent environments tended to be weakly associated (or even positively so) across them, indicating that cross-environment correlations throughout succession impose few limits to the adaptation of colony growth rates in *Hippopodina* and may even facilitate this process if they have a heritable basis (Agrawal and Stinchcombe 2009). The heritability of growth rates in our system, however, remains an open question. Strictly speaking, our estimates of among-colony variation are clonal repeatabilities, which are often used to infer broad-sense heritability for organisms that can be propagated clonally (Falconer and Mackay 1996). Such estimates may thus reflect genetic variation among focal colonies but also any environmental variation due to the conditions experienced prior to our experiment (which we made effort to control) or parental effects (which we could not). There is growing awareness that both sources of variation may contribute to microevolutionary processes (Day and Bonduriansky 2011; Bonduriansky 2012), but disentangling them will require complex breeding designs (e.g., Bonduriansky et al. 2012) that may prove challenging to implement for organisms with similar reproductive biology to *Hippopodina*.

Overall, our study offers new insight into the longstanding problem of why natural populations typically harbor abundant phenotypic variation in growth rates, against expectations that it should be depleted by selection in the absence of any costs (Arendt 1997; Mangel and Stamps 2001; Dmitriew 2011). While costs of accelerated growth could well manifest in other components of fitness than were explored here, our results imply that the variability of growth rates in nature may owe as much to fluctuating selection pressures, including periods of relaxed selection during the life history, as to intrinsic constraints on growing fast. Our results further highlight the importance of understanding how ecological conditions may act as agents of selection in natural populations.

Acknowledgments

We thank East Coast Marina and its residents for generous access to Manly Boat Harbour and for patience while the study was conducted, G. Dias and T. Sinclair-Taylor for help with laboratory and fieldwork, and K. Tilbrook for identifying the study organism. We also thank R. Bonduriansky and several anonymous reviewers for advice and comments that greatly improved the manuscript. K.M. and D.J.M. were supported by fellowships and grants awarded under the Australian Research Council's Discovery Projects funding scheme.

APPENDIX A

Supplementary Methods

Correction of Absolute Fecundity for Variation in Zooid Size

We corrected absolute fecundity for variation in zooid size by regressing it on the mean ln area of 10 mature zooids sampled adjacent to brood chambers. We used a separate regression for each environment because a preliminary test found the relationship between fecundity and zooid size to differ among them ($F_{\text{zooid} \times \text{environment}\,(2,\,116)} = 4.9$, $P < .01$), changing from positive at early succession to negative at late succession. We cannot currently explain this curious result, but it merits further study. Ultimately, this correction did not affect the outcome of our analyses (parameter estimates involving fecundity changed only little, and no tests of these parameters gained or lost significance) but was retained because unbiased measures of fecundity are central to the interpretation of our results. The correction was not done within the multivariate framework of our analyses because zooid size was measured only when assaying fecundity, ruling out its use as a covariate due to missing data against all other response variables. We wished to correct fecundity alone, moreover, because our goal was to study variation in colony growth rates, which incorporates variation in both zooid size and zooid number, inclusive of each component rather than corrected for one of them.

Exploratory Modeling of Colony Growth Rates Using Random Regression

We initially modeled the growth of focal *Hippopodina* colonies using the linear regression approach traditionally applied to plants (Paine et al. 2012). Briefly, we ln transformed size to improve linearity before regressing it against time in a multivariate random regression model (implemented in the MIXED procedure of SAS 9.3 and tested for fit using likelihood ratio tests, or LRTs, based on maximum likelihood). The model estimated the among-colony variation in regression slopes and intercepts within and across successional environments based on the random deviation of each colony from the population mean regression (Littell et al. 2006). Regression coefficients were also allowed to vary randomly at the level of panel within colony. Under this approach, each colony's slope is its relative growth rate (RGR, in $\text{cm}^2 \cdot \text{cm}^{-2} \cdot \text{d}^{-1}$), which is assumed to be constant (Paine et al. 2012). In the case of *Hippopodina*, however, model fit was improved by adding quadratic (LRT $\chi^2_{27} = 115.9$, $P < .01$) and cubic (LRT $\chi^2_{36} = 197.2$, $P < .01$) coefficients at the colony level, implying that relative growth rates varied through time as colonies aged. Given the limitations of modeling higher-order polynomials in a random regression framework (Stinchcombe et al. 2012), we dispensed with this approach and chose to model age-specific growth rates (see main article) as discrete traits with the potential to vary (and covary) through time. Doing so was no less parsimonious than the regression approach and meant that temporal variation in growth rates could be interpreted directly, rather than in the context of regression coefficients.

