ORIGINAL ARTICLE

Genetic correlations between adults and larvae in a marine fish: potential effects of fishery selection on population replenishment

Darren W. Johnson, Mark R. Christie, Jessica Moye and Mark A. Hixon

Department of Zoology, Oregon State University, Corvallis, OR, USA

Abstract

Correlated genetic responses have been hypothesized as important components of fishery-induced evolution, although predictive data from wild populations have been difficult to obtain. Here, we demonstrate substantial genetic correlations between a trait often subjected to fishery selection (adult body length) and traits that affect survival of larvae (length and swimming performance) in a wild population of a marine fish (bicolor damselfish, *Stegastes partitus*). Through both genetic covariance and size-dependent maternal effects, selection on adult size may cause a considerable, correlated response in larval traits. To quantify how variation in larval traits may affect survival, we introduce a flexible method that uses information from selection measurements to account for frequency dependence and estimate the relationship between phenotype and relative survival across a broad range of phenotypic values. Using this method, we synthesize studies of selective mortality on larval size for eight species of fish and show that variation in larval size may result in considerable variation in larval survival. We predict that observed rates of fishery selection on adult marine fishes may substantially reduce larval size and survival. The evolution of smaller larvae in response to fishery selection may therefore have substantial consequences for the viability of fished populations.

Introduction

For many wild populations, phenotypic changes in trait values can have contemporary effects that substantially influence population dynamics (Hairston et al. 2005; Coulson et al. 2006). Such effects may be especially strong for species that are subject to fishery selection (Law 2000; Allendorf and Hard 2009; Darimont et al. 2009). Fishing mortality rates often exceed natural mortality rates, and fishing practices can selectively remove larger individuals from the population, potentially resulting in rapid evolution of fished populations (reviewed by Stokes et al. 1993; Browman et al. 2000). Evolutionary changes such as reduced growth rate of adults and smaller size at maturity have been demonstrated conclusively in laboratory settings (Conover and Munch 2002). However, the full extent of evolutionary responses to fishery selection in natural populations may be complex. For example, even

if selection acts on only a single trait, other traits that are genetically correlated may also evolve (e.g. Lande 1979). Predicting the response of fish populations to fishery selection will therefore require accurate estimates of inheritance parameters for relevant traits in wild populations. Although such information may be difficult to obtain, there is a pressing need for estimates of additive genetic variances for traits under direct selection, as well as genetic correlations between related traits (Law 2000, 2007).

A major challenge for estimating inheritance parameters in marine fishes is that many species are broadcast spawners and most species have highly dispersive larvae. These life-history features make it difficult to find close relatives in the wild and difficult to compare the traits of relatives across generations. However, important responses to selection may occur in larval and early juvenile phases. Small changes in the survival rates of marine

fish larvae may result in extremely large fluctuations in recruitment (Bailey and Houde 1989). Likewise, small changes in mortality rates during the early postsettlement phase can have strong effects on population size (Myers and Cadigan 1993; Sogard 1997; Caley et al. 1996). If traits that affect larval and early juvenile survival are genetically correlated with adult traits that are under fishery selection (e.g. size or growth rate), then fishery selection may decrease population viability by selecting for individuals that are less able to replenish the population (Kirkpatrick 1993; Munch et al. 2005; Walsh et al. 2006). Because larval survival can be critically important to population dynamics and because little is known about the genetic (co)variance underlying larval traits, studies of model species whose larvae can be collected and measured in the field can be extremely useful in providing representative estimates of inheritance parameters, including genetic covariances that may be used to predict correlated evolutionary responses.

Genetic covariance between size and growth at different ages is likely due to pleiotropy, in which expression of single genes (e.g. those that code for growth factors) affect multiple traits (e.g. body sizes) at different ages (Cheverud et al. 1983). Although genetic covariance between body size at different ages has been demonstrated for many taxa (Kirkpatrick et al. 1990), such estimates are rare for fishes, especially in wild populations. Positive genetic covariance between size of adults and size during early life-history stages (eggs and larvae) has been previously demonstrated for a laboratory population of rainbow trout (*Oncorhynchus mykiss*; McKay et al. 1986), a laboratory population of Atlantic silversides (*Menidia menidia*; Munch et al. 2005; Walsh et al. 2006), and several populations of salmonids in hatcheries and farms (Heath et al. 1999; Carlson and Seamons 2008 and references therein). These results suggest that the presence of such covariance may be common in fishes. However, because it is the *magnitude* of genetic covariance that will determine how quickly larval traits can respond to selection on adults, predicting how larvae will respond to selection on adults in the wild requires accurate and representative estimates of genetic correlations between adult and larval traits.

Adult and larval traits may also be correlated through maternal effects mediated by associated, heritable traits (Kirkpatrick and Lande 1989). Previous research has demonstrated that for many fishes, variation in maternal provisioning of offspring can affect early life-history traits, such as egg and larval sizes (reviewed by Chambers and Leggett 1996; Heath and Blouw 1998). Moreover, for many fishes, maternal size and offspring size are phenotypically correlated (Berkeley et al. 2004a; Heath and Blouw 1998), suggesting that maternal effects may

partially depend on the body size of adult females. To our knowledge, existing measures of phenotypic correlations do not separate genetic resemblance from size-dependent maternal effects, and the actual magnitudes of size-dependent maternal effects are unclear. However, the presence of strong phenotypic correlations between maternal and offspring size suggests that size-dependent maternal effects may be substantial. Body size is a heritable trait for many fishes (Law 2000), and populations may experience a decline in average body size when subjected to size-selective fishing (Swain et al. 2007). Maternal effects mediated by changes in adult body size may therefore be an important pathway through which larval traits may change in response to selection on adults (Kirkpatrick and Lande 1989).

