QUANTIFYING EVOLUTIONARY POTENTIAL OF MARINE FISH LARVAE: HERITABILITY, SELECTION, AND EVOLUTIONARY CONSTRAINTS

Darren W. Johnson,[1,2,3] **Mark R. Christie,**[1,4] **and Jessica Moye**[1,5]

[1]Department of Zoology, Oregon State University, Corvallis, Oregon 97331

[2]E-mail: johnson@nceas.ucsb.edu

[4]E-mail: christim@science.oregonstate.edu

[5]E-mail: peachflower@sbcglobal.net

For many marine fish, intense larval mortality may provide considerable opportunity for selection, yet much less is known about the evolutionary potential of larval traits. We combined field demographic studies and manipulative experiments to estimate quantitative genetic parameters for both larval size and swimming performance for a natural population of a common coral-reef fish, the bicolor damselfish (*Stegastes partitus*). We also examined selection on larval size by synthesizing information from published estimates of selective mortality. We introduce a method that uses the Lande–Arnold framework for examining selection on quantitative traits to empirically reconstruct adaptive landscapes. This method allows the relationship between phenotypic value and fitness components to be described across a broad range of trait values. Our results suggested that despite strong viability selection for large larvae and moderate heritability ($h^2 = 0.29$), evolutionary responses of larvae would likely be balanced by reproductive selection favoring mothers that produce more, smaller offspring. Although long-term evolutionary responses of larval traits may be constrained by size-number trade-offs, our results suggest that phenotypic variation in larval size may be an ecologically important source of variability in population dynamics through effects on larval survival and recruitment to benthic populations.

KEY WORDS: Adaptive landscape, genetic correlation, larval quality, maternal effects, offspring size, quantitative genetics, recruitment.

Many species with complex life cycles have a life history in which early stages (e.g., eggs and larvae) are initially abundant, but experience high rates of mortality before transitioning to the juvenile stage (reviewed by Caley et al. 1996; Hixon et al. 2002). Furthermore, large variation in survival throughout early life-history phases can decouple local reproduction from local population input and lead to dramatic fluctuations in recruitment that can be a major source of variation in adult population dynamics (Houde 1987). Early in the life cycle may therefore be a critical period for natural selection because the combination of high initial abundance and variability in survival during the larval stage may provide ample opportunity for selection on important life-history traits. Additionally, phenotypic variation in early life-history traits may generate differences in survival that are a substantial source of variability in

[3]Present address: National Center for Ecological Analysis and Synthesis, Santa Barbara, CA, 93101.

population dynamics (Hairston et al. 2005; Saccheri and Hanski 2006).

Despite the large opportunity for selection on early life-history traits, the potential for such traits to evolve is unclear for several reasons. For traits that are strongly associated with larval survival, long-term selection may have caused fixation of favorable alleles and reduced additive genetic variance (Fisher 1930; Gustaffson 1986). Under such circumstances, heritability and evolutionary potential of larval traits would be low. On the other hand, there is increasing evidence that natural selection may vary substantially in both space and time (see reviews by Siepielski et al. 2009; Bell 2010). Variation in the strength and direction of selection could preserve both genetic and residual phenotypic variation (Roff 1997), suggesting that evolutionary potential may also be preserved, even if heritabilities of fitness-associated traits are driven down by increased residual variation (Houle 1992). Another consideration is the degree to which larval traits are coupled to traits expressed during other life-history stages. The "adaptive decoupling" hypothesis predicts that complex life cycles may allow larval traits to evolve independent of traits expressed in juveniles and adults (Moran 1994). However, much evidence suggests that parental effects may have a strong influence on offspring traits in a wide variety of taxa (reviewed by Mousseau and Fox 1998). If larval traits are coupled to juvenile and/or adult traits via genetic or maternal effects, then the evolutionary response of larval traits could be constrained by selection on correlated traits expressed during later life stages (Lande and Arnold 1983; Kirkpatrick and Lande 1989).

Conflict between maternal and offspring fitness is yet another potential constraint on the evolution of early life-history traits. This type of conflict may result from a trade-off between the quality (typically related to initial size) and quantity of offspring that a female can produce. Many theoretical models predict that maternal fitness, which is a function of both offspring size and offspring number, is optimized at the expense of offspring fitness, which is a function of offspring size (e.g., Vance 1973; Smith and Fretwell 1974; Parker and Begon 1986; Einum and Fleming 2000; Hendry et al. 2001). Under such conditions, average size of larvae within a population may remain below the phenotypic optimum for survival because viability selection on larvae is balanced by selection favoring adults that produce more larvae (albeit at a suboptimal size). Thus, the potential for larval traits to evolve may be influenced by links between larval traits and fitness of both mothers and larvae. Although most theoretical models assume that fecundity and offspring size are heritable traits that evolve toward an equilibrium state, empirical evaluations of the genetic covariance between these traits are rare (but see Smoker et al. 2000; Heath et al. 2003 for examples in salmonid fish).

For many species with complex life cycles, trait variation expressed as early as larval hatching is associated with differential survival throughout subsequent early life stages and during critical periods, such as metamorphosis or ontogenetic habitat shifts (e.g., Semlitsch and Gibbons 1990; Vigliola and Meekan 2002; Marshall et al. 2003). Among fish with pelagic larvae, mortality during larval and juvenile phases is affected by initial larval size, with larger larvae experiencing greater survival in most (Vigliola and Meekan 2002; Macpherson and Raventos 2005; Raventos and MacPherson 2005; Meekan et al. 2006; Robert et al. 2007; Vigliola et al. 2007; Durieux et al. 2009), but not all cases (Uparanen et al. 2005; Gagliano et al. 2007a). Although selection differentials on larval size can be strong, the potential for an evolutionary response to such selection remains unclear because, to our knowledge, there are no estimates of heritability of larval size for any wild populations of marine fish. Heritabilities have been estimated for larval size in laboratory populations of marine teleosts (e.g., Ma et al. 2007; Shimada et al. 2007) and for juvenile size in a wild population of lemon sharks (DiBattista et al. 2009). These estimates suggest that there can be appreciable genetic variation in larval and juvenile sizes. However, other factors that may constrain evolutionary responses of marine fish larvae in the wild have not been evaluated in depth.

In this study, we quantified both environmental and genetic sources of variation in larval traits for a field population of a common coral reef fish, the bicolor damselfish (*Stegastes partitus*). We used a combination of field demographic studies and manipulative experiments to estimate quantitative genetic parameters for both larval size and swimming performance—two traits that are associated with survival (Vigliola and Meekan 2002; Fuiman and Cowan 2003). In addition to quantifying sources of phenotypic variability in larval traits, we also examined several factors that may influence the evolution of larval traits. First, we estimated quantitative genetic parameters of larval traits, including additive genetic (co)variances and maternal effects. We then examined potential trade-offs between larval traits and larval number by evaluating the relationship between maternal fecundity and average trait values of her larval offspring. Finally, we compiled published estimates of viability selection on larval size from 10 species and 40 cohorts of fish to describe the form and magnitude of selection on this trait. We introduce a method that extends the Lande–Arnold theoretical framework for examining selection on quantitative traits and allows the relationship between mean trait value and mean fitness to be described and predicted across a broad range of phenotypic values. This analytical approach allowed us to better predict how phenotypic variation in larval size would affect larval survival, and to examine the influence of within-species variability in selection on expected evolutionary responses of larval traits.

Methods

STUDY SPECIES

Bicolor damselfish (*S. partitus*) inhabit coral reefs in the tropical Western Atlantic and live in small social groups (ca. 2–20 fish per coral head). Males hold breeding territories and females lay benthic eggs within nests defended by males (Appendix S1). Most courtship and spawning occurs during sunrise (Schmale 1981; Knapp and Warner 1991). Eggs are laid as a dense monolayer on top of benthic substrates (e.g., dead coral, sponges, shells) and are deposited in discrete clutches measuring 5–70 cm^2 (hereafter "egg masses"). Males guard and tend to the egg masses during benthic development, and eggs hatch at twilight after 3.5 days. Pelagic larval duration is about 30 days and most spawning occurs during the third quarter of the lunar cycle (Schmale 1981). Surviving individuals that were spawned during the same reproductive cycle tend to settle as part of the same cohort (i.e., the group of juveniles that settled to benthic habitat on or about the new moon of the next lunar cycle). Spawning cycles may occur year round (Schmale 1981; Robertson et al. 1988), though in our study area reproductive activity is greatest during the summer months. Previous behavioral studies have documented that females lay eggs up to every second day during the lunar breeding cycle (Knapp and Warner 1991). During each cycle males may mate with multiple females, and males may have up to five separate egg masses in the nest at one time.

