AN ABSTRACT OF THE DISSERTATION OF

Darren W. Johnson for the degree of Doctor of Philosophy in Zoology presented on August 6, 2009.

Title: Selection on Larval and Adult Body Size in a Marine Fish: Potential Evolutionary Responses and Effects on Population Dynamics

Abstract approved: _____

Mark A. Hixon

Many species have complex life cycles in which a dispersive larval stage is followed by a relatively sedentary adult stage. For such species, reproductive output is often high and large variation in survivorship throughout early life-history phases (eggs and larvae) can lead to dramatic fluctuations in recruitment which may in turn drive variation in the abundance of juveniles and adults. Early in the life cycle may therefore be a critical period for both natural selection and population dynamics. On one hand, variability in survival during early stages may provide ample opportunity for selection on early life-history traits. On the other hand, phenotypic variation in early life-history traits and selective mortality may be an important source of variability in population dynamics.

Variation in survival of marine fish larvae may be a major driver of variability in benthic population size. However, little is known about how variation in larval phenotype may affect larval survival, and less in known about the evolutionary potential of marine fish larvae. I quantified both environmental and genetic sources of variation in larval traits for a field population of a common Atlantic and Caribbean coral-reef fish, the bicolor damselfish (Pomacentridae: *Stegastes partitus*). I combined field demographic studies and manipulative experiments in the Bahamas to estimate heritability and quantitative genetic parameters for both larval size and swimming performance – two traits that are associated with early survival. I also compiled published estimates of viability selection on larval size from eight species of fish to estimate the average magnitude of selection on this trait. The initial results of these analyses were somewhat paradoxical. Despite ample heritability ($h^2 = 0.29$ for larval size), and strong selection on larval size (mean selection differential = 0.484), the observed mean larval size is quite far from the estimated phenotypic optimum (0.481 standard deviations greater than current mean size), suggesting that marine fish larvae are on average, maladapted with respect to survival during the larval and juvenile phases.

Further analyses focused on potential evolutionary constraints on larval size. First, I estimated trade-offs in individual reproductive output between larval quality and quantity. Mothers that produced larger larvae with greater swimming abilities tended to produce fewer larvae, and these effects explained a large component of the mismatch between mean larval size and the phenotypic optimum for survival.

Fluctuation in direct selection on larvae may also partially explain why mean larval size is less than optimal. Evolution of larval size may also be strongly influenced by genetic correlations with body size expressed at later ages. I demonstrated substantial additive genetic covariance between adult asymptotic size and both larval size-at-hatching and swimming performance (0.212 and 0.241 on variance-standardized traits, respectively). Adult asymptotic size was also linked to larval traits via size-dependent maternal effects, in which larger mothers provisioned offspring with more yolk resources. Selection on adult body size may therefore cause a substantial correlated genetic response in larval size that may strongly affect the overall evolutionary trajectory of larval traits.

I also examined natural selection on body size and growth form in *S. partitus*. Using data on size, growth and longevity of individual fish studied at 4 sites over a 7-year period, I analyzed both ontogenetic and spatial variation in the magnitude and direction of viability selection on body size. Selection on asymptotic (adult) size was strong and positive at some sites, but weak and negative at other sites. Moreover, fish that were small as juveniles generally experienced greater survival, even if large adult size conferred survival benefits later in life. Both spatial and ontogenetic reversals in selection on body size would be expected to produce similar reversals in the direction of correlated responses of larvae, thereby altering the evolutionary response of larvae and potentially preventing larval size from evolving toward its optimum value.

Although this research identified several potential constraints on the evolution of larval traits, there is still considerable scope for an evolutionary response to selection, especially if selection is consistent and strong. Many marine fishes are subject to size-selective fishing where larger, fast-growing individuals are selectively removed from the population. Such effects are usually strong because fishing mortality rates can greatly exceed natural mortality rates and fishing selectivity and intensity are often constant. Although correlated responses to selection have been hypothesized as potentially important consequences of fishery selection, estimates of quantitative genetic parameters required to predict correlated responses to such selection have been lacking. To my knowledge, my research provides the first estimates of quantitative genetic parameters for larval traits and their links to adult size in a wild population of fish. I used these data to predict how larval size would respond to selection on adults and how evolutionary shifts in larval size would in turn affect population replenishment. My results predict that observed rates of fishery selection on adult marine fishes may decrease average larval size by approximately 0.11 standard deviations after a single generation of selection. Such a reduction in larval size is predicted to reduce survivorship through the larval and early juvenile phases by about 16%. Because the dynamics of many fish populations are highly sensitive to changes in survival of early life stages, the evolution of a higher incidence of low-quality larvae in response to fishery selection may have substantial consequences for the viability of fished populations.

Overall, this research indicates that a complex interplay among trait variation, phenotypic selection, and demographic rates may have strong effects on both evolutionary responses and population dynamics. Our understanding of such interactions will be substantially advanced by applying evolutionary quantitative genetics to traditional studies of demography and population dynamics. A combination of these two approaches can yield significant insight into basic evolutionary questions (e.g., why larvae are smaller than expected), as well as applied conservation problems (e.g., predicting correlated responses to fishery selection).

Selection on Larval and Adult Body Size in a Marine Fish: Potential Evolutionary Responses and Effects on Population Dynamics

by

Darren W. Johnson

A DISSERTATION

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Presented August 6, 2009

Commencement June 2010

Doctor of Philosophy dissertation of Darren W. Johnson presented on August 6, 2009,

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Chair of the Department of Zoology

Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Darren W. Johnson, Author

ACKNOWLEDGMENTS

I sincerely thank my major advisor, Mark Hixon for many reasons, especially for his guidance, career advice, financial support, willingness to collaborate on projects, and thorough edits on my papers and talks. I am also extremely grateful to Mark for providing me with an office with such a delightful view. It was always a great place to work and brainstorm and helped to keep my spirits high during my time at OSU.

I also extend my thanks to the members of my graduate committee (in alphabetical order) for their advice and time spent helping me out with my research. Steve Arnold provided valuable advice on evolutionary quantitative genetic theory and numerous helpful reviews. Selina Heppell taught me much about quantitative conservation biology and helped to focus the application of my research to fisheries biology. Dan Schafer served as my statistics minor advisor and helped me to think critically about experimental design and statistical analyses. Douglas Robinson was a patient and flexible graduate representative as well as source of friendly and helpful advice on ecological studies.

Members of the Hixon Lab have been wonderful friends, colleagues, and collaborators. I always looked forward to lab meetings and scientific discussions. Chris Stallings was always ready and willing to provide helpful advice, listen to half-baked research ideas, or to review a manuscript. It was constantly a pleasure, though sometimes a mild visual horror to work with him in the field. D.Y.B., buddy. Mark

Christie is a wizard with molecular genetic analyses, R, and all things randomized. It was always fun to talk science with him. I guess it's true what they say about big 'fros – they cover big brains. Mark Albins has been a great resource for advice on statistics and experimental design. Tim Pusack was instrumental in making sure I attended seminars on Wednesdays and Thursdays and generally improved by academic life. Flower Moye was an absolute superstar in the field and an ace at keeping the crew in good spirits, even when the days were long and exhausting. Robert Lamb, fish counter extraordinaire and coconut-shucking machine, helped out tremendously with egg mass analyses and has been a great collaborator on other projects. I also owe Megan Cook, the OSU marine biology poster child, many thanks for her help in the lab and for her fun attitude at LSI.

I was extremely fortunate to have some outstanding assistants in both the field and laboratory, and I really can't thank them enough. Jenn Noell, Jenn Schellenger, Lisa Krigsman, Chris Soto, Nikita Schiel-Rolle, and Madeleine Weniger helped me out immensely during the long days of diving and data collection in the field. Robert Lamb, Megan Cook, Katie Borgen, Lanaya Fitzgerald, Leslie Armitage and Samantha Ferber provided valuable assistance with data processing and analysis.

People in the Zoology department have always been extremely supportive and helpful in all matters. Mike Westphal was an obliging colleague to discuss quantitative genetics with, and a great fishing buddy. I sincerely thank the Zo office staff, especially Tara Bevandich, Sarah Cain, Traci Durrell-Khalife, Mary Crafts, and

Torri Givigliano for all their help over the years. Joe Beatty, Bruce Menge, and Sally Hacker have been particularly supportive, and I appreciate their efforts in promoting quality of graduate studies and life in the Zoology department.

My thanks go out to the staff at the Perry Institute for Marine Sciences, Lee Stocking Island, Bahamas, especially Brenda Gadd and Ikemond Black. Working at LSI was both productive and fun and I am very fortunate to have spent several field seasons at such a great place. Brenda provided a great working atmosphere and much logistical assistance to our field crew over the years. Ikemond deserves special thanks for keeping boats afloat and the field station running.

I was very lucky to receive a postgraduate fellowship from the National Sciences and Engineering Research Council of Canada. I am also thankful for financial support from the American Museum of Natural History, the International Women's Fishing Association, and the College of Oceanographic and Atmospheric Sciences, Oregon State University. Further financial support was provided by research grants from the National Science Foundation and the National Undersea Research Program to M. Hixon. Without such funding, much of the research in this dissertation would not have been possible.

Finally, my deepest thanks go to Marla Ranelletti. She has been an extremely patient person, putting up with my prolonged absences (both physical and mental) during my PhD. I am extremely grateful for all her support and encouragement throughout my graduate education.

CONTRIBUTION OF AUTHORS

Dr. Mark Hixon collected and contributed data on size-at-age for the fish examined in the natural selection analysis in chapter 4 and for some of the adult fish examined in chapter 3. Mark Christie performed the molecular genetic analyses required to match samples of larvae to their parents in the local population in chapters 2 and 3. Jessica Moye contributed largely to the collection of data for chapters 2 and 3 and helped to design and execute cross-fostering experiments in the field.

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CHAPTER 1: GENERAL INTRODUCTION

It is increasingly apparent that trait variation among individuals may be an important source of variation in demographic rates. It is also clear that natural selection and evolution may have substantial, contemporary effects on population dynamics. Studies within the last two decades have revealed that significant evolutionary change may be rapid (e.g., occurring over tens of generations or fewer) across a wide range of taxa (reviewed by Thompson 1998, Hendry and Kinnison 1999, Palumbi 2001, Hairston et al. 2005). Such evolutionary change may then alter interactions both within and among species, thereby causing persistent changes in demographic rates and population dynamics (Thompson 1998). Additionally, even in the absence of a significant evolutionary response, natural selection may still have concomitant effects on population dynamics. Selective sources of variation in fitness components (i.e., trait-based differences in survival or reproduction) may be additive with non-selective variation in demographic rates (reviewed by Saccheri and Hanski 2006). As long as components of demographic variation that are independent of phenotypic value do not completely compensate for phenotype-dependent variation

in demography, natural selection may generate considerable variation in population dynamics.

Understanding the interplay among natural selection, contemporary evolution, and variation in demographic rates will substantially improve our understanding of population dynamics. For example, Hairston et al. (2005) estimated that for a population of Darwin's finches (*Geospiza fortis*) evolving in response to variation in rainfall, 63% of the variation in population growth rate could be explained by variation in mean body size. However, such effects have been little studied for marine fishes. Logistical constraints of working underwater make it difficult to study most marine fishes in situ, and there is little information about how natural selection operates in wild populations of fish. Moreover, many marine fishes have complex life cycles in which a dispersive larval stage is followed by a relatively sedentary adult stage. Dispersal and/or mortality of larvae during the planktonic phase may decouple local reproduction from local population input. Consequently, it is difficult to track changes in traits from one generation to the next, and difficult to estimate genetic variation underlying traits and therefore the capacity for evolutionary response. However, important responses to selection may manifest in the larval phase. For such species, reproductive output is often high and large variation in survivorship throughout early life history phases (eggs and larvae) can lead to dramatic fluctuations in recruitment which may in turn drive variation in the abundance of juveniles and adults. Early in the life cycle may therefore be a critical period for both natural selection and population dynamics.

My field studies focused on the bicolor damselfish (*Stegastes partitus*), a common coral reef fish. *S. partitus* is a superb species for in-situ demographic studies, as it moves very little (<10m) during the benthic phase of its life cycle following settlement from the plankton. Also, *S. partitus* readily lays demersal eggs in artificial collectors that can be experimentally manipulated and brought back to the lab. This life history feature allowed me to examine traits of both parents and their larval offspring and to perform quantitative genetic analyses for a field population of a marine fish. In chapter 2, I evaluated the evolutionary potential of size and swimming performance of marine fish larvae. I combined field demographic studies and manipulative experiments to quantify both environmental and genetic sources of variation in larval traits. In light of variation in larval size, I also conducted a summary and synthesis of studies that examined selective mortality based on larval size. This analysis explored demographic consequences of variation in larval size.

In chapter 3, I examined genetic correlations between adult size and larval size and swimming performance. One main application of these results is to examine how persistent changes in selection on adult body size may shift the selection balance demonstrated in chapter 2 and cause correlated responses in larval traits. Fishing mortality has been demonstrated to selectively remove smaller individuals from populations, and such effects are known to be relatively constant (reviewed by Law, 2000, 2007). If traits that affect larval survival are genetically correlated with adult traits that are under selection by commercial fishing (e.g., size

or growth rate), then fishing may impose evolutionary changes in the population that are not easily reversible (Kirkpatrick 1993, Munch et al. 2005, Walsh et al. 2006). These changes may decrease population viability by selecting for individuals that are less able to replace themselves and replenish the population. Using inheritance parameters for *S. partitus,* I evaluated how observed rates of fishery selection may cause a correlated evolutionary response in larval traits and how this may affect population replenishment.

Natural selection on adult and juvenile body size may also cause correlated response in larval traits. In chapter 4, I examined natural selection on body size in *S. partitus*, with an emphasis on ontogenetic and spatial variability in the magnitude and direction of selective mortality. Many studies have documented size-selective mortality of marine fish (reviewed by Sogard 1997). Although most studies suggest that large fish experience greater survival, the duration of most studies has been short and inferences about lifetime selection on size are limited. Few studies of fishes have examined survival of tagged individuals to estimate selection and fewer still have examined selection throughout the entire lifespan of the adult stage. This chapter detailed selection on growth form and also examined the roles of foraging behavior and population density in mediating selective mortality.

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CHAPTER 2:

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

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This manuscript is formatted for publication in *Evolution*

Abstract

For many marine fishes, intense larval mortality may provide considerable opportunity for selection, yet little 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 field population of a common coral reef fish, the bicolor damselfish (*Stegastes partitus*). We also used published estimates of viability selection on larval size to reconstruct an adaptive landscape relating larval size to survival. Our results suggested that despite strong phenotypic selection on larval size and moderate heritability ($h^2 = 0.29$), selection for large larvae that survive better may be fully balanced by fecundity selection favoring mothers that produce fewer, smaller offspring. In addition to larval quantity-quality tradeoffs, evolutionary response of larval traits may be affected by maternal effects and genetic correlations among size- and growth-related traits. With multiple factors affecting the evolutionary response of larval size, phenotypic variation in this trait may be a substantial and ecologically important source of variability in larval survival and recruitment to benthic populations.

Introduction

Many species with complex life cycles have a life history in which early life 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). Local populations of such species tend to exist as 'open' systems, in that dispersal and/or mortality of larvae may decouple local reproduction from local population input (Caswell 1978). Moreover, large variation in survivorship throughout early life history phases (eggs and larvae) can lead to dramatic fluctuations in recruitment (Houde 1987), that can be a major source of variation in adult population dynamics (Caley et al. 1996, Hixon et al. 2002). Early in the life cycle may therefore be a critical period for natural selection, because variability in survival during the larval stage may provide ample opportunity for selection on early life history traits. Additionally, phenotypic variation in early life history traits may generate survival variability that is an important source of variability in 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 (e.g., Weis et al.

1992, Grant and Grant 2002, McAdam and Boutin 2003, Garant et al. 2004, Seamons et al. 2007). Such variation could preserve genetic variation and evolutionary potential (Roff 1997). 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 independently of traits of 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 Bernardo 1996, 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 tradeoff between the quality (typically related to initial size) and quantity (fecundity) of offspring that a female can produce. Theoretical models generally 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., Lack 1947, Smith and Fretwell 1974, Vance 1973, Parker and Begon 1986, Hendry et al. 2001). Under such conditions, average size of larvae within a population may remain below the phenotypic optimum for survival because phenotypic selection on larvae is balanced by fecundity 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 architecture underlying these traits are rare (but see Heath et al. 2003).

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, Azvedo et al. 1997, Vigliola and Meekan 2002, Marshall et al. 2003). Among marine fishes, mortality during larval and juvenile phases is affected by initial larval size (Vigliola and Meekan 2002, Macpherson and Raventos 2005, Raventos and MacPherson 2005, Meekan et al. 2006, Robert et al. 2007, Gagliano et al. 2007, Vigliola et al. 2007). 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 wild populations of marine fish. Furthermore, other factors that may constrain microevolutionary 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 size and larval number by evaluating maternal fecundity selection on breeding value for larval size. Finally, we compiled published estimates of viability selection on larval size from many species of fish to estimate the average magnitude of selection on this trait. Using information on selection, we reconstructed an adaptive landscape relating expected survival to mean larval size across a broad range of phenotypic values. This analysis allowed us to 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 (*Stegastes 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. Most courtship and spawning occurs during sunrise (Knapp and Warner

1991). Eggs are laid as a monolayer on top of benthic substrates (e.g., dead coral, sponges, shells) and are deposited in discrete clutches of approximately 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. Within our study area in the Bahamas, reproduction occurs in cycles that are approximately 2 weeks long and centered on the 3rd quarter of the lunar phase, when the number of active spawners peaks. Pelagic larval duration is about 30 days and most settlement occurs during the new moon of the lunar cycle (Robertson et al. 1988). 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 (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 1-5 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 within two populations near Lee Stocking Island, Bahamas. In 2006, 37 breeding territories with artificial nests were monitored daily for a period of approximately two months. Artificial nests were 15cm lengths of 5cm diameter plastic pipe, lined with flexible

transparent plastic that could be removed to access the attached eggs. All adults within the populations (approximately 65 and 35 in the two populations each year) were individually tagged and monitored as part of a broader demographic study (Hixon et al. in prep). Small, non-lethal tissue samples (fin clips) were taken from all adults in the study area. Tissue was preserved and genomic DNA was extracted. Seven highly polymorphic microsatellite loci (Williams et al. 2003) were amplified using standard PCR techniques. This procedure provided a multi-locus genotype of adults that was used to identify parent-offspring relationships.

