

Ontogenetic and spatial variation in size-selective mortality of a marine fish

D. W. JOHNSON¹ & M. A. HIXON

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

Keywords:

balancing selection;
competition;
density-dependent selection;
foraging risk;
growth rate;
natural selection;
predation;
quantitative traits;
reef fish.

Abstract

Although body size can affect individual fitness, ontogenetic and spatial variation in the ecology of an organism may determine the relative advantages of size and growth. During an 8-year field study in the Bahamas, we examined selective mortality on size and growth throughout the entire reef-associated life phase of a common coral-reef fish, *Stegastes partitus* (the bicour damselfish). On average, 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 larger adult size. Large adults may be favoured because they are superior competitors and less susceptible to gape-limited predators. Laboratory experiments suggested that selective mortality of fast-growing juveniles was likely because of risk-prone foraging behaviour. These patterns 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 (reviews 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 risk of predation while foraging (Sih *et al.*, 2004; Stamps, 2007), delayed physiological development (Arendt, 1997; Metcalfe & 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 on fitness, are often unclear (Lynch & 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 (review by Blanckenhorn, 2000).

Correspondence: Darren W. Johnson, Department of Zoology, Oregon State University, 3029 Cordley Hall, Corvallis, OR, USA.

Tel.: +1 805 892 2519; fax: +1 805 892 2510;

e-mail: johnson@nceas.ucsb.edu

¹Present address: National Center for Ecological Analysis and Synthesis, 735 State St, Suite 300, Santa Barbara, CA 93101, USA.

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; Hoekstra *et al.*, 2001; Kingsolver *et al.*, 2001; Hereford *et al.*, 2004; Kingsolver & Pfenning, 2007; Siepielski *et al.*, 2009). 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 for only 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 single life stage transition) may provide an inaccurate description of the total effect of selection that operates within an entire generation (Arnold & Wade, 1984; Schluter *et al.*, 1991; Siepielski *et al.*, 2009).

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. fishes and many invertebrates), there is often considerable flexibility in size-at-age and age-specific growth rate (Wootton, 1990). For species with asymptotic growth, size-at-age will be influenced by both an individual's maximum attainable size (i.e. its asymptotic size), and how quickly it reaches 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 growth operates over an entire generation.

Size-selective mortality is common in marine fishes (reviewed by Sogard, 1997). Although most studies suggest that larger 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 specific individuals to estimate selection (e.g. DiBattista *et al.*, 2007; Olsen *et al.*, 2009) and fewer still have examined selection throughout the entire lifespan. In this study, we examined viability selection on size and relative growth rate of a marine fish from settlement through adulthood. Using data from an 8-year demographic study 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 on coral reefs in the Caribbean and tropical western Atlantic. Bicolor damselfish inhabit relatively complex coral heads that provide refuge from predators (Nemeth, 1998). Both adults and juveniles have extremely small (approximately 1–3 m) home ranges around home coral heads, except for occasional local excursions to neighbouring coral heads when mating (Schmale, 1981; Knapp & Warner, 1991). Bicolor damselfish deposit and fertilize eggs in holes on the reef

and nests are defended by males. Eggs develop on the seafloor for 3.5 days and larvae are pelagic for approximately 30 days before settling to reef habitat (Wilson & Meekan, 2002). Spawning activity follows the lunar cycle with peak reproduction occurring around the third quarter, with minimal spawning near the new moon (Robertson *et al.* 1988; D. W. Johnson, personal observation). Spawning cycles may occur year round, though in our study area reproductive activity is greatest during the summer months. Aggressive behaviour is common in larger social groups, which range from 2 to 15 fish 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 data).

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 data). During the time period of 1998–2006, tagging studies were conducted within four populations of *S. partitus* near Lee Stocking Island, Bahamas (23°46'N, 76°06'W). Local populations within each of the four coral reefs, each approximately 100 m in diameter, were sub-sampled within 22 permanent plots that were chosen haphazardly and distributed evenly over the reef. Plots measured 2 × 2 m and were centred 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, USA) just under the skin in the lightly pigmented posterior half of the body. To minimize stress, all handling and release of each fish occurred exactly where captured underwater, and each fish was handled for less than a minute. Previous studies have demonstrated that elastomer tags have negligible effects on mortality and growth of other coral-reef fishes, including damselfishes of similar size to *S. partitus* (Frederick, 1997; Hoey & McCormick, 2006), suggesting that our tagging procedure did not influence demographic rates. Tag loss was unlikely because, when fish were recaptured and measured, tags were inspected and re-applied, if necessary. Moreover, retention and visibility of elastomer tags has been demonstrated to be high over time periods comparable to the intervals between our measurements (e.g. 100% during a 76-day laboratory study; Frederick, 1997).

By using a combination of multiple tag locations (e.g. mid body vs. caudal, dorsal vs. ventral, left side vs. right side) and seven colours of elastomer, we were able to track the fates of individual fish from larval settlement (or subsequent immigration to study plots) until death. Mortality, known to occur mainly via predation (Booth & Hixon, 1999; Carr *et al.*, 2002; see also Hixon & Jones, 2005), was distinguished from local emigration by

exhaustive searches of the entire home reef and environs during each census. Movement of adults in our demographic study was minimal. The average, monthly, per-capita rate of emigration out of the 2×2 m study plots was 0.019, and all cases involved fish moving < 10 m and establishing residence on a nearby coral head. In all cases when individuals emigrated from plots, we continued to include them in the censuses and continued to re-measure them. Moreover, in our demographic study, only 9 of 484 (1.86%) fish were ever absent on one census but re-sighted on a subsequent census, and only 1 of 484 (0.21%) was absent on two consecutive censuses before being resighted on the next census. Importantly, these data summarizing encounter probabilities were collected over a 3-year period, suggesting that the encounter rate of living fish per census was effectively 100%.

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

Stegastes partitus is a conspicuous species that exhibits little post-settlement movement (Emery, 1968; Myrberg, 1972). Because our demographic study suggested that recapture rates were essentially 100%, and because each 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 (i.e. we did not need to adjust for recapture probabilities). The date of mortality was estimated as the mid-point between the first census when that individual was absent and the previous census when it was present. During the summer, when censuses were conducted weekly, the time of mortality could be estimated with a margin of error of no more than 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 < 2 months). However, even in the latter cases, the uncertainty in death age was small relative to the average lifespan of individuals in this study (530 days).

