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Sexual and lifetime selection on body size in a marine fish: the importance of life-history trade-offs

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optimal body size.

Abstract

Many field measurements of viability and sexual selection on body size indicate that large size is favoured. However, life-history theory predicts that body size may be optimized and that patterns of selection may often be stabilizing rather than directional. One reason for this discrepancy may be that field estimates of selection tend to focus on limited components of fitness and may not fully measure life-history trade-offs. We use an 8-year, demographic field study to examine both sexual selection and lifetime selection on body size of a coral reef fish (the bicolour damselfish, *Stegastes partitus*). Selection via reproductive success of adults was very strong (standardized selection differential = 1.04). However, this effect was balanced by trade-offs between large adult size and reduced cumulative survival during the juvenile phase. When we measured lifetime fitness (net reproductive rate), selection was strongly stabilizing and only weakly directional, consistent with predictions from life-history theory.

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Introduction

The measurement of selection in wild populations has been a major focus of modern evolutionary biology (Endler, 1986; Kingsolver *et al.*, 2001; Siepielski *et al.*, 2009). A common approach to measuring selection on quantitative traits is to examine the relationship between trait value and relative fitness (Lande & Arnold, 1983; Schluter, 1988; Brodie *et al.*, 1995). In practice, logistical constraints often require investigators to focus on fitness components (e.g. survival, mating success or fecundity during particular episodes), rather than lifetime measures of fitness. For example, only approximately 3% of the 1582 records of selection in Kingsolver *et al.*'s (2001) review were based on integrated measures that approach lifetime fitness (e.g. total offspring produced during a surviving adult's lifetime). Although studies of selection via fitness components may be very informative, using the results of such studies to make inferences about lifetime selection may be misleading.

Traits may be modified by several selective forces and may be subject to selection during different phases of the life cycle. Because lifetime selection results from the combination of all selection that occurs within a generation, patterns of selection via single fitness components and/or during different life stages may not accurately reflect lifetime selection (Schluter *et al.*, 1991). In some cases, successive episodes of selection may increase the net strength of selection (e.g. Arnold & Wade, 1984; Hunt *et al.*, 2009 and references therein). In other cases, selection via one fitness component (e.g. a positive relationship between trait value and fecundity) may be offset by selection on another component (e.g. a negative relationship with survival), resulting in weak selection favouring an intermediate phenotype (e.g. Preziosi & Fairbairn, 2000). Another common limitation of selection studies may be that selection measured during one life stage (e.g. survival of adults) may give no information about what happens during earlier stages (e.g. survival of juveniles), and total patterns of selection may be unknown. Nonetheless, studies that focus in detail on single fitness components may often reveal important details about mechanisms underlying selective forces (e.g. Howard & Kluge, 1985; Brodie, 1992; Young *et al.*, 2004). Still, understanding the overall direction, magnitude and mode of selection requires empirical study of lifetime fitness measures.

Body size is a trait that often exhibits a strong, positive relationship with fitness components such as survival and fecundity (reviewed by Kingsolver & Pfennig, 2004, 2007). In many cases, advantages of large size are obvious and

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readily measured. For example, large females often produce more offspring (e.g. Wootton, 1979), larger individuals may be superior competitors for territory or mates (e.g. Warner & Schultz, 1992) and larger individuals may be less susceptible to predation if predators are gape limited and the range of potential predators decreases with body size (e.g. Persson *et al.*, 1996). However, patterns of *lifetime* selection on body size are less clear. There may be disadvantages to being large, or costs associated with becoming large, though these drawbacks are less frequently measured (Blanckenhorn, 2000). Notably, if attaining a large adult size requires longer development time, then the expected survival to maturity may be reduced by greater juvenile mortality, even though rates of survival may be higher for larger adults (Stearns & Koella, 1986). Patterns of size-selective mortality can also be complex. In a prior study of the system examined in this paper, Johnson & Hixon (2010) investigated selective mortality of bicolour damselfish (*Stegastes partitus*) in detail, including explorations of mechanisms driving variation in selective mortality. They found that selective mortality may vary substantially among populations and that patterns of size-selective mortality may change throughout ontogeny (Johnson & Hixon, 2010). Complex patterns in mortality rates and their interactions with development time may be a major constraint on the evolution of body size (Roff *et al.*, 2006). However, empirical studies documenting such trade-offs are relatively rare, especially compared with the number of studies demonstrating selective advantages of large body size (general reviews by Blanckenhorn, 2000; Kingsolver & Pfennig, 2004, 2007; see Sogard, 1997 for a review specific to fishes).