REPRODUCTIVE MONITORING AND MEASUREMENT OF LARVAL TRAITS

During the summers of 2006 and 2007, we monitored reproduction at two sites near Lee Stocking Island, Bahamas. In 2006, breeding territories with artificial nests (*n* = 37) were monitored daily for a period of approximately two months. All reproductively active males at our study sites were given artificial nests that were composed of 15 cm lengths of 5 cm diameter plastic (PVC) pipe, lined with flexible transparent plastic that could be removed to access the attached eggs. All males switched to spawning in artificial nests within one to two days of nest placement and used artificial nests exclusively for the rest of the study (D. W. Johnson, pers. obs.; also see Knapp and Warner 1991; Cole and Sadovy 1995 for similar results). All adults within the populations (approximately 65 and 35 in the two sites) were individually tagged and monitored as part of a broader demographic study. Small, nonlethal tissue samples (fin clips) were taken from all adults in the study area.

In 2007, we conducted a cross-fostering experiment within these populations. Larvae were swapped among 21 nests shortly after eggs were deposited. Males of *S. partitus* would not guard foster eggs if they did not have previously deposited eggs in their own nest. Therefore, swapped eggs were randomly assigned to other nests that already contained eggs. During both years, we examined nests for newly deposited eggs daily. New egg masses were traced to provide an estimate of the number of eggs in each clutch. Eggs are deposited in a dense monolayer (average density of 215 eggs/cm^2; D.W. Johnson, unpubl. data) and egg size variation is extremely small compared to variation in clutch area, making clutch area a reliable proxy for egg number.

Throughout the duration of both summers, egg masses were recorded and eggs were collected 3.5 days later, immediately prior to larval hatching. Larvae were hatched in the laboratory, where we measured larval size and swimming performance (defined below), two traits that are likely to influence larval survival (Vigliola and Meekan 2002; Fuiman and Cowan 2003). We collected 55 larvae from each egg mass, 35 of which were size-measured under a microscope, 20 of which were used to evaluate average swimming performance. Swimming performance was measured as the duration of time that fish could swim against a standardized current of 3.2 cm/s within a swimming flume (e.g., Stobutski and Bellwood 1997). Tissue samples of all adults and larvae were amplified at seven highly polymorphic microsatellite loci (Williams et al. 2003; Christie et al. 2010) using established PCR methods (see Appendix S2 and Table S1 for additional details). This procedure provided the multilocus genotypes used to identify parent–offspring relationships. The probability of a single putative parent–offspring pair sharing alleles by chance was extremely low ($P < 0.00457$) (Christie 2010), which was not surprising given the large average number of alleles per locus ($n = 27.7$). Therefore, we first employed simple Mendelian incompatibility to assign larvae to parents. To account for genotyping errors, we also used standard likelihood-based methods as implemented in the program CERVUS (Marshall et al. 1998; Kalinowski et al. 2007). Larvae-parent relationships that were assigned with >95% confidence were included in our pedigree.

SOURCES OF VARIATION IN LARVAL TRAITS

We pooled the data from 2006 and 2007 and quantified the degree to which the variation in larval size and swimming performance could be explained by both environmental and genetic effects. We measured larval size for a total of 5872 individuals produced by 51 sires and 77 dams. Within this sample were 143 full-sibling families, 73 sets of paternal half-sibling families, and 12 sets of maternal half-sibling families. We measured swimming performance for 3474 individuals produced by 47 sires and 53 dams. Of the larvae we sampled to measure swimming performance, there were 126 full-sibling families, 70 sets of paternal half-sibling families, and 11 sets of maternal half-sibling families. Within our study population, sires and dams often mated multiple times with the same partners such that each set of half siblings was represented by 2–13 egg masses, with each egg mass representing a full-sibling family. Power analyses of these pedigrees indicated

that our pedigree information provided sufficient statistical power to detect modest amounts of additive genetic and maternal variation in larval traits, and that our analyses were robust to moderate error in parentage assignment (Appendix S3, Tables S2,S3).

Phenotypic variation for both larval size and swimming performance was evaluated using "animal model" analyses and restricted maximum likelihood (REML) estimation using the program ASreml (Gilmour et al. 2006). Because the same individuals were not used to measure both size and swimming performance, we analyzed variation in these traits separately. Variation among individual phenotypes was modeled as a combination of several causal components of variability using the following model:

$$z = \mathbf{X}\boldsymbol{\beta} + \mathbf{Y_a}\boldsymbol{a} + \sum_{k} \mathbf{Y_k}\mathbf{u_k} + \boldsymbol{e},$$

where z is a column vector of observed phenotypic values for n individuals ($n = 6003$ for size-at-hatching (SAH), $n = 3574$ for swimming performance), $\mathbf{X}$ is an n by 4 incidence matrix relating phenotypic values to the column vector of four fixed effects represented by $\boldsymbol{\beta}$, and $\mathbf{Y_a}$ is a n by n incidence matrix derived from the pedigree and used to relate each individual's phenotype to the column vector of additive genetic effects represented by $\boldsymbol{a}$. The $\mathbf{Y_k}$ matrices are n by p_i incidence matrices that relate each individual's phenotypic value to the p_i levels of each random effect within their corresponding column vectors ($\mathbf{u_k}$). $\boldsymbol{e}$ is a column vector of n residual effects (Lynch and Walsh 1998; Kruuk 2004). Our four fixed effects included overall mean value, water temperature (measurements were taken at 30-min intervals at each site and averaged over the development period for each egg mass), clutch area, and adult density (i.e., the number of conspecifics within a 2 m × 2 m plot centered on the breeding territory), because these factors have been demonstrated to affect SAH for other species of reef fish (e.g., McCormick 2006). Our six random effects included site ($p_1 = 2$), year ($p_2 = 2$), and lunar cycle ($p_3 = 6$) to account for temporal and spatial variation in factors that were not directly measured but may nonetheless affect offspring provisioning and development (e.g., ocean productivity and food supply). We also included random effects of nest of origin ($p_4 = 56$) to estimate environmental variation among breeding territories (some nests were used by multiple males due to deaths and/or relocation of reproductive males throughout the study), and nest of rearing ($p_5 = 56$) to estimate effects of paternal environment (e.g., variation in nest care provided by sires, especially foster sires), and a term for dam identity ($p_6 = 77$) to estimate maternal contributions to phenotype above and beyond the additive genetic effects transmitted by mothers (Kruuk 2004; Kruuk and Hadfield 2007).

HERITABILITY CALCULATIONS

For many marine fish, viability selection on larval size has been measured within cohorts (i.e., groups spawned within the same lunar reproductive cycle). To generate heritability estimates that were relevant to these selection measures, we again used an animal model to analyze variance components and estimate additive genetic variances and heritabilities. We did not include any fixed factors other than an estimate of the overall mean phenotypic value (i.e., an intercept term), because selection on cohorts of larvae was measured with respect to total observed phenotypic variation, rather than residual variation (e.g., corrected for temperature differences) (Wilson 2008). We included random effects terms for site, year, lunar cycle, additive genetic effects, maternal effects, nest of origin, nest of rearing, and estimated components of variance in phenotypic values that were attributable to these factors. Heritabilities were estimated as additive genetic variance divided by the total phenotypic variance within cohorts (sum of all variance components minus the among-year and among-cycle components). Standard errors of the heritability values were calculated using an approximation based on the "delta" method described by Hohls (1996). Because heritability estimates may depend on the random factors included in the model (Wilson 2008), we present heritability estimates for both full models (specified above) and reduced, statistically optimized models, although the differences were minor (see Results). Optimal models were generated by sequentially dropping the random effects with the smallest variance components until likelihood ratio tests indicated a significant reduction in the likelihood of model fit.

GENETIC CORRELATIONS BETWEEN LARVAL TRAITS

We used the covariance between full-sibling family mean values to estimate the genetic covariance ($\mathrm{Cov_G}$) between larval SAH and swimming performance because these traits were not measured for the same individuals, nor were they measured on parents. Because full-sibling family covariance contains both additive and nonadditive genetic covariance, our estimates were broad-sense genetic correlations. The covariance between family means estimates 1/2 of the genetic covariance plus 1/n of the within-family common environmental covariance, where n is the number of individuals within each family (Lynch and Walsh 1998). However, in this study the bias due to within-family common environmental variance is likely to be minimal because our within-family samples contained at least 20 individuals. Because multiple measurements were available for most full-sibling groupings (i.e., parents tended to pair for multiple matings), measurements of larval traits were averaged for each family so that in the final analysis, each full-sibling family contributed only one datapoint. To estimate the mean, variance, and 95% confidence intervals for the genetic covariance, we resampled family groups (mean values for both larval size and swimming performance) with replacement and calculated the covariance between family means for 1000 bootstrap replicates.