In 2007, we conducted a cross-fostering experiment within these populations. Larvae were swapped among 21 nests shortly after eggs were deposited. Because males of *S. partitus* would only foster eggs if they had eggs deposited in their own nest, swapped eggs were randomly assigned, but subject to the constraint that they could only go to other nests that had new eggs that day. 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 (previous research has indicated an average density of 215 eggs / cm^2). Egg masses were recorded and eggs were collected 3.5 days later, immediately prior to larval hatching. Larvae were hatched in the lab, where we measured larval size and swimming performance (defined below). We interpreted size and swimming performance as direct measures of larval quality because both of these traits 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 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). Samples of larvae from each egg mass were preserved and genotyped at the same loci as the adults in the study populations. Parentage of each clutch was determined using the program CERVUS (Marshall et al. 1998, Kalinowski et al. 2007).

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 ln-transformed swimming performance could be explained by both environmental and genetic effects. Microsatellite genotyping of larvae and adults within these populations allowed us to identify parentage of most egg masses and construct a pedigree matrix describing relatedness of individuals. We measured larval size for a total of 5872 individuals produced by 54 sires and 77 dams. Within this sample were 143 full-sib families, 73 sets of paternal half-sib families, and 12 sets of maternal half-sib 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-sib families, 70 sets of paternal half-sib families, and 11 sets of maternal half-sib families. Within our study population, sires and dams often mated multiple times with the same partners such that each set of half sibs was represented by 2-13 egg masses, with each egg mass representing a full-sib family.

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:

$$\boldsymbol{z} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Y}_a\boldsymbol{a} + \sum_k \mathrm{Y}_k \mathrm{u}_k + \boldsymbol{e},$$

where $\boldsymbol{z}$ is a column vector of observed phenotypic values for n individuals (n=6003 for size-at-hatching, n = 3574 for swimming performance), $\mathbf{X}$ is an n by 4 incidence matrix relating phenotypic values to the column vector of 4 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 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 (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 minute 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 2m X 2m plot centered on the breeding territory), since these factors have been demonstrated to affect size-at-

hatching for other species of reef fish (e.g., Green and McCormick 2005, 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 (e.g., due to within-site differences in temperature), nest of rearing ($p_5 = 56$) to estimate paternal effects (e.g., variation in nest care provided by 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

Although our main analysis focused on partitioning variance in larval traits observed over two summers, to predict the response to selection, it is also useful to express additive genetic variance as a fraction of the total phenotypic variation (i.e., as trait heritabilities). For many marine fishes, 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, though 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-sib family mean values to estimate the genetic covariance (Cov_G) between larval size-at-hatching and swimming performance because these traits were not measured on parents. Full-sib family covariance contains both additive and non-additive genetic covariance, so 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 = number of individuals within each family (Via 1984, Lynch and Walsh 1998). In this study, the bias due to within-family common environmental variance is likely to be minimal for several reasons. First, our within-family samples contained at least 20 individuals, such that the contribution of common environmental variance was less than or equal to $1/20^{th}$ of the actual common environment component. Second, larval size and swimming performance were measured on separate individuals from full-sib families, further reducing the effects of shared environment (Lynch and Walsh 1998). Finally, a large portion of the families were fostered in different nests, again reducing the effects of shared environment on the observed covariance between traits (Kruuk and Hadfield 2007). We therefore interpreted the covariance between family means as a reasonable estimate of the genetic covariance between larval traits. Because multiple measurements were available for most full-sib groupings (i.e., parents tended to pair for multiple reproductive bouts), measurements of larval traits were averaged for each family so that in the final analysis, each full-sib family contributed only one data point. 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 (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):

$$r_A = \frac{Cov_G\left(_{SAH,SWIM}\right)}{\sqrt{V_A(_{SAH}) \times V_A(_{SWIM})}}$$

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

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

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

Trade-offs between larval quality and quantity

Trade-offs between larval size and number may exist at multiple temporal scales. First, we tested whether larger clutches tended to contain lower quality larvae by including clutch size as a fixed factor in our mixed model analyses that examined sources of variation in larval size and swimming performance. However, trade-offs between larval quantity and quality may also manifest at longer time scales. For example, over their reproductive lifetime, females that produce more larvae may produce relatively low quality larvae. To test this hypothesis, we examined whether the predicted breeding values of mothers in this study (i.e., twice the deviation of the

mean phenotypic value of mother's offspring from the population mean) were related to estimates of relative fecundity during the reproductive season. We used best linear unbiased predictors (BLUP's) generated by the full animal model to estimate breeding values while simultaneously accounting for other factors that affected larval traits (e.g., temperature, density, maternal effects; Kruuk 2004). 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). Results of the parentage analysis indicated that in an overwhelming majority of cases, females mated with males that had nests < 4m away from their home territory (*unpublished data*), suggesting that females were extremely unlikely to mate outside of the study population. To obtain a standardized estimate of fecundity, we first used a linear model to account for the influence of site, maternal size, and average water temperature on fecundity. We next calculated individual deviations from expected fecundity values generated by linear model coefficients and covariate values. We then calculated relative fecundity by adding each individual's deviation to the population mean and then dividing by the population mean. Finally, we used a linear model to examine the relationship between predicted breeding value for larval size and relative fecundity. Within this

framework, the slope of the regression line estimates the strength of linear fecundity selection on breeding value of larval traits.

Larval size and selective mortality

Although larval quality may be best be measured by a suite of traits (e.g., size, growth rate, physiological performance, energy reserves), many of these traits are likely to be highly correlated. We focused on size-at-hatching because it was relatively easy to measure for field-reared larvae and because several studies had previously estimated selection on SAH. For many fishes, otolith size is directly proportional to body size throughout development (reviewed by Campana and Nielson 1985). Moreover, the calcium carbonate structures of otoliths are deposited in concentric rings, and ring size may provide a permanent record of an individual's size-at-age. For many species of fish, the size of otolith rings have been used to examine selective mortality on larval size-at-hatching by comparing distributions of otolith-estimated SAH for initial samples (e.g., settling larvae or early-stage larvae caught in plankton tows) to distributions for samples of survivors (e.g., larvae or juveniles sampled weeks to months later).

To examine general patterns of selection on SAH for cohorts of fish, we summarized measures of selection from the published literature. We included only those studies that measured selective mortality of multiple cohorts under similar field conditions and provided enough information to calculate selection differentials for SAH (i.e., mean SAH values before and after selection and estimates of initial

phenotypic variance). 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 (Lande and Arnold 1983, Brodie et al. 1995). Standardized selection differentials were therefore calculated as:

$$S = \bar{z}^* - \bar{z}, \qquad (1)$$

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 literature search yielded estimates of selective mortality on SAH for 37 cohorts from 8 different species (Appendix A).

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 (e.g., differences in survival of groups that vary in mean phenotypic values). Assuming that phenotypic values are normally distributed within populations, 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- and density-independent within populations. Then if selection is measured in multiple cohorts (within and among species) 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. Our results indicate that within species, the relationship between trait means after selection, $\bar{z}^*$, and the trait means before selection, $\bar{z}$, was well approximated by linear regression,

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

where b_0 is an intercept and b_1 is a regression slope. Substituting this expression into (1), we obtain the following approximation for the standardized selection differential,

$$S \approx (b_1 - 1)\bar{z} + b_0. \qquad (2)$$

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

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

where $\overline{W}$ is mean fitness (here defined as survival during early life history stages) (Lande 1979). Integrating (2) over $\bar{z}$ therefore provides a quadratic approximation of the natural log of mean fitness:

$$\ln \overline{W} = \int (b_1 - 1)\bar{z} + b_0 d\bar{z} = \frac{1}{2}(b_1 - 1)\bar{z}^2 + b_0 \bar{z} + C, \qquad (3)$$

where *C* is an undefined constant of integration. We used this approximation to model survival under selective mortality. 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 $\ln \overline{W}$, 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:

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

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 (3). However, fluctuations in the shape and location of the adaptive landscape about a long-term average may generate variation in selection differentials (Lynch and Lande 1993, Lande and Shannon 1996). In other words, within-species variability in the adaptive landscape may affect selection on larval traits. To account for such variation in the adaptive landscape for 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.

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 size-at-hatching (SAH) and swimming performance (Table 1, Table 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)(Table 1, Table 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, and residual variation was high (Table 2c). Heritabilities derived from optimal models were estimated as 0.289 (± 0.094 SE) for SAH and 0.203 (± 0.057 SE) for ln-transformed swimming performance. Note that heritiabilities calculated from the full models were very similar in magnitude (Table 1, Table 2). Genetic covariance between larval size and ln swimming performance was estimated as 0.00489 (± 0.00212 SE). When 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 quality and quantity

Predicted breeding values for both size-at-hatching and swimming performance were negatively related to estimates of fecundity (linear regression for fecundity as a function of size-at-hatching: slope = -0.203 (0.094 SE), $P = 0.036$, $r^2 = 0.13$; swimming performance: slope = -0.283 (0.095 SE), $P = 0.005$, $r^2 = 0.167$; Fig 1a, b). These estimates indicated that maternal fecundity selection favors the production of smaller larvae with lower swimming performance.

Larval size and selective mortality

Our literature survey indicated that viability selection on larval size-at-hatching was on average positive, but that the intensity, and in some cases, the direction of selection was variable. Figure 2a illustrates the variability among all selection estimates. Although much of the variability in Figure 2a is due to among-species variation, selection coefficients exhibited substantial variability within species as well. The overall average magnitude of selection was 0.484 and the average standard deviation of selection coefficients within each study was 0.362.

Our analysis of among-cohort variation in selection indicated that the average slope of relationship between $\bar{z}^*$ and $\bar{z}$ was less than one, (among-species mean values for slope, b_1, = 0.0292, 95% CI: -0.722 – 0.780, intercept, b_0, = 0.428, 95%

CI: 0.0122 – 0.844; Fig. 2b), suggesting that the linear selection decreased with increased mean SAH. These estimates indicated a curved adaptive landscape with a phenotypic optimum, $\bar{z}_{opt}$, 0.481 deviations greater than the current mean (Fig. 2c). However, within-species variability in the estimates of the parameters that describe the adaptive landscape was appreciable (average SD of slope = 0.184, intercept = 0.159). If such variability is attributed to fluctuation in the shape and location of the adaptive landscape, rather than sampling error, considerable variation in selection among cohorts could be expected.

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 marine fishes, and to our knowledge, all previous studies have been conducted on laboratory populations. Although it has been hypothesized that there is little additive genetic variance of larval traits of fishes (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 indicate 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 fishes, the Japanese flounder, *Paralichthys olivaceus* (h^2 = 0.36 ± 0.25 SE; Shimada

et al. 2007) and red drum, *Sciaenops ocellatus* ($h^2 = 0.24 \pm 0.06$ SE; Ma et al. 2007) suggesting larval size may evolve in response to natural selection for at least several marine fishes.

However, our synthesis of selection studies on larval fish suggested that, in general, 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 0.481 standard deviations greater than the observed mean. Because 2 of the 8 species in our analysis were damselfishes, we also reconstructed an adaptive landscape based on selection estimates for larval size-at-hatching of damselfishes. By this procedure, we estimated the phenotypic optimum to be 1.181 SD above the observed mean. These distance estimates suggest that the observed mean larval size may be quite maladaptive with respect to early survival (Hendry and Gonzalez 2008). 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. Because of trade-offs between

size and number of offspring, evolution of larval size may be constrained by the benefits of producing more, small offspring. Indeed, both theoretical (e.g., Smith and Fretwell 1974) and empirical (e.g., Einum and Fleming 2000, Marshall and Keough 2008) studies suggest that mean offspring size evolves to a value that maximizes maternal fitness even though offspring survival may be less than optimal. Because the effects of trait values on maternal fitness will depend on both the number of offspring produced (i.e., maternal fecundity selection) and offspring survival (i.e., offspring viability selection), maternal fitness will be maximized when the net value of linear selection is zero (Arnold and Wade 1984). Our results suggest that, despite strong viability selection on SAH, these effects are almost equally balanced by maternal fecundity selection. In this study, maternal fecundity selection on breeding value for larval size was moderate ($S = -0.203 \pm 0.094$ SE). Because this estimate is a measure of selection acting on the genetic component of variation (i.e., the breeding value), it provides a direct prediction of the selection response. However, because selection only acts on females and the sex ratio is approximately 1:1, this estimate needs to be halved. In contrast, viability selection on SAH was measured on phenotypes. In the absence of any environmentally-induced bias, the predicted selection response is calculated by multiplying the phenotypic selection differential by the heritability value (reviewed by Postma 2006). Predicted response to viability selection is therefore mean S_{SAH} (0.484) $\times$ h^2_{SAH} (0.29) = 0.140, only slightly higher in magnitude than the predicted response to fecundity selection (-0.101). Using estimates of mean selection for damselfishes (0.530) yielded a slightly

higher value (0.154). Net linear selection on SAH was therefore 0.039 (0.053 based on selection on larval damselfishes), indicating weak total selection for larger larvae. Overall, these results suggest that mean SAH is relatively close to the value that maximizes maternal fitness, but far from the value that maximizes larval and juvenile survival. Such results are consistent with theoretical predictions (e.g., Smith and Fretwell 1974) and empirical results for other species of fish (e.g., Einum and Fleming 2000).

Although in general SAH appears to be near an equilibrium value set by the balance between fecundity and viability selection, equilibrium values may fluctuate in response to variation in selection (reviewed by Roff 1997), with potential consequences for population dynamics. Our survey of selection estimates for larval size indicated considerable variability in the magnitude of selection (Fig. 2). Although our analysis suggested that much of the variation in selection resulted from variation in mean phenotypic values of cohorts (Fig. 2b), the remaining variation in selection estimates may have been in response to variation in ecological factors. Indeed, mechanistic studies suggest that there may be considerable variation in the magnitude and direction of viability selection on early life history traits of larval and juvenile fishes. Several factors have been identified as sources of variability, including the abundance and behavior of conspecifics (McCormick and Meekan 2007), 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). Traits such as SAH may evolve in response to variable selection, but because SAH is only moderately heritable, mean SAH may persistently lag behind stochastic fluctuations in natural selection, resulting in mean phenotypes that temporarily deviate from the optimum value (in this case the balance between maternal and larval selection on SAH).

In addition to responding to variation in direct selection on SAH, larval size may exhibit correlated responses to selection on other traits. Our research has also identified several genetic links between SAH and other traits. The genetic correlation between larval size and swimming performance was substantial (0.486). Swimming performance is a trait that may be important for resisting drift toward unfavorable habitats, avoiding predators, and acquiring food (reviewed by Leis 2006). Selection on swimming performance would likely induce an appreciable correlated response in larval size-at-hatching.

Within these populations, maternal effects were a substantial source of variability in larval traits. In a related study (Johnson et al. in prep), we found that the maternal effect on larval size was largely dependent on maternal body size (coefficient of size-dependent maternal effect = 0.178, on variance-standardized traits 95% CI: 0.0245 – 0.3260). Because body size is a heritable trait for marine fishes (mean $h^2 = 0.30$; Law 2000), selection on adult body size and associated changes in maternal effects may have both short- and long-term effects on larval size (Kirkpatrick and Lande 1989). Although few studies have examined maternal effects on SAH, egg size is closely related to SAH (Chambers and Leggett 1996) and

our findings are consistent with studies of many other teleosts which have indicated substantial, size-dependent maternal effects on egg size (reviewed by Heath and Blouw 1998). Finally, like many size- and growth-related traits, larval size-at-hatching is likely to be phenotypically and genetically correlated with measures of size and growth throughout ontogeny (Cheverud et al. 1983). Indeed, for our study population the genetic covariance between adult asymptotic size and larval size was relatively high (0.212 on variance-standardized traits 95% CI: 0.0407 – 0.367; Johnson et al. in prep). In general, genetic correlations among size-at-age increase as the time between measurements decreases (Kirkpatrick and Lofsvold 1992), suggesting that genetic correlations between larval size and juvenile size are also likely to be substantial.

We conclude that larval size is unlikely to evolve independently and that larval size and swimming performance are not adaptively decoupled from traits expressed during juvenile and adult stages. The substantial genetic links between larval size and size expressed later in development suggest that selection on juvenile or adult size will cause a substantial correlated genetic response in larval size. Natural selection on juvenile and adult body size may vary substantially among populations of *S. partitus* (Johnson and Hixon, in prep.). Furthermore patterns of viability selection on body size may vary throughout ontogeny for marine fishes, even reversing direction (Gagliano et al. 2007, Johnson and Hixon in prep). Variation in selection on juvenile and adult body size may alter the direction and magnitude of correlated responses in larvae. Such effects may offset any balance

between maternal fecundity selection and offspring viability selection, driving mean larval phenotypes away from their fitness optima (Lande 1976, 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 adult traits is consistent and sufficiently strong, it may result in a long-term shift in larval traits away from their fitness optima.

Size-at-hatching, selective mortality and population dynamics

Overall, our study identified several sources of variability in traits that affect larval survival. We focused on size-at-hatching because direct 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 non-genetic sources of variation) may therefore be a substantial source of variability in larval and juvenile survival (cf. Fig. 2c). For example, cohorts of larvae 0.5 SD below the overall mean are expected to experience greater selective mortality and reduced relative survival (ca. 0.65 times the survival at the phenotypic optimum, ca. 0.71 times the survival at the overall mean value; Fig. 2c). Even small differences in larval and juvenile survival can drive large fluctuations in recruitment

for marine species (Houde 1987). 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) or persistent shifts in selection on adults (Johnson et al. in prep.). 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 evolutionary potential of such traits (Pechenik et al. 1998, McCormick 1998, Hairston et al. 2005, Saccheri and Hanski 2006).