In this study, we examined both sexual selection and total lifetime selection on adult male body size in a common coral reef fish (the bicolour damselfish, *S. partitus*). Our first set of analyses examined sexual selection on adult males in detail and focused on potential mechanisms generating the observed differences in male reproductive success. Our second set of analyses used data from an 8-year field study of damselfish demography to quantify the relationship between adult body size and net reproductive rate. We compared the results of these two analyses to illustrate how selection analyses that use an incomplete, though reasonably integrated measure of fitness (observed reproductive success throughout adult life of breeding males) may differ greatly from those that examine a fully integrated measure of fitness (net reproductive rate associated with a particular phenotype).

Methods

Study species

The bicolour damselfish (*S. partitus*) is an abundant coral reef fish found throughout the tropical western Atlantic and Caribbean. Several characteristics make bicolour damselfish highly amenable to an *in situ* study of growth and reproduction. Adults and juveniles usually stay within 1–2 m of their home territories, with the exception of local excursions to nearby territories during courtship and mating (Knapp & Warner, 1991). This high degree of site fidelity facilitates tag-recapture studies to collect individual size-at-age data. In this study, we focused on male (rather than female) fitness because male fitness was readily calculated from field data. Males guard benthic nests (allowing measurement of offspring production) and mature males can be identified by field behaviour. In contrast, tracking female fecundity is extremely difficult and we have no data on timing of female maturity – a key life-history trait. Males often mate with multiple females and may have up to five separate egg masses in the nest at one time (Johnson *et al.*, 2010). Eggs are deposited in a monolayer and laid in discrete masses, allowing reproductive output to be measured in the field. Both spawning and settlement follow a cyclical pattern that is closely related to the lunar cycle (Schmale, 1981; Robertson *et al.*, 1988). Little to no spawning occurs between the new moon and first quarter. Spawning activity increases and then decreases throughout the rest of the cycle, typically peaking during the 3rd quarter. Although reproduction and settlement may occur throughout the year, in the Bahamas most reproduction and settlement occurs during the summer months.

At our study site in the Bahamas, *S. partitus* is commonly found in groups of 1–12 fish that inhabit the same local area (i.e. clusters of coral or other natural habitats). Males compete for territories, and *S. partitus* exhibits a strong, size-dependent social hierarchy in which larger fish often harass smaller conspecifics with relative impunity (Myrberg, 1972a). Although larger individuals are at an advantage when competing for territories (Myrberg, 1972b), it is not always clear whether larger size leads to greater mating success (positive relationships were found by Schmale, 1981; Cole & Sadovy, 1995, whereas no significant relationship was found by Knapp & Warner, 1991). Still, large size may contribute to reproductive success if size is positively related to the quality of a breeding territory, or the length of time a breeding territory is held, via increases in either adult survival or competition for nest sites.

Demographic monitoring

Survival and growth of *S. partitus* were monitored from 1998 to 2005 at Norman's Pond Reef, an approximately 100-m-diameter coral reef located near Lee Stocking Island, Bahamas (23°46′N, 76°06′W). This population was 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 captured using hand nets and the anaesthetic quinaldine and individually tagged with 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. Handling and release of each fish occurred exactly where captured underwater, and each fish was handled for less than a minute. Elastomer tags have been shown to 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 minimal effects of our tagging procedure on demographic rates. Tag loss was unlikely because, when fish were recaptured and measured, tags were inspected and re-applied, if necessary. Reproduction was monitored from 2000 to 2005. Reproductive activity was identified by specific courtship behaviours (Myrberg, 1972a) and/or the presence of eggs in natural nests. All reproductively active males were given artificial nests that were 15 cm lengths of 5-cm-diameter plastic pipe, placed in the vicinity of the natural nest and lined with flexible transparent plastic that could be removed to access attached eggs. We assume that our use of artificial nests allowed us to accurately characterize reproduction. Evidence from this study and many others (e.g. Schmale, 1981; Knapp & Warner, 1991; Cole & Sadovy, 1996) suggests that males given artificial nests quickly begin using them exclusively and tend to continue doing so throughout their reproductive life. Moreover, male reproductive behaviour is very conspicuous, and reproductive males without artificial nests could be readily identified and given new artificial nests.

Monitoring took place weekly during the main summer breeding season (June–September) and 1–3 times between summers. During each census, reproduction was measured by counting and tracing egg masses, if present. Because eggs are laid in a dense monolayer and because variation in egg size is extremely small compared with variation in egg area (unpublished data), the area of egg masses within each nest provided a direct and robust measure of number of offspring. Egg mass area was calculated by digital analysis of egg mass tracings using the program ImageJ (Rasband, 2009). Eggs hatch after 3.5 days of benthic development, so weekly censuses did not count the same egg masses twice.