This estimate of genetic covariance ($\mathrm{Cov_G}$) was combined with estimates of additive genetic variance (V_A) obtained from the animal model analyses to calculate the genetic correlation (r_A):

$$r_A = \frac{\mathrm{cov_G}(_{SAH,SWIM})}{\sqrt{V_A(_{SAH}) \times V_A(_{SWIM})}}$$

where SAH = larval SAH and $SWIM$ = ln swimming performance. Standard errors for the estimated genetic correlation were calculated using the following approximation (Falconer and Mackay 1996):

$$\sigma_{r_A} = \left(1 - r_A^2\right)\sqrt{\left[\frac{\sigma_{(h_{SAH}^2)}\sigma_{(h_{SWIM}^2)}}{h_{SAH}^2 h_{SWIM}^2}\right]},$$

where r_A = genetic correlation, h^2 = heritability, and $\sigma_{(h^2)}$ = standard error of heritability.

TRADE-OFFS BETWEEN LARVAL SIZE AND NUMBER

If there is a trade-off between larval size and number, females that produce more larvae may produce relatively small larvae. We examined this potential trade-off in two different ways. First, we included a measure of the number of eggs per clutch (clutch area) as a fixed factor in our analyses evaluating variation in larval traits. A negative relationship between clutch area and larval traits would indicate a (phenotypic) trade-off between larval size and number within each reproductive event. However, trade-offs between offspring size and number may manifest at longer timescales. We also examined potential trade-offs by evaluating whether mean size and swimming performance of a mother's larval offspring were related to maternal fecundity (estimated over 1–2 summer reproductive seasons). Ideally, one would evaluate offspring size-number trade-offs using lifetime measures of reproduction (Marshall and Uller 2007), and we acknowledge that patterns in the relationship between the mean value of larval traits and fecundity may have been different if we were able to measure each individual's complete, lifetime reproduction. We proceed with our analyses, but because the fecundity values we were able to measure may not necessarily reflect an individual's lifetime reproduction, we suggest that the quantitative results be interpreted with this limitation in mind.

Individual fecundity was estimated as the sum of the area of all egg masses produced by each female during the sampled reproductive period. Microsatellite-based parentage analysis allowed us to assign clutches of eggs to females in the breeding population. Although not all clutches produced during the study were genotyped, this procedure provided a reasonably large sample of identified egg clutches throughout the two breeding seasons ($n = 168$). Many egg masses that were sampled in the field did not survive to be genotyped as larvae (mean survival of egg masses during the egg stage = 0.60 ± 0.035 SE). However, there was no indication of significant spatial variation in egg survival or that survival varied with characteristics of the nest or parents (Appendix S4, Table S4). Furthermore, results of the parentage analysis indicated that in an overwhelming majority of cases, females mated with males that had nests <4 m away from their home territory (D.W. Johnson, unpubl. data; also see Cole and Sadovy [1995] for similar results based on direct spawning observations), suggesting that females were unlikely to mate outside of the study area. Thus, the total area of egg masses that could be assigned to each mother likely provided a reasonable estimate of her fecundity.

We used a linear model to estimate the relationship between the mean trait values of a mother's larval offspring and her relative fecundity (individual fecundity/population mean fecundity), while also accounting for the effects of site, maternal size, and year on fecundity. Within this framework, the partial regression coefficient describing the relationship between mean trait value and a component of fitness (fecundity) provides an approximate measure of selection via maternal fecundity that can be compared to estimates of selection on larval traits via differences in larval viability. Because SAH and larval swimming performance were strongly correlated (see Results), we analyzed these traits separately to avoid problems with collinearity in the analysis. Larval traits were expressed as the deviation of the mean values of a mother's larval offspring from the overall population mean. This deviation was then divided by the within-cohort standard deviation in trait values to make maternal selection values comparable to estimates of viability selection on larvae. To estimate nonlinear selection, we also included the squared value of larval traits in these analyses. Assuming that epistatic genetic effects are negligible, the deviation of the mean value of a mother's offspring from the overall population mean reflects half her breeding value plus any deviations due to maternal effects (Lynch and Walsh 1998). Additional study of *S. partitus* has revealed that maternal effects on larval traits are almost completely explained by variation in maternal body size (D.W. Johnson, M. R. Christie, J. Moye, and M. A. Hixon, unpubl. ms), a covariate included in our selection analyses. We therefore interpreted partial regression coefficients relating relative fecundity rate to mean phenotypic value of offspring as estimates of half the value of selection on the genetic component of larval traits via differences in maternal fecundity (Rausher 1992). This estimate is an approximation because the variance of family means also includes a fraction (1/average number of individuals in a family) of the within-family variance. However, within our study the average number of individuals per family was high (76.0 for larval size, 43.5 for swimming performance), suggesting that partial regression coefficients provided a reasonable estimate of selection coefficients.

LARVAL SIZE AND SELECTIVE MORTALITY

Although larval survival may be associated with a suite of traits (e.g., size, physiological performance, energy reserves), many of these traits are likely to be highly correlated (e.g., Chambers and Trippel 1997; Sponaugle and Grorud-Colvert 2006). We focused on SAH because it was possible to measure for field-reared larvae and because many studies had previously estimated selection on SAH. To examine general patterns of selection on SAH for cohorts of fish, we summarized measures of selection from the published literature by compiling and analyzing a total of 40 selection estimates from 10 species (Appendix S5, Table S5). Although this review of selection differentials summarized the magnitude of selection within single populations (settling cohorts), evolutionary dynamics may be better understood by characterizing selection among multiple populations and across a broader range of phenotypic values. Toward this goal, we analyzed among-cohort variation in selective mortality for a subset of studies that measured selective mortality of multiple cohorts under similar field conditions (e.g., at the same location). Most of the studies in this database examined differences in selection among cohorts that settled in monthly or weekly intervals—a time period over which the chance of large changes in environmental selective forces would be reduced (Siepielski et al. 2009; Bell 2010). This feature allowed us to estimate the relationship between the magnitude of selection and the mean phenotypic value of cohorts. This dataset included a total of 37 selection estimates of selection from eight species (Appendix S5).

Selection on quantitative traits can be visualized using an adaptive landscape, a theoretical surface relating population mean fitness to mean phenotypic values (Lande 1976, 1979). If the adaptive landscape can be described across a broad range of mean phenotypic values, then this surface can be used to predict both the direction and magnitude of selection as a function of mean phenotype and to evaluate the demographic consequences of a change in mean values (e.g., differences in survival of groups that vary in mean phenotypic values). Assuming that phenotypic values are normally distributed within populations, standardized linear selection gradients (equal to standardized selection differentials in the univariate case) provide a local estimate of the slope of the adaptive landscape evaluated at the population mean phenotypic value (Lande 1979; Lande and Arnold 1983). We assume that the adaptive landscape is constant, or at least stationary in shape and position among populations, and that selection is frequency-independent within populations. Then, if selection is measured for multiple cohorts that vary in mean phenotypic values, variation in the values of selection differentials may be used to generate a global description of the average adaptive landscape by providing multiple estimates of the slope of the landscape at various points along the phenotypic trait scale. By expressing selection differentials as a continuous function of mean phenotypic value, one can obtain a functional approximation of the adaptive landscape.

To compare studies of different species on a similar scale, mean phenotypic values were standardized by dividing by the phenotypic standard deviation in the initial group and expressed as deviations from the overall mean value of initial SAH for that species. Standardized selection differentials were therefore calculated as

$$S = \bar{z}^* - \bar{z}, \tag{1}$$

where $\bar{z}^*$ and $\bar{z}$ are, respectively, the mean phenotypic trait values of SAH for the survivor and initial groups, and both $\bar{z}^*$ and $\bar{z}$ are expressed in units of initial group phenotypic standard deviations from the overall mean value of initial SAH. Our results indicate that within species, the relationship between trait means after selection, $\bar{z}^*$, and the trait means before selection, $\bar{z}$, could be described by a linear model,

$$\bar{z}^* = b_0 + b_1 \bar{z}, \tag{2}$$

where b_0 is an intercept and b_1 is a regression slope. This approach allowed us to calculate the relationship between selection differentials and initial mean value while avoiding statistical bias associated with directly modeling the relationship between estimated selection differentials ($\bar{z}^* - \bar{z}$) and initial mean value ($\bar{z}$) Substituting our expression for $\bar{z}^*$ into (1), we obtain the following approximation for the standardized selection differential:

$$S \approx (b_1 - 1)\bar{z} + b_0. \tag{3}$$

In the univariate case, the standardized selection differential (S) is also the slope of the adaptive landscape

$$S = \frac{\partial \ln \bar{W}}{\partial \bar{z}}, \tag{4}$$

where $\bar{W}$ is mean fitness (here defined as survival during early life-history stages) (Lande 1979). Integrating (3) over $\bar{z}$ therefore provides a quadratic approximation of the natural log of mean fitness

$$\ln \bar{W} = \int (b_1 - 1)\bar{z} + b_0 \, d\bar{z} = \frac{1}{2}(b_1 - 1)\bar{z}^2 + b_0 \bar{z} + C, \tag{5}$$

where C is an undefined constant of integration. We used this approximation to model survival under selective mortality. If $(b_1 - 1) < 0$, then at the phenotypic optimum ($\bar{z}_{opt}$), survival is maximal and $S = 0$, so $\bar{z}_{opt} = \frac{-b_0}{(b_1-1)}$. To scale our estimate of $\ln \bar{W}$, we defined the value of mean survival for a cohort with $\bar{z} = \bar{z}_{opt}$ as one. This definition allowed us to solve for the integration constant

$$C = -\frac{1}{2}(b_1 - 1)(\bar{z}_{opt})^2 - b_0\bar{z}_{opt}. \tag{6}$$

By using the above framework to obtain information from multiple selection estimates, one can obtain a robust, global estimate of the adaptive landscape. Although equation (5) provides a simple expression for the adaptive landscape, Appendix S6 demonstrates that equations (3) and (5) can be reparameterized to express the adaptive landscape in terms that are similar to Lande's (1979) formulation (also see Estes and Arnold 2007).