Acknowledgments

We especially thank L. Krigsman, N. Schiel-Rolle, C. Soto, and M. Weigner for all their hard work and assistance in the field and lab. We also thank B. Gadd, I. Black, and the staff at the Perry Institute for Marine Sciences, Lee Stocking Island, Bahamas. This manuscript comprises a chapter from the senior author's doctoral dissertation (M.A.H. Major Professor), and benefited greatly from reviews by his graduate committee: S.J. Arnold, S.A. Heppell, D.W. Schafer, and D. Robinson. Financial support was provided by an NSERC postgraduate scholarship to D.W.J., awards from the Lerner-Grey fund of the American Museum of Natural History and the International Women's Fishing Association to D.W.J.., by NSF grants OCE-00-93976, OCE-05-50709 and OCE-08-51162 to M.A.H., and by grants from NOAA's National Undersea Research Program, courtesy of the Caribbean Marine Research Center, to M.A.H.

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Table 2.1. 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.

Table 2.1.

(a) Fixed effects:

Variable	Estimate	SE	Wald statistic	df	*P*
Density	0.000774	0.00143	0.542	1	0.58
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	0.00044	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	0.001107	0.0901	0.104
Residual	0.003192	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	0.00047	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	0.0011	0.121	0.14
Lunar cycle	0.00039331	0.000355	N/A	N/A
Residual	0.00352004	0.000269	0.395	0.022
Total	0.00930			

Table 2.2. 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*
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	7.91E-09	6.30E-10	4.34E-08	1.72E-08
Year	0.00385	1.31E-02	N/A	N/A
Site	1.36E-08	9.99E-10	7.45E-08	5.52E-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	0.018
Residual	0.134	0.00987	0.736	0.057
Total	0.202			

(c) Random effects - Reduced (optimal) model:

Source	Estimate	SE	Proportion of total variation within reproductive cycles	SE
Additive genetic	0.03470	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			

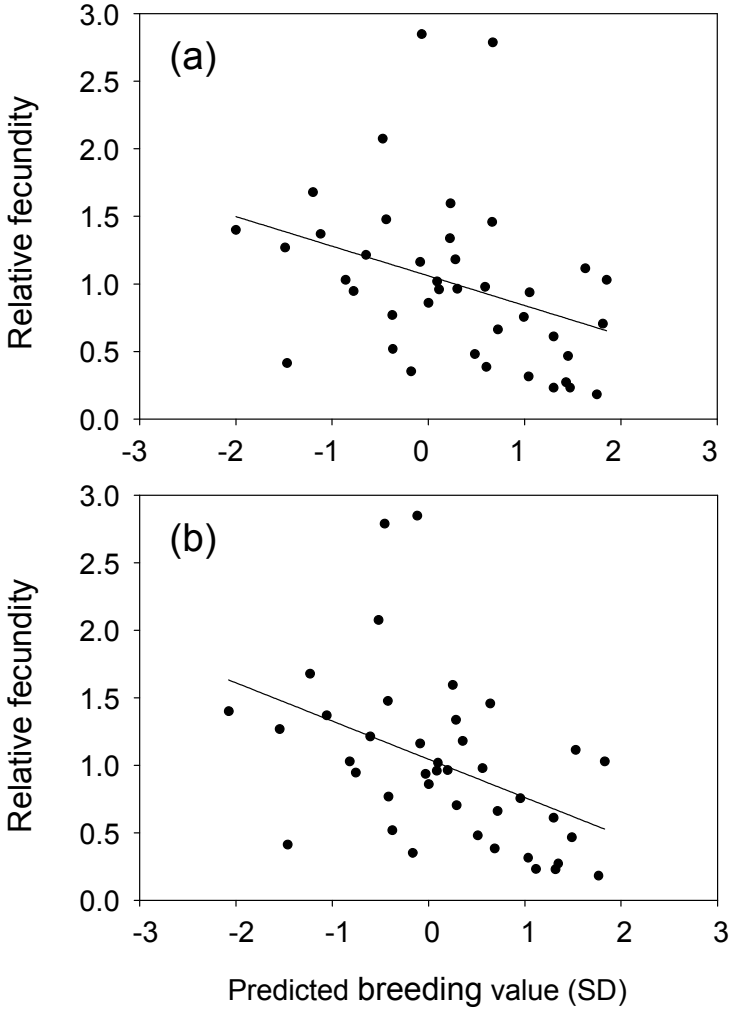

Figure 2.1 Maternal fecundity selection on predicted breeding values for larval traits. (a) Larval size-at-hatching (SAH), (b) Larval swimming performance. Breeding values were standardized by dividing by the within-cohort standard deviation in larval traits – the same measure of variance used to standardize mean cohort SAH in the analysis of selective mortality of larvae.

Figure 2.2. Summary and synthesis of published estimates of selective mortality on larval size-at-hatching (SAH). (a) Histogram illustrating the distribution of standardized selection differentials, S, (n=37 cohorts from 8 species; average study duration = 30 days). (b) Relationship between mean value in the survivor group ($\bar{z}^*$) and mean value in the initial sample ($\bar{z}$). Dashed trendline illustrates the average of the within-species regressions of $\bar{z}^*$ and $\bar{z}$. 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). (c) Approximated adaptive landscape relating mean larval SAH to mean survival under selective mortality. Relative survival is expressed as a decimal fraction of expected mean survival of a cohort with $\bar{z} = \bar{z}_{opt}$.

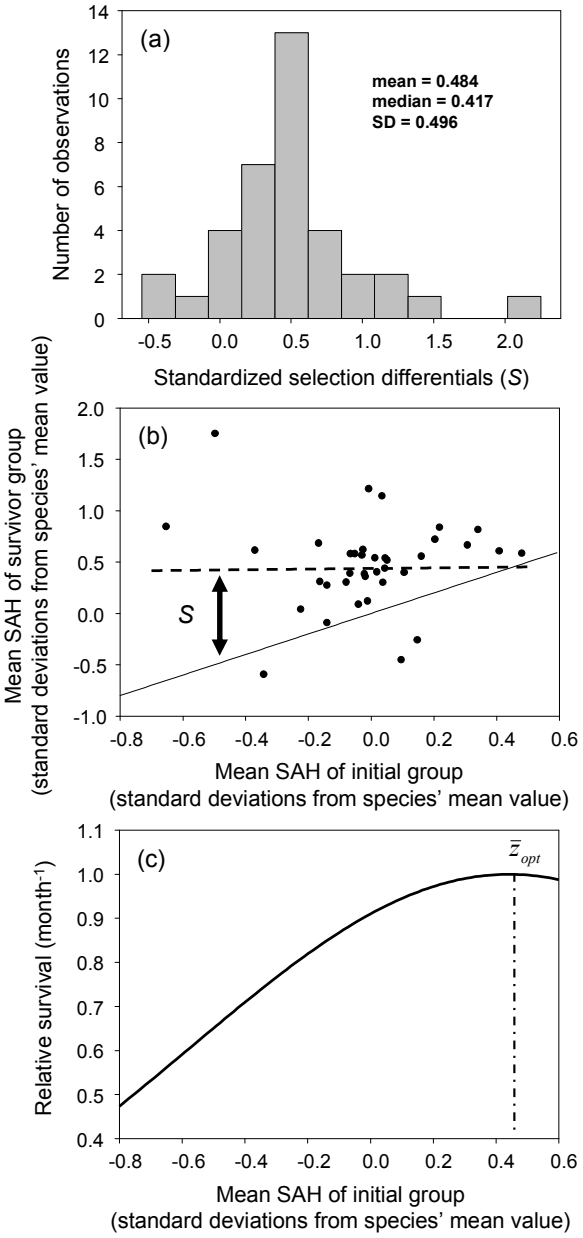
(a)
mean = 0.484
median = 0.417
SD = 0.496
Number of observations
Standardized selection differentials (S)
(b)
S
Mean SAH of survivor group
(standard deviations from species' mean value)
Mean SAH of initial group
(standard deviations from species' mean value)
(c)
$\bar{z}_{opt}$
Relative survival (month-1)
Mean SAH of initial group
(standard deviations from species' mean value)

Figure 2.2

CHAPTER 3:

FISHERY SELECTION MAY REDUCE POPULATION REPLENISHMENT THROUGH GENETIC CORRELATIONS BETWEEN LARVAE AND ADULTS

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This manuscript is formatted for publication in *Ecology Letters*

Abstract

Correlated genetic responses have been hypothesized as important components of fishery-induced evolution, though predictive data from wild populations have been difficult to obtain. We demonstrate substantial genetic links between a trait subject to fishery selection (adult body size) and traits that affect survival of larvae (size and swimming performance) in a wild population of a marine fish (the bicolor damselfish, *Stegastes partitus*). We also synthesize studies of selective mortality on larval size in many fishes and show that variation in larval size may result in considerable variation in population replenishment. Assuming our genetic parameter estimates can be extended to fishery species, we predict that observed rates of fishery selection on adult marine fishes may decrease larval size and reduce survivorship through early life stages by ~16% after one generation. The evolution of lower quality larvae in response to fishery selection may have substantial consequences for the viability of fished populations.

Introduction

For many wild populations, evolutionary changes in trait values can have contemporary effects that strongly influence population dynamics (Hairston et al. 2005; Coulson et al. 2006; Carroll et al. 2007). Such effects may be especially strong for species that are subject to fishery selection (Law 2000). Fishing mortality rates often exceed natural mortality rates, and fishing practices can selectively remove larger individuals from the population, resulting in rapid evolution of fish

populations (reviewed by Stokes et al. 1993; Browman et al. 2000). Although evolutionary changes such as reduced growth rate of adults and smaller size at maturity have been documented (Conover & Munch 2002; Kuparinen & Merila 2007), the full extent of evolutionary responses to fishery selection may be complex. Even if selection acts only on a single trait, other traits that are genetically correlated may also evolve (Falconer and Mackay 1996). Predicting the response of fish populations to fishery selection will therefore require accurate estimates of inheritance parameters 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 among related traits (Law 2000; 2007).

A major challenge for estimating inheritance parameters in marine fishes is that most species have highly dispersive larvae, so it is 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 (Houde 1987). Likewise, small changes in mortality rates during the early post-settlement phase can have strong effects on population size (Myers & Cadigan 1993; Caley et al. 1996; Johnson 2007). 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).

Genetic covariance between size or growth at different ages is likely due to pleiotropy, in which expression of single genes (e.g., growth factors) affect multiple traits (e.g., body sizes) at different ages (Cheverud et al. 1983). Adult and larval traits may also be connected by indirect genetic effects (e.g., maternal effects mediated by associated, heritable traits) (Kirkpatrick & 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 & Leggett 1996, Heath & Blouw 1998). Furthermore, for some species, the magnitude of these maternal effects may at least partially depend on the body size of adult females (Heath & Blouw 1998). Because body size is a heritable trait for many fishes (Law 2000), populations may evolve a smaller average body size when subjected to size-selective fishing (Swain et al. 2007). Maternal effects mediated by evolving body size may therefore be an important pathway through which larval traits may evolve in response to selection on adults (Kirkpatrick & Lande 1989).

We evaluated the degree to which two traits that affect the survival of larval fish – size at hatching and swimming performance – were genetically connected to 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. Although the life history of *S.*

partitus differs in several ways from many fishery species, (it is a benthic spawner with paternal care, site fidelity, and strong site-based density dependence), we believe that it shares enough important life history similarities (iteroparity, a high degree of gene flow, planktonic larvae, and large population sizes) that genetic parameter estimates for *S. partitus* may be useful in making general predictions about how larval traits may respond to selection on adult size, with a focus on fishery selection.

The degree to which larval traits are genetically correlated with adult body size will determine how quickly these traits may evolve in response to selection on adult size. However, the effects of a correlated response of larval traits on population dynamics will depend on how changes in the values of larval traits affect demographic rates (Munch et al. 2005). Therefore, we also examined the demographic consequences of variation in larval size-at-hatching by synthesizing information from studies that estimated selective mortality of larval fishes. Using information on the magnitude of selective mortality, we estimated how variation in larval size-at-hatching among cohorts would affect relative rate of larval and post-settlement survival within species. We then combined this information with our estimates of genetic connections between adult and larval traits to make general predictions about (*i*) how a given intensity of selection on adult size (in particular, example estimates of fishery selection) would cause a correlated response in the size of larvae, and (*ii*) how this response would affect relative rates of survival during

larval and early post-settlement life – key demographic phases for many marine fishes (Houde 1987; Myers & Cadigan 1993; Caley et al. 1996).

Methods

Demographic monitoring

The bicolor damselfish (*Stegastes partitus*) is an abundant species that inhabits coral reefs and lives in small social groups (≈ 2-20 fish) within distinct coral heads. Males hold breeding territories and will often mate with multiple females. Females lay benthic eggs and will readily deposit eggs on artificial substrates that can be manipulated and brought back to the laboratory for analysis. 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 38 breeding territories with standard, artificial nests were monitored daily for approximately two months. Artificial nests were 15cm lengths of 5cm diameter plastic pipe, lined with flexible transparent plastic that could be removed to access the attached eggs. Adult fish at these sites (n=65 and 35) were individually tagged as part of a broader long-term demographic study. Most of these fish had been monitored periodically since settlement and their age, size, and growth rate were measured directly. Maximum size of each adult was expressed as the asymptotic size estimated from a Von Bertalanffy growth function fit to individual size-at-age data. We used asymptotic, rather than current size in all parent-offspring analyses to avoid confounding the effects current age and size. Adult body size is a

heritable trait for marine fish (Law 2000), and asymptotic size provides an age-invariant measure of size that is useful when comparing phenotype to estimated breeding value. Small, non-lethal tissue samples (fin clips) were taken from all adults in the study area to identify parent-offspring relationships.

To quantify genetic covariance between larval and adult traits, we monitored breeding adults in the field, collected larvae immediately prior to hatching, examined hatched larvae in the lab, and compared traits of both larvae and adults. We measured larval size and swimming performance (defined below) as indicators of larval quality because both of these traits may influence larval survival (Vigliola & Meekan 2002; Fuiman & Cowan 2003). We sampled 55 larvae from each egg mass (n=143) collected in the field. Thirty-five of these larvae were 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 standardized 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 screened at seven highly polymorphic microsatellite loci (Williams et al. 2003) using standard methods. This procedure provided multi-locus genotypes of all sampled adults and larvae, which we used to determine parentage (see methods in supporting information (SI), appendix S1). Given the large numbers of alleles per locus, the probability of a single putative parent-offspring pair sharing alleles by chance was extremely low ($p < 0.00457$) (see methods in Jamieson & Taylor 1997; Christie 2009). Thus we used simple

Mendelian incompatibility to assign parentage. To cross-validate our 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; Kalinowski et al. 2007).

Genetic covariance among larval and adult traits

We examined the potential for a genetic relationship between asymptotic adult size and larval quality 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 (Falconer & Mackay 1996). For graphical display, we plotted mean offspring 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 the all offspring of each sire on 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). We acknowledge that because most of the offspring from sires in this study came from the same nest, this design confounds sire and nest effects. However, additional studies using these artificial nests within this system suggest that nest effects are small (accounting for < 5% of the variation in

larval traits) and unlikely to be correlated with sire asymptotic size (D. Johnson, unpublished data).

We evaluated sire-offspring relationships for a large sample of offspring from naturally breeding adults (2006 data). 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 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 at the same two study populations, there was very little overlap between individuals breeding in 2006 and 2007 because of high turnover in the population (5 sires and 6 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 (3.5d) 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 asymptotic size but no environmental effects that depended on sire size (see Results), we pooled the data from both years to calculate genetic covariances and size-dependent maternal effects. Analysis of multi-locus microsatellite genotypes suggested that the

overall relatedness in the population was very low and that breeding pairs were unlikely to be related (SI text and Fig. S1). Genetic covariances (Cov_G), corrected for assortative mating, were calculated according to the following formula (Falconer & Mackay 1996):

$$Cov_G = \frac{2b}{(1+r)} - rm$$

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. Because the causal mechanisms underlying mother-offspring regressions include both genetic covariance and size-dependent maternal effects and sire-offspring relationships reflect genetic covariance only, the difference between mother-offspring and sire-offspring regression slopes was used to estimate m (Lande & Price 1989). Mean and 95% confidence intervals for estimates of size-dependent maternal effects and genetic covariances were generated using standard resampling procedures (SI text).

Larval size and relative mortality

We evaluated demographic consequences of changes in larval size by estimating how a given shift in mean larval size (predicted after a generation of selection on adults) would affect relative survival of larvae and juveniles. The relationship between larval size and relative survival was estimated by synthesizing information from published studies that examined whether larval size-at-hatching

(SAH) influences larval and/or post-settlement survival for multiple cohorts under similar field conditions. Our search yielded estimates of selective mortality on SAH for 37 cohorts from 8 species of fish (SI text and Table S5). 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:

$$S = \bar{z}^* - \bar{z}, \qquad (1)$$

where $\bar{z}^*$ and $\bar{z}$ are, respectively, the mean phenotypic trait values of SAH for the survivor and initial groups (Lande & Arnold 1983).

Although selection differentials summarized selective mortality on SAH *within* cohorts, the demographic consequences of long-term changes in larval traits may be better predicted by the relationship between trait value and relative survival *across* cohorts (Saccheri & Hanski 2006). Assuming that components of mortality that do not depend on larval size remain similar across cohorts, estimates of selective mortality can be used to estimate the adaptive landscape – a theoretical surface relating the population mean fitness (here defined as survival under selective mortality) to mean phenotypic value (Lande 1976, 1979). If phenotypic values are normally distributed within populations, 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). We assume that the adaptive landscape is constant, or at least

stationary in shape and position among populations, and that selection is frequency- and density-independent within populations. Then if selection is measured in 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.