Size and growth were measured by capturing and measuring fish within the population several times throughout the year (at least early summer, late summer and winter). Fish were also measured when they were first encountered. 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. Size-at-age (total length) of *S. partitus* is well described by a Von Bertalanffy growth function (VBGF):

$$L_t = L_\infty(1 - \mathrm{e}^{-k(t-t_0)}) \tag{1}$$

where L_∞ is asymptotic size, k is a growth constant, t is age and t_0 is the estimated time at which size is zero. Parameters describing the VBGF for each individual were estimated in one of two ways. For fish that were initially found at settlement or as young juveniles (≤ 4 cm TL), parameters were estimated using eqn 1 and numeric values for census dates. This approach allowed us to estimate L_∞, k and birth (hatch) date (t_0 + 3.5 days in the egg stage). Although we were not able to critically evaluate the fit of a VBGF to growth during the larval stage, variation in larval growth and larval duration (range = 26–36 days, Sponaugle & Cowen, 1996) is small compared with variation in estimated age at maturity (range = approximately 380–1150, this study). These patterns suggest that for fish initially tagged as juveniles, the growth function we fit could be used to estimate birthdate with reasonable precision. However, some fish took up residence in our study area between summers when sampling was infrequent. For fish that were initially found as adults or late juveniles (> 4 cm TL), growth parameters were estimated using the method of Gulland & Holt (1959). This approach allowed us to estimate L_∞ and k, but for these individuals, t_0 could not be reliably estimated and age was unknown. For a subset of 20 individuals, VBGF parameters were estimated using both methods. L_∞ values obtained through the two methods were highly correlated (r = 0.97).

Selection via reproductive success

For reproductively active males, we measured selection via differential reproductive success by examining the relationship between asymptotic body size (L_∞) and number of eggs sired. To investigate this relationship in detail, we separated reproductive success into three components, (i) average size of egg masses (clutches) in each male's nest, (ii) number of clutches per unit time observed and (iii) duration of time the nest was held. Nesting duration was measured as the midpoint between the observed, minimum breeding time (time between first and last observations of eggs in the nest, minus any time the nest was occupied by another male) and the maximum breeding time (time between the census prior to first observed breeding and disappearance date). The first two components measure aspects of male mating success effected through female choice and/or male–male competition and thus reflect sexual selection on asymptotic size. Males with breeding territories will hold them until death or until ousted by another male. The third component thus represents sexual selection (via competition for nest sites), but may also represent a component of viability selection (via effects of longevity). Because the observation period varied among males and because we did not measure all clutches sired by males throughout their entire reproductive lifetimes, we estimated the total number of eggs sired by each male as the product of average size of egg masses, number of egg masses per unit time and nesting duration. It is likely that this measure also directly reflects the number of larvae produced by each male, because survival of eggs in the nest is not related to male body size (Knapp & Warner, 1991; Cole & Sadovy, 1995). However, survival of offspring beyond the larval stage is unknown, because larvae disperse away from the reef and into the plankton.

To calculate selection differentials, asymptotic size (L_∞) was standardized by subtracting the mean value from each individual estimate and dividing by the phenotypic standard deviation. Selection differentials were then estimated by the estimate of the slope between standardized asymptotic size and relative fitness (observed value of individual fitness components divided by the population mean; Lande & Arnold, 1983). Because L_∞ values were estimated with some uncertainty, model 2 regression was more appropriate for estimating slope values in some of our analyses (Legendre & Legendre, 1998). When relative fitness was measured by egg area or number of clutches per unit time, estimated error variation in L_∞ (the average, estimated variation in individual L_∞ values) was similar in magnitude to the estimated error variation in relative fitness (estimated by the error variance in an ordinary least squares regression of relative fitness on standardized L_∞), suggesting that major axis regression was the most appropriate analysis (McArdle, 1988). When relative fitness was measured by nesting duration or by total reproductive success, estimated error variation in relative fitness was much larger (i.e. > 3×) than estimated variation in L_∞, indicating that the data better fit the assumptions of least squares regression (McArdle, 1988). For analyses in which nesting duration was part of the response variable, we used weighted least squares to estimate slope values. Each case was weighted by the inverse of the estimated standard deviation of nesting duration (i.e. cases where nesting time was observed with greater certainty were given more weight in the analyses). For graphical display, raw data are plotted and regression lines were back-calculated to the original units.