To reconstruct an approximation of the adaptive landscape for survival based on SAH, we first plotted the relationship between $\bar{z}^*$ and $\bar{z}$ for all species. We then used linear regression to describe the relationship between $\bar{z}^*$ and $\bar{z}$ for each species. Because sample sizes to estimate selection differentials varied among cohorts, within this analysis each cohort was weighted by the number of individuals in the initial or survivor samples, whichever was smaller, (i.e., estimates of selection differentials with less certainty were downweighted). If selection differentials do not depend on $\bar{z}$, one would expect the slope of such a regression to be equal to one (i.e., the difference between $\bar{z}^*$ and $\bar{z}$ would be constant). If the slope is less than 1, then selection differentials decrease as $\bar{z}$ increases. Conversely, if the slope is greater than 1, then selection differentials increase as $\bar{z}$ increases. Within-species estimates of the slope and intercept were then averaged across species ($n = 8$) to provide an overall estimate for the relationship between selection differentials and cohort mean SAH. Regression estimates for each species were weighted by the number of cohorts measured. The overall relationship between S and mean SAH was integrated to estimate the average adaptive landscape as described above.

The average adaptive landscape for survival was approximated by the average of linear regressions for each species, using (5). However, fluctuations in the shape and location of the adaptive landscape about a long-term average may generate variation in selection differentials (e.g., Lande and Shannon 1996). In other words, within-species variability in the adaptive landscape may affect selection on larval traits. To evaluate such variation in selection on larval size, we averaged the within-species variability for the slope and intercept estimates from the linear models relating $\bar{z}^*$ to $\bar{z}$. These estimates could then be combined with estimates of the among-species average of the slope and intercept values to generate estimates of the mean and variance of the parameters that describe the adaptive landscape.

TOTAL SELECTION ON SAH

Because we were able to obtain estimates of selection on SAH through associations with both maternal fecundity and larval survival, we were able to combine these estimates to generate an overall description of the relationship between the value of SAH and relative fitness of mothers. However, because of the limitations in our data (incomplete measures of lifetime fecundity, pooling data on selective mortality of larvae from multiple species),

we present this analysis as an illustration of how adaptive landscapes for maternal fitness may qualitatively differ from those for offspring fitness and we place less emphasis on the quantitative results.

We modeled the parental fitness landscape by adding components of the adaptive landscape of maternal fecundity to components of the adaptive landscape for larval survival. However, maternal and larval selection analyses estimated slightly different quantities (i.e., genetic vs. phenotypic selection) and needed to first be converted to a common scale. Because our estimate of selection on SAH via maternal fecundity was calculated on mean phenotypic value of offspring, selection coefficients from this analysis estimate half the selection on the genetic component of SAH. In this case, we did not double our selection coefficients because we assume that the sex ratio in the population is 1:1, and in a similar analysis of paternal offspring number, we detected no appreciable selection on mean SAH. In contrast to maternal fecundity selection, viability selection on SAH was measured on phenotypes. In the absence of any environmentally induced bias and concurrent selection on correlated traits, the selection differential for the genetic component of phenotypic values may be calculated by multiplying the phenotypic selection differential by the heritability value (reviewed by Postma 2006). The parental fitness landscape for the genetic component of SAH was calculated by first generating an expression for S_G, the genetic selection differential. This was done by multiplying the relationship between mean size of larvae and phenotypic selection differentials (eq. 3 above) by h_{SAH}^2, the heritability value for larval SAH, and then adding these terms to estimates of maternal selection based on maternal selection coefficients:

$$S_G = \beta_M + \left(\gamma_M - \beta_M^2\right)\bar{a} + h_{SAH}^2((b_1 - 1)\bar{z} + b_0), \quad (7)$$

where $\bar{a} =$ mean breeding value $= \bar{z}h^2$, β_M estimates the slope of the maternal fecundity landscape at the population mean, and $\gamma_M - \beta_M^2$ provides a point estimate the curvature of the landscape, that is, the degree to which the slope of the landscape changes as a function of the population mean phenotypic (or breeding) value (Phillips and Arnold 1989). Collecting like terms and integrating equation (7) over $\bar{a}$ yields a quadratic approximation of the natural log of mean fitness, similar to equation (5). After solving for the integration constant as described above, we used this surface to illustrate maternal fitness as a function of mean breeding value.

Results

SOURCES OF VARIATION IN LARVAL TRAITS

Of the fixed effects that we included in our analyses, only temperature had a strong effect on larval SAH and swimming performance

Table 1. Results of animal model analyses examining variation in larval size-at-hatching. (A) Estimates and significance tests for fixed effects. (B) Predicted values for variance components associated with random effects in the full model. (C) Predicted values for variance components associated with random effects in an optimized model that retained only those variance components that significantly improved the likelihood of model fit. Models summarized by (B) and (C) excluded fixed effects, such that predicted values are components of total variance in phenotypic values.

(A) Fixed effects					
Variable	Estimate	SE	Wald statistic	df	P
Adult density	0.000774	0.00143	0.542	1	0.580
Clutch area	0.000411	0.000720	0.570	1	0.568
Temperature	0.0299	0.00476	6.279	1	<0.001

(B) Random effects—full model				
Source	Estimate	SE	Proportion of total variation within reproductive cycles	SE
Additive genetic	0.00268	0.000440	0.279	0.073
Maternal	0.00154	0.000443	0.160	0.0539
Year	6.85E-06	2.57E-11	N/A	N/A
Site	0.000726	0.00144	0.0755	0.121
Lunar cycle	0.000519	0.000794	N/A	N/A
Nest of origin	0.000505	0.000307	0.0525	0.031
Nest of rearing	0.000866	0.00111	0.0901	0.104
Residual	0.00319	0.000254	0.332	0.0366
Total	0.0100			

(C) Random effects—reduced (optimal) model				
Source	Estimate	SE	Proportion of total variation within reproductive cycles	SE
Additive genetic	0.00258	0.000470	0.289	0.094
Maternal	0.00132	0.000481	0.148	0.063
Nest of origin	0.000413	0.000386	0.046	0.049
Nest of rearing	0.00108	0.00110	0.121	0.140
Lunar cycle	0.000393	0.000355	N/A	N/A
Residual	0.00352	0.000269	0.395	0.022
Total	0.00930			

(Tables 1 and 2). Both SAH and swimming performance increased at higher temperatures, but neither of these traits strongly varied with clutch area (directly related to egg number) or local density (number of conspecifics in the vicinity of the breeding territory)(Tables 1 and 2). Of the random effects included in the models, we identified substantial effects of several sources of variation in SAH (Table 1B). The largest effects of interest (in order of decreasing magnitude) were additive genetic variance, maternal effects, environmental effects of rearing, and environmental variation among nests of origin (Table 1B,C). For swimming performance, the components of variance that were due to maternal effects, environmental effects of rearing, and environmental variation among nests of origin were all very small and not included in the statistically optimized model (Table 2B,C). Additive genetic variance was a moderate source of variation for swimming performance, and residual variation was high (Table 2C). Heritabilities derived from optimal models were estimated to be 0.289 (±0.094 SE) for SAH and 0.203 (±0.057 SE) for ln-transformed swimming performance. Note that heritabilities calculated from the full models were very similar in magnitude (Tables 1 and 2). Genetic covariance between larval size and ln swimming performance was estimated to be 0.00489 (±0.00212 SE). When

Table 2. Results of animal model analyses examining variation in (ln-transformed) larval swimming performance. (A) Estimates and significance tests for fixed effects. (B) Predicted values for variance components associated with random effects in the full model. (C) Predicted values for variance components associated with random effects in an optimized model that retained only those variance components that significantly improved the likelihood of model fit. Models summarized by (B) and (C) excluded fixed effects, such that predicted values are components of total variance in phenotypic values.