Estimation of 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 (equivalent to birth in each local population) and measured at least three times. Although recent settlers could be readily identified by their size and behaviour,

we restricted our analysis to those individuals that settled sometime between weekly censuses, such that their estimated post-settlement age was never off the true value by more than 3.5 days. Size-at-age of *S. partitus* is well described by a Von Bertalanffy growth equation (VBGE), a model of asymptotic growth that is commonly used to describe the growth form of fish:

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

where TL is the total length, TL_{\max} is the asymptotic size and k is a growth constant describing how quickly the asymptotic size is reached (Fig. 1). The model was fit to individual size-at-age data using nonlinear least squares regression, and growth trajectories were modelled from hatching (day 0) through post-settlement life. To model growth during the early stages, we used an initial size at hatching of 2.17 mm (average from a sample of 103 fish) and a 30-day larval duration (Wilson & 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 & 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 with $TL_{\max} = 7.15$ cm and $k = 0.007$. Although in our study area individual asymptotic size ranged from 6.2 to 9.7 cm, a value of 7.15 cm TL is near the overall average for fish in our selection study. 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 \pm a normally distributed random error term with mean of 0 and standard deviation of 2.5% 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

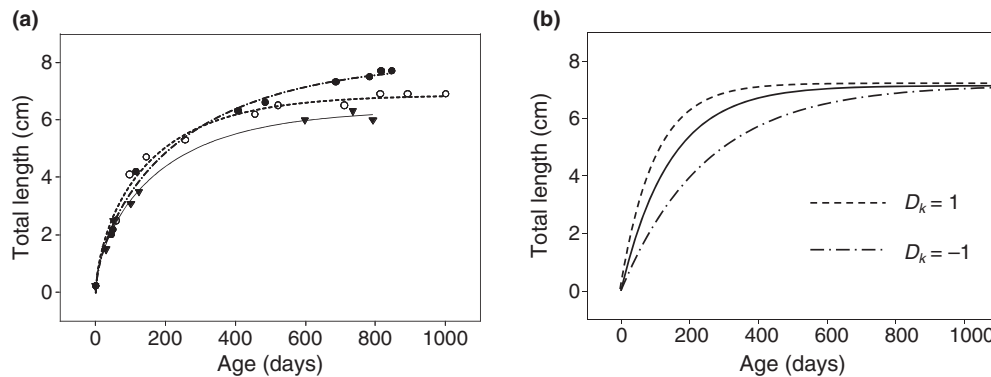


Fig. 1 (a) Three examples of the Von Bertalanffy growth equation fit to individual size-at-age data for three bicolor damselfish (*Stegastes partitus*). Age is expressed as days after hatching. (b) An illustration of variation in relative growth rate (D_k). For a fixed asymptotic size of 7.15-cm TL, growth curves are plotted for the mean D_k (solid line) and values one standard deviation above (dashed line) and one standard deviation below (dot-and-dashed line) the mean.

compared distributions of parameter estimates among samples of individuals with four observations (ages 0, 50, 100, 150 days), six observations (ages 0, 50, 100, 150, 200, 300 days) and ten 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 therefore allows 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 & Arnold, 1988). However, estimates of growth parameters will allow a comparison of trait values of survivors to the estimated trait values of nonsurvivors, thereby allowing a more accurate measurement of lifetime selection.

Size, growth rate and selective mortality

We quantified selection on size and growth rate by analysing asymptotic size (TL_{\max}) and relative growth rate (D_k) as quantitative traits. We used multiple linear regression to test the relationship between an individual's relative fitness (defined as an individual's lifespan/population mean lifespan) and that individual's values of TL_{\max} and D_k . This procedure allowed estimation of the strength and form of natural selection acting directly on each trait, assuming that selection is frequency independent, that traits have a multivariate normal distribution before selection, and that the fitness surface can be reasonably approximated by quadratic polynomials (Lande & 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 the 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 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 & 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 earlier. We used quadratic regression to estimate selection coefficients and conduct statistical tests. However, we also examined the form of the univariate selection

surfaces. For each site and trait combination, we used generalized additive models to fit cubic splines by generalized cross-validation using the program R (R development core team 2009).

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 mortality among sites was evaluated with respect to these ecological characteristics. Mean survival rates were calculated using all tagged individuals at each site in our demographic study. For each yearly cohort, we used maximum likelihood estimation to fit a 2-parameter Weibull function to the survivorship data. Survival of juveniles was summarized over a period of 0–30 days post settlement. Survival of adults was summarized over a period of 365–395 days post settlement. Survival estimates were then averaged over all 8 years of the study.

Our main analyses examined patterns of viability selection within the local population. To complement this analysis, we also calculated the correlation between lifespan and relative body size within local groups (i.e. all conspecifics within 2×2 m plots centred on home patches of coral). Such information may help identify the scale at which selective processes occur. For example, a correlation between relative size within the local group and lifespan would suggest that size-dependent interactions *within* groups are important mechanisms generating selection. In contrast, if there was no correlation between lifespan and relative size within groups, but selective mortality at the scale of the population, then it would suggest that size-selective processes occur *among* groups (e.g. because of within-site spatial differences in growth and predation). Each individual in our study was assigned a rank based on their body size relative to other conspecifics within each 2×2 m plot (1 = largest, 2 = second largest, etc.). For each study population, we calculated the correlation between body size rank and lifespan.

Selection on size-at-age

Although the parameters TL_{\max} and D_k provided an accurate summary of individual growth (see Results section) and our main selection analysis provided a summary of lifetime selection on growth form, it is also useful to compare the effects of selection on size-at-age. We examined ontogenetic variation in selection on size-at-age by examining whether, for each of eight different ages (50, 100, 200, 300, 400, 500, 600 and 700 days), size-at-age was related to survival during the next 200 days. For each interval, fitness was defined as equalling one for individuals that survived for > 200 days past the beginning of the interval, and

equalling 0 for individuals that survived for < 200 days past the beginning of the interval. We used logistic regression to test for selection on size-at-age and to estimate the average selection differential using the method described by Janzen & Stern (1998). Total length at each age was estimated from an individual's VBGE parameter estimates, and sizes were standardized by subtracting the mean value from each individual value, then dividing by the standard deviation before selection (Lande & Arnold, 1983). Mean and variance for size at each age were calculated based on estimated size values for all individuals in the study, including those that did not survive to the beginning of the interval. However, for each interval we estimated selection only for the subset of individuals that were alive at the beginning of the interval (i.e. we calculated conditional selection differentials; Lynch & Arnold, 1988). Consequently, statistical power to test for selection was much reduced for older age groups in which there were relatively few survivors. Nonetheless, this approach provides a useful means of visualizing variation in selection on size-at-age and was meant to complement our main analysis of lifetime selection on growth parameters.