Larval mortality may increase with decreasing body size (reviewed by Morse 1989; Pepin 1993), suggesting that an evolutionary reduction in larval size owing to the selective removal of large adults may result in lower larval survival and reduced recruitment. A previous study by Munch et al. (2005) investigated potential for correlated responses of larvae to affect recruitment, using estimates of genetic correlations between adult and juvenile body size from a laboratory population of Atlantic silversides (*Menidia menidia*) and measures of size-dependent mortality estimated by comparing mortality rates for species of different size. The authors concluded that, despite the potential for a moderate, correlated response of larval size to selection on adults, effects on size-dependent survival (and therefore recruitment) were likely to be negligible. However, for a given rate of selection on adults, responses of larval traits and effects on recruitment will depend critically on both the magnitude of genetic correlations and the rate at which mortality depends on body size, two quantities that are not easily estimated with much certainty. Making general predictions of how fishery selection is likely to affect larval survival, and population replenishment will therefore require further investigation into genetic covariance, maternal effects, and size-dependent mortality of larvae.

In this study, we evaluated the degree to which two traits that affect the survival of larval fish – size at hatching (hereafter 'SAH') and swimming performance – were genetically correlated with adult size in a wild population of bicolor damselfish (*Stegastes partitus*) in the Bahamas. We estimated genetic covariances among adult and larval traits as well as size-dependent maternal effects on larval traits. These estimates of inheritance parameters allowed us to predict how larval traits may evolve in response to selection on adults, especially in the light of potentially large maternal effects on larvae. We also examined the demographic consequences of variation in larval SAH by analyzing size-dependent mortality of larvae and juveniles

in two separate ways. We first characterized size-dependent mortality by comparing published estimates of mortality among species that varied in body size. We also introduce a method for inferring size-dependent mortality within species by synthesizing information from field studies of selective mortality. We then combined both estimates of size-dependent mortality with our estimates of genetic correlations between adult and larval traits to illustrate (i) how a given intensity of selection on adult size (in particular, estimates of fishery selection) may cause a correlated response in the size of larvae and (ii) how this response affects relative rates of survival during larval and early postsettlement life – key demographic phases for many marine fishes (Bailey and Houde 1989; Myers and Cadigan 1993; Caley et al. 1996; Sogard 1997).

Methods

Demographic monitoring

The bicolor damselfish (*S. partitus*) is an abundant species that inhabits coral reefs and lives in small social groups ($\approx$2–20 fish) on distinct coral heads. This is an excellent model species for estimating genetic parameters in the field. Adults remain within a few meters of their home territory, permitting *in situ* monitoring of individual growth and reproduction. Males hold small breeding territories and will often mate with multiple females (Schmale 1981). Females lay benthic eggs and will readily deposit eggs on artificial substrates that can be manipulated and brought back to the laboratory for analysis. We used artificial nests comprised of 15 cm lengths of 5-cm-diameter plastic pipe, lined with flexible transparent plastic that could be removed to access the attached eggs. Eggs hatch at twilight after 3.5 days of benthic development.

In 2006, we monitored reproduction at two sites near Lee Stocking Island, Bahamas. A total of 37 breeding territories with artificial nests were monitored daily for approximately 2 months. Adult fish at these sites ($n = 65$ and 35) were individually tagged as part of a broader long-term demographic study. Small tissue samples (fin clips) were taken from all adults in the study population to identify parent–offspring relationships. Most adults had been monitored periodically because settlement and their age, size, and growth rate were measured directly. Size-at-age of *S. partitus* is well described by a Von Bertalanffy growth function (Johnson and Hixon 2010), and maximum size of each adult (L_{max}) was expressed as the asymptotic size described by the growth function fit to individual size-at-age data. We used L_{max} in parent–offspring analyses because we believe that it is more useful and direct to predict correlated responses to changes in average values of L_{max} (a parameter that relates to growth trajectories) than to changes in average adult size (which also depends on

age). Nonetheless, we also conducted parent–offspring analyses using current size, rather than L_{max} (see Supporting Information). However, because the adults in our study were within 86–99% of their estimated L_{max} values, genetic parameter estimates were very similar.

To quantify genetic covariance between larval and adult traits, we monitored breeding adults in the field, collected eggs immediately prior to hatching, and compared traits of both larvae and adults. We measured larval size and swimming performance as indicators of larval quality because both of these traits may influence larval survival (Vigliola and Meekan 2002; Fuiman and Cowan 2003). We sampled 55 larvae from each of 143 egg masses collected in the field. Thirty-five of these larvae were size-measured under a microscope, and 20 larvae were used to evaluate average swimming performance. Swimming performance was measured as the duration of time that fish could swim against a current of 3.2 cm/s within a swimming flume. Three larvae from each egg mass were individually preserved for genetic analysis.

Adults and larvae were genotyped at seven highly polymorphic microsatellite loci (Williams et al. 2003). This procedure provided multi-locus genotypes of all sampled adults and larvae, which we used to determine parentage (Appendix S1, also see Methods in Christie et al. 2010). Given the large numbers of alleles per locus, the probability of a single putative parent–offspring pair sharing alleles by chance was extremely low ($P < 0.00457$) (Christie 2010). Thus, we used simple Mendelian incompatibility to assign parentage. To cross-validate results as well as to fully account for genotyping errors, we also used likelihood-based methods as implemented in the program CERVUS (Marshall et al. 1998).

Genetic covariance among larval and adult traits

We examined the potential for a genetic relationship between L_{max} and larval traits by plotting offspring phenotype against the phenotype of the sire. All traits were expressed as phenotypic standard deviations from the population mean. If there is no environmental covariation between parent and offspring phenotype, then the slope of such a regression line estimates one-half the additive genetic covariance between traits (Lynch and Walsh 1998). For graphical display, we plotted mean values for all larval families (egg masses) sampled. However, because observations of multiple clutches of offspring from a single father were not independent, we regressed the mean standard length of all offspring of each sire on maximum total length of sire. In this analysis, each sire–offspring case was weighted by the number of clutches used to determine the average of larval traits. We also included effects of average water temperature, site, and average

density of damselfish within breeding territories as covariates, because these factors may affect larval size (McCormick 2006; Appendix S2, Table B1). We acknowledge that because most of the offspring from sires in this study came from the same nest, this design confounded sire and nest effects. However, additional studies using our artificial nests within this system suggested that nest effects were small (accounting for <5% of the variation in larval traits) and unlikely to be correlated with sire asymptotic size (D. W. Johnson, unpublished data).