Our results indicate that within species, the relationship between trait means after selection, $\bar{z}^*$, and the trait means before selection, $\bar{z}$, was well approximated by linear regression,

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

where b_0 is an intercept and b_1 is a regression slope. Substituting this expression into (1), we obtain the following approximation for the standardized selection differential,

$$S \approx (b_1 - 1)\bar{z} + b_0. \qquad (2)$$

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

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

where $\overline{W}$ is mean fitness (here defined as survival during early life history stages) (Lande 1979). Integrating (2) over $\bar{z}$ therefore provides a quadratic approximation of the natural log of mean fitness:

$$\ln \overline{W} = \int (b_1 - 1)\bar{z} + b_0 d\bar{z} = \frac{1}{2}(b_1 - 1)\bar{z}^2 + b_0\bar{z} + C, \qquad (3)$$

where *C* is an undefined constant of integration. By setting C = 0, we scaled relative fitness such that mean survival rate was equal to 1 in the absence of selection on adults (i.e., when mean SAH = 0 standard deviations away from the pre-selection mean). Survival consequences of changes in mean SAH via correlated responses to selection on adults could be directly evaluated with reference to this surface. Because the average duration of selection studies was ca. 30 days, we expressed survival as a monthly rate.

To empirically 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. 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 approximate the average adaptive landscape, using equation 3 as described above.

Fishery selection, larval responses, and population replenishment

Assuming our genetic parameter estimates for *S. partitus* can be extended to fishery species, we predicted the response of larval traits to fishery selection on adults by multiplying fishery selection differentials by the combined genetic covariance and size-dependent maternal effects. We used a range of published selection estimates (Sinclair et al. 2002; Swain et al. 2007) as example measures of fishery selection on adult body size. Net selection differentials were calculated from the weighted average of selection differentials relating mean body size at age 4 to body size at age 4 for fish sampled at later ages (Swain et al. 2007). Differentials were weighted by the average proportion of each age class in the population (calculated from Table 1 in Sinclair [2001]). Selection differentials were standardized to standard deviation in body length of 4-yr old fish (calculated from Fig. 3 in Sinclair et al. [2002]). These studies of Atlantic cod (*Gadus morhua*) in the Gulf of St. Lawrence have indicated that, over a 13-year period of moderate-to-heavy fishing effort (1981-1993), average standardized selection differentials for

different adult age classes ranged from -0.12 to -0.6, with a mean of -0.29. These values were used as example measures of selection on adults to predict the correlated response of larval size-at-hatching. The effect of correlated larval response on relative survivorship throughout the larval and early juvenile phases was predicted using the adaptive landscape relating SAH to relative survival rate (Fig. 3B) and assuming that effects of SAH on survival persist for 90 days (the maximum duration of selection studies in our analysis). Uncertainty in these predictions was estimated from combined uncertainty in both genetic parameter estimates and the fitness surface (SI Text).

Results

Genetic covariance among larval and adult traits

Sires with larger asymptotic sizes (hereafter referred to as '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 ± 0.063SE, t_{32} = 2.682, P = 0.012; larval swimming duration: slope = 0.176 ± 0.060SE, t_{26} = 2.93, P = 0.007, Fig. 1). Average values of larval traits were not affected by average temperature, site, or average density of conspecifics, and excluding these factors from the analysis had little effect on regression parameters (Table S1). However, direct estimates of genetic covariances derived from these relationships may have been biased by assortative mating. Values for sizes of sires and mothers were weakly correlated (r = 0.34, P = 0.038), though there was no evidence for assortative

mating based on other, measured characteristics of adults nor was there any correlation between parental age and larval traits (Tables S2, S3). 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 quality, 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 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 differences in size or swimming performance between fostered, and non-fostered larvae (P = 0.307 and 0.421, respectively). Again, there was some evidence for an association between asymptotic sizes 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 S2). All sire-offspring regressions are summarized in Table S1. Based on sire-offspring regressions for the combined 2006 and 2007 data, the genetic covariance (on standardized variables) between sire size and larval size was

estimated to be 0.212 (95% CI: 0.0407 – 0.367), and that between sire size and larval swimming performance was 0.241 (95% CI: 0.027 – 0.471). Mother-offspring regressions on standardized variables had higher slope values, indicating size-dependent maternal effects on larval size (Lande and Price 1989)(m = 0.178; 95% CI: 0.0245 – 0.326) and swimming performance (m = 0.09: 95% CI: -0.079 – 0.345).

Larval size and relative mortality

Results from the literature survey indicated that, on average, early post-settlement survival of marine fishes was selective, and individuals that were larger at hatching had a greater chance of surviving the larval-juvenile transition (mean, standardized selection differential = 0.484, SEM = 0.0805)). Moreover, the average slope of relationship between $\bar{z}^*$ and $\bar{z}$ was less than one, (among-species mean values for slope = 0.0331, 95% CI: -0.720 – 0.783, intercept = 0.465, 95% CI: 0.0492 – 0.881), suggesting that within each species, cohorts of larvae with greater mean values of size-at-hatching experienced less selective mortality (Fig 3a). Our estimate of the adaptive landscape suggested that monthly survival may vary considerably in response to variation in mean size-at-hatching (Fig. 3b)

Fishery selection, larval responses, and population replenishment

Based on our estimates of genetic covariance and size-dependent maternal effects, we predicted how larval quality would 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 size at hatching (Table 1). For fishery selection in the middle of this range (mean observed value = -0.29),

larval size would be expected to decrease by 0.113 SD in a single generation. Based on our estimates of size-dependent larval survival (Fig. 3), this decrease in phenotype is predicted to decrease relative monthly survivorship through larval and juvenile phases by 16% (95% CI: 6- 30%)(Fig. 3b, Table 1).

Discussion

We demonstrated that traits affecting larval quality (size and swimming performance) in a wild population of marine fish may have substantial, genetic connections with adult traits (asymptotic size). These connections were comprised of both genetic covariance between larval and adult traits, as well as an indirect genetic effect in which maternal contributions to larval quality depended on body size, a heritable trait (mean heritability of body length for marine fish = 0.30, SD = 0.21; [Law 2000]). Selection on adult size may therefore induce a substantial, correlated response in larval traits. Our results suggest that even moderate selection on adult size (e.g., a variance-standardized selection differential of -0.12), may cause an appreciable decrease in relative survivorship, and that intense selection (e.g., a standardized differential of -0.29) may cause a substantial reduction in relative survivorship (a difference of 16% after one generation of selection on adults).

Predicting the long-term response to the combined effects of fishery selection on adults and natural selection on larvae presents an additional challenge, and empirically reconstructing an adaptive landscape relating larval size to survival provides a useful starting point. Although natural selection for larger larvae may be persistent and strong, these effects are likely balanced by maternal fecundity

selection for a greater number of larvae such that mean larval size is smaller than the size that optimizes larval survival (i.e., mean larval size is below the peak of the adaptive landscape; Smith & Fretwell 1974; see Einum & Fleming 2000; Heath et al. 2003 for examples of balanced selection on offspring size in fish). When the balance between maternal and larval selection is offset, larval size may exhibit a rapid evolutionary response (Heath et al. 2003). Through correlated responses, selection for smaller adult body size would offset the balance of selective forces and result in the evolution of smaller larvae (with mean survival values 'lower' on the landscape). However, the estimated adaptive landscape suggests that as larvae evolve toward smaller sizes, the strength of larval viability selection for larger SAH (indicated by the logarithmic slope of the landscape) would increase. Because of the genetic correlation between adult and larval size, natural selection on larvae is expected to cause a correlated response in adults that opposes responses to fishery selection. However, it is likely that selection on larvae only partially counters the effects of selection on adults. Size-dependent maternal effects are asymmetric in that the correlated response of larvae to selection on adults is greater than the correlated response of adults to selection on larvae (Kirkpatrick & Lande 1989). Moreover, fishery selection on adults may be strong, and the reduction in larval size would have to be large before selection on larvae was sufficiently strong to balance selection on adults. All told, it is likely that larval size and survival would continue to decline after multiple generations of selection on adults, though the rate of decline would decelerate.

Genetic correlations between adult size and traits that affect larval and juvenile survival highlight a mechanism whereby fishery selection may disrupt and/or reduce recruitment. Several large-scale studies have empirically linked selective removal of large individuals with reduced recruitment (Marteinsdottir & Thorarinsson 1998; Venturelli et al. 2009) and increased recruitment variability (Hseih et al. 2006; Andersen et al. 2007). However, the processes responsible for these large-scale patterns were not directly investigated. Reduced recruitment may be a consequence of lower reproductive output associated with loss of large individuals (either by evolution of smaller adult body size or age-truncation)(Law 2007). However, reduction in larval quality may also have large effects on recruitment (Houde 1987), particularly if larval quality affects survival during larval and juvenile phases (which may be demographic 'bottlenecks' regulating abundance of benthic populations) (Sissenwine 1984).

Genetic covariance between adult size and early life-history traits (e.g., egg size, larval size, and growth) has been demonstrated in a laboratory population of rainbow trout (McKay et al. 1986) and a laboratory population of Atlantic silversides (Munch et al. 2005, Walsh et al. 2006). While the presence of such covariance may be a general phenomenon among fishes, the degree to which larvae may evolve in response to selection on adults may vary among species. Using Atlantic silversides as a model organism, Munch et al. (2005) examined the potential for selection on adults to generate correlated responses in larval size and larval survival. Munch et al. (2005) suggested that selection on adults would produce a weak response in larvae

and would have negligible effects on survivorship through early life history stages. The results from our study differ, largely because the estimated magnitude of genetic covariance between adult and larval size measured for bicolor damselfish (estimated as 0.212 on standardized trait values) was considerably higher than published estimates for Atlantic silversides (0.043 – 0.071; estimated from Fig. 1 in Walsh et al. 2006). Also, we considered the effects of size-dependent maternal effects when predicting correlated responses of larvae. Despite the potential for among-species variability in the values of inheritance parameters, some indirect evidence suggests that the values measured for *S. partitus* may be representative of a broad group of fishes. Heath and Blouw (1998) reviewed phenotypic correlations between maternal body size and egg size for many fishes and found that such correlations are substantial (all species mean correlation = 0.392, SD = 0.307, n = 25). Though the extent to which these correlations are due to genetic covariance (cov_G) vs. size-dependent maternal effects (*m*) is unclear (mother-offspring correlations are equal to $1/2cov_G + m$ when traits are expressed as variance-standardized values), the summarized values suggest that selection on adults may strongly affect egg size (and presumably larval size) in future generations. Moreover, comparable values observed for *S. partitus* ($1/2cov_G + m = 0.284$) are reasonably close to the overall mean correlation, suggesting that these genetic parameter estimates may be useful for making general predictions of how larval fish may respond to selection on adults. Although indirect maternal effects may require a few generations of selection on adults before they fully manifest (Kirkpatrick & Lande 1989), we believe they are

important because fishery selection can persist for many generations and many fishery species show evidence of maternal effects on recruitment (Venturelli 2009).

Fisheries-induced evolution should be a major concern for conservation and management of fished species partially because the expected evolutionary responses - smaller adult size, reduced growth, earlier maturity - are thought to reduce reproduction and have negative effects on population abundance, biomass, and/or fishery yields (Stokes et al. 1993; Browman et al. 2000; Law 2000). Here we demonstrate that a substantial correlated response to selection (reduced larval quality) may occur relatively quickly and may have additional negative consequences for population dynamics. For marine fishes, survival during larval and early juvenile stages may be a demographic bottleneck and a major determinant of adult population size (Houde 1987; Caley et al. 1996). Evolution of lower-quality larvae in response to fishery selection may therefore have substantial effects on 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. 2004) will likely slow fishery selection (Trexler & Travis 2000; Baskett et al. 2005) and slow or prevent the evolution of low-quality larvae. Retaining large fish in the population would allow greater reproduction by individuals with genotypes that produce high-quality larvae (Law 2007). Conserving large fish would thereby promote recruitment success and ensure greater resilience of fished populations.

Acknowledgments

Our sincerest thanks go to L. Krigsman, N. Schiel-Rolle, C. Soto, and M. Weigner for all their hard work and assistance in the field and lab. We also thank B. Gadd, I. Black, and the staff at the Perry Institute for Marine Sciences, Lee Stocking Island, Bahamas. This manuscript comprises a chapter from the senior author's doctoral dissertation (M.A.H. Major Professor), and benefited greatly from reviews by his graduate committee: S.J. Arnold, S.A. Heppell, D.W. Schafer, and D. Robinson. Financial support was provided by an NSERC postgraduate scholarship to D.W.J, by NSF grants OCE-00-93976, OCE-05-50709, and OCE-08-51162 (Hixon), and by grants to M.A.H. from the National Undersea Research Program, courtesy of the Caribbean Marine Research Center.

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Table 3.1. 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). Relative survivorship is expressed as proportion of survivorship in the absence of selection on adult size. Values of selection on adult size were based on the range and mean of selection differentials published by Sinclair et al. (2002) and Swain et al. (2007) (also see text).

Standardized adult selection differential	Predicted change in SAH (in SD units)	Relative survivorship per 90d		
		Mean	95% CI	
-0.12	-0.047	0.93	0.88	0.98
-0.29	-0.11	0.84	0.70	0.94
-0.6	-0.23	0.67	0.44	0.86

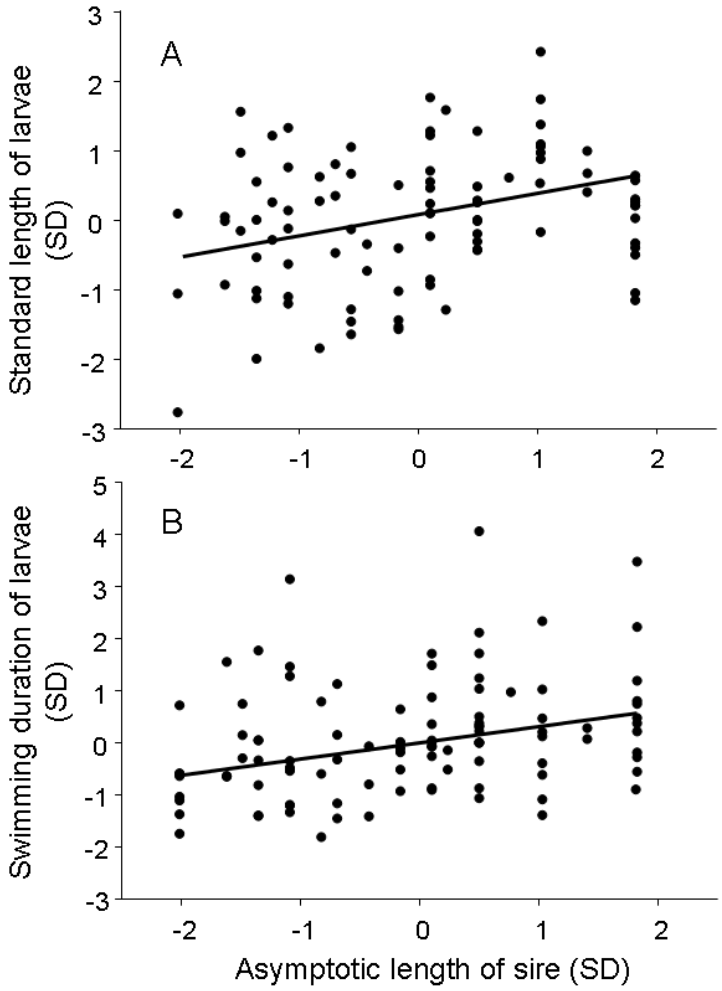

Figure 3.1. Parent-offspring regression illustrating the relationship between the maximum total length of sire (asymptotic length from individual Von Bertalanffy growth curves) and two traits of larval offspring: (A) standard length and (B) swimming duration. Each data point illustrates the mean value from a sample of larvae collected from a single clutch of eggs (n=35 for standard length, n=20 for swimming performance). All family 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. Each sire-offspring case was weighted by the number of families used to determine the average.

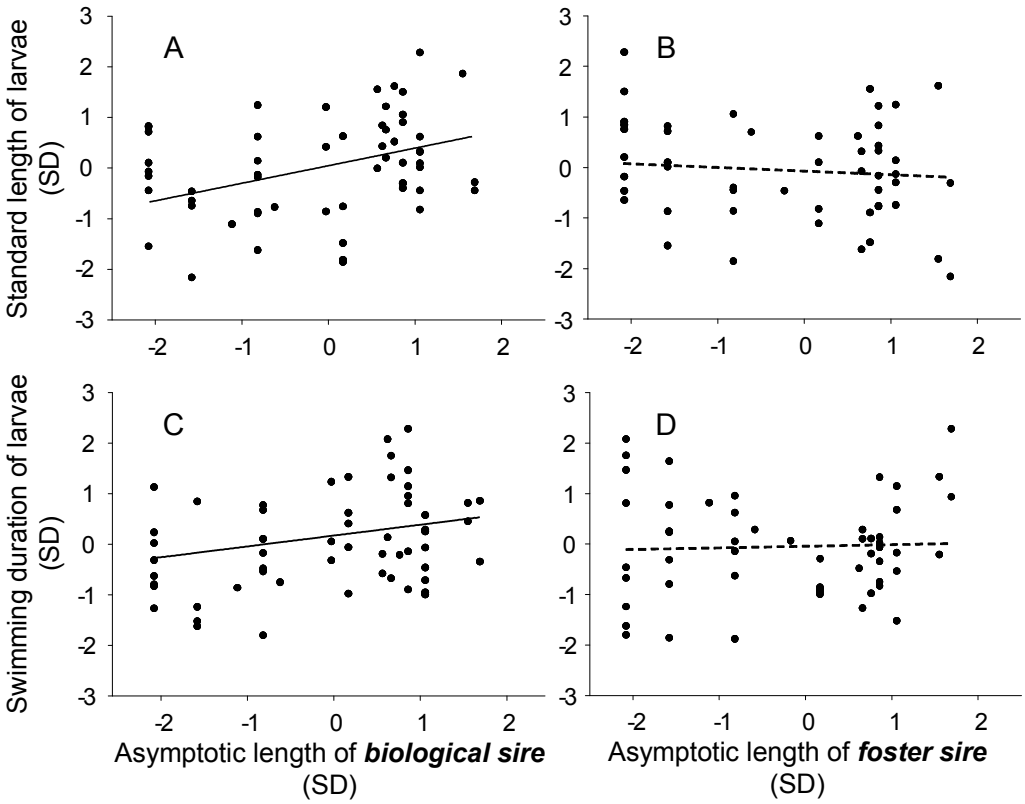

Figure 3.2. Parent-offspring regressions for cross-fostered larvae. Graphs A and C illustrate relationships between biological sire size and larval traits. Graphs B and D illustrate relationships between foster sire size and larval traits (foster sires were males rearing unrelated egg clutches during 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 family 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. Each sire-offspring case was weighted by the number of families used to determine the average.