Juvenile growth rate and foraging risk

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

We collected recently settled fish (< 1 week post settlement) from the field and housed them in laboratory aquaria (15 fish per 144 L 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), then randomly assigned to either high (10% body weight per day) or low (5% body weight per day) feeding treatments 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 1.2-m long \times 0.6-m high \times 0.2-m wide ($n = 4$). Shelter was provided by a small plastic tube that was placed at the base of a standpipe drain located 10 cm from the wall of the aquarium. Nylon twine was attached around the

exterior of the aquarium to delineate distance from shelter at standard intervals (0, 10, 20, 40, 60 and 80 cm). Opaque black plastic was wrapped around each tank to minimize the effects of observer presence on fish behaviour. Approximately 5 min 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, and each feeding trial began once a fish had emerged from shelter and resumed 'normal' swimming behaviour (i.e. once the fish had moved > 10 cm away from shelter). Unless feeding, fish never moved further than 15–20 cm from shelter. To examine foraging risk, we added food to the water column and measured the distance that an individual travelled from shelter when feeding. In these experimental trials, damselfish would typically remain near shelter (within 5–12 cm) until food was detected. Food detection was marked by a pause in routine swimming behaviour and an alignment of the fish towards the food in the water column. Feeding did not always immediately follow detection, but eventually fish swam directly towards the food, often pausing halfway en route.

Delivery of food began at a distance of 80 cm 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). Each addition of food comprised 1 mL of homogenized fish flakes in seawater delivered to the top of the water column with a pipette. This amount of food took 20–30 s to sink to the bottom of the aquarium. After 30 s, more food was added

at the next closest distance to the shelter. Food additions stopped once fish began feeding.

We used a multiple linear regression to analyse the effects of initial size, feeding treatment, and growth rate on the distance 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.

Results

Estimation of growth form

Simulations suggested 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. 2). Increasing the number of observations per individual increased the precision of the VBGE estimates. However, relatively few samples per individual growth curve did not appear to bias the parameter estimates substantially (Fig. 2).

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 selection on both of these traits (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, suggesting the

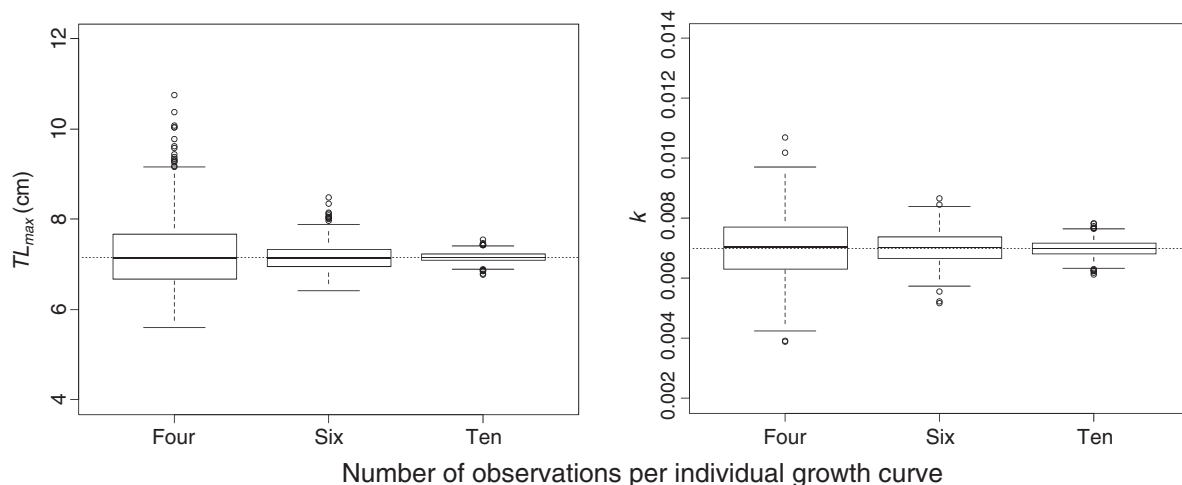


Fig. 2 Effect of the number of observations per individual growth curve on estimates of Von Bertalanffy growth parameters. For each replicate, parameters describing an individual Von Bertalanffy growth curve were estimated by fitting a nonlinear least squares regression to simulated size-at-age data. True parameter values were based on population means and are represented by the dashed lines ($TL_{max} = 7.15$, $k = 0.007$, random error SD for individual size-at-age = 2.5% of 'true' size-at-age). Boxplots summarize the distributions of parameter values generated for each group (i.e. individual growth curves with four, six and ten observations). $n = 1000$ randomizations within each group.

Table 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. Sample size refers to number of individuals included in the analysis of selection. (b) Ancillary data on mean population density and mean survival rates in each population over 8 years of demographic monitoring.

Study population		Normans Pond Reef			Windsock Reef			NW Barracuda Reef			SE Barracuda Reef		
Sample size		89			66			32			87		
(a) Phenotypic selection summaries	Symbol	Coef.	SE	<i>P</i>	Coef.	SE	<i>P</i>	Coef.	SE	<i>P</i>	Coef.	SE	<i>P</i>
Linear selection gradients													
TL_{max}	β_1	0.251	0.052	6.41E-6	0.145	0.050	5.45E-3	-0.107	0.085	0.212	0.063	0.052	0.232
D_k	β_2	-0.198	0.052	2.34E-4	-0.012	0.072	0.869	-0.187	0.125	0.148	-0.166	0.055	3.35E-3
Quadratic selection gradients													
TL_{max}	γ_{11}	-0.131	0.071	0.067	-0.056	0.062	0.373	-0.315	0.162	0.054	-0.161	0.066	9.08E-3
D_k	γ_{22}	0.183	0.070	0.010	0.224	0.106	0.039	-0.048	0.141	0.735	0.009	0.072	0.894
$TL_{max} \times D_k$	γ_{12}	-0.125	0.057	0.032	0.035	0.049	0.483	-0.079	0.094	0.409	-0.084	0.057	0.141
(b) Population characteristics													
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Population density (m^{-2})													
Juveniles		0.992	0.109	1.099	0.357	0.315	0.107	1.264	0.550				
Adults		2.402	0.237	1.643	0.279	1.079	0.215	1.286	0.286				
Monthly survival													
Juveniles		0.734	0.058	0.709	0.042	0.772	0.045	0.695	0.097				
Adults		0.924	0.006	0.899	0.009	0.912	0.019	0.859	0.019				