We evaluated sire–offspring relationships for a large sample of offspring from naturally breeding adults in 2006. Although significant relationships were observed (see Results section), they may have been caused by a combination of environmental, maternal, and/or additive genetic effects. To examine possible assortative mating and maternal influences, we used parentage analysis to identify mothers of each clutch and tested whether maternal size and/or age was correlated with paternal size. Finally, we separated genetic effects from any environmental effects that depended on paternal size (e.g. greater care of offspring) by conducting a cross-fostering experiment in the summer of 2007. Although the experiment was conducted in the same two study populations, there was very little overlap between individuals breeding in 2006 and 2007 because of high turnover in the population (only five sires and six mothers bred in both years). We monitored adult size and larval quality as before, except during this experiment; egg masses were swapped among nests for the duration of benthic egg development (3.5 day) by moving eggs on plastic collectors among nests. We compared offspring and sire phenotype for both biological and foster fathers.

Because our results indicated some assortative mating based on L_{max} but no environmental effects that depended on sire size (see Results), we pooled the data from both years (2006 and 2007) to calculate genetic covariances and size-dependent maternal effects. Additive genetic covariances (Cov$_A$), corrected for assortative mating, were calculated according to the following formula, derived from Lynch and Walsh (1998):

$$\mathrm{Cov}_A = \frac{(b - rm)(2 - m)}{(1 + r)} \qquad (1)$$

where b is the slope of the sire–offspring regression, r is correlation between maternal and paternal size, and m is size-dependent maternal effect coefficient (Appendix S3). We estimated m as the difference between mother–offspring and sire–offspring regression slopes divided by $(1 - r)$. Mean and 95% confidence intervals for estimates of size-dependent maternal effects and genetic covariances were generated using standard resampling procedures (Appendix S3).

We acknowledge that parental effects may depend on age (e.g. Berkeley et al. 2004a; Marteinsdottir and Steinarsson 1998) and that because of the correlation between age and size, our study (like many others) did not allow us to cleanly separate age-dependent effects from those that depend on size. However, because fishery selection is likely to reduce both the mean age of adults and the mean values of maximum length, our estimates of Cov$_A$ and m should be robust and useful for predicting correlated responses of larvae.

Fishery selection, larval responses, and population replenishment

Using our genetic parameter estimates for *S. partitus*, we explored how larval traits may respond to fishery selection on adults. We predicted the response of larvae to a single (initial) generation of selective fishing by multiplying fishery selection differentials by the combined genetic covariance and size-dependent maternal effects. This approach provides a suitable approximation if one assumes no net selection in previous generations that would cause a lagged response arising from maternally transmitted effects (Kirkpatrick and Lande 1989). (Multigeneration responses to selection are much more complex and are considered further in the Discussion.) To describe fishery selection on adult body size, we used a range of standardized selection differentials (−0.05, −0.15, and −0.3) that were based on values estimated from several empirical studies (e.g. Rijnsdorp 1993; Law 2000; Swain et al. 2007). Importantly, these values served as estimates of the net selection differential (i.e. the total effects of fishery selection and natural selection on adults) and were used to predict correlated responses of SAH.

The effect of correlated larval response on relative survivorship (cumulative survival) throughout the larval and early juvenile phases was predicted by two different approaches. First, we used the method described by Munch et al. (2005) that uses information on growth and genetic covariance between adult size and size at younger ages to predict correlated changes in body length. This approach characterizes length-dependent mortality of larvae and juveniles by combining published estimates of daily, instantaneous mortality among species that varied in size. An advantage of this approach is that there are enough data available to describe overall patterns in mortality with reasonable precision across a broad range of sizes. Disadvantages are that this approach requires explicit information on growth rates and genetic covariance functions and that predictions may be sensitive to these inputs. Furthermore, this approach assumes that rates of size-dependent mortality within a single species can be approximated by comparing rates of total mortality across

species that differ in size. By comparing total mortality among species, these estimates of size-dependent mortality may be confounded with species-specific differences in mortality that are attributable to other factors that may have strong effects on estimates of mortality rates (e.g. age, experience, catchability, life-history adaptations).

Our second approach to estimate the effects of changes in mean larval size on mortality rates was to synthesize information from studies of selective mortality on SAH. An advantage of this approach is that it can be used to compare mortality among cohorts of the same age and species and derive estimates of size-dependent mortality under similar field conditions. Disadvantages are that multiple estimates of selection have been made for relatively few species and that estimates of mortality are calculated indirectly using information on selection. Both methods of estimating size-dependent mortality assume that components of survival that do not depend on body size are the same for selected and unselected populations.

Larval size and relative mortality: approach 1

To predict survival consequences for a change in larval size, we followed the procedure described by Munch et al. (2005). In brief, we estimated expected survivorship of larvae after a single generation of selection on adults and compared this value as a fraction of expected larval survivorship in the absence of selection on adults. Relative survivorship of larvae and juveniles after a single generation of selection on adults was estimated as follows:

$$RS_{90} = \exp\left(-1.613 \int_0^{90} L_t^{-1.125} - [L_t + S(m + \text{cov}_{A(t)})]^{-1.125} dt\right), \quad (2)$$

where t is days posthatching, L_t is length at age t, S is the standardized selection differential on adult body size, m is the coefficient describing size-dependent maternal effects, and $\text{cov}_{A(t)}$ is the genetic covariance function (see Appendix S4 for further details). We examined length-dependent mortality over the first 90 days posthatching (dph) to make these estimates comparable with our estimates of larval mortality derived from analyses of natural selection (90 days was the maximum duration of selection studies in our review.).

Larval size and relative mortality: approach 2

The relationship between larval size and relative survival was also estimated by synthesizing information from published studies that examined whether larval SAH

influences larval and/or postsettlement survival for multiple cohorts under similar field conditions. Our search yielded estimates of selective mortality on SAH for 37 cohorts from eight species of fish (Macpherson and Raventos 2005; Raventos and Macpherson 2005; Urpanen et al. 2005; Robert et al. 2007; Vigliola et al. 2007; Appendix S5). For each cohort, these studies provided estimates of the mean value before selection, $\bar{z}$, mean value after selection, $\bar{z}^*$, variance before selection, $\text{var}(z)$ and variance after selection, $\text{var}(\bar{z}^*)$.