(A) Fixed effects					
Variable	Estimate	SE	Wald statistic	df	*P*
Adult density	−0.00368	0.011	−0.339	1	0.735
Clutch area	−0.0410	0.031	−1.320	1	0.186
Temperature	0.113	0.021	5.258	1	<0.001

(B) Random effects—full model				
Source	Estimate	SE	Proportion of total variation within reproductive cycles	SE
Additive genetic	0.0393	0.0144	0.216	0.0803
Maternal	7.91×10^{-09}	6.30×10^{-10}	4.34×10^{-08}	1.72×10^{-08}
Year	0.00385	0.0131	N/A	N/A
Site	1.36×10^{-08}	9.99×10^{-10}	7.45×10^{-08}	5.52×10^{-08}
Lunar cycle	0.0166	0.0177	N/A	N/A
Nest of origin	0.00243	0.000306	0.0134	0.00823
Nest of rearing	0.00616	0.00459	0.0339	0.0180
Residual	0.134	0.00987	0.736	0.0570
Total	0.202			

(C) Random effects—reduced (optimal) model				
Source	Estimate	SE	Proportion of total variation within reproductive cycles	SE
Additive genetic	0.0347	0.0125	0.203	0.057
Lunar cycle	0.0178	0.0187	N/A	N/A
Residual	0.136	0.00977	0.797	0.063
Total	0.189			

combined with estimates of additive genetic variance for these traits, the genetic correlation was estimated to be 0.486 (±0.231 SE).

TRADE-OFFS IN LARVAL SIZE AND NUMBER

Mean phenotypic values for both SAH and swimming performance were negatively related to estimates of relative fecundity rate (Table 3). Estimated selection gradients for genetic components of larval SAH were −0.299 (0.135 SE) for linear selection and −0.248 (0.130 SE) for nonlinear selection (Table 3A). Selection gradients for larval swimming performance were −0.253 (0.106 SE) for linear selection and −0.232 (0.112 SE) for nonlinear selection (Table 3B). Note that although these selection coefficients estimate half the selection on breeding value, to de-

scribe selection in a parental population with a 1:1 sex ratio, we did not double these values because the similar analysis of paternal offspring number detected no appreciable selection on mean SAH.

LARVAL SIZE AND SELECTIVE MORTALITY

Our literature survey indicated that viability selection on larval SAH was on average positive and strong, but that the intensity, and in some cases, the direction of selection was variable. Figure 1 illustrates the variability among all selection estimates from our literature review. Although much of the variability in Figure 1 is due to among-species variation, selection coefficients exhibited substantial variability within species as well. The overall average magnitude of selection was 1.330 and the average

Table 3. Regression table summarizing the relationships between maternal fecundity and mean trait values of her larval offspring. (A) Larval size-at-hatching (SAH), (B) Larval swimming performance (ln-transformed). Offspring mean trait values were expressed as deviations from the overall population mean and standardized by dividing by the within-cohort standard deviation in larval traits—the same measure of variability used to standardize mean cohort SAH in the analysis of selective mortality of larvae.

	Coefficient	SE	t	P
(A) SAH				
Offspring mean	−0.299	0.135	−2.216	0.031
Offspring mean^2	−0.124	0.065	−1.906	0.062
Mother's size	0.327	0.079	4.124	<0.001
Site	−0.333	0.191	−1.748	0.086
Year	−0.198	0.169	−1.171	0.247
Density	−0.097	0.086	−1.124	0.266
(B) Swimming performance				
Offspring mean	−0.253	0.106	−2.385	0.021
Offspring mean^2	−0.116	0.056	−2.071	0.043
Mother's size	0.144	0.082	1.762	0.084
Site	−0.529	0.209	−2.536	0.014
Year	−0.354	0.183	−1.938	0.058
Density	−0.256	0.090	−2.835	0.006

standard deviation of selection coefficients within each study was 0.344.

Our analysis of among-cohort variation in selection indicated that the average slope of relationship between $\bar{z}^*$ and $\bar{z}$ was less
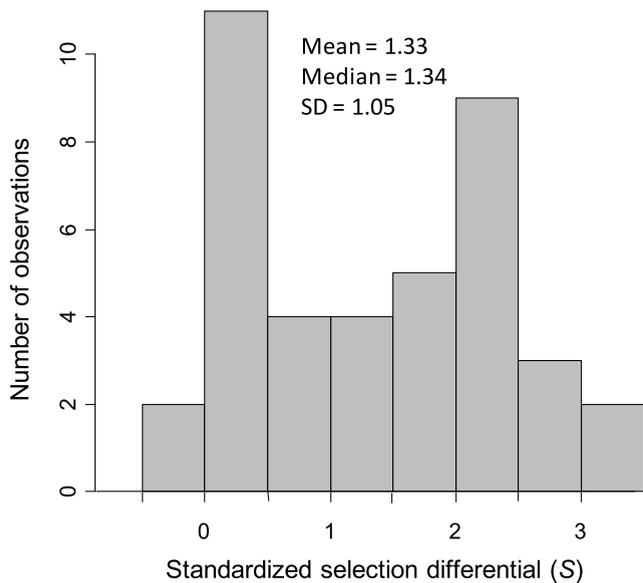

Figure 1. Histogram illustrating the distribution of standardized selection differentials, *S*, calculated from published estimates of selective mortality on larval size-at-hatching (SAH). Data compiled from 40 cohorts from eight species; average study duration was approximately 1 month.

than one, (among-species mean values for slope, b_1, = 0.339, 95% CI: −0.290 to 0.968, intercept, b_0, = 1.343, 95% CI: 0.455–2.231; Fig. 2A), suggesting that the linear selection decreased with increased mean SAH. Although the among-species variation
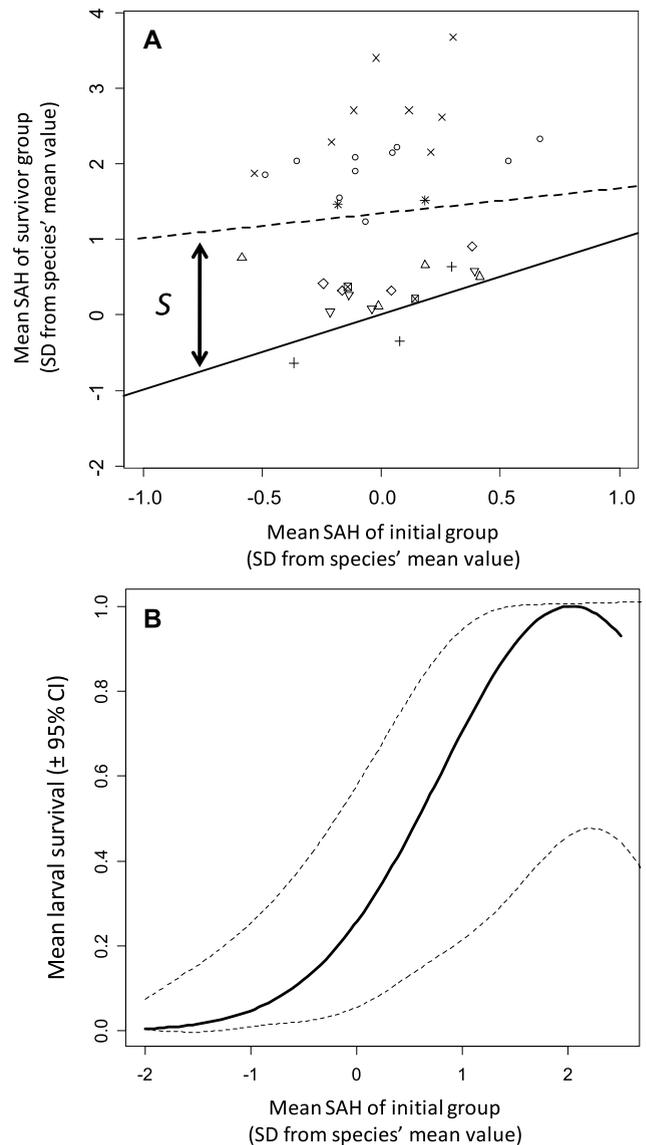

Figure 2. Summary and synthesis of published estimates of selective mortality on larval size-at-hatching (SAH). (A) Relationship between mean value in the survivor group ($\bar{z}^*$) and mean value in the initial sample ($\bar{z}$). Dashed trend line illustrates the average of the within-species regressions of $\bar{z}^*$ on $\bar{z}$. Solid line represents a 1:1 relationship between $\bar{z}^*$ and $\bar{z}$. The difference between the dashed and solid lines (i.e., $\bar{z}^* − \bar{z}$) is equal to the average, standardized selection differential (*S*). Plotting symbols vary by species ($n = 8$). (B) Adaptive landscape relating mean larval SAH to mean, monthly survival under selective mortality. The survival landscape was estimated based on the averaged relationship between mean SAH and *S* as illustrated in (A). Relative survival is expressed as a decimal fraction of the expected mean survival of a cohort with $\bar{z} = \bar{z}_{opt}$. Dashed lines represent bootstrapped confidence intervals.

in selection estimates was substantial, the average relationship between $\bar{z}^*$ and $\bar{z}$ indicated a curved adaptive landscape with a phenotypic optimum, $\bar{z}_{opt}$, 2.032 deviations greater than the current mean (Fig. 2B). Moreover, the curve of the landscape was steep, especially in the vicinity of the overall population mean, where mean survival was ca. 0.26 times the expected survival at the phenotypic optimum (Fig. 2C). These results suggest that selective mortality of larvae may be substantial and that variation in mean cohort size may have large effects on relative survival of larvae. However, within-species variability in the estimates of the parameters that describe the adaptive landscape was also appreciable (average SD of slope = 0.743, intercept = 1.060). If such variability is attributed to environmentally driven fluctuation in the shape and location of the adaptive landscape, rather than to sampling error, considerable variation in selection among cohorts could be expected above and beyond variation in selective mortality that is due to variation in mean cohort size.