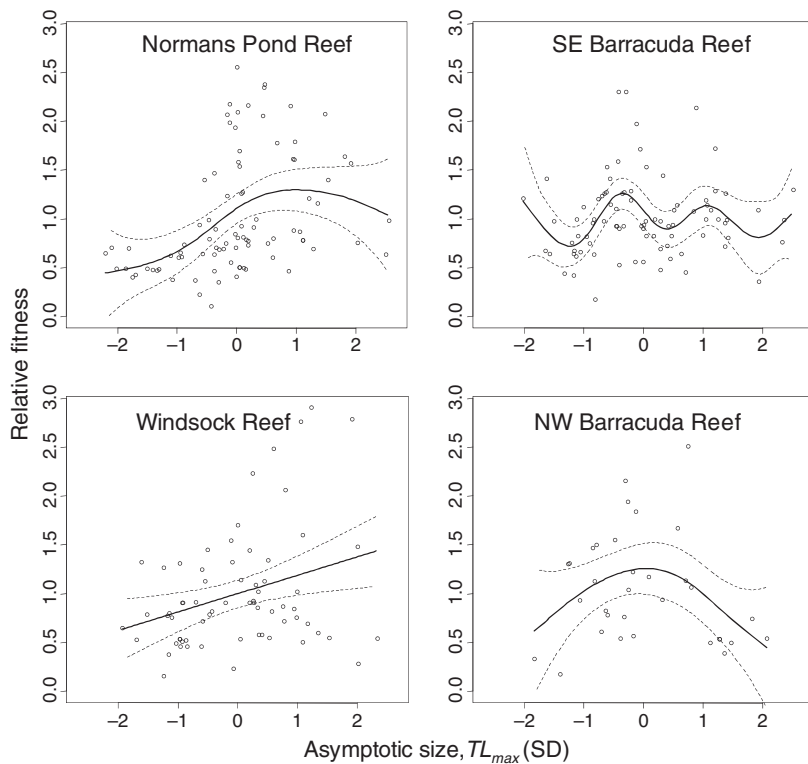


Fig. 3 Relationship between asymptotic size (TL_{max}) and relative fitness (lifespan) for each of four study populations. Asymptotic size is expressed as standard deviations from the population mean value. Solid lines are cubic spline smoothers ± 2 SE (dashed lines).

selective loss of individuals with extreme values of this trait (Table 1a). Linear selection on D_k was always 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, Normans Pond Reef (Table 1a).

Visualization of selection surfaces with cubic spline smoothers confirm overall patterns identified by

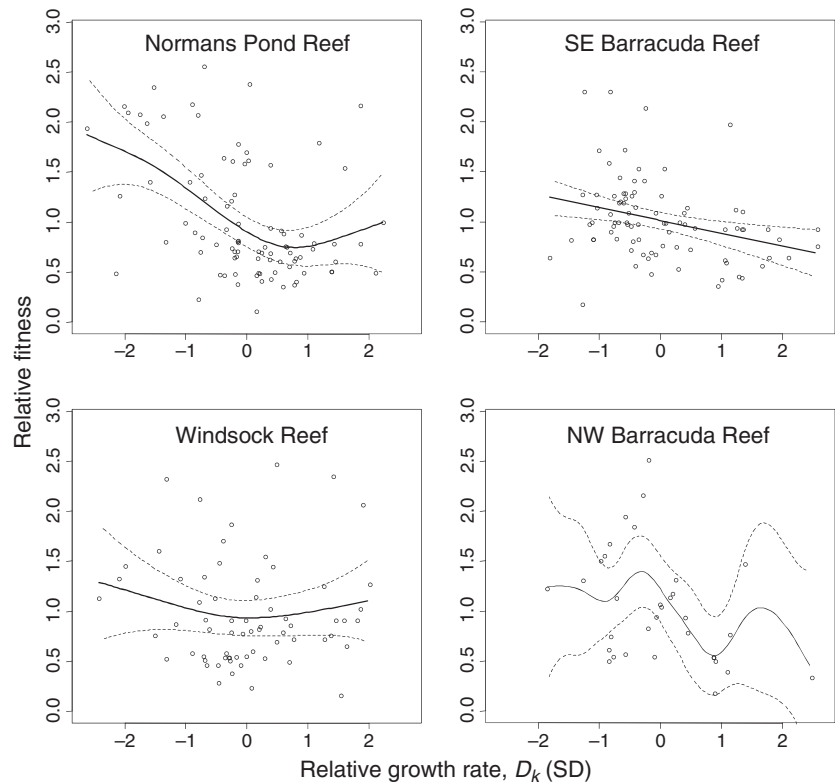


Fig. 4 Relationship between relative growth rate (D_k) and relative fitness (lifespan) for each of four study populations. Relative growth rate is expressed as standard deviations from the population mean value. Solid lines are cubic spline smoothers \pm 2 SE (dashed lines).

quadratic regression. Selection on asymptotic size was both directional and stabilizing at Normans Pond Reef, mainly directional at Windsock Reef, mainly stabilizing at NW Barracuda Reef, and possibly multimodal at SE Barracuda Reef (Fig. 3). Selection on relative growth rate was both directional and disruptive at Normans Pond Reef, slightly disruptive at Windsock Reef, directional and possibly bimodal at NW Barracuda Reef and directional at SE Barracuda Reef (Fig. 4). However, because of the low sample size at NW Barracuda Reef, complexities in the selection surface were estimated with considerable uncertainty (Fig. 4).