Selective mortality of larval and juvenile fish is likely to be a mix of both 'soft' selection (i.e. frequency-dependent selection in which selective mortality is substitutable with nonselective, background mortality) and 'hard' selection (i.e. frequency-independent selection which generates survival variation in addition to any background mortality; Wallace 1975). Because measurements of selection are likely to reflect both frequency-dependent and frequency-independent components and because frequency-dependent selection may not have direct effects on population dynamics (Saccheri and Hanski 2006), we used the following procedure to estimate both frequency-independent and frequency-dependent components of selection on size-at-hatching.

We obtained overall estimates of size-dependent mortality by estimating the amount of selective mortality required to generate the observed changes in the distribution of trait values between initial samples of fish (i.e. the before selection sample) and samples of fish that survived to a later date. We assumed that before selection, the distribution of phenotypic values in the ith cohort, $p(z|\bar{z}_i, \text{var}(z_i))$, is normal with mean and variance specified by $\bar{z}_i$ and $\text{var}(\bar{z}_i)$, respectively. We also assumed that the expected value of relative fitness (defined in this case as daily survival) can be described as a smooth function of phenotypic value, $W(z)$, Given known values for $\bar{z}$, $\bar{z}^*$, $\text{var}(z)$, and $\text{var}(\bar{z}^*)$ for each cohort, parameter values defining $W(z)$ can be obtained by finding the best solution to the following inverse problem, where

$$\bar{z}_i^* = \frac{\int z p(z|\bar{z}_i, \text{var}(z_i)) W(z)^{t_i} dz}{\int p(z|\bar{z}_i, \text{var}(z_i)) W(z)^{t_i} dz}, \quad (3)$$

and

$$\text{var}(\bar{z}_i^*) = \frac{\int z^2 p(z|\bar{z}_i, var(z_i)) W(z)^{t_i} dz}{\int p(z|\bar{z}_i, var(z_i)) W(z)^{t_i} dz} - \left[\frac{\int z p(z|\bar{z}_i, var(z_i)) W(z)^{t_i} dz}{\int p(z|\bar{z}_i, var(z_i)) W(z)^{t_i} dz}\right]^2 \quad (4)$$

where t_i is duration of the study (in days) for the ith cohort. We estimated the relationship between SAH and survival under selective mortality by numerically solving

for parameters in $W(z)$ that minimized the sum of absolute differences between predicted and observed values of $\bar{z}_i^*$ and $\text{var}(\bar{z}_i^*)$. This analysis assumes that there is a component of the selective surface that is constant and that sampling multiple cohorts across a range of phenotypic values can reveal the constant selective surface underlying any independent variation in selection (e.g. owing to environmental variation). $W(z)$ may be described by a number of different functional forms. Following earlier studies that model hard and soft selection on quantitative traits (e.g. Wade 1985; Goodnight et al. 1992), we modeled hard selection as a component in which individual fitness depends on absolute phenotypic value, and soft (frequency-dependent) selection as a component in which fitness depends on relative phenotypic value (deviations from the cohort mean). Specifically, we modeled fitness as

$$W(z) = \left(\left[\frac{1}{1 + e^{-(\alpha + \beta z + \gamma z^2)}} \right] \times \left[\frac{1}{1 + e^{-(\delta + \varepsilon(z - \bar{z}) + \theta(z - z)^2)}} \right] \right). \quad (5)$$

The first term describes how phenotype affects expected individual fitness, regardless of the frequency of other phenotypes in the cohort. The second term describes how individual fitness depends on *relative* phenotypic value (i.e. value relative to the group mean). This added term describes the expected (average) value of soft selection. Note that in the absence of hard selection (i.e. when the first term in eqn 5 is constant with respect to phenotypic value), the relative survival of cohorts would be equal. Because both hard and soft selection may take several functional forms (i.e. directional, stabilizing, or disruptive), our approach was to start by fitting a relatively complex model to the data (i.e. eqn 5 in which each component of selection was described by a flexible, three-parameter logistic function). Variation in our parameter estimates was assessed by a bootstrapping procedure. For each of 200 iterations, 37 cohorts were sampled with replacement and parameters defining $W(z)$ were estimated. If appropriate, we simplified the model by dropping those parameters whose bootstrapped 95% confidence intervals included zero.

To obtain an overall estimate of $W(z)$, we pooled data from all eight species. Phenotypic values for each species were standardized by dividing by the average phenotypic standard deviation within the initial samples and expressed as deviations from the overall mean for that species. Although selective surfaces are unlikely to be exactly the same across species, this approach matched our goal of describing an average pattern of selective mortality based on size-at-hatching. Our estimate of $W(z)$ was then used to predict how a given shift in mean SAH would change the average value of survival. However, we were interested in comparing survival of cohorts of larvae produced after a generation of selection on adults to the

average survival of larvae in the absence of such selection. We therefore calculated relative survival by dividing the mean survival of a cohort of larvae whose mean SAH shifted in response to selection on adults, $\bar{W}_{(\Delta \bar{z})}$, by mean survival for a cohort of larvae whose mean SAH was equal to the overall mean before selection on adults (i.e. $\bar{z} = 0$). Relative survivorship (cumulative survival at time t) was therefore calculated as follows:

$$\text{RS}_t = \prod_{i=1}^{t} \left[\frac{\int p(z \mid \Delta \bar{z}) W(z)^t dz}{\int p(z \mid \Delta \bar{z}) W(z)^{t-1} dz} \div \frac{\int p(z \mid \bar{z} = 0) W(z)^t dz}{\int p(z \mid \bar{z} = 0) W(z)^{t-1} dz} \right], \quad (6)$$

where $W(z)$ is as described above and t is days posthatching (see Appendix S6 for details). We evaluated relative survivorship at 90 days posthatching (90 day was the maximum duration of selection studies in our review). Distributions of larval SAH were assumed to be normal, and variance in SAH was assumed to be equal before and after selection on adults.