Literature Cited

Aarssen, L. W., and T. Keogh. 2002. Conundrums of competitive ability in plants: what to measure? Oikos 96:531–542.

Agrawal, A. F., and J. R. Stinchcombe. 2009. How much do genetic covariances alter the rate of adaptation? Proceedings of the Royal Society B: Biological Sciences 276:1183–1191.

Arendt, J. D. 1997. Adaptive intrinsic growth rates: an integration across taxa. Quarterly Review of Biology 72:149–177.

Arnold, S. J., and M. J. Wade. 1984. On the measurement of natural and sexual selection: theory. Evolution 38:709–719.

Badyaev, A. V., and T. E. Martin. 2000. Individual variation in growth trajectories: phenotypic and genetic correlations in ontogeny of the house finch (*Carpodacus mexicanus*). Journal of Evolutionary Biology 13:290–301.

Barrett, R. D. H., and D. Schluter. 2008. Adaptation from standing genetic variation. Trends in Ecology and Evolution 23:38–44.

Barton, N., and L. Partridge. 2000. Limits to natural selection. BioEssays 22:1075–1084.

Bell, G. 2010. Fluctuating selection: the perpetual renewal of adaptation in variable environments. Philosophical Transactions of the Royal Society B: Biological Sciences 365:87–97.

Benjamini, Y., and Y. Hochberg. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. Journal of the Royal Statistical Society B: Statistical Methodology 57:289–300.

Blanckenhorn, W. U., and M. Demont. 2004. Bergmann and converse Bergmann latitudinal clines in arthropods: two ends of a continuum? Integrative and Comparative Biology 44:413–424.

Bonduriansky, R. 2012. Rethinking heredity, again. Trends in Ecology and Evolution 27:330–336.

Bonduriansky, R., A. J. Crean, and T. Day. 2012. The implications of nongenetic inheritance for evolution in changing environments. Evolutionary Applications 5:192–201.

Case, T. J. 1978. On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. Quarterly Review of Biology 53:243–282.

Chayes, F. 1949. On ratio correlation in petrography. Journal of Geology 57:239–254.

Christiansen, F. B. 1975. Hard and soft selection in a subdivided population. American Naturalist 109:11–16.

Connell, J. H., and M. J. Keough. 1985. Disturbance and patch dynamics of subtidal marine animals on hard substrata. Pages 125–152 *in* S. T. A. Pickett and P. S. White, eds. The ecology of natural disturbance and patch dynamics. Academic Press, New York.

Crow, J. F. 1958. Some possibilities for measuring selection intensities in man. Human Biology 61:763–775.

Day, T., and R. Bonduriansky. 2011. A unified approach to the evolutionary consequences of genetic and nongenetic inheritance. American Naturalist 178:E18–E36.

Dmitriew, C. M. 2011. The evolution of growth trajectories: what limits growth rate? Biological Reviews 86:97–116.

Ebenman, B., and L. Persson. 1988. Dynamics of size-structured populations: an overview. Pages 3–9 *in* B. Ebenman and L. Persson, eds. Size-structured populations. Springer, Berlin.

Eitan, G. 1972. Types of metamorphosis and early astogeny in *Hippopodina feegeensis* (Busk) (Bryozoa: Ascophora). Journal of Experimental Marine Biology and Ecology 8:27–30.

Falconer, D. S., and T. F. C. Mackay. 1996. Introduction to quantitative genetics. Longman, Harlow.

Ferguson, N., C. R. White, and D. J. Marshall. 2013. Competition in benthic marine invertebrates: the unrecognized role of exploitative competition for oxygen. Ecology 94:126–135.

Fry, J. D. 2004. Estimation of genetic variances and covariances by restricted maximum likelihood using Proc MIXED. Pages 11–34 *in* A. M. Saxton, ed. Genetic analysis of complex traits using SAS. SAS, Cary, NC.

Garant, D., S. E. Forde, and A. P. Hendry. 2007. The multifarious effects of dispersal and gene flow on contemporary adaptation. Functional Ecology 21:434–443.

Grime, J. P., and R. Hunt. 1975. Relative growth-rate: its range and adaptive significance in a local flora. Journal of Ecology 63:393–422.

Hanzawa, F. M., and S. Kalisz. 1993. The relationship between age, size, and reproduction in *Trillium grandiflorum* (Liliaceae). American Journal of Botany 80:405–410.

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.

Hendry, A. P., T. Day, and E. B. Taylor. 2001. Population mixing and the adaptive divergence of quantitative traits in discrete populations: a theoretical framework for empirical tests. Evolution 55: 459–466.