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 reefs was therefore examined with these ecological factors in mind. At Norman's Pond Reef, 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 Reef, a site that had medium population density, but a low value for juvenile survival, there was strong evidence only for linear selection for larger asymptotic size (Table 1). At NW and SE Barracuda

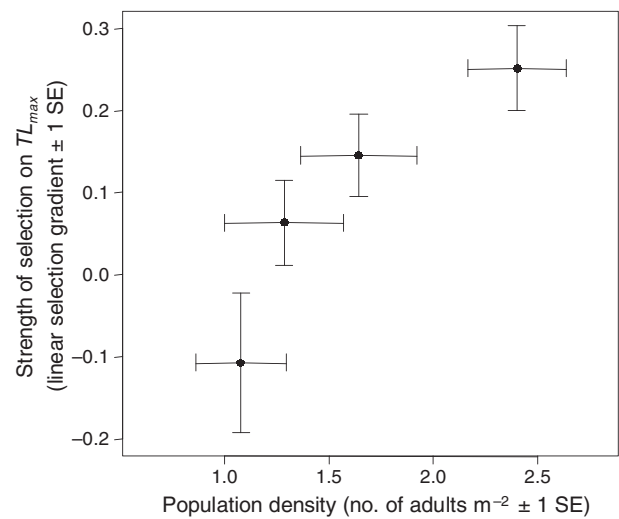


Fig. 5 Relationship between strength of selection on asymptotic size and population density for the four study populations.

Reefs, two sites with low densities of adults, 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, reefs with a greater density of adults experienced stronger selection on

asymptotic size (Table 1; Fig. 5), suggesting a mechanistic link between population density and the magnitude of linear selection on asymptotic size. Indeed, a similar pattern was observed for correlations between body size rank and lifespan. Correlation coefficients were negative at all reefs, and increased in magnitude as population density increased (NW Barracuda Reef: $r = -0.088 \pm 0.190$ SE; SE Barracuda Reef: $r = -0.178 \pm 0.131$ SE; Windsock Reef: $r = -0.294 \pm 0.122$ SE; Normans Pond Reef: $r = -0.350 \pm 0.105$ SE).

Emigration from study plots was low. Only 30 of 274 (10.95%) fish in our selection study left their focal plot and all moved to nearby coral heads (mean migration distance = 4.1 m). On average, emigrating fish tended to be larger than those that stayed on their original plots ($t_{272} = 2.21$, $P = 0.028$), though moving to a nearby head was often associated with an increase in size rank, i.e. fish tended to move to coral heads with fewer conspecifics larger than themselves. For those cases that involved fish moving to another study plot (where all fish were tagged and measured), rather than to a nearby coral head (where we did not collect data on nontagged individuals) 12 of 13 (92.31%) cases resulted in an increase in size rank for the fish that moved. Overall, emigrating fish tended to survive longer than nonemigrating fish ($t_{272} = 3.01$, $P = 0.003$), consistent with the results of our selection analysis indicating greater survival of large adults.

Selection on size-at-age

Interpretation of selection on TL_{\max} and D_k can be aided by examining the degree to which each of these parameters influenced length-at-age. For *S. partitus*, this influence 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. On average, this pattern was observed. Selection differentials on size at 50 days were negative at three of four reefs, indicating that larger individuals experienced greater mortality early in life (Fig. 6). However, the overall trend was for selection on body size to become positive later in life, especially at Normans Pond Reef, Windsock Reef, and to a lesser extent, NW Barracuda Reef (Fig. 6). Overall, these results suggest that as adults, large size was associated with greater survival probability.

Table 2 Correlations between estimated growth parameters of individuals and total length (TL) at different ages (expressed as days after hatching).

	Size-at-age (mm TL)				
	50	100	200	500	700
TL_{\max}	-0.02	0.42	0.83	0.98	1.00
D_k	0.95	0.82	0.45	-0.18	0.03

Juvenile growth rate and foraging risk

Juvenile fish housed in the laboratory exhibited a wide range of growth rates [0.0018–0.0340 mm day⁻¹; Coefficient of variation (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. Food ration treatments did not affect the distance away from shelter that individuals would swim and feed ($P = 0.93$; Table 3). However, both initial size and growth rate were positively associated with greater foraging distance (Table 3).

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 (review by 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 populations studied. Second, at least at some populations, 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 to have large asymptotic sizes, but also tended to be those that grew relatively slowly, especially 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 6).

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). Bicolour damselfish are largely planktivorous, 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

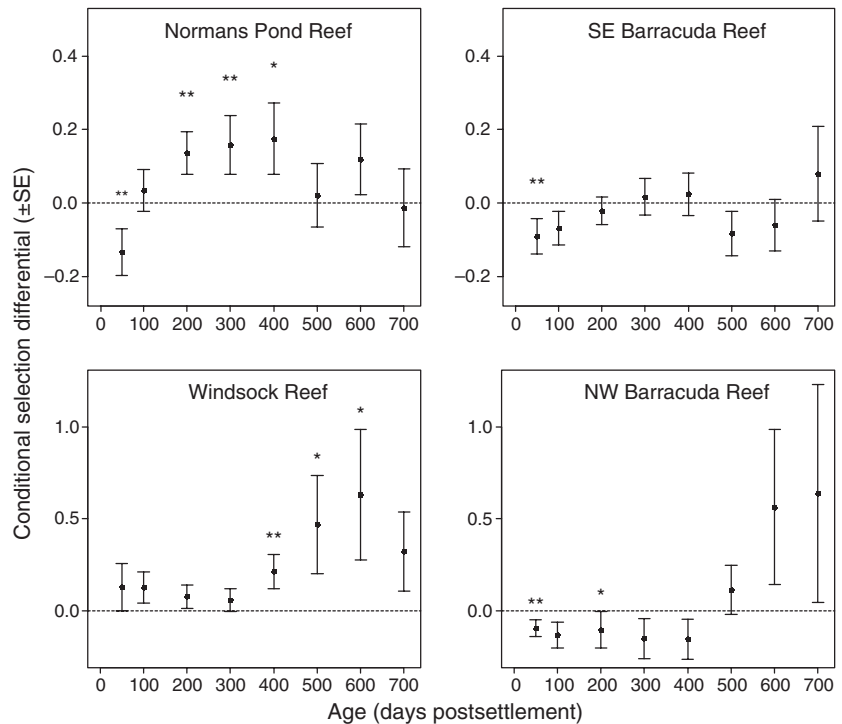


Fig. 6 Ontogenetic variation in size-selective mortality. Conditional selection differentials were calculated for body length at each of eight ages. For the sample of fish that remained alive at each age, fitness was defined as 0 if individuals survived less than an additional 200 days, and 1 if fish survived > 200 days. At each age, logistic regression was used to analyse selection and to estimate average selection differentials. ** $P < 0.05$, * $P < 0.1$.

Table 3 Linear model analysis 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 day^{-1}).