TOTAL SELECTION ON SAH

Our results suggest that, when selection on the genetic component of SAH is considered, selection via maternal fecundity may substantially balance selection via larval survival (Fig. 3). The optimum breeding value for parental fitness was approximately 0.16—very close to the observed population mean (where deviation = 0). Moreover, the slope of the parental fitness landscape in the vicinity of the overall population mean was gradual, suggesting that fitness consequences of variation in mean (breeding) value of SAH were small (Fig. 3), especially compared to variation in larval survival expected for comparable variation in mean phenotypic values of SAH (Fig. 2B).

Discussion

By combining field demographic studies with manipulative experiments, we were able to estimate genetic and environmental sources of variation in larval traits for a wild population of marine fish. Estimates of genetic sources of variability in larval traits are rare for fully marine fish, and to our knowledge, all previous studies have been conducted on laboratory populations. Although it has been hypothesized that there may be little additive genetic variance in larval traits of fish (e.g., Heath and Blouw 1998) our results indicated a moderate amount of genetic variation in both larval size and swimming performance for *S. partitus* ($h^2 = 0.29$ and 0.21, respectively). These values suggest appreciable scope for an evolutionary response to selection on these traits in the wild. Furthermore, our estimate of heritability of larval size is comparable to laboratory estimates from at least two other marine teleost fish, the Japanese flounder, *Paralichthys olivaceus* ($h^2 = 0.36 \pm 0.25$ SE; Shimada et al. 2007) and red drum, *Sciaenops ocellatus* ($h^2 = 0.24 \pm 0.06$ SE; Ma et al. 2007), although consid-
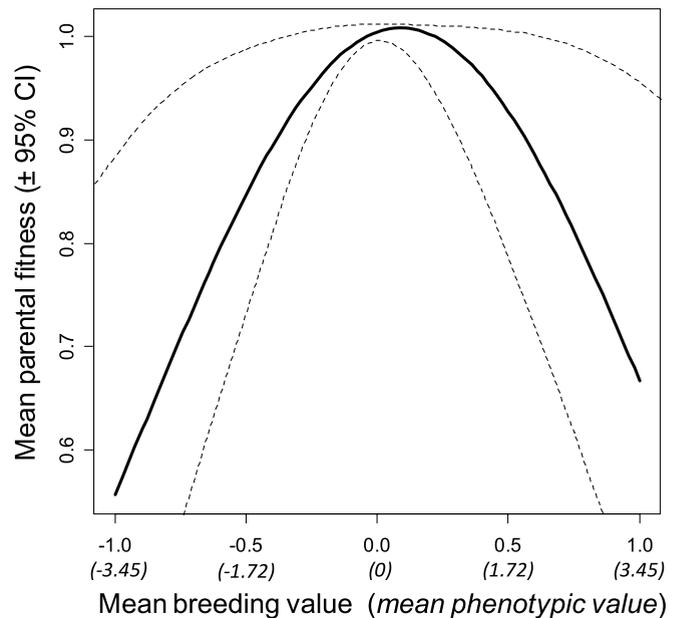

Figure 3. Adaptive landscape relating mean breeding value for SAH to mean parental fitness. Breeding values ($\bar{a}$) are expressed as deviations from the overall mean value of SAH divided by the within-cohort standard deviation in SAH. Values in parentheses express mean phenotypic values to facilitate comparison with Figure 2B. Mean breeding values were converted to phenotypic values assuming that the estimated heritability of SAH accurately describes the degree to which phenotypic value reflects breeding value (i.e., phenotypic values were calculated by dividing breeding values by a heritability value of 0.29). Fitness of parents was calculated by combining estimates of the relationships between SAH and maternal fecundity and SAH and larval survival (eq. 6 in main text). Relative survival is expressed as a decimal fraction of the expected mean survival of a cohort with $\bar{a} = \bar{a}_{opt}$. Dashed lines represent bootstrapped confidence intervals.

erably smaller than heritability estimates for body length of newborn and juvenile sharks in the field ($h^2 = 0.38$–0.85; DiBattista et al. 2009). Overall, these results suggest that larval size may evolve in response to natural selection for at least several marine fish.

However, our synthesis of selection studies on larval fish suggested that average values of larval size may be far from the value that optimizes survival during the larval and juvenile stages. Based on our overall estimate of an adaptive landscape for larval survival, we estimated the phenotypic optimum to be approximately two standard deviations greater than the observed mean. Because two of the eight species in our analysis were damselfish with life histories similar to *S. partitus*, we also reconstructed an adaptive landscape based on selection estimates for larval SAH of damselfish. By this procedure, we estimated the phenotypic optimum to be approximately 3.05 SD above the observed mean (data not shown). Although we treat these derived values as

approximations because of the uncertainty in selection estimates, on average, these figures suggest that the observed mean larval size may be quite maladapted with respect to early survival. For example, the estimated value of relative survival for larvae at the observed mean size was ca. 0.26 of their potential optimum (0.16 if the larval survival landscape is based on estimates of selection from damselfish species; see Hendry and Gonzalez 2008 for a full description of measures of maladaptation). Given ample heritability of larval size and strong observed values of viability selection on larval size, the large mismatch between mean and optimal values suggests the presence of constraints on the evolutionary potential of larval size. Although there are many reasons why no evolutionary response may be observed for heritable traits despite the presence of direct selection (reviewed by Merila et al. 2001), we focus our discussion on potential constraints that we were able to assess directly.

Larval size is strongly influenced by maternal investment per larva, a factor that is also important in determining maternal fitness. Offspring size can influence maternal fitness by constraining the number of offspring produced (i.e., selection via maternal fecundity) and by affecting offspring survival (i.e., selection via offspring viability). In this study, we detected a trade-off between these two fitness components. Although on average, larger larvae tended to experience greater survival, mothers that produced smaller larvae tended to produce more offspring. Maternal fitness gains via increases in one component (e.g., more, smaller offspring) would therefore be offset to some extent by necessary decreases in the other (e.g., lower survival of small larvae). Our reconstruction of the parental fitness landscape suggested that, despite strong phenotypic selection on larval size, when selection on the genetic component of SAH is considered, selection via maternal fecundity may substantially balance selection via larval survival (cf. Fig. 3). Although there is appreciable uncertainly in our estimate of the maternal fitness landscape, the general finding was that mean SAH is close to the value that maximizes maternal fitness, but relatively far from the value that maximizes larval and juvenile survival. Overall, these results are consistent with both theoretical predictions (e.g., Smith and Fretwell 1974), and results from empirical studies in other systems (e.g., Einum and Fleming 2000; Marshall and Keough 2008) suggesting that mean offspring size evolves to a value that maximizes maternal fitness even though average offspring survival may be much less than optimal.

Although the mean value of SAH may be near an equilibrium value strongly influenced by the balance between fecundity and viability selection, equilibrium values may fluctuate in response to variation in selection (Bell 2010), and such variation may have potential consequences for population dynamics. Our survey of selection estimates for larval size indicated considerable variability in the magnitude of selection (Fig. 1). Although

our analysis suggested that much of the within-species variation in selection resulted from variation in mean phenotypic values of cohorts (Fig. 2A), the remaining variation in selection estimates may have been in response to variation in ecological factors. Indeed, many studies have documented substantial variation in the magnitude and direction of viability selection on traits of juvenile fish (e.g., Carlson et al. 2004; Dibattista et al. 2007). For early life-history traits of marine fish, several factors have been identified as sources of variability in selection, including the abundance and behavior of conspecifics (Johnson and Hixon 2010), predator abundance (Holmes and McCormick 2006), and predator type (Takasuka et al. 2004). Such variation in selection may be envisioned as fluctuations in the shape and location of the adaptive landscape about a long-term average (Lande 2007; Siepielski et al. 2009). Traits such as SAH may evolve in response to such short-term variation in larval and/or maternal selection, but because SAH is only moderately heritable, mean SAH may persistently lag behind fluctuations in natural selection, resulting in mean phenotypes that temporarily deviate from the optimum value set by the balance between maternal and larval selection.