Body size and lifetime reproductive success

Although analyses of selection via fitness components (e.g. relative number of eggs sired) can be informative, understanding and predicting rates of evolution may be better achieved by examining more comprehensive measures of fitness. Populations of *S. partitus* are regulated by density-dependent survival of juveniles (Carr *et al.*, 2002; Johnson, 2008) such that the long-term growth rate (r) is equal to zero (Hixon *et al.*, in prep.). Assuming no genetic variation in density-dependent survival or that L_∞ is genetically uncorrelated with components of density regulation, an appropriate measure of fitness is R_0, the net reproductive rate (Roff, 2002), defined as:

$$R_0 = \int_{\alpha}^{\infty} l_{(t)} m_{(t)} \mathrm{d}t \qquad (2)$$

where t is age (in days), α is the age at first reproduction, $l_{(t)}$ is the age schedule of mortality (i.e. the probability of surviving to age t) and $m_{(t)}$ is the age schedule of fecundity (i.e. the production of offspring at age t). To examine lifetime selection on asymptotic size, we calculated and compared expected values of R_0 for a range of observed asymptotic sizes. Each of the major components of fitness (age at first reproduction and the age schedules of mortality and fecundity) was described as a function of size and estimated from demographic data collected in the field. Size-specific demographic rates could then be combined with growth data (eqn 1) to express survival and fecundity as functions of age.

Age at first reproduction (α)

For those males whose birth dates could be reliably estimated ($n = 26$), we estimated date of first reproduction as the midpoint of the date at which eggs first appeared in the nest and the date of the previous census. We then subtracted the estimated birth date from this value to obtain an estimate of age at first reproduction. For some individuals, e.g. those who began reproducing during the summer months when censuses were weekly, age at first reproduction was well estimated. For others, e.g. those whose first eggs were observed in the winter when censuses were less frequent, age at first reproduction was estimated with less certainty. We therefore used weighted least squares to estimate the relationship between asymptotic size and age at first reproduction. Each case was weighted in inverse proportion to the standard deviation of the estimate for age at first reproduction (i.e. cases where age at first reproduction was estimated with greater certainty were given more weight in the analyses).

Age schedule of fecundity ($m_{(t)}$)

To estimate the age schedule of fecundity, we re-examined our data on male reproductive success (i.e. eggs received), this time analysing the relationship between reproduction and observed size during each census. We estimated the age schedule of fecundity as the product of two component functions. One function ($p_{(t)}$) described the probability of reproducing during each census. The other ($f_{(t)}$) described the expected fecundity, given that the fish had received eggs. We estimated both of these functions using general, linear mixed-effects models. Because multiple observations were made on each fish, fish identity was included as a random factor. As fixed factors, we included effects of male size and two environmental factors known to affect reproductive output: lunar phase and season. Lunar phase was expressed as the number of days between the census date and the nearest 3rd quarter moon, the peak of the spawning cycle (Schmale, 1981; Robertson *et al.*, 1988). Season was coded as 1 if the observations took place during June–September, 0.5 if observations were made during March–May and

October–November and 0 if observations were made during December–February. Our approach was to fit all fixed terms and their interactions in a full model and retain terms that significantly contributed to the variation explained by the model. To model egg presence (a binary response), we used a logit link. Following recommendations by Bolker *et al.* (2008), we used Laplace approximation to the likelihood surface to estimate model parameters. We used the lme4 package in R (R Development Core Team, 2009). Likelihood ratio tests (LRT) were used to assess contribution of fixed and random effect terms dropped from the model. Terms were included if *P*-values were < 0.05. Because likelihood approximation and inference can be difficult with binary data (Bolker *et al.*, 2008), we also used penalized quasi-likelihood and Wald's *t*-tests to select a reduced model describing egg presence (using the glmmPQL package in R). To model expected fecundity (egg mass area), we used a log link. *F*-tests were used to assess contribution of fixed effect terms dropped from the model, and the contribution of the random term was evaluated with a likelihood ratio test (Bolker *et al.*, 2008). Terms were included if *P*-values were < 0.05. All analyses were conducted using the lme4 package in R (R Development Core Team, 2009).

Age schedule of mortality ($l_{(t)}$)

To describe the age schedule of mortality within our analytical framework, we needed to evaluate how mortality rates varied with body size. To estimate size-specific mortality rates, we estimated survival of fish within 10 size bins, starting with a bin for recently settled fish ($1.4 \text{ cm} \le x < 1.6 \text{ cm}$) and continuing in 0.5-cm bins for each larger size class ($1.6 \text{ cm} \le x < 1.99 \text{ cm}$, $2.0 \text{ cm} \le x < 2.49 \text{ cm}$, etc.). Included in this data set were 693 fish tagged at the study site from 1998 to 2005. Male and females of *S. partitus* are indistinguishable as juveniles. However, as males mature, they can be identified by their courtship and reproductive behaviour (Myrberg, 1972a). We therefore estimated 'prematurity' (< 6.5 cm TL; Schmale, 1981) mortality rates using all fish and estimated 'post-maturity' mortality rates using a subset of fish that could be identified as males. Survival was scored as 1 if fish survived for > 30 days after tagging and 0 otherwise. To model size-specific survival $s_{(t)}$, we plotted estimated proportional survival for each size bin.