Figure 3.3. Effects of larval size-at-hatching (SAH) on relative survival of larval and juvenile fishes. (a) Selective mortality illustrated by comparing mean SAH for initial samples of cohorts ($\bar{z}$) to mean SAH for samples of surviving fish ($\bar{z}^*$). Phenotypic values were standardized by dividing by the phenotypic standard deviation in the initial sample and expressed as standard deviations from the overall mean value of SAH for that species. Dashed trendline 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 selection differential (*S*). (b) Estimated adaptive landscape relating mean SAH (expressed as standard deviations from the pre-selection mean) to the expected value of monthly survival (relative to the expected survival in the absence of selection on adults). Arrows indicate the reduction in relative survival associated with a decrease in SAH of 0.113 SD (cf. Table 1).

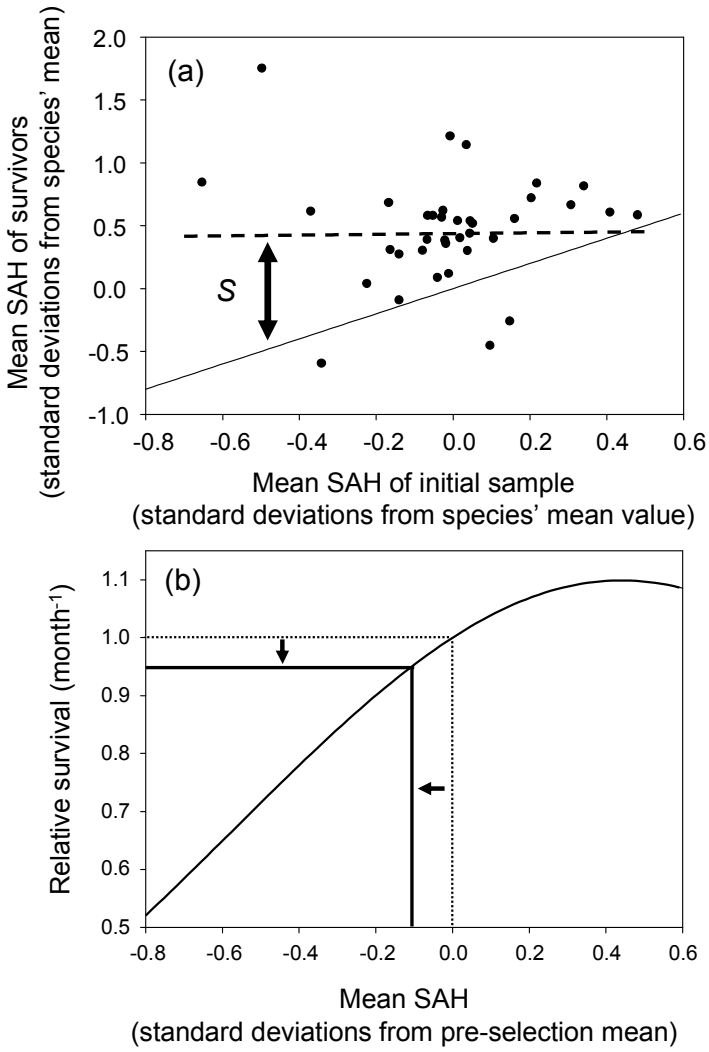
(a)
Mean SAH of survivors
(standard deviations from species' mean)
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
S
-0.8
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6
Mean SAH of initial sample
(standard deviations from species' mean value)
(b)
Relative survival (month-1)
1.1
1.0
0.9
0.8
0.7
0.6
0.5
-0.8
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6
Mean SAH
(standard deviations from pre-selection mean)

Figure 3.3

CHAPTER 4:

ONTOGENETIC AND SPATIAL VARIATION IN SIZE-SELECTIVE MORTALITY OF A MARINE FISH

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This manuscript is formatted for publication in *Journal of Evolutionary Biology*

Abstract

Although body size and growth can affect individual fitness, ontogenetic and spatial variation in the ecology of an organism may determine the relative advantages of these traits. During a 7-year field study, we examined how selective mortality operated on size and growth throughout the entire reef-associated life phase of a common coral-reef fish, the bicolor damselfish (*Stegastes partitus*). In general, faster-growing juveniles experienced greater mortality, though as adults larger individuals had higher survival. Comparing patterns of selection observed at four separate populations revealed that greater population density was associated with stronger selection for large adult size. Large adults may be favored because they are superior competitors and less susceptible to gape-limited predators. Laboratory experiments suggested that selective mortality of fast-growing juveniles was likely due to an association with risky foraging. Overall, our results suggest that variation in ecological interactions may lead to complex patterns of lifetime selection on body size.

Introduction

Both body size and growth rate can influence individual survival probabilities (reviewed by Roff 1992, Stearns 1992). Because larger size is often associated with a higher probability of survival, rapid growth may confer a survival benefit by allowing individuals to reach a large size sooner (Case 1978, Arendt 1997). However, rapid growth may also be associated with a suite of costs, including

increased foraging risk (Sih et al. 2004, Stamps 2007), delayed physiological development (Arendt 1997, Metcalfe and Monaghan 2001), and decreased locomotory performance (Billerbeck et al. 2001). Because size and growth are often strongly correlated, their direct effects on survival probability, and therefore fitness, are often unclear (Lynch and Arnold 1988). Moreover, the relative costs and/or benefits of rapid growth and large size may vary throughout the lifetime of an organism and among the locations it inhabits (reviewed by Blanckenhorn 2000).

Recent reviews suggest that natural selection on morphological traits such as body size can be strong, but that the magnitude of selection is highly variable (Endler 1986, Kingsolver et al. 2001, Hoekstra et al. 2001, Hereford et al. 2004, Kingsolver and Pfenning 2007). For estimates of viability selection (i.e., fitness differences among individuals measured by differences in survival probabilities), some of the variability in intensity of selection can be explained by study duration. Hoekstra et al. (2001) found that the largest estimates of selection came from studies that measured differences in survival over short time scales (days), and suggested that intense selective mortality is typically sustained only for brief episodes. Over longer intervals, the strength of selection is likely to be balanced by periods of no selection, or by reversals in selection. These findings suggest that studies that focus on short-duration episodes of selection (e.g., during a life stage transition) may provide an inaccurate description of the total effect of selection that operates within a generation of an organism (Arnold and Wade 1984a,b, Schluter et al. 1991).

Understanding the lifetime effects of selection on size and growth may be complicated by ontogenetic variation in both of these traits. This complication is especially prevalent in species that exhibit indeterminate growth, i.e., growth that continues throughout the lifespan of an individual (though typically at a decelerating rate). For such species (e.g., fish, many invertebrates), there is often considerable flexibility in size-at-age and age-specific growth rate (Wooton 1990). For species with an asymptotic growth form, size-at-age will be influenced by both an individual's maximum attainable size (i.e., its asymptotic size), and how quickly it approaches that size (Von Bertalanffy 1938). Both of these components of growth are ecologically important and may be subject to natural selection. For example, an individual's asymptotic size may influence its competitive ability or vulnerability to predators (Persson et al. 1996), and relative growth rate may be directly associated with foraging risk and/or physiological costs (Blanckenhorn 2000). Moreover, the importance of growth components may vary with ontogeny. Adult size is largely determined by asymptotic size, whereas juvenile size is mostly influenced by relative growth rate (Francis 1996). An examination of lifetime selection on components of growth can detect ontogenetic changes in size-selective mortality and may therefore provide a clear picture of how selection on size and growth form operates within a generation of an organism.

Many studies have documented size-selective mortality of marine fish (reviewed by Sogard 1997). Although most studies suggest that large fish experience greater survival rates, the duration of most studies has been short and

inferences about lifetime selection on size are limited. Few studies of marine fishes have examined survival of tagged individuals to estimate selection and fewer still have examined selection throughout the entire lifespan of the adult stage. In this study, we examined viability selection on size and relative growth rate of a marine fish, the bicolor damselfish (*Stegastes partitus*). Using data from 7-year demographic studies of four separate populations in the wild, we examined how individual lifespan was related to two different components of growth: asymptotic size and relative growth rate. Analyses focused on ontogenetic variation in size-selective mortality and spatial variation in the intensity of selection.

Methods

Study Species

The bicolor damselfish (*Stegastes partitus*) is a common species found on coral reefs in the Caribbean and western Atlantic. Bicolor damselfish inhabit relatively complex coral heads that provide refuge from predators (Nemeth 1998). Both adults and juveniles have extremely small (~1-3m) home ranges around their home coral heads, except for occasional local excursions to neighboring coral heads when mating (Schmale 1981, Knapp and Warner 1991). Aggressive behavior is common in larger social groups, which range from 2-20 individuals at our study sites. Long-term research in the Bahamas has revealed no long-distance (i.e., between-reef) post-settlement movement of adults (M.A. Hixon et al., unpublished manuscript).

Demography of study populations

Data on individual growth and survival were obtained from a long-term, large-scale demographic study of *S. partitus* (M.A. Hixon et al., unpublished). During the time period of 1998-2005, tagging studies were conducted within four populations of *S. partitus* near Lee Stocking Island, Bahamas (23°46'N, 76°06'W). Populations within each of the four study locations (coral reefs that were approximately 100m in diameter) were sub-sampled with 21 permanent plots that were chosen haphazardly and distributed evenly over the reef. Plots measured 2m x 2m and were centered on large coral heads that were inhabited by groups of *S. partitus*. All resident fish within each plot were individually tagged with subcutaneous injections of visibly identifiable elastomer (Northwest Marine Technologies, Shaw Island, WA). Within these plots we followed the fates of all resident fish from larval recruitment (or subsequent immigration to the study plots) until death. Mortality, known to occur mainly via predation (Booth and Hixon 1999, Carr et al. 2002, see also Hixon and Jones 2005), was distinguished from local emigration by exhaustive searches of the entire home reef during each census and occasional searches of neighboring reefs (>100m away). Emigration was low throughout the duration of the study and almost all cases involved individuals moving < 10m from the study plot and taking up residence on a nearby coral head. In all cases when individuals emigrated from study plots, we continued to include them in the censuses and continued to re-measure them.

Study populations were monitored weekly during the main recruitment season (June-Sept) and 1-2 times during each winter. Growth was measured by capturing and measuring fish within each population at certain times throughout the year (early summer, late summer and during the winter censuses) and special effort was made to capture and measure new individuals upon first encounter. Individuals may therefore have been measured up to five times each year. However, because of natural differences in settlement date, individuals were measured at different ages.

Because *S. partitus* is a conspicuous species that exhibits little post-settlement movement (Emery 1968, Myrberg 1972) and because the study area was thoroughly searched during each census, the date of mortality (and therefore the lifespan) of each individual could be reliably estimated from the date of disappearance. The date of mortality was estimated as the mid-point between the first census when that individual was absent and the previous census. During the summer, when censuses were conducted weekly, the time of mortality could be estimated with a margin of error of $\leq$ 3.5 days. For those individuals that died at some point between summer and winter censuses, date of mortality was estimated with less precision (margin of error $\leq$ 2 months). However, even in these cases the uncertainty in death age was small relative to the average lifespan of individuals in this study (530 days).

Measuring growth form

To quantify patterns of natural selection on size and growth, we compiled a subset of data that included all individuals that had been monitored from settlement and measured at least three times. Although recent settlers could be readily identified by their size and behavior, we restricted our analysis to those individuals that settled sometime between weekly censuses, such that their estimated post-settlement age was never off by more than 3.5 days. Size-at-age of *S. partitus* is well-described by a VonBertalanffy growth equation (VBGE), a model of asymptotic growth that is commonly used to describe the growth form of fish:

$$TL = TL_{\max}\left[1 - \exp(-k * age)\right]$$

where TL = total length, TL_{max} = asymptotic size, and k = a growth constant describing how quickly the asymptotic size is reached (Figure 1). The model was fit to individual size-at-age data using nonlinear least squares regression and growth trajectories were modeled from hatching (day 0) through the benthic life stage. To model growth during the early stages, we used an initial size at hatching of 2.17mm (average from a sample of 103 fish) and a 30-day larval duration (Wilson and Meekan 2002). This procedure provided estimates of k and TL_{max} for each individual (Fig. 1A). The parameters of the VBGE or simple measurements of growth derived from these values (e.g., body size attained at a standard age [Francis 1996, Wang and Milton 2000]) can be treated as age-invariant, quantitative traits that may be under selection (Cock 1966). Asymptotic size (TL_{max}) is technically never reached within an individual's lifetime and it is not a trait that is "expressed" in the conventional sense. However, asymptotic size influences growth at all ages and can be accurately

estimated with relatively few observations per individual, i.e., even when the individual is small relative to its estimated asymptotic size.

Within this data set, fish that lived longer tended to be measured more often. To examine whether this phenomenon affected estimates of growth parameters, we conducted a simulation analysis to assess potential biases in the procedure used to estimate growth of individual fish. The goal of the simulation analysis was to determine whether estimates of a "true" growth function change as more observations become available. The true function was a Von Bertalanffy growth curve based on mean observed values for a subset of the growth data (TL_{max} = 6.15 cm, k = 0.00995). Each replicate of the simulation produced an individual growth curve by generating size values at various ages. Size was randomly generated from the true size-at-age function +/- a normally-distributed random error term (mean = 0 and variance = 10% of "true" size-at-age value). Sizes were generated at 50, 100, 150, 200, 300, 400, 500, 600 and 700 days of age. These ages provided an approximation of how frequently individuals were sampled in the field, and encompassed most of the variation in lifespan. For each replicate (an "individual" in the simulated study), a VBGE was fit to the simulated size-at-age data using nonlinear least squares regression. Estimates of TL_{max} and k for each individual were compiled, and we compared three classes of individuals to examine how estimates of the true growth function changed with number of observations. The distribution of parameter estimates were compared among samples of individuals with 4 observations (ages 0, 50, 100, 150 days), 6 observations (ages 0, 50, 100, 150, 200,

300 days) and 10 observations (ages 0, 50, 100, 150, 200, 300, 400, 500, 600, 700 days).

If growth function parameters can be reliably estimated with relatively few observations, then comparisons of size- or growth-at-age can be made by interpolation or extrapolation from individual growth functions. Such a procedure will therefore allow estimation of the "invisible fraction" –the subset of phenotypic values that are not normally measured because individuals die before those traits are expressed (e.g., size at 500 days cannot be measured if the individual only lives 300 days). Ignoring the invisible fraction can lead to biased and unreliable measures of lifetime selection (Lynch and Arnold 1988). However, estimates of growth parameters will allow a comparison of the trait values of survivors to the estimated trait values for non-survivors. This procedure will result in a more accurate measurement of lifetime selection.

Size, growth rate, and selective mortality

We quantified selection on size and growth rate by analyzing asymptotic size (TL_{max}) and relative growth rate (D_k) as quantitative traits. We used multiple regression analyses to quantify the relationship between an individual's relative fitness (defined as an individual's lifespan / population mean lifespan) and their values of TL_{max} and D_k. This procedure allowed us to estimate the strength and form of natural selection acting directly on each trait, assuming that selection is frequency-independent, traits have a multivariate normal distribution before selection, and that

the fitness surface can be reasonably approximated by quadratic polynomials (Lande and Arnold 1983).

When growth can be described by a VBGE and when comparing growth rate among individuals (or other groupings such as populations or species) that vary in their asymptotic size, it is often most useful to compare how quickly that asymptote is reached by comparing values of *k* (Francis 1996). However, among individuals in this study, estimates of TL_{max} and *k* were strongly correlated, causing problems with interpretation of the regression analyses. We removed this correlation by expressing k as a power function of TL_{max}:

$$k = a(TL_{\max})^b,$$

where a and b are constants estimated by nonlinear least squares regression. We then calculated the deviations from this relationship for each individual. Deviations in *k* (D_k) provided a measure of whether an individual's growth rate was relatively fast or slow (positive and negative values, respectively; Fig 1B) after accounting for individual values of TL_{max}, which influence absolute growth rate. Consequently, TL_{max} and D_k were phenotypically uncorrelated (r = 0). For the analyses both TL_{max} and D_k were expressed as standardized traits (mean = 0 and phenotypic SD before selection = 1; Lande and Arnold 1983). Specifically, we fit the following statistical model:

$$w = \alpha + \beta_1 TL_{\max} + \beta_2 D_k + \frac{1}{2}\gamma_{11}(TL_{\max})^2 + \frac{1}{2}\gamma_{22}(D_k)^2 + \gamma_{12} TL_{\max} D_k + \varepsilon,$$

where w is relative fitness (individual longevity / mean longevity), α is an intercept term, β_1 and β_2 are linear selection gradients, γ_{11} and γ_{22} are quadratic selection gradients, γ_{12} is a correlational selection coefficient, and ε is residual variation. TL_{max} and D_k are as defined above.