In addition to responding to variation in direct selection on SAH, larval size may exhibit correlated responses to selection on other traits. The genetic correlation between larval size and swimming performance was substantial (0.486), suggesting that direct selection on swimming performance would likely induce an appreciable correlated response in larval SAH. Additionally, like many size- and growth-related traits, larval SAH is likely to be phenotypically and genetically correlated with measures of size and growth throughout ontogeny (Cheverud et al. 1983; Kirkpatrick and Lofsvold 1992; see Munch et al. 2005 for an example in fish). We suggest that larval size and swimming performance are not decoupled from traits expressed during juvenile and adult stages and that larvae are unlikely to evolve independently. Selection on juvenile or adult size may cause a correlated genetic response in larval size (Munch et al. 2005). Such effects may offset any balance between maternal fecundity and offspring viability selection, and cause an evolutionary change in mean larval phenotypes (Lande 1979; Lande and Arnold 1983). If selection on juvenile and adult traits is weak and variable, correlated responses of larval traits may generate small, fluctuating perturbations away from the optimum. If selection on juvenile and adult traits is consistent and sufficiently strong, it may result in a long-term shift in larval traits away from their fitness optima (Munch et al. 2005; Walsh et al. 2006).

SAH, SELECTIVE MORTALITY, AND POPULATION DYNAMICS

Overall, our study identified several sources of variability in traits that affect larval survival. We focused on SAH because estimates

of the relationship between SAH and survival are available. Phenotypic variation in SAH may affect population dynamics through the mortality costs incurred during viability selection. Assuming selective mortality is additive, rather than substitutable with non-selective mortality, stronger viability selection should result in a greater selective load and greater total mortality (Lande 1976). Because the intensity of selection varied with mean phenotypic value, phenotypic variation in SAH (including nongenetic sources of variation) may therefore be a substantial source of variability in larval and juvenile survival (cf. Fig. 2B). For example, cohorts of larvae 0.5 SD below the overall mean are expected to experience greater selective mortality and reduced relative survival (ca. 0.47 times the survival at the overall mean value), whereas larvae 0.5 SD above the overall mean would experience greater survival (ca. 1.8 times the survival at the overall mean value; Fig. 2B). Even small differences in larval and juvenile survival can drive large fluctuations in recruitment for marine species (Houde 1987; Johnson 2007). Variation in early life-history traits such as SAH may therefore contribute substantially to recruitment variability. Such effects may occur on short time scales (e.g., via effects of recent feeding history or variation in local density; McCormick 2003, 2006) or in response to long-term effects, such as climate change (Gagliano et al. 2007b). Given the importance of recruitment variability for populations with an "open" structure (Caley et al. 1996; Hixon et al. 2002), understanding the replenishment and dynamics of such populations may require a more detailed understanding of sources of variation in early life-history traits, and a particular emphasis on the potential for such traits to evolve in response to environmental change (Moran 1994; Podolsky and Moran 2006).

LITERATURE CITED

Bell, G. 2010. Fluctuating selection: the perpetual renewal of adaptation in variable environments. Philos. Trans. R. Soc. Lond. B 365:87–97.

Caley, M. J., M. H. Carr, M. A. Hixon, T. P. Hughes, G. P. Jones, and B. A. Menge. 1996. Recruitment and the local dynamics of open marine populations. Annu. Rev. Ecol. Syst. 27:477–500.

Carlson, S. M., A. P. Hendry, and B. H. Letcher. 2004. Natural selection acting on body size, growth rate and compensatory growth: an empirical test in a wild trout population. Evol. Ecol. Res. 6:955–973.

Chambers, R. C., and E. A. Trippel. 1997. Early life history and recruitment in fish populations. Chapman and Hall, London.

Cheverud, J. M., J. J. Rutledge, and W. R. Atchley. 1983. Quantitative genetics of development: genetic correlations among age-specific trait values and the evolution of ontogeny. Evolution 37:895–905.

Christie, M. R. 2010. Parentage in natural populations: novel methods to detect parent-offspring pairs in large data sets. Mol. Ecol. Res. 10:115–128.

Christie, M. R., D. W. Johnson, C. D. Stallings, and M. A. Hixon. 2010. Self-recruitment and sweepskaes reproduction amid extensive gene flow in a coral-reef fish. Mol. Ecol. 19:1042–1057.

Cole, K. S., and Y. Sadovy. 1995. Evaluating the use of spawning success to estimate reproductive success in a Caribbean reef fish. J. Fish Biol. 47:181–191.

Dibattista, J. D., K. A. Feldheim, S. H. Gruber, and A. P. Hendry. 2007. When bigger is not better: selection against large size, high condition and fast growth in juvenile lemon sharks. J. Evol. Biol. 20:201–212.

DiBattista, J. D., K. A. Feldheim, D. Garant, S. H. Gruber, and A. P. Hendry. 2009. Evolutionary potential of a large marine vertebrate: quantitative genetic parameters in a wild population. Evolution 63:1051–1067.

Durieux, E. D. H., M. G. Meekan, D. Ponton, and L. Vigliola. 2009. Temperature, selective mortality and early growth in the short-lived clupeid *Spratelloides gracilis*. J. Fish Biol. 74:921–938.

Einum, S., and I. A. Fleming. 2000. Highly fecund mothers sacrifice offspring survival to maximize fitness. Nature 405:565–567.

Estes, S., and S. J. Arnold. 2007. Resolving the paradox of stasis: models with stabilizing selection explain evolutionary divergence on all timescales. Am. Nat. 169:227–244.

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

Fisher, R. A. 1930. The genetical theory of natural selection. Oxford Univ. Press, London.

Fuiman, L. A., and J. H. Cowan. 2003. Behavior and recruitment success in fish larvae: repeatability and covariation of survival skills. Ecology 84:53–67.

Gagliano, M., M. I. McCormick, and M. G. Meekan. 2007a. Survival against the odds: ontogenetic changes in selective pressure mediate growth-mortality trade-offs in a marine fish. Proc. R. Soc. Lond. B 274:1575–1582.

———. 2007b. Temperature-induced shifts in selective pressure at a critical developmental transition. Oecologia 152:219–225.

Gilmour, A. R., B. J. Gogel, B. R. Cullis, and R. Thompson. 2006. ASReml user guide release 2.0. VSN International Ltd.

Gustafsson, L. 1986. Lifetime reproductive success and heritability: empirical support for Fisher's fundamental theorem. Am. Nat. 128:761–764.

Hairston, N. G. Jr., S. P. Ellner, M. A. Geber, T. Yoshida, and J. A. Fox. 2005. Rapid evolution and the convergence of ecological and evolutionary time. Ecol. Lett. 8:1114–1127.

Heath, D. D., and M. Blouw. 1998. Are maternal effects in fish adaptive or merely physiological side-effects? Pp. 178–201 in T. A. Mousseau and C. W. Fox, eds. Maternal effects as adaptations. Oxford press, Oxford, UK.

Heath, D. D., J. W. Heath, C. A. Bryden, R. M. Johnson, and C. W. Fox. 2003. Rapid evolution of egg size in captive salmon. Science 299:1738–1740.

Hendry, A. P., and A. Gonzalez. 2008. Whither adaptation? Biol. Philos. 23:673–699.

Hendry, A. P., T. Day, and A. B. Cooper. 2001. Optimal size and number of propagules: allowance for discrete stages and effects of maternal size on reproductive output and offspring fitness. Am. Nat. 157:387–407.

Hixon, M. A., S. W. Pacala, and S. A. Sandin. 2002. Population regulation: historical context and contemporary challenges of open vs. closed systems. Ecology 83:1490–1508.

Hohls, T. 1996. Setting confidence limits to genetic parameters estimated by restricted maximum likelihood analysis of North Carolina design II experiments. Heredity 77:476–487.

Holmes, T. H., and M. I. McCormick. 2006. Location influences size-selective predation on newly settled reef fish. Marine Ecology-Progress Series 317:203–209.

Houde, E. D. 1987. Fish early life dynamics and recruitment variability. Am. Fish. Soc. Symp. Series 2:17–29.

Houle, D. 1992. Comparing evolvability and variability of quantitative traits. Genetics 130:195–204.

Jamieson, A., and S. S. Taylor. 1997. Comparisons of three probability formulae for parentage exclusion. Anim. Genet. 28:397–400.

Johnson, D. W. 2007. Habitat complexity modifies post-settlement mortality and recruitment dynamics of a marine fish. Ecology 88:1716–1725.

Johnson, D. W., and M. A. Hixon. 2010. Ontogenetic and spatial variation in size-selective mortality of a marine fish. J. Evol. Biol. 23:724–737.

Kalinowski, S. T., M. L. Taper, and T. C. Marshall. 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. Mol. Ecol. 16:1099–1106.

Kirkpatrick, M., and R. Lande. 1989. The evolution of maternal characters. Evolution 43:485–503.