	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

greater risk of predation (reviews by Hixon, 1991; Hobson, 1991). Results of the laboratory experiments in this study indicated that, even after accounting for greater boldness with increased body size, faster-growing juveniles fed farther away from shelter. These results may be because faster-growing fish are bolder and/or better at detecting food at greater distances. Either way, our laboratory results support 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 6 days of feeding in the laboratory, groups of high-ration fish were much more aggressive after being returned to their natural habitat (Johnson, 2008). Similar results have been documented for other species of damselfish (Booth & Beretta, 2004).

Greater mortality of small adults may be explained by interference competition and size-dependent susceptibil-

ity to predation. Indeed, our observations of negative correlations between lifespan and relative body size within groups suggest that within-group interactions are important drivers of selective mortality. 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 (Carr *et al.*, 2002; Holbrook & Schmitt, 2002; Hixon & Jones, 2005). Larger adults may also take the territories of smaller adults (A. A. Myrberg, 1972; D. W. Johnson, personal observation), possibly relegating small individuals to inferior territories where risk of predation is higher (e.g. because of territory location or reef structural complexity; Holbrook & Schmitt, 2002). Larger adults may also be less susceptible to gape-limited predators (Stephens & Krebs, 1986), leading to greater probability of survival. All three of these factors may act separately or in combination, and it is likely that 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*, and although there were only four populations to compare,

some of the spatial variation in selective mortality may be explained by variation in population density. 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 be a greater number of large fish to harass small fish, thereby increasing the susceptibility of smaller fish to predation (see Persson *et al.*, 1996; Carr *et al.*, 2002, for other examples). Indeed, within this study, the correlation between body-size rank and lifespan was negative and greater in magnitude for reefs with greater population densities, suggesting that the consequences of size-dependent interactions become more severe as the average number of fish per plot increases. Selection on deviation in growth rate exhibited less spatial variability than selection on asymptotic size. The only obvious difference among populations was that there was little to no selection on deviation in growth rate at one site (Windsock Reef). However, reasons for this pattern are unclear.

Limitations of this study

Although this study estimated selection on size and growth throughout the entire post-settlement lifespan of individuals, there are two important limitations to the approach used here. First, we were unable to reliably describe growth form for individuals with less than three measurements. Although the Von Bertalanffy 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 (D. W. Johnson, unpublished data). In this study, we only considered selective mortality of those individuals that survived long enough to be measured at least three times (approximately 100 days 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. Multiple 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 & Cowen, 1997; Searcy & Sponaugle, 2001; Shima & Findlay, 2002; McCormick & Hoey, 2004; Raventos & Macpherson, 2005; Holmes & McCormick, 2006; Vigliola *et al.*, 2007). Selection on size- and growth-related traits may also be strong during the larval phase. Larvae of many marine fishes, including *S. partitus*, experience high rates of mortality during the planktonic phase (Houde, 1987). Although intense mortality may provide considerable opportunity for selection, selection during the larval phase has been difficult to study for fishes (but see Urpanen *et al.*, 2005; Robert *et al.*, 2007), and it is unclear whether patterns of

viability selection would be similar during larval and post-settlement life. Additionally, selection on post-settlement (rather than presettlement) 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 & Neilson, 1985).

A second limitation is that the method of estimating growth parameters may have inflated the magnitude 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 selection analysis used here, the quadratic terms reflect change in trait variances and covariances (Lande & 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 nonlinear selection among sites may therefore be heuristically valuable, despite potential bias in the absolute values.

Response to selection on growth form

Growth rate of bicolor damselfish is likely to be 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 towards 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 behaviour. 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 behaviour, then the association between growth and foraging risk would be because of 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 genes that promote large size tend to affect size throughout an organism's life (Cheverud *et al.*, 1983). Genetic covariances tend to be high between sizes at nearby ages and relatively low between ages that are further apart (Kirkpatrick & Lofsvold, 1992). Although we have no measurements of the underlying genetic architecture for size-at-age throughout post-settlement life in *S. partitus*, it is likely that there is a moderate-to-high degree of additive genetic covariance among sizes because traits as distant as larval and adult size show appreciable genetic covariance in other fishes (Munch *et al.*, 2005). Because of 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 Reef, direct selection on asymptotic size was strong (linear selection gradient = 0.251), but the response to direct selection may be 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 & Pfennig, 2007). However, both ontogenetic and spatial variation in viability selection on body size may lead to a complex evolutionary response to selection on body size. Although previous studies of fish populations have documented differences in the intensity of selection on body size at different ages (e.g. Hendry *et al.*, 2003; Carlson *et al.*, 2004; DiBattista *et al.*, 2009), 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; Kirkpatrick *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 like marine fishes that are subject to both natural selection and artificial selection via fishing mortality on body size (Gardmark *et al.*, 2003; Carlson *et al.*, 2007).

Acknowledgments

We are very thankful to many people who helped in the field and made this labour-intensive study possible: G. Almany, A. Altieri, T. Anderson, 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, J. Noell, M. Novak, K. Overholtzer-McLeod, C. Stallings, 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. Moyer 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. We also thank two anonymous reviewers for their helpful suggestions and insight. 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.A.H., and by grants to M.A.H. from NOAA's National Undersea Research Program, courtesy of the Caribbean Marine Research Center.

References

- Arendt, J.D. 1997. Adaptive intrinsic growth rates: an integration across taxa. *Q. Rev. Biol.* **72**: 149–177.
- Arnold, S.J. & Wade, M.J. 1984. On the measurement of natural and sexual selection: applications. *Evolution* **38**: 720–734.
- von Bertalanffy, L. 1938. A quantitative theory of organic growth (inquiries on growth laws, II). *Hum. Biol.* **10**: 181–213.
- Billerbeck, J.M., Lankford, T.E. & Conover, D.O. 2001. Evolution of intrinsic growth and energy acquisition rates. I. Trade-offs with swimming performance in *Menidia menidia*. *Evolution* **55**: 1863–1872.
- Biro, P.A., Abrahams, M.V., Post, J.R. & Parkinson, E.A. 2004. Predators select against high growth rates and risk-taking behaviour in domestic trout populations. *Proc. R. Soc. Lond. B Biol. Sci.* **271**: 2233–2237.
- Blanckenhorn, W.U. 2000. The evolution of body size: what keeps organisms small? *Q. Rev. Biol.* **75**: 385–407.
- Booth, D.J. & Beretta, G.A. 2004. Influence of recruit condition on food competition and predation risk in a coral reef fish. *Oecologia* **140**: 289–294.