Analyses of selection were conducted for each of the study populations to assess spatial differences in selection. Although there were only four study populations to compare, we also examined spatial differences in population density and survival rates, two characteristics of the study populations that may affect the presence and/or intensity of selective mortality (Sogard 1997). Variation in selective morality among sites was evaluated with respect to these ecological characteristics.

Although the parameters TL_{max} and D_k provided an accurate summary of individual growth (see *Results* section), it may also be useful to compare the effects of selection on size-at-age. To illustrate the effects of selection on size-at-age, we compared the distributions of length-at-age among individuals that died during particular intervals of time and those that survived. We compared the distributions of length at 50 days of age for individuals that died in the subsequent interval of 50 – 300d post-settlement, and those that survived greater than 300d. To illustrate ontogenetic variation in selection on size-at-age, we performed a similar comparison on the distributions of length at 200 days of age for those individuals that died in the interval 200-400d post-settlement and those that survived greater than 400d. Although this illustrative procedure was only conducted for the one site that had the strongest statistical evidence for selection (see *Results* section), it reflects the general

pattern that results from the values of selection gradients averaged across the four sites.

Juvenile growth rate and foraging risk

Under natural conditions in the field, damselfish typically remain near shelter, but will occasionally swim a short distance away (10-50 cm) and feed in the water column. Swimming farther away from shelter may incur a greater risk of predation by piscivorous fishes that feed in the water column (Hixon 1991, Hobson 1991, Hixon and Carr 1997). Because faster growth rate and larger size may be correlated with greater risk-taking behavior (Stamps 2007, Biro et al. 2004), and because variation in foraging distance may be a mechanism contributing to selective mortality of *Stegastes partitus*, we conducted a laboratory experiment to examine the effects of growth rate and body size on individual willingness to take risks while foraging.

We collected recently settled fish (< 1 week post settlement) from the field and housed them in laboratory aquaria (15 fish per 144L aquarium) where they were reared on a diet of household aquarium fish flakes. Fish were measured and individually tagged with a subcutaneous injection of elastomer (Northwest Technologies, Shaw Island WA). Fish were randomly assigned to either high (10% body weight per day) or low (5% body weight per day) feeding treatments and kept in laboratory aquaria for 68 days. The experiment was designed to measure how far away from shelter an individual would swim when feeding. Experimental trials were

conducted in seawater flow-through glass aquaria that measured 1.2m long X 0.6m high X 0.2m wide (n=4). Shelter was provided by a small PVC tube that was placed at the base of a standpipe drain located 10cm from the wall of the aquarium (Fig. 2). Nylon twine was attached around the exterior of the aquarium to delineate the distance away from shelter at standard intervals (0, 10, 20, 40, 60, and 80cm). Opaque black plastic was wrapped around each tank to minimize the effects of observer presence on fish behavior. Approximately 5 minutes prior to each trial the flow of seawater into the tank was stopped to minimize water flow in the tank.

For each trial, a single fish was introduced into the aquarium and directed into the shelter. Fish were allowed to acclimate within the shelter until they began to make regular swimming bouts at short distances away from the shelter (5-12cm). Feeding trials began once fish had emerged from shelter and resumed "normal" swimming behavior within the tanks (i.e., once fish had swam >10cm away from shelter). Unless feeding, fish never swam further than 15-20cm from shelter. To examine foraging risk, we added food to the water column and measured the distance that an individual was willing to travel from shelter when feeding. In these experimental trials, damselfish would typically remain near shelter (within 5-12cm) until food was detected. Food detection was marked by a pause in routine swimming behavior and an alignment of the fish toward the food in the water column. Feeding did not always immediately follow detection, but eventually fish typically swam directly toward the food, often pausing halfway before resuming swimming toward the food. Feeding began at a distance of 80cm away from the shelter and subsequent

additions of food were delivered progressively closer to the shelter (i.e., at distances of 60, 40, 20, 10 and 0 cm from the shelter). During each addition of food, 1ml of homogenized fish flakes in seawater was delivered to the top of the water column with a pipette. This amount of food took 20-30 seconds to sink to the bottom of the aquarium. After 30 seconds, more food was added at the next closest distance to the shelter. Food additions were stopped once fish began feeding. The distance from shelter that fish began feeding was visually estimated with the aid of nylon lines that regularly marked distance at 10cm intervals from the shelter. We used a multiple linear regression to analyze the effects of initial size, feeding treatment, and growth rate on the distance away from shelter that individuals would travel and feed. Including initial size as a covariate allowed us to statistically control for the effects of initial size and directly test the effects of growth rate on foraging risk of damselfish.

Genetic variation in juvenile growth

To get a rough estimate of environmental versus genetic effects on growth rate, we conducted a common garden experiment where juvenile fish were grown in the laboratory. A total of 20 recently settled juveniles were collected from sites near the research station and brought back to the lab, where fish were housed individually in separate 9.5 L aquaria. Aquaria received flow-through seawater at similar flow rates. Seawater came from a common source and was filtered to remove food particles. Water temperature varied throughout the study, but there was no

difference in water temperature among the individual tanks. Each individual received a standard amount of household aquarium fish food per day (0.010 g [dry weight] per day at the beginning of the experiment and later increased to 0.02 g/day). Fish were periodically measured and the experiment lasted for 54 days.

Variation in growth will have both genetic and environmental components. To assess how much of the phenotypic variation in growth rate was due to genetic sources of variation, we compared the observed variation in lab growth to variation in early growth rate for fish that were measured in natural populations in the field. Assuming no appreciable environmental differences in the lab, variation in lab growth rates should represent only genetic variation. In contrast, natural growth rates should reflect both genetic and environmental variation. Expressing lab variation as a fraction of natural variation should therefore provide an estimate of the coefficient of genetic determination for growth rate (Falconer and Mackay 1996). We first tested for an effect of location within the lab (three aquaria were situated on each lab bench and tanks on lab benches may have received differences in light levels or visual stimuli) by a one-way ANOVA with "location" (bench) as a factor. Because no effects of aquarium location were detected (see *Results* section), we compared the observed variance in juvenile growth rate of the lab-grown individuals to the observed variance in growth for a sample of 20 of 91 fish that were tagged and re-measured at one of our study populations located near our collection location. To estimate the mean and 95% confidence interval for the coefficient of genetic determination, we divided the variation in growth rate for the 20 lab-grown fish by

the variation in growth rate for a sample of 20 field-tagged fish, repeated this procedure for 1000 randomized samples from the distribution of the 91 tagged fish in the wild population. We calculated the mean value, and used the 2.5 and 97.5 percentiles as the lower and upper limits for the 95% confidence interval.

Results

Estimating growth form

Results of the simulations suggest that the VBGE provided an accurate description of individual growth for *S. partitus* with as little as four observations including initial size at hatching (Fig. 3). Increasing the number of observations per individual increased the precision of the VBGE estimates. However, having relatively few samples per individual growth curve did not appear to bias the parameter estimates (Fig. 3).

Size, growth rate, and selective mortality

Quadratic regression analyses of the relationship between relative fitness and phenotypic values for both asymptotic size (TL_{max}) and deviations in growth rate (D_k) revealed that selection on both of these traits could be strong (Table 1A). Linear selection on TL_{max} was positive at most sites, indicating that individuals that were large as adults experienced greater survival, on average. However, nonlinear selection coefficients for TL_{max} were negative, also suggesting the selective loss of individuals with extreme values of this trait (Table 1A). Linear selection on D_k was

generally negative, indicating lower average survival for individuals that grew fast as juveniles. However, positive nonlinear selection coefficients suggest that relative survival was high for some individuals with relatively fast or slow growth rates. There was strong evidence of correlational selection at only one site, Norman's Pond Cay (Table 1A).

The four study populations also varied in several factors that may affect the presence and/or intensity of selective mortality. Most notably, adult population density and juvenile survival varied appreciably among the study populations (Table 1B) and were correlated with the intensity of selection. Variation in the intensity of selection among sites was therefore examined with these ecological factors in mind. At Norman's Pond Cay, a site characterized by high adult population density, structurally complex habitat, and relatively high survival, there was strong evidence for linear selection for large asymptotic size and slower-than-average growth rate (Table 1A). At Windsock Cay, a site that had medium population density, but the lowest value for juvenile survival, there was strong evidence only for linear selection for larger asymptotic size (Table 1). At NW and SE Barracuda Rocks, two sites with low densities of adults and high survival of juveniles, there was little evidence of linear selection on asymptotic size, but evidence for linear selection for slower-than-average growth rate (Table 1A). In general, sites with a greater density of adults experienced stronger selection on asymptotic size (Table 1; Fig.4), suggesting a mechanistic link between population density and the magnitude of linear selection on asymptotic size.

Selection on size-at-age

Interpretation of selection on TL_{max} and D_k can be aided by examining how each of these parameters influenced length-at-age. For *S. partitus*, the degree to which each parameter influenced length-at-age depended on age. Table 2 summarizes correlations between growth parameters and size at various ages post-settlement (50, 100, 200, 500 and 700 days). Early in life, length at age is uncorrelated with TL_{max}. However, most individuals had approached TL_{max} by about 500 days post-settlement, and size during the later phase of life was well correlated with this parameter. In contrast, relative growth rate (D_k) was strongly correlated with length at age early, but not late in life (Table 2).

Because D_k influences size-at-age early in life and TL_{max} influences size-at-age later in life, the pattern of linear selection for large values of TL_{max} and small values of D_k may indicate an ontogenetic shift in the direction of size-selective mortality. This pattern was observed at Norman's Pond Cay, the site with the strongest statistical evidence for selection on TL_{max} and D_k. Figure 5A illustrates differences in the distributions of length at 50 days post-settlement for fish that died as juveniles (i.e., between 50 and 300 days post-settlement) vs. those that survived longer (> 300 days). Individuals that survived this phase tended to be slower growing and smaller (Fig. 5A). However, later in life an opposite pattern was observed. Of those individuals that survived > 200 days post-settlement, fish that survived > 400 days tended to be larger than those that died sometime between 200

and 400 days post-settlement (Fig. 5B). Although data are presented only for Norman's Pond Cay, the general pattern of ontogenetic variation in selective mortality is consistent with the overall average values of selection (average linear selection gradients weighted by number of observations at each site were 0.126 and -0.142, for TL_{max} and D_k).

Juvenile growth rate and foraging risk

Juvenile fish housed in the lab exhibited a wide range of growth rates (0.0018-0.034 mm/d; CV = 88%) during the 68-day experiment. On average, fish in the high-ration treatments grew faster. However, there was considerable overlap in the distribution of growth rates for fish in the high- and low-ration treatments. Differences in food ration between treatments did not affect the distance away from shelter that individuals would swim and feed (P = 0.93; Table 2). However, both initial size and growth rate were positively associated with greater foraging distance (Table 2).

Genetic variation in juvenile growth

Juveniles grown in the common garden experiment exhibited considerable variation in growth rate (range = 0.001-0.026 mm/d; CV = 69%). There was no effect of tank location within the lab (ANOVA, P = 0.57), so the blocking term was removed from further analysis. Comparing the observed variance in juvenile growth rate of the 20 lab-grown individuals to the variance in growth rate for 1000

randomly-selected samples of 20 individuals from a group of 91 individuals that were tagged and re-measured in the field, the coefficient of genetic determination (i.e., the proportion of variation in growth rate that can be attributed to genetic causes) was estimated to be 0.658 (bootstrapped 95% CI = 0.365-0.951).

Discussion

By estimating growth parameters for each individual fish and following the fate of these individuals throughout their life on the reef, we found substantial net effects of selection on both asymptotic size and relative growth rate. Although previous studies of selective mortality of teleost fishes have generally concluded that large fish experience greater survival rates (Sogard 1997), the results of this study highlight two sources of variability in viability selection on body size. First, patterns of selection on size and growth varied considerably among the four sites studied. Second, at least at some sites the observed pattern of selection corresponded to an ontogenetic reversal in the direction of viability selection on size-at-age. Individuals that survived longest tended have large asymptotic sizes, but also tended to be those that grew relatively slow, resulting in small size-at-age during the juvenile phase. This pattern appeared to be driven by greater mortality of fast growing juveniles followed by greater mortality of small adults (cf. Fig 5).

The loss of fast-growing juveniles may be explained by a correlation between growth rate and foraging risk (Sih et al. 2004, Stamps 2007). Juvenile *S. partitus* are vulnerable to many reef-associated predators and generally remain close to shelter

(Nemeth 1998, Carr et al. 2002). Bicolor damselfish are planktivores, and although individuals that forage farther away from shelter may be rewarded with greater food availability (particularly if there is competition for food), feeding excursions away from protective habitat may incur a greater risk of predation (Hixon 1991, Hobson 1991). Results of the lab experiments in this study indicated that even after accounting for greater boldness with increased body size, faster growing juveniles were willing to feed farther away from shelter, supporting the idea that faster growth is correlated with greater risk of predation. However, it is unclear whether boldness causes fast growth or fast growth causes boldness. An earlier study with individual *S. partitus* randomly assigned to high or low feeding treatments demonstrated that after six days of feeding in the lab, groups of high-ration fish were much more aggressive when transported back to natural habitat (Johnson 2008). Similar results have been documented for other species of damselfish (Booth and Beretta 2004)

Greater mortality of small adults may be explained by interference competition and size-dependent susceptibility to predation. Adult *S. partitus* are aggressively territorial and groups on coral heads often form size-dependent hierarchies where larger fish chase and harass smaller fish with relative impunity (Myrberg 1972). Although predation is likely to be the proximate agent of mortality for most reef fishes (Hixon 1991), such competitive effects can have a strong influence on susceptibility to predation (Holbrook and Schmitt 2002, Hixon and Jones 2005). Larger adults may also take over the territories of smaller adults (Myrberg 1972, personal observation), possibly relegating small individuals to

inferior territories where risk of predation is higher (e.g., due to territory location or reef structural complexity; Holbrook and Schmitt 2002). Larger adults may also be less susceptible to gape-limited predators (Stephens and Krebs 1986), leading to greater probability of survival. All three of these factors may act separately or in combination, and it is likely that they all contribute to the observed pattern of selection for larger asymptotic size.

This study also revealed considerable variation in the patterns of selective mortality among populations. Although the data we used to evaluate selective mortality came from a long-term, large-scale demographic study that was not designed to investigate selection per se (Hixon et al. unpublished), and although there are only four sites to compare, some of the spatial variation in selective mortality may be explained by variation in population density and overall survival rates. Selection for larger asymptotic size appeared to increase with greater population density of adults. Because adult *S. partitus* form size-dependent dominance hierarchies where large fish harass small fish (but not vice versa; Myrberg 1972), small fish may be at a greater disadvantage when densities of adults are high. In such situations there would simply be a greater number of large fish to harass them, thereby increasing their susceptibility to predation (see Persson et al. 1996, Zabel and Achord 2004 for similar examples). Selection on deviation in growth rate exhibited less spatial variability than selection on asymptotic size. The only obvious difference among sites was that there was little to no selection on deviation in growth rate at one site (Windsock Cay). Although reasons for this

pattern are unclear, it is worth noting that average survival of juveniles was lowest at this site, and it may be that a high overall rate of mortality precludes or obfuscates any selective mortality based on growth rate.

Limitations of this study

Although this study estimated selection on size and growth throughout the entire benthic lifespan of individuals, there are important limitations to the approach used here. We were unable to reliably describe growth form for individuals with less than three measurements. Although the VonBertalanffy growth function describes size-at-age of *S. partitus* extremely well, fitting the function to less than four data points (including initial size) resulted in imprecise parameter estimates (results not shown). In this study we only considered selective mortality of those individuals that survived long enough to be measured at least three times (~100d post settlement and greater). Because many individuals died before this point, we were unable to assess whether selective mortality operated within the first few months post-settlement. Several studies of reef fish have documented that early life history traits (e.g., growth during the planktonic larval phase, size at settlement) are positively associated with greater survival during early post-settlement life (Hare and Cowan 1997, Searcy and Sponaugle 2001, Shima and Findlay 2002, McCormick and Hoey 2004, Raventos and Macpherson 2005, Holmes and McCormick 2006, Vigliola et al. 2007). However, selection on post-settlement (rather than planktonic) growth remains little studied (Gagliano et al. 2007). Investigating the influence of growth

on immediate, post-settlement mortality would require much more frequent measurements of individuals or the use of otolith measures to provide an indirect, but continuous record of growth history (Campana and Neilson 1985).

Another limitation of this study is that the method of estimating growth parameters may have inflated the estimates of nonlinear (quadratic) selection gradients. Simulation analyses demonstrated that although VBGE parameter estimates were unbiased with as little as four measurements per individual, the precision of parameter estimates increased with the number of measurements. Individuals with low fitness (short lifespans) had relatively few measurements of size-at-age, and growth parameter estimates based on a low number of post-settlement measurements were more likely to generate extreme values. In the type of selection analysis used here, the quadratic terms reflect change in trait variances and covariances (Lande and Arnold 1983). Variance in a trait can be reduced by the loss of individuals with extreme phenotypes. However, in this study, the magnitude of the quadratic terms may have also been increased by the decrease in the variability of growth parameter estimates associated with long life (and more measurements per individual). Although the procedure used to estimate growth may have biased quadratic selection terms, it is unlikely that the bias varied systematically among sites. Comparing non-linear selection among sites may therefore be heuristically valuable, despite potential bias in the absolute values.

Response to selection on growth form

Juvenile growth rate is likely to be under a moderate degree of genetic control. The coefficient of genetic determination calculated from the common garden growth experiment was relatively high (mean = 0.658, 95% CI = 0.365-0.951). Although subtle sources of environmental variation among individuals grown in the lab will tend to inflate such estimates, the procedure used here provided a rough estimate of broad-sense heritability for juvenile growth (Falconer and Mackay 1996). Even if the estimate of genetic determination is inflated, it is nevertheless likely that juvenile growth rate in *S. partitus* is a moderately heritable trait. Although the amount of information is limited, heritability values for body length in other species of fish average 0.30 (SD = 0.21 from 17 studies; reviewed by Law 2000).