Because the data suggested a nonlinear pattern, our approach was to first estimate a suitable shape for the survival function by fitting the data with a generalized additive model (GAM). This analysis used cross-validation to estimate a flexible, nonparametric smoother that best fit the data. We then fit to the data a parametric function that approximated the shape suggested by the GAM smoother. Specifically, we used nonlinear least squares to fit the following function to the survival data: $S_{(t)} = a \times (L_t \times \exp[b \times L_t])^c$. For the calculation of R_0, our survival function $s_{(t)}$ was then converted to $M_{(t)}$, a function describing daily mortality rate ($M_{(t)} = -\ln[s_{(t)}]/30$).

In this data set, the number of fish sampled within each size bin varied from 16 to 185 (mean = 61.5). Consequently, size-specific mortality rates were estimated with varying precision. To fit the overall relationship, we therefore weighted each estimate by the square root of the initial number in fish each bin. We were not able to measure mortality during the larval stage. However, for many marine fish larvae, the instantaneous rate of mortality decreases with larval size in a pattern similar to what we observed for post-settlement stages of *S. partitus* (reviews by Morse 1989; Pepin, 1991). In the absence of direct data, we assumed that the rate of size-dependent mortality observed for juveniles could be used to also describe size-dependent mortality of larvae.

Estimated lifetime fitness

We used our estimates of demographic rates to calculate expected values of R_0 for a range of plausible asymptotic sizes (6–11 cm TL). The net reproductive rate associated with each value of adult asymptotic size $R_{0(L_\infty)}$ was calculated as:

$$R_{0(L_\infty)} = \frac{1}{2} \int_{\alpha_{(L_\infty)}}^{\infty} \mathrm{e}^{-\int_0^t M_{(t)} \mathrm{d}t} p_{(t)} f_{(t)} \mathrm{d}t \tag{3}$$

where the age schedules of mortality and fecundity are described as component functions of both age and size and all other symbols are as described above (see Table 1 for a full description of component functions). Age at first reproduction (α) and the Von Bertalanffy growth constant (k) were both described as functions of asymptotic size and estimated from field data. Functions $M_{(t)}$, $p_{(t)}$ and $f_{(t)}$ were also estimated from field data and are described in Table 1. Equation 3 was multiplied by ½ to calculate expected number of male offspring (assuming a 1 : 1 sex

Table 1 Summary of functions used to calculate lifetime fitness (R_0).

Trait or demographic process	Function
Age at first reproduction	$\alpha = 131.79 \times L_\infty - 438.81$
Growth constant	$k = 3.82 \times L_\infty^{-3.29}$
Body size	$L_t = L_\infty(1 - e^{-k(t)})$
Probability of reproduction	$\text{Logit}(p_{(t)}) = -29.37 + 3.77 \times L_t + 1.41 \times \text{Lunar phase} + 2.25 \times \text{Season} - 0.189 \times L_t \times \text{Lunar phase} - 0.241 \times \text{Lunar phase} \times \text{Season}$
Fecundity (egg mass area per adult male)	$f_{(t)} = \exp(-1.623 + 0.421 \times L_t + 0.56 \times \text{Season})$
Instantaneous mortality rate	$M_{(t)} = -\ln[0.724 \times (L_t \times \exp[-0.179 \times L_t])^{0.342}]/30$

ratio). For each value of L_∞ (range = 6–11 cm TL), we calculated the expected value of R_0 by evaluating eqn 3 at all possible combinations of season and lunar day values and calculating the overall average.

Equation (3) was used to generate a continuous surface describing the relationship between relative fitness (R_0/mean R_0) and phenotypic value (L_∞). The slope of the relative fitness surface evaluated at the population mean describes the direction and strength of selection (i.e. the selection differential; Lande, 1979). To compare lifetime selection on asymptotic size to selection measured as differences in reproductive success, we calculated the standardized selection differential by estimating the slope of the surface relating relative fitness to standardized L_∞ values at the overall population mean.

Each of the component functions making up eqn 3 was estimated with some uncertainty. To propagate this uncertainty to the final calculation of R_0 and the lifetime selection surface, we conducted a randomization procedure where we examined both the mean and the distribution of R_0 values. For each of 26 values of L_∞ (every 0.2 cm from 6 to 11 cm TL), we calculated 30 R_0 values using eqn 3 and 30 sets of randomly generated parameters that defined $s_{(t)}$, $p_{(t)}$, $f_{(t)}$, α and k. Parameters defining each function were drawn from a multivariate normal distribution using the estimated mean parameter values and the estimated covariance matrices associated with each function (see Table 1 for a full description of functions). Randomizations were conducted using the MASS package in R (R Development Core Team, 2009). Quantiles of the distributions of R_0 values were used to display confidence regions associated with the mean fitness surface relating R_0 to L_∞.