- Booth, D.J. & Hixon, M.A. 1999. Food ration and condition affect early survival of the coral reef damselfish, *Stegastes partitus*. *Oecologia* **121**: 364–368.
- Campana, S.E. & Neilson, J.D. 1985. Microstructure of fish otoliths. *Can. J. Fish. Aquat. Sci.* **42**: 1014–1032.
- Carlson, S.M., Hendry, A.P. & Letcher, B.H. 2004. Natural selection acting on body size, growth rate and compensatory growth: an empirical test in a wild trout population. *Evol. Ecol. Res.* **6**: 955–973.
- Carlson, S.M., Edeline, E., Vollestad, L.A., Haugen, T.O., Winfield, I.J., Fletcher, J.M., James, J.B. & Stenseth, N.C. 2007. Four decades of opposing natural and human-induced artificial selection acting on Windermere pike (*Esox lucius*). *Ecol. Lett.* **10**: 512–521.
- Carr, M.H., Anderson, T.W. & Hixon, M.A. 2002. Biodiversity, population regulation and the stability of coral-reef fish communities. *Proc. Natl Acad. Sci. USA* **99**: 11241–11245.
- Case, T.J. 1978. General explanation for insular body size trends in terrestrial vertebrates. *Ecology* **59**: 1–18.
- Cheverud, J.M., Rutledge, J.J. & Atchley, W.R. 1983. Quantitative genetics of development: genetic correlations among age-specific trait values and the evolution of ontogeny. *Evolution* **37**: 895–905.
- Cock, A.G. 1966. Genetical aspects of metrical growth and form in animals. *Q. Rev. Biol.* **41**: 131–190.
- DiBattista, J.D., Feldheim, K.A., Gruber, S.H. & Hendry, A.P. 2007. When bigger is not better: selection against large size, high condition and fast growth in juvenile lemon sharks. *J. Evol. Biol.* **20**: 201–212.
- DiBattista, J.D., Feldheim, K.A., Garant, D., Gruber, S.H. & Hendry, A.P. 2009. Evolutionary potential of a large marine vertebrate: quantitative genetic parameters in a wild population. *Evolution* **63**: 1051–1067.
- Emery, A.R. 1968. *Comparative Ecology of Damselfishes at Alligator Reef, Florida Keys*. PhD Thesis, University of Miami, Miami.
- Endler, J.A. 1986. *Natural Selection in the Wild*. Princeton university press, Princeton.
- Francis, R.I.C.C. 1996. Do herring grow faster than orange roughy? *Fish. Bull.* **94**: 783–786.
- Frederick, J.L. 1997. Evaluation of fluorescent elastomer injection as a method for marking small fish. *Bull. Mar. Sci.* **61**: 399–408.
- Gagliano, M., McCormick, M.I. & Meekan, M.G. 2007. Survival against the odds: ontogenetic changes in selective pressure mediate growth-mortality trade-offs in a marine fish. *Proc. R. Soc. Lond. B Biol. Sci.* **274**: 1575–1582.
- Gardmark, A., Dieckmann, U. & Lundberg, P. 2003. Life-history evolution in harvested populations: the role of natural predation. *Evol. Ecol. Res.* **5**: 239–257.
- Hare, J.A. & Cowen, R.K. 1997. Size, growth, development, and survival of the planktonic larvae of *Pomatomus saltatrix* (Pices: Pomatomidae). *Ecology* **78**: 2415–2431.
- Hendry, A.P., Letcher, B.H. & Gries, G. 2003. Estimating natural selection acting on stream-dwelling Atlantic salmon: implications for the restoration of extirpated populations. *Conserv. Biol.* **17**: 795–805.
- Hereford, J., Hansen, T.F. & Houle, D. 2004. Comparing strengths of directional selection: how strong is strong? *Evolution* **58**: 2133–2143.
- Hixon, M.A. 1991. Predation as a process structuring coral reef fish communities. In: *The Ecology of Fishes on Coral Reefs* (P.F. Sale, ed.), pp. 475–508. Academic Press, San Diego.
- Hixon, M.A. & Carr, M.H. 1997. Synergistic predation, density dependence, and population regulation in marine fish. *Science* **277**: 946–949.
- Hixon, M.A. & Jones, G.P. 2005. Competition, predation, and density-dependent mortality in demersal marine fishes. *Ecology* **86**: 2847–2859.
- Hobson, E.S. 1991. Trophic relationships of fishes specialized to feed on zooplankters above coral reefs. In: *The Ecology of Fishes on Coral Reefs* (P. F. Sale, ed.), pp. 69–95. Academic Press, San Diego.
- Hoekstra, H.E., Hoekstra, J.M., Berrigan, D., Vignieri, S.N., Hoang, A., Hill, C.E., Beerli, P. & Kingsolver, J.G. 2001. Strength and tempo of directional selection in the wild. *Proc. Natl Acad. Sci. USA* **98**: 9157–9160.
- Hoey, A.S. & McCormick, M.I. 2006. Effects of subcutaneous fluorescent tags on the growth and survival of a newly settled coral reef fish, *Pomacentrus amboinensis* (Pomacentridae). In: *Proceedings of the 10th International Coral Reef Symposium*, pp. 420–424. Okinawa, Japan.
- Holbrook, S.J. & Schmitt, R.J. 2002. Competition for shelter space causes density-dependent predation mortality in damselfish. *Ecology* **83**: 2855–2868.
- Holmes, T.H. & McCormick, M.I. 2006. Location influences size-selective predation on newly settled reef fish. *Mar. Ecol. Prog. Ser.* **317**: 203–209.
- Houde, E.D. 1987. Fish early dynamics and recruitment variability. *Am. Fish. Soc. Symp.* **2**: 17–19.
- Janzen, F.J. & Stern, H.S. 1998. Logistic regression for empirical studies of multivariate selection. *Evolution* **52**: 1564–1571.
- Johnson, D.W. 2008. Combined effects of condition and density on post-settlement survival and growth of a marine fish. *Oecologia* **155**: 43–52.
- Kingsolver, J.G. & Pfenning, D.W. 2007. Patterns and power of phenotypic selection in nature. *Bioscience* **57**: 561–572.
- Kingsolver, J.G., Hoekstra, H.E., Hoekstra, J.M., Berrigan, D., Vignieri, S.N., Hill, C.E., Hoang, A., Gilbert, P. & Beerli, P. 2001. The strength of phenotypic selection in natural populations. *Am. Nat.* **157**: 245–261.
- Kirkpatrick, M. & Lofsvold, D. 1992. Measuring selection and constraint in the evolution of growth. *Evolution* **46**: 954–971.
- Kirkpatrick, M., Lofsvold, D. & Bulmer, M. 1990. Analysis of the inheritance, selection and evolution of growth trajectories. *Genetics* **124**: 979–993.
- Knapp, R.A. & Warner, R.R. 1991. Male parental care and female choice in the bicolor damselfish, *Stegastes partitus*: bigger is not always better. *Anim. Behav.* **41**: 747–756.
- Lande, R. & Arnold, S.J. 1983. The measurement of selection on correlated characters. *Evolution* **37**: 1210–1226.
- Law, R. 2000. Fishing, selection, and phenotypic evolution. *ICES J. Mar. Sci.* **57**: 659–668.
- Lynch, M. & Arnold, S.J. 1988. The measurement of selection on size and growth. In: *Size-Structured Populations* (B. Ebenman & L. Persson, eds), pp. 47–59. Springer-Verlag, Berlin.
- McCormick, M.I. & Hoey, A.S. 2004. Larval growth history determines juvenile growth and survival in a tropical marine fish. *Oikos* **106**: 225–242.
- Merila, J., Sheldon, B.C. & Kruuk, L.E.B. 2001. Explaining stasis: microevolutionary studies in natural populations. *Genetica* **112**: 199–222.
- Metcalfe, N.B. & Monaghan, P. 2001. Compensation for a bad start: grow now, pay later? *Trends Ecol. Evol.* **16**: 254–260.