Given moderate heritability of growth and the observed rates of selection on both components of growth, evolution toward larger asymptotic size and slower-than-average growth rate is expected. However, the predicted response to selection on growth may be complicated by interdependencies in growth, food availability and behavior. In this study, a measure of boldness (foraging risk) was positively correlated with juvenile growth rate. However, a previous study (Johnson 2008) found that feeding history had a causal effect on another measure of boldness (intraspecific aggression). If increased foraging risk is a consequence of previous feeding experience, rather than a genetic predisposition to risk-taking behavior, then the association between growth and foraging risk would be due to a shared environmental factor, rather than a genetic one. In the former case, selection against

increased growth and increased foraging risk would operate on an environmental source of phenotypic variation and would not result in a genetic response (Price et al. 1988, Merila et al. 2001). In the latter case, selection would operate on a genetic source of variation and a genetic response would be expected. Future studies would benefit from disentangling how selection affects both genetic and environmental sources of variation in growth rate.

Assuming that selection on size and growth is at least partially operating on an underlying genetic effect, the response to selection may still be difficult to predict because of ontogenetic variation in selection on size-at-age. Body sizes at different ages are expected to be genetically correlated traits, in part because the genes that promote large size tend to affect size throughout an organism's life (Cheverud et al. 1983). Genetic covariance tends to be relatively high for nearby ages and low for ages that are further apart (Kirkpatrick and Lofsvold 1992). Although we have no measurements of the underlying genetic architecture for size-at-age throughout benthic life in *S. partitus*, it is likely that there is a moderate-to-high degree of additive genetic covariance among sizes since traits as distant as adult and larval size show appreciable genetic covariance (Johnson et al. in prep). Because of the genetic covariance among body sizes and the opposite patterns of selection on size-at-age for juveniles vs. adults, genetic response of growth form may be minimized. For example, at Norman's Pond Cay direct selection on asymptotic size was strong (linear selection gradient = 0.251) but the response to direct selection may be substantially countered by a correlated response to opposing selection on relative

growth rate (linear selection gradient = -0.198), a trait that was strongly correlated with juvenile size.

The values of linear selection for larger asymptotic size documented in this study are consistent with the general pattern of selection for larger body size in many organisms (Kingsolver and Pfenning, 2007). However, both ontogentic and spatial variation in viability selection on body size may lead to a complex evolutionary response to selection on body size. The results of this study suggest that different aspects of growth form (adult size and early growth) may be subject to strong linear selection in opposite directions. Understanding the evolutionary response to such selection will require measurement of the quantitative genetic parameters of growth form (i.e., additive genetic [co]variances of body size at different ages; Kirpatrick et al. 1990). Particularly needed are quantitative genetic estimates for size and growth in wild populations of marine fishes (e.g., Shikano 2008, DiBattista et al. 2009). Because body size influences other ecologically important traits (e.g., reproductive output and timing), evolutionary responses to selection on body size may exert considerable influence on the dynamics of populations. A more detailed understanding of selection on size and growth may therefore be very useful in informing management and conservation, particularly for species such as marine fish that are subject to both natural selection and artificial selection via fishing mortality on body size (Gardmark et al. 2003, Conover 2007, Edeline et al. 2007).

Acknowledgments

We are very thankful to many people who helped out in the field and made this labor-intensive study possible: G. Almany, A. Altieri, C. Bartels, E. Bartels, A. Bartholomew, M. Bond, K. Buch, B. Byrne, M. Carr, M. Christie, N. Ehlers, D. Frerich, L. Hatley, W. Head, S. Hixon, B. Kakuk, K. Kroecker, A. King, B. McLeod (super assistant), J. Noell, M. Novak, K. Overholtzer-McLeod, A. Stier, M. Webster, and T. Young. We are also grateful to the staff of the Caribbean Marine Research Center (CMRC), especially T. Wolcott and B. Gadd, for greatly facilitating our long-term research. F. Moye assisted with the laboratory experiments. This manuscript comprises a chapter from the senior author's doctoral dissertation (M.A.H. Major Professor), and benefited greatly from reviews by his graduate committee: S.J. Arnold, S.A. Heppell, D.W. Schafer, and D. Robinson. Financial support was provided by an NSERC postgraduate scholarship to D.W.J; by NSF grants OCE-00-93976, OCE-05-50709, and OCE-08-51162 to M. Hixon, and by grants to M. Hixon from the National Undersea Research Program, courtesy of the Caribbean Marine Research Center.

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Table 4.1. Summary of selection analyses and population characteristics. A: Phenotypic selection gradients for asymptotic size (TL_{max}) and relative growth rate (D_k) at each of the four study populations. B: Ancillary data on mean population density and mean survival rates in each population over 7 years of demographic monitoring.

Site		Normans Pond Cay	Windsock Cay	NW Barracuda Rocks	SE Barracuda Rocks
No. of individuals		89	66	32	87
A. Phenotypic selection summaries					
Linear selection gradients	Symbol				
TLmax	β_1	0.251***	0.212**	-0.107	0.0631
Dk	β_2	-0.198**	-0.0119	-0.187	-0.166**
Quadratic selection gradients					
TLmax	γ_{11}	-0.131*	-0.056	-0.315*	-0.161**
Dk	γ_{22}	0.183*	0.224*	-0.0480	0.0096
TLmax X Dk	γ_{12}	-0.125*	0.0348	-0.079	-.0839
	Note: *** P < 0.001, ** P < 0.01, * P < 0.05				
B. Population characteristics					
Mean population density (per 21 plots)					
Juveniles		45	48	13.87	45.4
Adults		40.85	31.6	20.9	27.0
Mean survival (monthly)					
Juveniles		0.78	0.69	0.83	0.86
Adults		0.92	0.90	0.91	0.86

Table 4.2. Correlations between estimated growth parameters of individuals and total length at different ages (expressed as days after hatching).

	Size-at-age				
	50	100	200	500	700
TLmax	-0.02	0.42	0.83	0.98	1.00
D_k	0.95	0.82	0.45	-0.18	0.03

Table 4.3. Analysis of covariance describing how foraging risk (distance individual fish travelled from shelter and fed) was affected by initial body size (TL), food ration (high vs. low), and growth rate (mm/d).

	Coefficient	SE	*t*	*P*
Initial body size	33.9	7.51	4.524	< 0.0001
Food ration	-0.843	9.51	-0.089	0.93
Growth rate	1957.1	458.8	4.267	0.0002

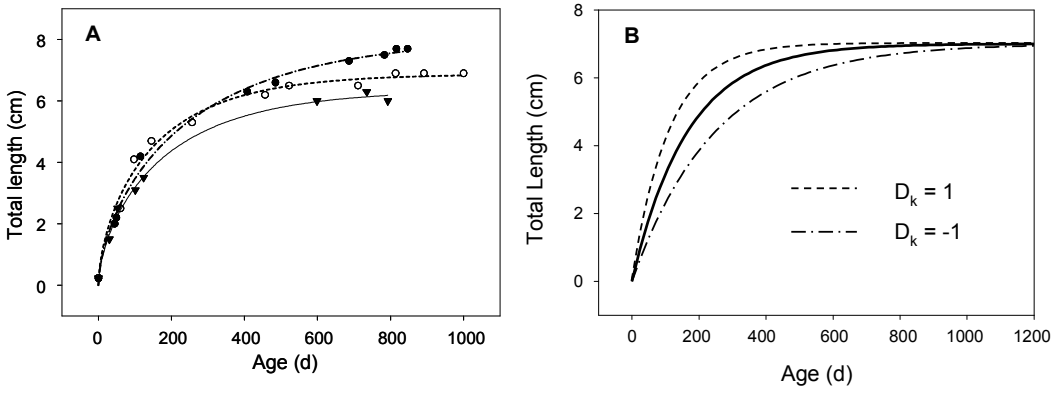

Figure 4.1. Illustration of the growth form for body size of *S.partitus* and growth parameters used in the selection analysis. Panel A illustrates three examples of the Von Bertalanffy growth equation fit to individual size-at-age data for the bicolor damselfish, *Stegastes partitus*. Age is expressed as days after hatching. Panel B illustrates the relationship between relative growth rate (D_k) and growth form. For a fixed asymptotic size, example growth curves are plotted for (D_k) values 1 standard deviation above the mean (dashed line) and 1 standard deviation below the mean (dot-and-dashed line).

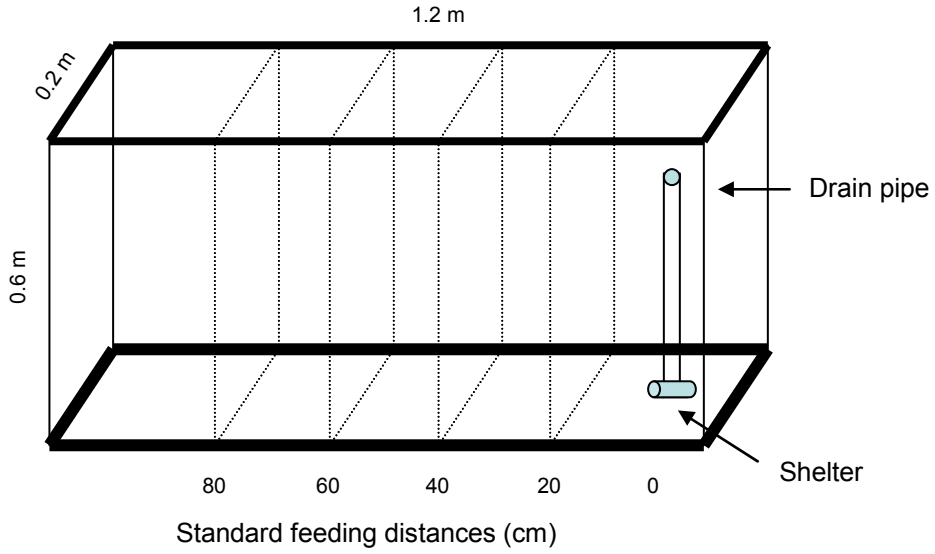

Figure 4.2. Experimental apparatus used to examine variation in the distance that individual fish were willing to leave shelter and forage. Food was delivered at progressively closer distances until the fish left the shelter and began feeding.

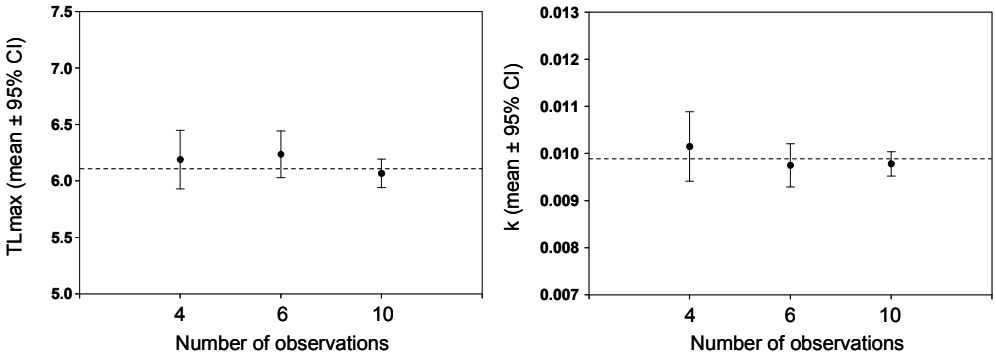

Figure 4.3. Effect of the number of observations per individual growth curve on estimates of Von Bertalanffy growth parameters. For each replicate, parameters describing an individual Von Bertalanffy growth curve were estimated by fitting a nonlinear least squares regression to simulated size-at-age data. True parameter values were based on population means and are represented by the dashed lines (TL_{max} = 6.15, k = 0.00995, random error SD for individual size-at-age = 10% of "true" size-at-age). Mean and confidence intervals for each group (i.e., individual growth curves with 4, 6, and 10 observations) were calculated from 100 randomizations.

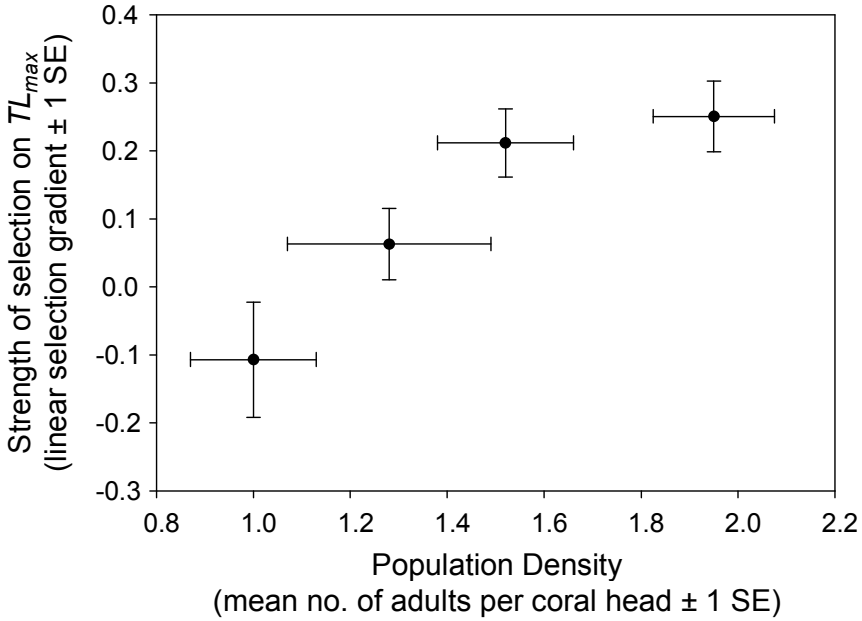

Figure 4.4. Relationship between strength of selection on asymptotic size and population density for the four sites studied.

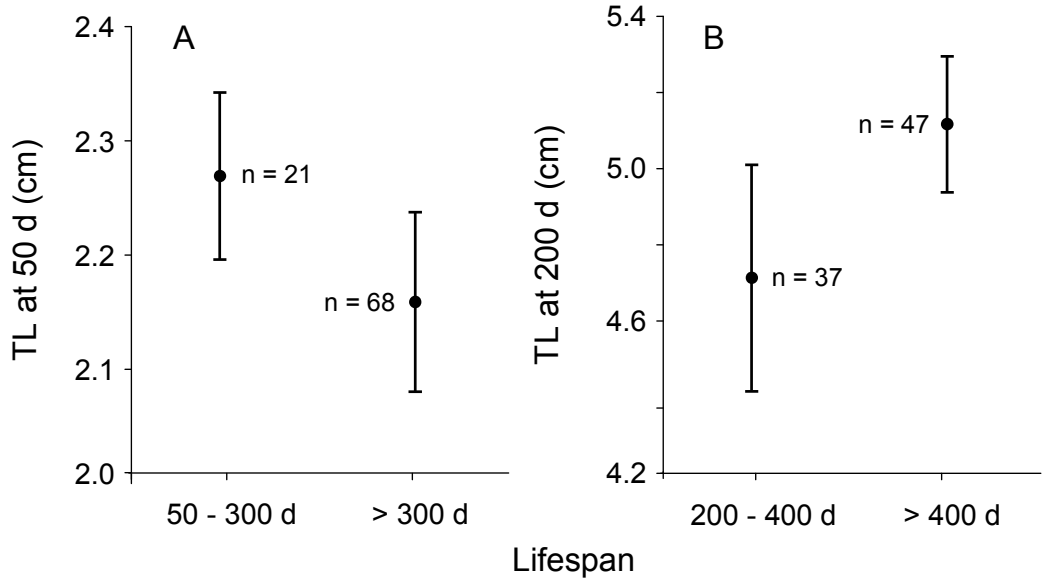

Figure 4.5. Ontogenetic variation in size-selective mortality of *S. partitus* at Norman's Pond Cay. Each panel illustrates an episode of selective mortality by comparing the distribution of size-at-age (means ± 95% CI) between individuals that died during particular intervals of time and those that survived. A: Relationship between juvenile survival and length at 50 days post-settlement. B: Relationship between adult survival and length at 200 days post-settlement.

CHAPTER 5: GENERAL CONCLUSIONS

The results of this study suggest that viability selection on larval size can be substantial, and that the selective component of mortality during the larval and juvenile phases is likely to be a significant driver of variation in population replenishment. Moreover, the review of studies examining selection on larval size suggested that even small changes in mean larval size may result in considerable changes in the relative magnitude of selective mortality. For example, predicted values of relative monthly survival during larval and early juvenile phases for larvae with mean sizes at hatching 0.5 SD below and 0.5 SD above the observed mean were approximately 70% and 111% of the predicted value for averaged sized larvae. However, strong viability selection on larval size appears to be balanced by maternal selection favoring the production of more, smaller larvae. Consistent with theoretical predictions (e.g., Smith and Fretwell 1974) the observed mean size was estimated to be near the value that optimizes maternal fitness, rather than larval survival.

Traits such as larval size are still likely to be capable of adaptive phenotypic evolution. Heritability values for both larval size at hatching and swimming performance were moderate ($h^2 = 0.29$ and 0.21, respectively), suggesting appreciable capacity for an evolutionary response to selection. Indeed, the balance of maternal and larval selection may have contributed to the preservation of additive genetic variation underlying larval traits (reviewed by Roff 1997). Any shift in the

selection balance would be expected to produce an evolutionary response in larval traits. However, in the absence of major environmental or ecological changes, shifts in selection are more likely to manifest as fluctuations in the magnitude of selection (Lande 2007). Over long time periods, the balance between larval and maternal selection on larval size may keep the mean value of larval size near an equilibrium value. However, larval traits may still respond to fluctuations in selection. Because of moderate heritability values, there may be persistent, small mismatches between observed mean size and the phenotypic value that maximizes maternal fitness (Hendry and Gonzalez 2008).

Additionally, larvae may exhibit a substantial evolutionary response if shifts in the selection balance are maintained. This study revealed strong genetic correlations between adult size and larval traits. Constant selection on adult size, as expected under fishery selection, may therefore cause a correlated evolutionary response in larval traits. The additional effects of selection for smaller adults (typical of fishery selection; Law 2000, 2007) are predicted to shift the balance between larval viability selection and maternal selection on larval size and result in the evolution of smaller larvae. The results in chapter 3 demonstrate that such effects may have potentially severe consequences for long-term changes in population replenishment.