Results

Genetic covariance among larval and adult traits

Sires with larger L_{max} values (hereafter referred to simply as larger 'size') produced larvae that were larger at hatching and exhibited greater swimming performance (linear model for larval size as a function of sire size: slope $= 0.169 \pm 0.063$SE, $t_{32} = 2.682$, $P = 0.012$; larval swimming duration: slope $= 0.176 \pm 0.060$SE, $t_{26} = 2.93$, $P = 0.007$, Fig. 1). Average values of larval traits were not affected by average temperature, spawning site, or average density of conspecifics, and excluding these factors from the analysis had little effect on regression parameters (Table B1 in Appendix S2). However, direct estimates of genetic covariances derived from these relationships may be biased by assortative mating. Values for L_{max} of sires and mothers were moderately correlated ($r = 0.34$, $P = 0.038$), although there was no evidence for assortative mating based on other, measured characteristics of adults (Table B2 in Appendix S2).

Although assortative mating and associated maternal effects could be accounted for by identification of mothers, relationships in Fig. 1 may have been influenced by paternal, environmental effects (e.g. if greater parental care by larger sires accelerated development of larvae). To separate environmental and genetic contributions to covariance between sire size and larval traits, we compared sire–offspring regressions for biological and foster sires in the cross-fostering experiment (Fig. 2). Both larval size and swimming performance significantly increased
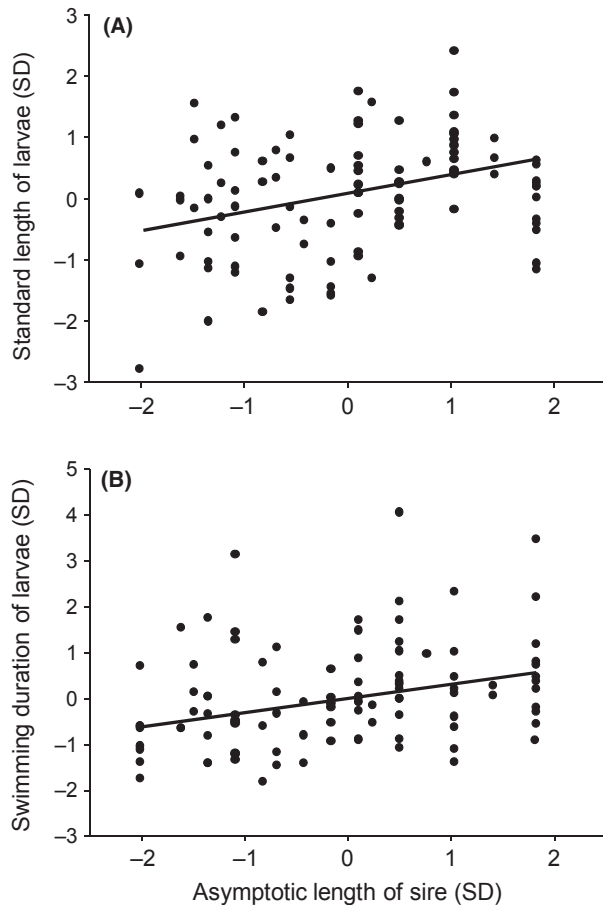
Figure 1 Parent–offspring regression illustrating the relationship between the maximum total length of the biological sire (asymptotic length from individual Von Bertalanffy growth curves) and two traits of larval offspring: (A) standard length at hatching and (B) swimming duration. Each data point illustrates the mean value from a sample of larvae collected from a single clutch of eggs ($n = 35$ larvae per clutch for standard length, $n = 20$ for swimming performance). All clutch means were plotted, but the regression lines were generated using a weighted least-squares regression of the mean standard length of the offspring of each sire on total length of sire ($n = 37$). Each sire–offspring case was weighted by the number of clutches used to determine the average.

with size of the biological sire (linear model for larval size: slope = 0.241 ± 0.085SE, $t_{16} = 2.835$, $P = 0.012$, Fig. 2A; swimming duration: slope = 0.223 ± 0.092SE, $t_{16} = 2.424$, $P = 0.028$, Fig. 2C), but there was no detectable relationship between larval traits and size of the foster sire (linear model for larval size: slope = -0.079 ± 0.175SE, $t_{16} = -0.452$, $P = 0.658$, Fig. 2B; swimming duration: slope = 0.061 ± 0.110SE, $t_{16} = 0.555$, $P = 0.587$, Fig. 2D), nor did we detect overall differences in size or swimming performance between fostered and nonfostered larvae ($P = 0.307$ and 0.421, respectively). In 2007, there was also some evidence for an association

between L_{max} of biological mothers and fathers ($r = 0.18$, $P = 0.096$), but no evidence for assortative mating based on other measured characteristics of adults (Table B2 in Appendix S2). All sire–offspring regressions are summarized in Table B1 in Appendix S2.

Based on sire–offspring regressions for the combined 2006 and 2007 data and equation 1, the genetic covariance (on standardized variables) between sire size and larval size was estimated to be 0.202 (95% CI: 0.025 – 0.407), and that between sire size and larval swimming performance was 0.264 (95% CI: 0.039 – 0.467). Mother–offspring regressions on standardized variables had higher slope values, suggesting size-dependent maternal effects on larval size (Lande and Price 1989) ($m = 0.229$; 95% CI: 0.027 – 0.452) and swimming performance ($m = 0.115$: 95% CI: −0.064–0.310). Changes in the regression procedures used to estimate genetic parameters (i.e. using current size rather than L_{max} and using major axis regression to account for uncertainty in estimates of L_{max}) had minor effects on overall parameter estimates (Table C1 in Appendix S3).

Larval size and selective mortality

Our analysis of selective mortality on SAH indicated that hard selection could be adequately modeled by a two-parameter logistic function ($\alpha = 1.430$, bootstrap 95% CI: 0.997, 1.883; $\beta = 0.272$, bootstrap 95% CI: 0.095, 0.462), which suggested that hard selection on SAH was predominantly directional (Fig. 3A). In contrast, soft selection was, on average, disruptive, as individuals with phenotypic values near the cohort mean experienced greater mortality (Fig 3B). The confidence interval for the parameter describing directional, soft selection was centered near zero ($\varepsilon = 0.663$, bootstrap 95% CI: −3.301, 4.823), suggesting that soft selection could be adequately described by a two-parameter logistic function ($\delta = 1.760$, bootstrap 95% CI: 0.919, 2.738; $\theta = 1.526$, bootstrap 95% CI: 0.374, 2.902). Patterns of total selection reflected both directional selection favoring larger larvae and disruptive selection favoring phenotypes that deviated from the cohort mean (Fig. 3C).