Hine, E., and M. W. Blows. 2006. Determining the effective dimensionality of the genetic variance-covariance matrix. Genetics 173: 1135–1144.

Hoffmann, W. A., and H. Poorter. 2002. Avoiding bias in calculations of relative growth rate. Annals of Botany 90:37–42.

Houle, D. 1998. How should we explain variation in the genetic variance of traits? Genetica 102/103:241–253.

Hughes, R. N. 2005. Lessons in modularity: the evolutionary ecology of colonial invertebrates. Scientia Marina 69:S169–S179.

Hughes, T. P., and J. H. Connell. 1987. Population dynamics based on size or age? a reef-coral analysis. American Naturalist 129:818–829.

Kalisz, S. 1986. Variable selection on the timing of germination in *Collinsia verna* (Scrophulariaceae). Evolution 40:479–491.

Kimball, S., J. R. Gremer, T. E. Huxman, D. L. Venable, and A. L. Angert. 2013. Phenotypic selection favors missing trait combinations in coexisting annual plants. American Naturalist 182:191–207.

Kingsolver, J. G., S. E. Diamond, S. A. Seiter, and J. K. Higgins. 2012. Direct and indirect phenotypic selection on developmental trajectories in *Manduca sexta*. Functional Ecology 26:598–607.

Kirkpatrick, M., and N. Heckman. 1989. A quantitative genetic model for growth, shape, reaction norms, and other infinite-dimensional characters. Journal of Mathematical Biology 27:429–450.

Kirkpatrick, M., and D. Lofsvold. 1992. Measuring selection and constraint in the evolution of growth. Evolution 46:954–971.

Kuparinen, A., and M. Björklund. 2011. Theory put into practice: an R implementation of the infinite-dimensional model. Ecological Modelling 222:2027–2030.

Legendre, P., and L. Legendre. 2012. Numerical ecology. Elsevier Science, Amsterdam.

Littell, R. C., G. A. Milliken, W. W. Stroup, R. D. Wolfinger, and O. Schabenberger. 2006. SAS for mixed models. SAS, Cary, NC.

Mangel, M., and S. B. Munch. 2005. A life-history perspective on short- and long-term consequences of compensatory growth. American Naturalist 166:E155–E176.

Mangel, M., and J. Stamps. 2001. Trade-offs between growth and mortality and the maintenance of individual variation in growth. Evolutionary Ecology Research 3:583–593.

Marshall, D. J., C. N. Cook, and R. B. Emlet. 2006. Offspring size effects mediate competitive interactions in a colonial marine invertebrate. Ecology 87:214–225.

Merilä, J., B. C. Sheldon, and L. E. B. Kruuk. 2001. Explaining stasis: microevolutionary studies in natural populations. Genetica 112/113:199–222.

Meyer, K. 2009. Factor-analytic models for genotype × environment type problems and structured covariance matrices. Genetics Selection Evolution 41:21.

Monro, K., and D. J. Marshall. 2013. Evolutionary constraints and the maintenance of individual specialization throughout succession. Evolution 67:3636–3644.

———. 2014. Data from: Faster is not always better: selection on growth rate fluctuates across life history and environments. American Naturalist, Dryad Digital Repository, http://dx.doi.org/10.5061/dryad.30vn6.

Nylin, S., and K. Gotthard. 1998. Plasticity in life-history traits. Annual Review of Entomology 43:63–83.

Ostrovsky, A. N. 2013. From incipient to substantial: evolution of placentotrophy in a phylum of aquatic colonial invertebrates. Evolution 67:1368–1382.

Paine, C. E. T., T. R. Marthews, D. R. Vogt, D. Purves, M. Rees, A. Hector, and L. A. Turnbull. 2012. How to fit nonlinear plant growth models and calculate growth rates: an update for ecologists. Methods in Ecology and Evolution 3:245–256.

Pease, C. M., and J. J. Bull. 1988. A critique of methods for measuring life history trade-offs. Journal of Evolutionary Biology 1:293–303.

Petraitis, P. S. 1995. The role of growth in maintaining spatial dominance by mussels (*Mytilus edulis*). Ecology 76:1337–1346.

Roff, D. A. 1992. The evolution of life histories: theory and analysis. Chapman & Hall, New York.

Rose, K. E., R. L. Atkinson, L. A. Turnbull, and M. Rees. 2009. The costs and benefits of fast living. Ecology Letters 12:1379–1384.

Schluter, D. 2009. Evidence for ecological speciation and its alternative. Science 323:737–741.

Schluter, D., T. D. Price, and L. Rowe. 1991. Conflicting selection

pressures and life history trade-offs. Proceedings of the Royal Society B: Biological Sciences 246:11–17.