Natural selection on body size may also cause correlated responses in larvae. However, fishery selection is typically much stronger and more consistent than natural selection (Edeline et al. 2007, Carlson et al. 2007). Chapter 4 examined

viability selection on body size in *Stegastes partitus*. By estimating growth parameters for individually-tagged fish and following the fate of these individuals throughout their life on the reef, I found substantial net effects of selection on both adult size and relative growth rate. Although previous studies of selective mortality of teleost fishes have generally concluded that large fish experience greater survival (Sogard 1997), the duration of most studies has been short and inferences about lifetime selection on size are limited. This study highlighted two sources of variability in lifetime viability selection on body size. First, patterns of selection on size and growth varied considerably among the four sites studied. Second, at least at some sites the observed pattern of selection corresponded to an ontogenetic reversal in the direction of viability selection on size-at-age. Individuals that survived longest tended have large asymptotic sizes, but also tended to be those that grew relatively slow, resulting in small size-at-age during the juvenile phase. This pattern appeared to be driven by differential mortality of fast growing juveniles followed by differential mortality of small adults, suggesting that the relative advantage of size and growth may change throughout ontogeny.

Overall, this research indicates that a complex interplay among trait variation, phenotypic selection, and demographic rates may have strong effects on both evolutionary responses and population dynamics. Our understanding of such interactions will be substantially advanced by applying evolutionary quantitative genetics to traditional studies of demography and population dynamics. A combination of these two approaches can yield significant insight into both basic

evolutionary questions (e.g., what forces determine optimal size of larvae?) and applied ecological problems (e.g., can fishery selection cause a correlated, evolutionary response in larval traits?). Because variation in larval survival can be such a large source of variability in population replenishment, understanding how trait variation, selection, and evolutionary responses affect larval traits and survival will extremely useful in informing successful conservation and management of marine fishes.

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APPENDIX

APPENDIX A, SUPPLEMENTARY MATERIALS, CHAPTERS 2 & 3

Demographic monitoring and quantitative genetics

DNA extraction and microsatellite typing

Tissue was placed in a urea-based storage solution consisting of 10mM Tris, 125mM NaCl, 10mM EDTA, 1% SDS, 8M urea, pH adjusted to 7.5 with HCL. DNA was extracted using a protocol for urea stored samples (J.F.H. Purcell, University of Miami, personal communication). Tissue was incubated in extraction buffer (75mM NaCl, 25mM EDTA, 1% SDS) along with proteinase K (2uL of 20mg/ml) at 55°C for 2 hours. One half volume of Ammonium acetate (7.5M) was added followed by a standard isopropanol precipitation (Sambrook & Russell, 2001). DNA was diluted to approximately 100ng/ μL.

Samples were genotyped at seven microsatellite loci originally described by Williams *et al.* (2003). The seven loci employed in this study were *Sp*GATA16, *Sp*GATA40, *Sp*AAC41, *Sp* AAC42, *Sp*AAC33, and *Sp*AAC47. PCR reactions contained 1.5mM $MgCl_2$, 0.2mM dNTPs, 0.2 U *Taq* DNA polymerase (Promega), 10 μM of each primer, and 2.0μL template in a total reaction volume of 15 μL. Thermocycling profiles consisted of an initial denature at 94°C followed by 35 cycles of 30 seconds at 94°C, 45 seconds at 52°C, and 45 seconds at 72°C. Some loci had different optimal annealing temperatures and this information can be obtained from the authors upon request. PCR products were electrophoresed on an ABI 3100 automated sequencer and allele sizes were determined with the fragment

analysis software GENOTYPER 3.7 (Applied Biosystems). Approximately 5% of individuals were re-run through the entire procedure due to difficulties in scoring alleles and to calculate an approximate error rate. Low quality electropherograms were more common in larvae, though a second round of genotyping usually resulted in clearly defined alleles. A small portion of larvae (<1%) were dropped from analyses due to unsuccessful amplification, which was likely due to insufficient amounts of template DNA for successful PCR.

Data assessment

Each locus was tested for departure from Hardy-Weinberg equilibrium (HWE) using GENEPOP 3.4 (Raymond & Rousset, 1995). A total of 10,000 batches and 5,000 iterations per batch were employed to reduce the standard errors below 0.01 (Table S1). The same number of batches and iterations were used to calculate linkage disequilibrium among all pairs of loci (Table S2). All loci were in linkage equilibrium justifying the multiplicative combination of exclusion probabilities. One locus, GATA 40, showed deviation from HWE after a Bonferroni correction, suggesting possible null alleles. Because CERVUS can explicitly account for genotyping error and null alleles, we decided to keep this locus in our analyses. Furthermore, we allowed for one locus to mismatch based upon study-specific error rates, which resulted in few differences between parent-offspring pairs that were identified by CERVUS and those identified by Mendelian incompatibility.

Tests of relatedness

We first calculated an overall measure of relatedness among breeding adults using Queller and Goodnight's relatedness metric[1]. Mean relatedness values and confidence intervals were calculated using 1000 bootsraps in GENALEX [2]. Overall relatedness values were negative suggesting that these adults are not related to one another (mean: -0.008, 95% confidence interval: -.02 to -.001). Calculations employing other relatedness metrics (e.g., Lynch and Ritland 1999[3]) yielded a similar pattern.

Because the above relatedness measures consider every pair-wise comparison among breeding adults, we performed a more detailed analysis by examining the number of alleles shared by each breeding pair. None of the breeding adults were parent-offspring pairs, as no pairs shared alleles at enough loci even after accounting for genotyping errors (see methods in Christie 2009). We used simulations to test whether the distribution of shared alleles among breeding pairs was greater than expected under random mating among unrelated individuals. Simulated individuals were created by drawing alleles, at random, from a pool of potential alleles based on the allele frequencies at each locus. We created simulated individuals until 135 pairs were created, the number of observed breeding pairs. For each simulated pair, we calculated the number of loci that shared at least one allele. This procedure was repeated 1000 times. To create a distribution of the expected number of loci to share

an allele among simulated unrelated individuals, we calculated the mean (out of the 1000 simulated data sets) number of pairs that shared an allele at 0, 1, 2 etc. loci (Figure S1). A one-tailed Kolmogorov-Smirnov two-sample test determined that the observed distribution of alleles shared among our breeding pairs was not greater than expected by mating among unrelated individuals (p-value = 0.61). Furthermore, the average number of loci (out of 7 total) among the 135 breeding pairs that shared an allele was 1.79 (range: 0 to 4), well within the range of values expected for unrelated individuals. These results, along with the stochastic nature and high mortality rates associated with larval dispersal in marine organisms, suggest that adults in this study were unrelated.

Genetic covariance estimates

Mean and 95% confidence intervals for estimates of size-dependent maternal effects and genetic covariances were generated using standard resampling procedures. For each of 1000 iterations, the 54 sires within the data set were sampled with replacement. Sires contributed multiple families (often from different mothers) to each iteration, but because measurements of larvae reared by the same sire are not independent, the resampling was conducted at the level of the sire. At each iteration, size-dependent maternal effects and genetic covariances were estimated as described above. The 2.5^{th} and 97.5^{th} quantiles of the distribution of resampled replicates were used to estimate the 95% confidence limits.

Selective mortality of larvae

We compiled estimates of size-selective mortality from published studies that examined whether size-at-hatching (SAH) of fishes influences larval and/or post-settlement survival for multiple cohorts. In these studies, size at hatching was inferred from size of otolith increments and selection was measured by comparing the distributions of SAH values for initial samples of settling fish (typically collected from light traps or plankton tows) to the distribution for groups of survivors collected in the field weeks to months later (i.e., the same cohort sampled at a later age). These measurements of selection assume that the same cohort is sampled at both times. We believe that this assumption is likely to hold for these studies. Otolith structure permitted the estimation of ages for all fish in these studies. Settlement dates were back-calculated for survivors to ensure that they settled at the same time as the initial sample. Many of the species studied (e.g., all the species studied in sources 5-7 in Table S6) are relatively sedentary as benthic juveniles. For such species, randomly-selected samples of settlers should be representative of the original population of settlers. Other species (those listed in sources 7-9 in Table S6) are more mobile, but were sampled within gulfs and lakes, such that migration from or to the study region was unlikely.

Larval responses to selection on adults

We calculated response of larvae to selection on adults by multiplying adult selection differentials by the sum of the values of genetic covariance and size-dependent maternal effects. Relative survival of larvae was then calculated by inserting this value into our equation describing relative, daily survival of larvae. We quantified uncertainty in these predictions by repeatedly calculating relative survival values from resampled data. For each iteration we calculated resampled genetic parameter estimates as described above. We then used a similar resampling procedure to calculate regression statistics relating selection differentials on larval size-at-hatching to the mean values of SAH in each cohort. These regression statistics were used to estimate the relative survival surface. Relative survival was calculated for each of 1000 iterations and the 2.5^{th} and 97.5^{th} quantiles of these resampled values were used to delineate 95% confidence intervals about our predicted survival values. We examined variation in fishery selection differentials by predicting larval response to adult selection operating at three different intensities.

Table A1. Summary statistics for parent-offspring regressions. All variables were averaged across all clutches produced by each sire in the study. Each of the averaged response variables were weighted by the number of clutches used to estimate the average and weighted least squares was used to estimate regression parameters.

Table A1

2006 - Effect of sire size on larval size (SL)

		coef	SE	t-value	*P*
Full model:	Intercept	3.270	10.160	0.322	0.750
(resid. df = 32)	Asymptotic size	0.169	0.063	2.682	0.012
	Average density	0.046	0.030	1.547	0.132
	Average temperature	-0.106	0.346	-0.309	0.760
	Site	-0.253	0.240	-1.058	0.299
Reduced model:					
(resid. df = 35)	Intercept	0.023	0.271	-1.058	0.297
	Asymptotic size	0.183	0.076	2.408	0.021

2006 - Effect of sire size on larval swimming performance

		coef.	SE	t-value	*P*
Full model:	Intercept	3.760	8.420	0.447	0.659
(resid. df = 26)	Asymptotic size	0.176	0.060	2.930	0.007
	Average density	0.073	0.046	1.582	0.126
	Average temperature	-0.023	0.205	-0.114	0.910
	Site	-0.101	0.270	-0.374	0.711
Reduced model:					
(resid. df = 29)	Intercept	-0.067	0.197	-0.340	0.736
	Asymptotic size	0.169	0.072	2.347	0.026

2007 - Effect of biological sire size on larval size (SL)

		coef.	SE	t-value	*P*
Full model:	Intercept	6.370	9.180	0.694	0.498
(resid. df = 16)	Asymptotic size	0.241	0.085	2.835	0.012
	Average density	0.088	0.086	1.033	0.317
	Average temperature	-0.234	0.312	-0.750	0.464
	Site	0.411	0.421	0.976	0.344
Reduced model:					
(resid. df = 19)	Intercept	-0.041	0.186	0.976	0.341
	Asymptotic size	0.248	0.075	3.320	0.004

2007 - Effect of biological sire size on larval swimming performance

		coef.	SE	t-value	*P*
Full model:	Intercept	4.638	7.237	0.641	0.531
(resid. df = 16)	Asymptotic size	0.223	0.092	2.424	0.028
	Average density	-0.013	0.067	-0.190	0.852
	Average temperature	-0.153	0.246	-0.620	0.544
	Site	-0.255	0.332	-0.768	0.454
Reduced model:					
(resid. df = 19)	Intercept	0.032	0.210	0.152	0.881
	Asymptotic size	0.239	0.091	2.611	0.017

2007 - Effect of foster sire size on larval size (SL)

		coef.	SE	t-value	*P*
Full model:	Intercept	14.890	7.008	2.125	0.050
(resid. df = 16)	Asymptotic size	-0.079	0.175	-0.452	0.658
	Average density	0.114	0.103	1.107	0.287
	Average temperature	-0.435	0.238	-1.828	0.088
	Site	0.422	0.397	1.063	0.305
Reduced model:					
(resid. df = 19)	Intercept	-0.070	0.200	-0.350	0.730
	Asymptotic size	-0.128	0.177	-0.723	0.478

2007 - Effect of foster sire size on larval swimming performance

		coef	SE	t-value	*P*
Full model:	Intercept	3.879	4.435	0.875	0.395
(resid. df = 16)	Asymptotic size	0.061	0.110	0.555	0.587
	Average density	0.088	0.065	1.342	0.198
	Average temperature	-0.144	0.151	-0.954	0.354
	Site	-0.048	0.252	-0.191	0.851
Reduced model:					
(resid. df = 19)	Intercept	0.018	0.115	0.160	0.875
	Asymptotic size	-0.008	0.103	-0.076	0.940

Table A2. Correlations among size-related traits of adults in this study. In this data set, father-mother pairs often mated with each other more than once, so p-values associated with each correlation were calculated using Mantel (randomization) tests.

Year		Actual size of sire		Asymptotic size of dam		Actual size of dam	
		r	*P*	*r*	*P*	*r*	*P*
	Asymptotic size of sire	0.712	< 0.001	**0.340**	**0.038**	0.101	0.314
2006	Actual size of sire			0.153	0.138	0.186	0.064
	Asymptotic size of dam					0.600	< 0.001
	Asymptotic size of sire	0.820	< 0.001	0.180	0.096	0.059	0.598
2007	Actual size of sire			0.083	0.470	0.182	0.090
	Asymptotic size of dam					0.694	< 0.001

Table A3. Correlations between parental age and larval traits.

	SAH				Swimming performance			
	2006		2007		2006		2007	
	r	*P*	*r*	*P*	*r*	*P*	*r*	*P*
Paternal age	0.111	0.466	0.075	0.684	0.153	0.246	0.095	0.760
Maternal age	-0.089	0.704	0.160	0.506	-0.083	0.618	0.143	0.444

Table A4. Observed and expected heterozygosity in microsatellite loci used in parentage analysis.

Locus	K§	H_O†	H_E‡
AAT40	14	0.889	0.888
GATA16	48	0.875*	0.974
GATA40	41	0.722**	0.957
AAC33	15	0.856	0.881
AAC41	29	0.958	0.955
AAC42	22	0.944	0.945
AAC47	19	0.903	0.917

§ Mean number of alleles per locus
† Observed heterozygosity
‡ Expected heterozygosity
* Significant deviation from HWE at the 0.05 level
** Significant deviation from HWE after a Bonferroni correction

Table A5. Summary of linkage disequilibrium probabilities for microsatellite loci used in parentage analysis.

Locus 1	Locus 2	p-value*
GATA16	AAT40	0.365
GATA40	AAT40	0.552
GATA40	GATA16	0.873
AAC33	AAT40	0.594
AAC33	GATA16	0.042
AAC33	GATA4	0.428
AAC41	AAT40	0.019
AAC41	GATA16	1
AAC41	GATA40	1
AAC41	AAC33	0.035
AAC42	AAT40	0.219
AAC42	GATA16	1
AAC42	GATA40	1
AAC42	AAC33	0.02
AAC42	AAC41	0.379
AAC47	AAT40	0.188
AAC47	GATA16	0.858
AAC47	GATA40	0.198
AAC47	AAC33	0.103
AAC47	AAC41	0.19
AAC47	AAC42	0.954

* probability that any two pairs of loci are in linkage equilibrium

Table A6. Summary of studies of larval size and selective mortality

Stage sampled	Species	Family	No. of cohorts	Mean selection differential	Replicate type	Source
Benthic Juveniles	*Neopomacentrus filamentosus*	Pomacentridae	4	0.55	Temporal	5
Benthic Juveniles	*Symphodus roissali*	Labridae	2	0.74	Temporal	6
Benthic Juveniles	*Symphodus ocellatus*	Labridae	2	0.30	Temporal	6
Benthic Juveniles	*Lipophyrys trigloides*	Bleniidae	8	0.81	Temporal	7
Benthic Juveniles	*Chromis chromis*	Pomacentridae	10	0.52	Temporal	7
Pelagic larvae	*Coregonus albula*	Salmonidae	4	0.57	Spatial	8
Pelagic larvae	*Coregonus lavaretus*	Salmonidae	3	-0.15	Spatial	8
Pelagic larvae	*Scombrus scombrus*	Scombridae	4	0.25	Temporal	9†

5 Vigliola et al. 2007, *Ecology*
6 Raventos and Macpherson 2005, *Marine Ecology Progress Series*
7 Macpherson and Raventos 2005, *Marine Biology*
8 Urpanen et al. 2005, *Boreal Environment Research*
9 Robert et al. 2007, *Marine Ecology Progress Series*
† Information on day 0 not available, day 1 increment used as proxy for size-at-hatching

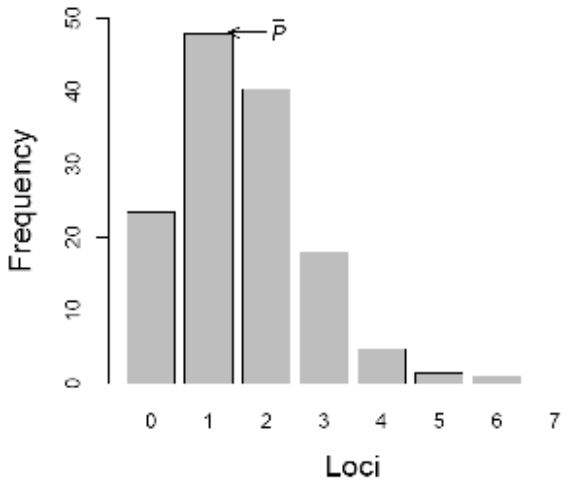

Figure A1. Distribution of the expected number of loci to share an allele averaged from 1000 sets of 135 simulated unrelated pairs. $\overline{P}$ equals the average number of loci that shared an allele among the observed breeding pairs.

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