Fishery selection, larval responses, and population replenishment

Based on our estimates of genetic covariance and size-dependent maternal effects, we predicted how larval size might respond to fishery selection on adult size. Fishery selection can be strong, and our results suggested that such selection could result in a substantial, correlated response in larval SAH (Table 1). For fishery selection in the middle of this range ($S = -0.15$), larval size would be
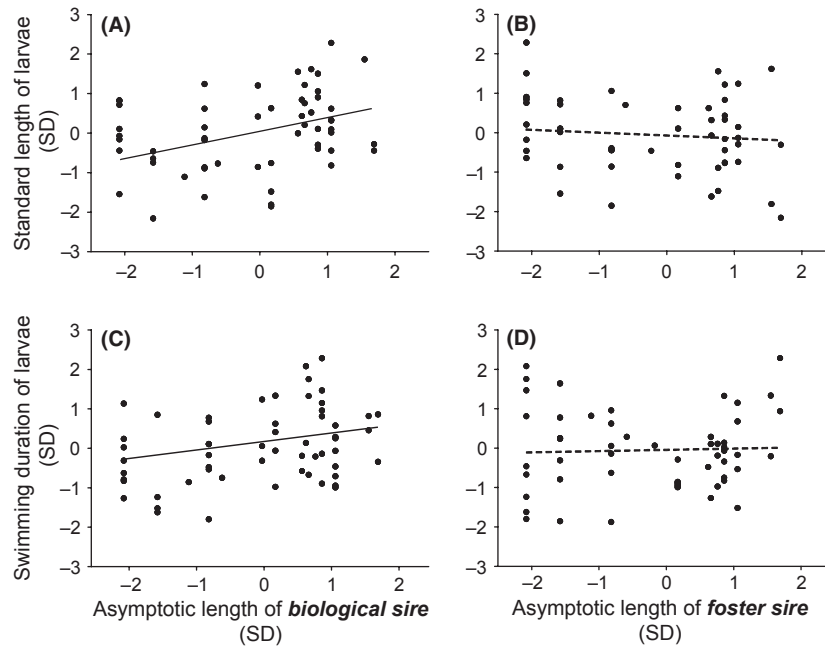
Figure 2 Parent–offspring regressions for cross-fostered larvae. Graphs A and C illustrate relationships between biological sire size and larval traits. Graphs B and D illustrate relationships between foster sire size and larval traits (foster sires were males rearing unrelated egg clutches during benthic development). Each data point illustrates the mean value from a sample of larvae collected from a single clutch of eggs ($n = 35$ larvae per clutch for standard length, $n = 20$ for swimming performance). All clutch means were plotted, but the regression lines were generated using a weighted least-squares regression of the mean standard length of the offspring of each sire on total length of sire ($n = 21$ biological sires and 21 foster sires). Each sire–offspring case was weighted by the number of clutches used to determine the average.

expected to decrease by 0.06 SD after a single generation of selection. This change in phenotype is predicted to decrease relative survival through a 90-day larval and juvenile phase by approximately 8% as predicted by approach 1% and 14% as predicted by approach 2 (Table 1). Stronger selection on adults would result in a greater reduction in larval and juvenile survival (Table 1).

Discussion

We have demonstrated that larval SAH and swimming performance may have substantial genetic correlations with adult length (L_{max}) in a wild population of marine fish. Larval size and swimming performance covaried with the L_{max} of their fathers, and results from the cross-fostering experiment suggest that the parent–offspring resemblance was attributable to genetic, rather than environmental, covariance. Furthermore, the covariance between larval size and L_{max} of mothers was greater than the covariance observed for larvae and fathers, suggesting that maternal contributions to larval size and swimming performance were substantial and depended, in part, on maternal body size.

Although genetic correlations between body size at different ages are expected to be positive (Kirkpatrick et al.