Results

Selection via reproductive success

All three components of reproductive success increased with asymptotic size, although the strength of these relationships varied (Fig. 1a–c). Both the mean number of eggs received per clutch (clutch area) and the mean rate at which egg masses were received exhibited a moderate increase with male asymptotic size (clutch area = $3.769 \times L_\infty - 11.171$, $P < 0.0258$; clutch rate = $0.0379 \times L_\infty - 0.137$, $P < 0.0360$). When these relationships were expressed as standard selection differentials (S), estimated values were 0.128 (major axis regression 95% CI: 0.0295, 0.230) and 0.147 (major axis regression 95% CI: 0.0108, 0.288), respectively. The relationship between asymptotic size and average nest duration was stronger [weighted least squares: ln(nest duration) = $1.278 \times L_\infty - 5.236$, $P = 6.66 \times 10^{-8}$, df = 59; Fig. 1c], resulting in a larger selection differential ($S = 0.945$; 95% CI: 0.640, 1.251). The overall relationship between asymptotic size and reproductive success (here defined as the product of clutch area, clutch rate and nesting duration) was very strong [weighted least squares: ln(reproductive success) = $1.61 \times L_\infty - 7.03$, $P = 7.44 \times 10^{-9}$, df = 59; Fig. 1d], suggesting extremely strong selection for large asymptotic size ($S = 1.04$, 95% CI: 0.704, 1.372). Although the selection differentials calculated for each of the components of reproductive success are not expected to be strictly additive (Wade & Kalisz, 1989), their values suggest that the relationship between L_∞ and nest duration had the largest influence on relative reproductive success.

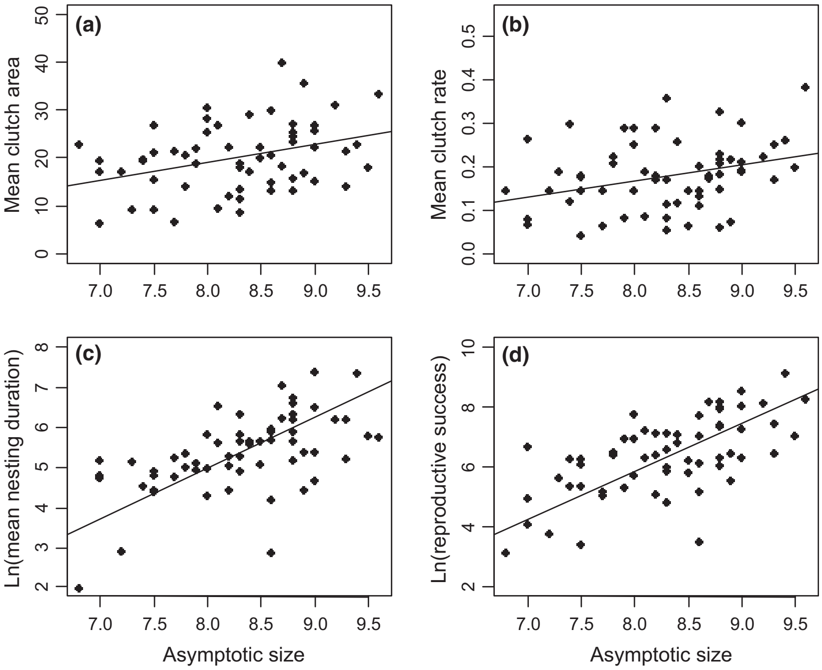

Fig. 1 Observed reproductive selection on body size of adult males. Panels (a–c) display relationships between asymptotic size and components of reproductive success ($n = 61$ in all panels). Panel (d) displays the relationship between asymptotic size and reproductive success, which is the product of the components shown in panels a–c.

One reason for the strongly positive relationship between male asymptotic size and nesting duration may be size-dependent competition for nest sites. Of the 61 males monitored, 14 lost their nests to other males (i.e. the ousted male stayed within the plot but was not observed reproducing). In 20 cases, competition was likely but not observed with certainty (i.e. the former defender disappeared between censuses and a new defender occupied the nest). In 27 cases, there was no evidence of competition (i.e. the defender disappeared and the nest remained vacant). Of the 14 cases where competition for nests could be clearly identified (i.e. when surviving males yielded the nest to other males), larger males took over nests 12 times. Of the two cases where smaller males successfully acquired nests, the difference in length was < 0.3 cm, and in one case, the larger male eventually regained the nest.