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

Knapp, R. A., and R. R. Warner. 1991. Male parental care and female choice in the bicolor damselfish, *Stegastes partitus*: bigger is not always better. Anim. Behav. 41:747–756.

Kruuk, L. E. B. 2004. Estimating genetic parameters in natural populations using the 'animal model'. Philos. Trans. R. Soc. Lond. B 359:873–890.

Kruuk, L. E. B., and J. D. Hadfield. 2007. How to separate genetic and environmental causes of similarity between relatives. J. Evol. Biol. 20:1890–1903.

Lande, R. 1976. Natural selection and random genetic drift in phenotypic evolution. Evolution 30:314–334.

———. 1979. Quantitative genetic analysis of multivariate evolution, applied to brain-body size allometry. Evolution 33:402–416.

———. 2007. Expected relative fitness and the adaptive topography of fluctuating selection. Evolution 61:1835–1846.

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

Lande, R., and S. Shannon. 1996. The role of genetic variation in adaptation and population persistence in a changing environment. Evolution 50:434–437.

Lynch, M., and B. Walsh. 1998. Genetics and analysis of quantitative traits. Sinauer, Sunderland, MA.

Ma L, E. Saillant, D. M. Gatlin, and J. R. Gold. 2008. Estimates of heritability of larval and early juvenile growth traits in red drum (*Sciaenops ocellatus*). J. Appl. Aquaculture 20:134–147.

Macpherson, E., and N. Raventos. 2005. Settlement patterns and post-settlement survival in two Mediterranean littoral fishes: influences of early-life traits and environmental variables. Marine Biol. 148:167–177.

Marshall, D. J., and M. J. Keough. 2008. The relationship between offspring size and performance in the sea. Am. Nat. 171:214–224.

Marshall, D. J., and T. Uller. 2007. When is a maternal effect adaptive? Oikos 116:1957–1963.

Marshall, T. C., J. Slate, L. E. B. Kruuk, and J. M. Pemberton. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. Mol. Ecol. 7:639–655.

Marshall, D. J., T. F. Bolton, and M. J. Keough. 2003. Offspring size affects the post-metamorphic performance of a colonial marine invertebrate. Ecology 84:3131–3137.

McCormick, M. I. 2003. Consumption of coral propagules after mass spawning enhances larval quality of damselfish through maternal effects. Oecologia 136:37–45.

———. 2006. Mothers matter: crowding leads to stressed mothers and smaller offspring in marine fish. Ecology 87:1104–1109.

Meekan, M. G., L. Vigliola, A. Hansen, P. J. Doherty, A. Halford, and J. H. Carleton. 2006. Bigger is better: size-selective mortality throughout the life history of a fast-growing clupeid, *Spratelloides gracilis*. Marine Ecology-Progress Series 317:237–244.

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

Moran, N. A. 1994. Adaptation and constraint in the complex life cycles of animals. Annu. Rev. Ecol. Syst. 25:573–600.

Mousseau, T. A., and C. W. Fox. 1998. Maternal effects as adaptations. Oxford Univ. Press, Oxford.

Munch, S. B., M. R. Walsh, and D. O. Conover. 2005. Harvest selection, genetic correlations, and evolutionary changes in recruitment: one less thing to worry about? Can. J. Fish. Aquat. Sci. 62:802–810.

Parker, G. A., and M. Begon. 1986. Optimal egg size and clutch size: effects of environment and maternal phenotype. Am. Nat. 128:573–592.

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

Podolsky, R. D., and A. L. Moran. 2006. Integrating function across marine life cycles. Integr. Comp. Biol. 46:577–586.

Postma, E. 2006. Implications of the difference between true and predicted breeding values for the study of natural selection and micro-evolution. J. Evol. Biol. 19:309–320.

Rausher, M. D. 1992. The measurement of selection on quantitative traits—biases due to environmental covariances between traits and fitness. Evolution 46:616–626.

Raventos, N., and E. Macpherson. 2005. Effect of pelagic larval duration and size-at-hatching on post-settlement survivorship in two temperate labrid fish of genus *Symphodus*. Marine Ecology-Progress Series 285:205–211.

Robert, D., M. Castonguay, and L. Fortier. 2007. Early growth and recruitment in Atlantic mackerel *Scomber scombrus*: discriminating the effects of fast growth and selection for fast growth. Marine Ecology-Progress Series 337:209–219.

Robertson, D. R., D. G. Green, and B. C. Victor. 1988. Temporal coupling of production and recruitment of larvae of a Caribbean ref fish. Ecology 69:370–381.

Roff, D. A. 1997. Evolutionary quantitative genetics. Chapman and Hall, New York.

Saccheri, I., and I. Hanski. 2006. Natural selection and population dynamics. Trends Ecol. Evol. 21:341–347.

Schmale, M. C. 1981. Sexual selection and reproductive success in males of the bicolor damselfish, *Eupomacentrus partitus* (Pices: pomacentridae). Anim. Behav. 29:1172–1184.

Semlitsch, R. D., and J. W. Gibbons. 1990. Effects of egg size on success of larval salamanders in complex aquatic environments. Ecology 71:1789–1795.

Shimada, Y., T. Shikano, N. Murakami, T. Tsuzaki, and T. Seikai. 2007. Maternal and genetic effects on individual variation during early development in Japanese flounder *Paralichthys olivaceus*. Fisheries Sci. 73:244–249.

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

Smith, C. C., and S. D. Fretwell. 1974. Optimal balance between size and number of offspring. Am. Nat. 108:499–506.

Smoker, W. W., A. J. Gharrett, M. S. Stekoll, and S. G. Taylor. 2000. Genetic variation of fecundity and egg size in anadromous pink salmon *Oncorhynchus gorbuscha* Walbaum. Alaska Fishery Res. Bull. 7:44–50.

Sponaugle, S., and K. Grorud-Covert. 2006. Environmental variability, early life-history traits, and survival of new coral reef fish recruits. Integr. Comp. Biol. 46:623–633.

Stobutzki, I. C., and D. R. Bellwood. 1997. Sustained swimming abilities of the late pelagic stages of coral reef fishes. Marine Ecology Progress Series 149:35–41.

Takasuka, A., Y. Oozeki, R. Kimura, H. Kubota, and I. Aoki. 2004. Growth-selective predation hypothesis revisited for larval anchovy in offshore waters: cannibalism by juveniles versus predation by skipjack tunas. Marine Ecology-Progress Series 278:297–302.

Urpanen, O., H. Huuskonen, T. J. Marjomaki, and J. Karjalainen. 2005. Growth and size-selective mortality of vendace (*Coregonus albula* (L.)) and whitefish (*C. lavaretus* L.) larvae. Boreal Environ. Res. 10:225–238.

Vance, R. R. 1973. Reproductive strategies in marine benthic invertebrates. Am. Nat. 107:339–352.

Vigliola, L., and M.G. Meekan. 2002. Size at hatching and planktonic growth determine post-settlement survivorship of a coral reef fish. Oecologia 131:89–93.

Vigliola, L., P. J. Doherty, M. G. Meekan, D. M. Drown, M. E. Jones, and P. H. Barber. 2007. Genetic identity determines risk of post-settlement mortality of a marine fish. Ecology 88:1263–1277.

Walsh, M. R., S. B. Munch, S. Chiba, and D. O. Conover. 2006. Maladaptive changes in multiple traits caused by fishing: impediments to population recovery. Ecol. Lett. 9:142–148.

Williams, D. A., J. Purcell, C. R. Hughes, and R. K. Cowen. 2003. Polymorphic microsatellite loci for population studies of the bicolor damselfish, *Stegastes partitus* (Pomacentridae). Mol. Ecol. Notes 3:547–549.

Wilson, A. J. 2008. Why h^2 does not always equal V_A/V_P? J. Evol. Biol. 21:647–650.

Associate Editor: J. Wolf

Supporting Information

The following supporting information is available for this article:

Appendix S1. Photographs of *Stegastes partitus*.

Appendix S2. Additional details regarding microsatellite parentage analyses.

Appendix S3. Power to detect additive genetic variance and maternal effects.

Appendix S4. Variation in egg mass survival.

Appendix S5. Summary of studies examining selective mortality of larval and juvenile fishes.

Appendix S6. An alternative expression to describe the form of the adaptive landscape.

Figure S1. Analyses of the power to detect variation in larval traits that was due to additive genetic and maternal effects.

Table S1. Mean per-locus allelic diversity and deviations from Hardy-Weinberg Equilibrium in sampled bicolor damselfish.

Table S2. Estimated heritability and maternal effect values for larval size.

Table S3. Estimated heritability and maternal effect values for larval swimming performance.

Table S4. Output from a generalized linear mixed effects model describing variation in egg mass survival.

Table S5. Summary of studies of larval size and selective mortality.

Supporting Information may be found in the online version of this article.

Please note: Wiley-Blackwell is not responsible for the content or functionality of any supporting information supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.