- Munch, S.B., Walsh, M. R. & Conover, D.O. 2005. Harvest selection, genetic correlations, and evolutionary changes in recruitment: one less thing to worry about? *Can. J. Fish. Aquat. Sci.* **62**: 802–810.
- Myrberg, A.A. 1972. Social dominance and territoriality in the bicolor damselfish, *Eupomacentrus partitus*. *Behaviour* **4**: 207–231.
- Nemeth, R.S. 1998. The effect of natural variation in substrate architecture on the survival of juvenile bicolor damselfish. *Environ. Biol. Fish* **53**: 129–141.
- Olsen, E.M., Carlson, S.M., Gjosaeter, J. & Stenseth, N.C. 2009. Nine decades of decreasing phenotypic variability in Atlantic cod. *Ecol. Lett.* **12**: 622–631.
- Persson, L., Andersson, J., Wahlstrom, E. & Eklov, P. 1996. Size-specific interactions in lake systems: predator gape limitation and prey growth rate and mortality. *Ecology* **77**: 900–911.
- Price, T.D., Kirkpatrick, M. & Arnold, S.J. 1988. Directional selection and the evolution of breeding date in birds. *Science* **240**: 798–799.
- R Development Core Team 2009. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna.
- Raventos, N. & Macpherson, E. 2005. Effect of pelagic larval duration and size-at-hatching on post-settlement survivorship in two temperate labrid fish of genus *Symphodus*. *Mar. Ecol. Prog. Ser.* **285**: 205–211.
- Robert, D., Castonguay, M. & Fortier, L. 2007. Early growth and recruitment in Atlantic mackerel *Scomber scombrus*: discriminating the effects of fast growth and selection for fast growth. *Mar. Ecol. Prog. Ser.* **337**: 209–219.
- Roff, D.A. 1992. *The Evolution of Life Histories: Theory and Analysis*. Chapman and Hall, New York.
- Schluter, D., Price, T.D. & Rowe, L. 1991. Conflicting selection pressures and life history trade-offs. *Proc. R. Soc. Lond. B Biol. Sci.* **246**: 11–17.
- Schmale, M.C. 1981. Sexual selection and reproductive success in males of the bicolor damselfish, *Eupomacentrus partitus* (Pices: Pomacentridae). *Anim. Behav.* **29**: 1172–1184.
- Searcy, S.P. & Sponaugle, S. 2001. Selective mortality during the larval–juvenile transition in two coral reef fishes. *Ecology* **82**: 2452–2470.
- Shikano, T. 2008. Estimation of quantitative genetic parameters using marker-inferred relatedness in Japanese flounder: a case study of upward bias. *J. Hered.* **99**: 94–104.
- Shima, J.S. & Findlay, A.M. 2002. Pelagic larval growth rate impacts benthic settlement and survival of a temperate reef fish. *Mar. Ecol. Prog. Ser.* **235**: 303–309.
- Siepielski, A.M., DiBattista, J.D. & Carlson, S.M. 2009. It's about time: the temporal dynamics of phenotypic selection in the wild. *Ecol. Lett.* **12**: 1261–1276.
- Sih, A., Bell, A. & Johnson, J.C. 2004. Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol. Evol.* **19**: 372–378.
- Sogard, S.M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bull. Mar. Sci.* **60**: 1129–1157.
- Stamps, J.A. 2007. Growth-mortality tradeoffs and 'personality traits' in animals. *Ecol. Lett.* **10**: 355–363.
- Stearns, S.C. 1992. *The Evolution of Life Histories*. Oxford university press, Oxford.
- Stephens, D.W. & Krebs, J.R. 1986. *Foraging Theory*. Princeton University Press, Princeton, New Jersey.
- Urpanen, O., Huuskonen, H., Marjomaki, T.J. & Karjalainen, J. 2005. Growth and size-selective mortality of vendace (*Coregonus albula* (L.)) and whitefish (*C. lavaretus*) larvae. *Boreal Environ. Res.* **10**: 225–238.
- Vigliola, L., Doherty, P.J., Meekan, M.G., Drown, D.M., Jones, M.E. & Barber, P.H. 2007. Genetic identity determines risk of post-settlement mortality of a marine fish. *Ecology* **88**: 1263–1277.
- Wang, Y.G. & Milton, D.A. 2000. On comparison of growth curves: how do we test whether growth rates differ? *Fish. Bull.* **98**: 874–880.
- Wilson, D.T. & Meekan, M.G. 2002. Growth-related advantages for survival to the point of replenishment in the coral reef fish *Stegastes partitus* (Pomacentridae). *Mar. Ecol. Prog. Ser.* **231**: 247–260.
- Wootton, R.J. 1990. *Ecology of Teleost Fishes*. Chapman and Hall, New York.

Received 12 October 2009; revised 24 November 2009; accepted 28 December 2009