1990; Carlson and Seamons 2008), the magnitude of genetic correlations we observed suggested that selection on adult length (L_{max}) may result in considerable correlated responses of larval size and swimming performance. Moreover, we believe that the genetic parameters we estimated for a small, reef-associated damselfish may be representative of a broader group of marine fishes. Although to our knowledge, genetic covariance between adult length and larval SAH has only been measured for one other species of fully marine fish, when calculated on standardized trait values, genetic covariance between adult size and larval SAH for Atlantic silversides (*Menidia menidia*) was estimated to be 0.194 (S. Munch, personal communication), very similar in magnitude to values we estimated for the distantly related bicolor damselfish (0.202). Similarly, indirect evidence suggests that the values of size-dependent maternal effects we measured for *Stegastes partitus* may be representative of many fishes. Heath and Blouw (1998) reviewed phenotypic correlations between maternal body size and egg size for a variety fishes and found that such correlations are substantial (all species mean correlation = 0.392, SD = 0.307, $n = 25$). Although the extent to which these correlations are attributable to genetic covariance (cov_A) vs size-dependent maternal effects (m) is unclear (mother–offspring
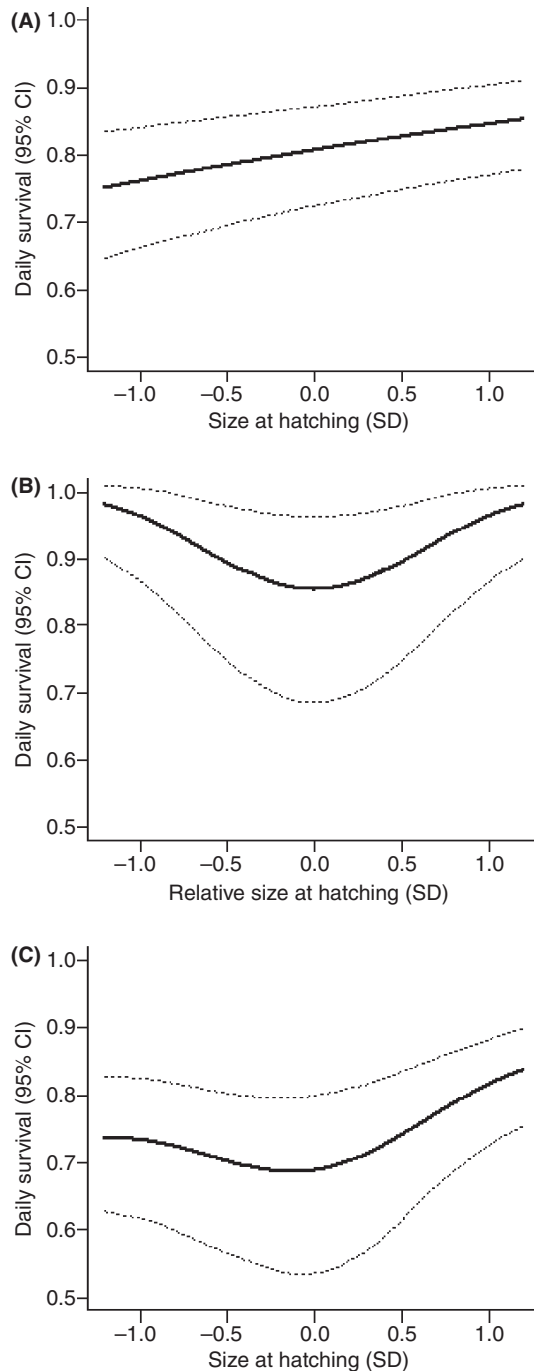
Figure 3 Effects of larval size-at-hatching on relative survival during larval and juvenile phases. Each panel illustrates the expected values of the component survival function ±95% confidence bands. (A) Hard selection, in which survival probability depends on an individual's phenotypic value regardless of the frequency of other phenotypes in the cohort. (B) Average pattern of soft selection, in which survival probability depends on an individual's phenotypic value relative to the cohort mean. (C) Combined effects of hard and soft selection, illustrated for a cohort whose mean value was equal to the overall mean (i.e. $\bar{z} = 0$).

correlations are equal to $1/2\text{cov}_A + m$ when traits are expressed as variance-standardized values), the summarized values suggest that selection on adults may strongly affect size of eggs and larvae for many fishes (egg and larval size are strongly correlated ($r = 0.611$, SD = 0.246, $n = 17$ spp.; Heath and Blouw 1998). Moreover, comparable values we observed for $S. partitus$ ($1/2\text{cov}_A + m = 0.33$) are reasonably close to the average correlation between maternal size and egg size. Overall, these results suggest that estimates of genetic parameters made for $S. partitus$ may be useful for making predictions of how larval fish in general may respond to selection on adults.

Size-at-hatching and selective mortality

Both swimming ability and larval length are likely to influence survival probabilities. However, because these two traits are related and because we have more direct information on how SAH influences survival, we focus our discussion on larval size. Our results suggest that even small changes in SAH can have strong effects on survival during larval and juvenile phases, although the patterns of selective mortality may reflect a complex mix of frequency-independent and frequency-dependent selection. Hard (frequency-independent) selection was predominantly directional. Hard selection favoring large larvae may result from a narrowing of the potential predator field, as larger larvae escape a greater number of gape-limited predators (Miller et al. 1988; Sogard 1997; Bailey and Houde 1989). These findings are consistent with comparisons of mortality estimates across species that indicate an overall decline in mortality rate with body length (Morse 1989; Pepin 1993). Survival within cohorts was also strongly influenced by relative phenotypic value (i.e. frequency-dependent selection). Our analyses suggested that frequency-dependent selection was, on average, disruptive. Such patterns may result from one or more frequency-dependent mechanisms (e.g. if overlap in resource use depends on similarity in size and competition reduces survival probability, or if predators use a particular search image that matches the cohort average size). Disruptive selection on body size may be common for larval and juvenile fishes (Perez and Munch 2010), and future studies investigating mechanisms of frequency-dependent selection may be especially valuable in advancing our understanding of how variation in larval size affects survival.

Natural selection, fishery selection, and long-term responses of larvae

Our analyses focused on predicting the correlated response of larval size after a single generation of selection on

Table 1. Predicted evolutionary responses of larval size-at-hatching (SAH) to fishery selection on adult body size and predicted consequences for relative survivorship through the larval and juvenile phases (90 days).

Standardized adult s election differential	Predicted change in SAH (in SD units)	Relative survival to 90 days post hatching					
		Approach 1			Approach 2		
		Mean	95% CI		Mean	95% CI	
−0.05	−0.02	0.97	0.92	1.00	0.95	0.92	0.98
−0.15	−0.06	0.92	0.80	0.98	0.86	0.77	0.96
−0.30	−0.13	0.85	0.62	0.96	0.74	0.62	0.89

Relative survival is expressed as proportion of survivorship in the absence of selection on adult size. Confidence intervals for relative survival include uncertainty in both the genetic parameter estimates and estimates' size-dependent mortality.

adults. Predicting the long-term response to the combined effects of fishery selection on adults and natural selection on larvae is much more complex and beyond the scope of this study. However, we can offer some insight into predicted selection response in the short term (i.e. after a few generations). Although selective mortality favoring larger larvae is strong, in the absence of fishery selection on adults, responses to selective mortality of larvae are likely balanced by reproductive selection in which mothers that produce smaller larvae benefit from greater fecundity (e.g. Smith and Fretwell 1974; see Einum and Fleming 2000; Heath et al. 2003; Johnson et al. 2010 for examples of balanced selection on offspring size in fish). Fishery selection may upset this balance by selecting for smaller adults and causing a correlated reduction in larval size. After the correlated response to selection on adults, selective mortality of larvae may then cause a shift in mean SAH toward larger sizes. However, because of the asymmetry in maternal effects (maternal size affects SAH but not vice versa) and because fishery selection is likely to be stronger than natural selection on larvae, we expect larval size to continue to decline, though at a slower rate after the first generation of selection (Kirkpatrick and Lande 1989). Similarly, correlated responses of adults to natural selection on larvae are likely to slow, but not stop, long-term decline in adult size. Shifts in mean SAH are predicted to occur in a cyclic pattern within each generation, decreasing in response to fishery selection on adults and increasing in response to selective mortality of larvae. Importantly, within each generation, a demographic cost will be incurred as larvae that are increasingly smaller suffer additional selective mortality (Fig. 4).