Sebens, K. P. 1982. Competition for space: growth rate, reproductive output, and escape in size. American Naturalist 120:189–197.

Siepielski, A. M., J. D. DiBattista, and S. M. Carlson. 2009. It's about time: the temporal dynamics of phenotypic selection in the wild. Ecology Letters 12:1261–1276.

Smith, A., B. Cullis, and R. Thompson. 2001. Analyzing variety by environment data using multiplicative mixed models and adjustments for spatial field trend. Biometrics 57:1138–1147.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford.

Stinchcombe, J. R., Function-Valued Traits Working Group, and M. Kirkpatrick. 2012. Genetics and evolution of function-valued traits: understanding environmentally responsive phenotypes. Trends in Ecology and Evolution 27:637–647.

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.

Ström, R. 1977. Brooding patterns of bryozoans. Pages 23–55 *in* R. M. Woollacott and R. L. Zimmer, eds. Biology of bryozoans. Academic Press, New York.

Sutherland, J. P., and R. H. Karlson. 1977. Development and stability of the fouling community at Beaufort, North Carolina. Ecological Monographs 47:425–446.

Tilbrook, K. J. 1999. Description of *Hippopodina feegeensis* and three other species of *Hippopodina* Levinsen, 1909 (Bryozoa: Cheilostomatida). Journal of Zoology 247:449–456.

Turelli, M., and N. H. Barton. 2004. Polygenic variation maintained by balancing selection: pleiotropy, sex-dependent allelic effects and G × E interactions. Genetics 166:1053–1079.

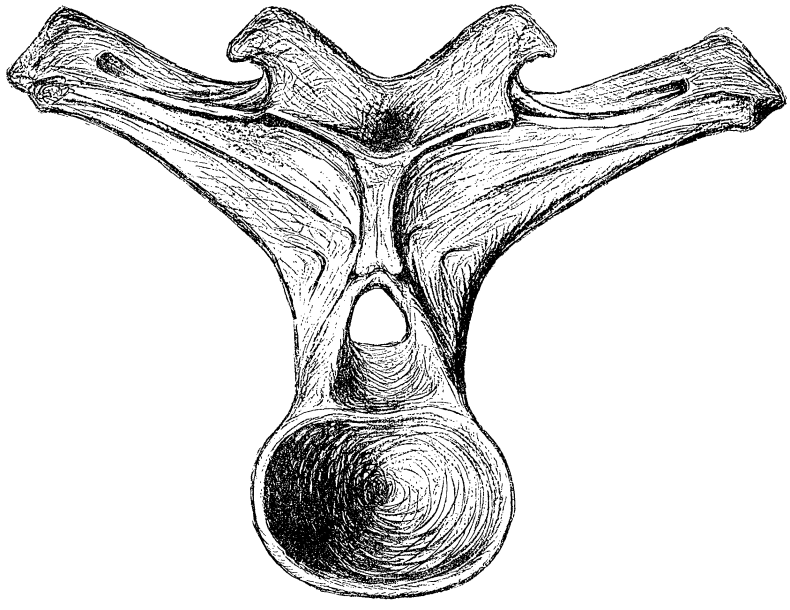
Walsh, B., and M. W. Blows. 2009. Abundant genetic variation + strong selection = multivariate genetic constraints: a geometric view of adaptation. Annual Review of Ecology, Evolution, and Systematics 40:41–59.

Weis, A. E., E. L. Simms, and M. E. Hochberg. 2000. Will plant vigor and tolerance be genetically correlated? effects of intrinsic growth rate and self-limitation on regrowth. Evolutionary Ecology 14:331–352.

Werner, P. A., and H. Caswell. 1977. Population growth rates and age versus stage-distribution models for teasel (*Dipsacus sylvestris* Huds.). Ecology 58:1103–1111.

West, G. B., J. H. Brown, and B. J. Enquist. 2001. A general model for ontogenetic growth. Nature 413:628–631.

Associate Editor: Russell Bonduriansky
Editor: Susan Kalisz



"The second sending [of fossils] included a number of vertebræ, which apparently represent a much more gigantic animal, and I believe the largest or most bulky animal capable of progression on land, of which we have any knowledge. This reptile I described in my palæontological bulletin No. 26, under the name of *Camarasaurus supremus*. Subsequent sendings included many of the more important bones of the skeleton, which render it comparatively easy to determine the general character of this monster." From "On the Saurians Recently Discovered in the Dakota Beds of Colorado" by E. D. Cope (*The American Naturalist*, 1878, 12:71–85).