Age at first reproduction (α)

Males with large asymptotic sizes tended to mature at later ages. This relationship could be reasonably described by a linear model (age at first reproduction = 121.9 × L_∞ – 358.7, $P = 0.0219$, df = 24, $r^2 = 0.20$; Fig. 2). Note that although we could only estimate age at first reproduction for a subset of adult males within our study ($n = 26$), we believe the estimated relationship between asymptotic length and age at maturity to be robust because very similar relationships were observed for this species at three other sites (unpublished data).

Age schedule of fecundity ($m_{(t)}$)

The probability of a male having eggs in its nest during a census was well described by a model that included terms for size, season, lunar phase, a season by lunar phase interaction and a size by lunar day interaction (Table 1). Likelihood ratio tests indicated that dropping any one of these terms from the model resulted in a large increase in the amount of unexplained variation (all LRT P-values < 0.01). Dropping terms based on penalized quasi-likelihood and Wald's t-tests resulted in an identical model. Probability of reproducing increased strongly with size ($P < 2.0 \times 10^{-16}$; Fig. 3a), though the magnitude of this effect also depended on lunar phase (Table 1). *Stegastes partitus* spawns on a regular lunar cycle (Schmale, 1981; Robertson *et al.*, 1988), and our data confirm that, on average, less reproduction occurred on days that are further from the 3rd quarter of the lunar phase. Similarly, most reproduction occurred in the summer (Table 1). Fecundity (area of eggs received per census) was optimally described by a model containing terms for size and season (Table 1). Statistical support for including both of these terms was strong (LRT P-values < 1.0×10^{-6}). Egg production increased in summer months and area of eggs received increased exponentially with male body size (Table 1, Fig. 3b).

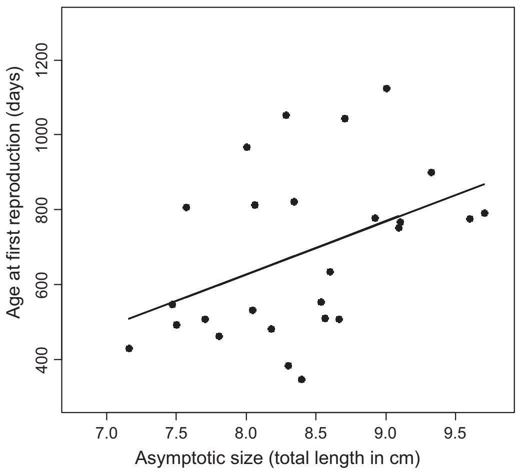

Fig. 2 Relationship between age at maturity (estimated by age at first reproduction) and asymptotic size of males (L_∞).

Age schedule of mortality ($l_{(t)}$)

Survival initially increased with body size, reaching a maximum at approximately 6 cm TL before decreasing slightly for larger size classes (mainly reproductively active males)(Fig. 4). The relationship between mean size and mean survival was well approximated by a three-parameter function, $S_{(t)} = a \times (L_t \times \exp[b \times L_t])^c$, where estimated values of each of the parameters were $a = 0.724$ (SE = 0.0372, $P = 5.39 \times 10^{-11}$), $b = -0.179$ (SE = 0.0221, $P = 1.96 \times 10^{-6}$) and $c = 0.342$ (SE = 0.107, $P = 7.26 \times 10^{-3}$)(Fig. 4).

Asymptotic size and estimated lifetime fitness

In contrast to the observed patterns of sexual selection, which indicated strong directional selection for large asymptotic size, the estimated surface relating lifetime fitness to asymptotic size was unimodal, indicating stabilizing selection towards an intermediate optimum (Fig. 5a). Moreover, the expected fitness surface was steeply peaked and centred very close to the observed mean value for male asymptotic size (mean = 8.49 cm TL, predicted optimum = 8.35 cm TL; Fig. 5b). Although we acknowledge substantial uncertainty in our final calculations, the results suggest that stabilizing selection was strong and that directional selection was, on average, relatively weak in this population (standardized, directional selection differential = −0.130). Overall, the distribution of male asymptotic body sizes matched the estimated fitness surface quite well, suggesting that body size was fine-tuned to fitness in this population (Fig. 5).