Fishery selection and correlated responses of larvae

Our results suggest that fishery selection on adult size may induce a substantial, correlated response in larval size and a considerable reduction in relative survival of larvae and juveniles (Table 1). These results contrast with an earlier study by Munch et al. (2005) that used Atlantic
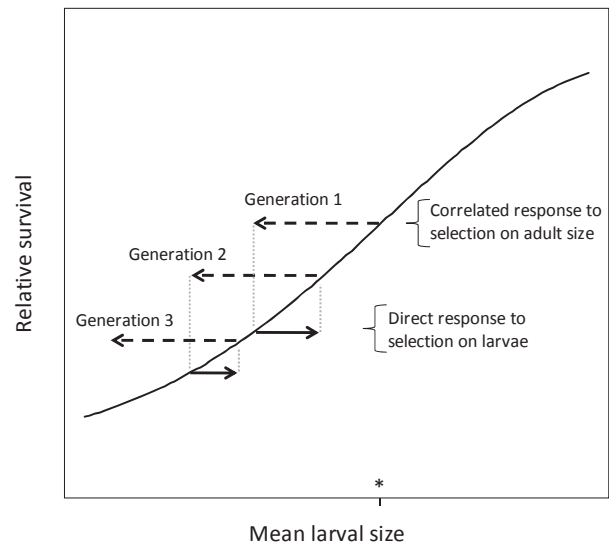
Figure 4 An illustration of the response of larval size to fishery and natural selection over multiple generations. Solid curve illustrates the relationship between mean larval size and relative survival. Asterisk denotes mean larval size in the absence of fishery selection on adults. Within each generation, there are two shifts in mean larval size. Fishery selection on adults results in a correlated reduction mean larval size (dashed arrows), the magnitude of which is influenced by both genetic covariance and size-dependent maternal effects. Natural selective mortality of larvae then results in an increase in mean larval size (which is proportional to additive genetic variance of larvae). Although natural selection on larvae may slow the multi-generation reduction in larval size, the additional, selective mortality of larvae each generation will affect population replenishment. See main text for additional details.

silversides as a model species and concluded that selection on adults would have negligible effects on survivorship. The results from our study differ for multiple reasons. First, we included the effects of size-dependent maternal effects when predicting correlated responses of larvae, resulting in a greater predicted response of larval size to selection on adults. Second, the approach to estimating size-dependent mortality introduced by Munch et al. (2005) (Approach 1 above) appears to be sensitive to

species-specific estimates of growth and genetic covariance between adult size and sizes throughout larval and juvenile phases. For a similar rate of selection on adults, data from *S. partitus* resulted in a greater predicted reduction in relative survival in response to selection on adults, although we acknowledge that our indirect method of calculating a genetic covariance function for *S. partitus* (Appendix S4) introduced additional uncertainty in our predictions. Finally, our method of estimating size-dependent mortality from studies of selection suggested slightly stronger effects of larval phenotype on subsequent survival. Although correlated responses of larvae and effects on relative survival may vary between species, our results suggest that at least under some circumstances, correlated responses to selection on adults may have important effects on survival.

Our analyses sought to provide a general, illustrative example of how correlated responses of larvae may affect input into benthic populations. The effects that variation in larval and juvenile survival ultimately has on the abundance of adults will depend on variation in demographic rates during later life stages. For example, a reduction in adult abundance (through reduced survival of larvae) may result in increased per capita reproductive success, which may then compensate for decreases in larval survival. Additionally, density dependence at later stages may weaken (but not completely negate) the relationship between larval input and adult population size (Caley et al. 1996). Nevertheless, detailed studies of recruitment of marine fishes have revealed that even in the presence of strong density dependence, limitation by larval and juvenile survival can be substantial (Schmitt et al. 1999; Shima 1999; Johnson 2007), especially when recruitment levels are relatively low (as might be expected under fishery selection). Moreover, the magnitude of density-dependent mortality may itself depend on characteristics of settling larvae (Shima et al. 2006), further suggesting that declines in SAH and associated effects on survival may substantially affect the size of density-regulated populations. In any case, exact predictions of the effects of reduced larval survival on adult abundance will depend on the demographic details of the particular species of interest.

Several large-scale studies have empirically linked selective removal of large individuals with reduced recruitment (e.g. Marteinsdottir and Thorarinsson 1998; Venturelli et al. 2009) and increased recruitment variability (e.g. Hseih et al. 2006; Anderson et al. 2008). Although processes responsible for these large-scale patterns were not directly investigated, reduced recruitment may be a consequence of both lower reproductive output associated with loss of large individuals (Berkeley et al. 2004b; Law 2007) and reductions in larval survival. Here, we demonstrate that a correlated response to selection (reduced larval

size) may occur relatively quickly and may have substantial, negative consequences for survival of larvae and juveniles. Because survival of larvae and juveniles may strongly limit the abundance of benthic populations (Bailey and Houde 1989; Caley et al. 1996), reduction in larval size may have important consequences for population dynamics. Management actions that guard against the selective removal of large adults (e.g. reduced harvest rates, slot limits on size of harvested fish, and/or establishment of marine protected areas; Berkeley et al. 2004b) will likely slow fishery selection (Trexler and Travis 2000; Baskett et al. 2005) and slow or prevent the evolution of smaller larvae. Retaining large fish in the population would allow greater reproduction by individuals with genotypes that produce larger larvae with greater survival rates. Conserving large fish may therefore promote recruitment success and help ensure greater sustainability and resilience of fished populations.

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Supporting Information

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

Appendix S1. Additional details on parentage analyses.

Appendix S2. Regression summaries and supporting statistics for parent-offspring regressions.

Appendix S3. Estimation of genetic covariances and size-dependent maternal effects.

Appendix S4. Larval size and relative mortality: approach 1.

Appendix S5. Summarizing selective mortality of larvae.

Appendix S6. Estimation of average survival of cohorts.

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