Discussion

Our two approaches to measuring selection on asymptotic size yielded substantially different conclusions. The cor-

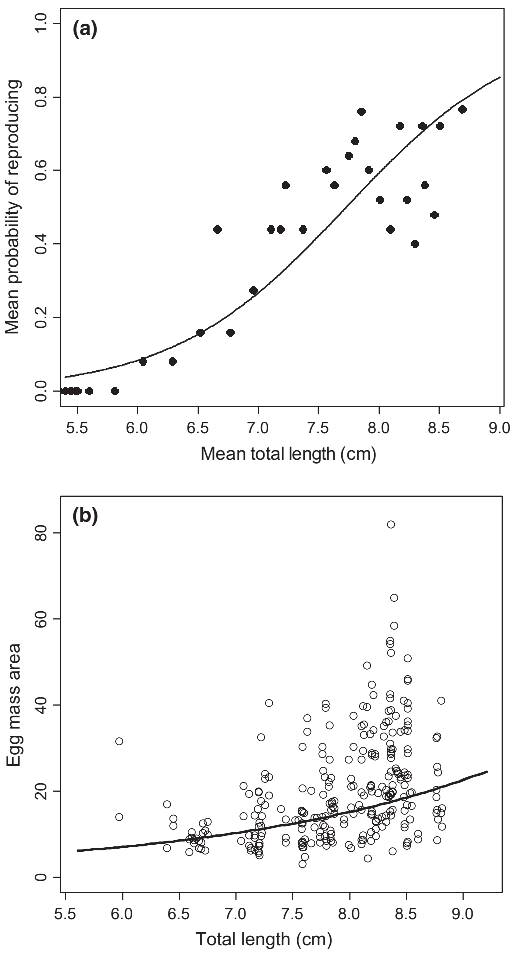

Fig. 3 Male body size and fecundity (number of eggs received). Panel (a) illustrates the relationship between probability of receiving eggs in the nest during each census and body size. Dots indicate the average values for 25 observations. Curve illustrates $p_{(t)}$ evaluated at average values of lunar phase and season. Panel (b) displays the relationship between egg mass area (directly proportional to number of offspring) and body size, given that eggs were present during the census. Curve illustrates $f_{(t)}$ evaluated at average values of season. See Table 1 for full description of functions.

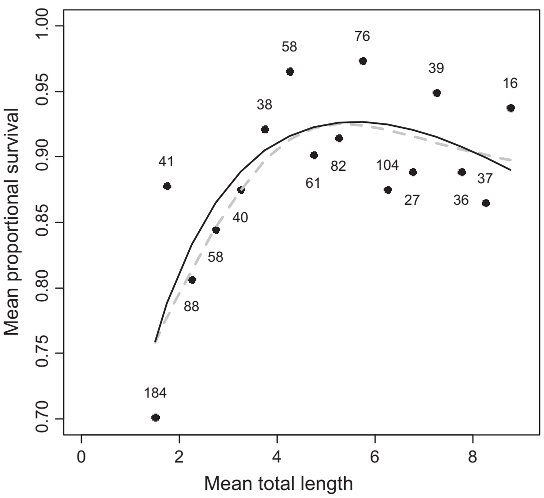

Fig. 4 Size-specific survival of juveniles and adults. Dashed line indicates the best-fit, nonparametric smoother generated by a generalized additive model. Solid line illustrates the parametric function used to model the relationship between body length and survival (see text and Table 1 for further details). For display, each data point represents average survival for fish within a 0.5 cm size bin centred on the *x*-axis value. Numbers associated with each data point indicate the number of fish within each size bin.

relative analysis examining the relationship between body length and reproductive success of adults suggested selection was strongly directional (standardized, linear selection differential = 1.04). In contrast, our analysis of lifetime fitness (net reproductive rate, R_0) suggested that selection on asymptotic size was strongly stabilizing and only moderately directional (standardized, linear selection differential = −0.130). We emphasize that neither analytical approach is necessarily superior. The main difference in our results was due to which portion of the life cycle was sampled, rather than any limitation of the analytical approaches. Our correlative analysis focused on breeding males only and was unable to measure selection that occurred before breeding – a key component of lifetime fitness. In contrast, calculating R_0 based on life-history data allowed us to examine selection throughout a much longer portion of the life cycle. We discuss each of these approaches in turn, focusing on mechanistic details of selection revealed by our correlative analysis and focusing on life-history trade-offs revealed by our approach to estimating net reproductive rate.

Of the reproductively active males of bicolour damselfish that were observed during this study, larger males tended to produce many more offspring. Much of this effect was because larger males held nests for longer periods of time, though a substantial portion was also due to males receiving more eggs while at the nest. Regarding the number of eggs received per unit time, several mechanisms may be driving these patterns. First, large males may receive more eggs because of greater access to breeding females. Male size was positively correlated with the number of adults within the same plot ($r = 0.41$). Because females tend to mate with nearby males (< 3 m away, Knapp & Warner, 1991), these results suggest that larger males may hold higher-quality territories with more adult females nearby and thus experience greater opportunity for mating. Second, breeding females within large groups may also be, on average, larger if there is a size-mediated competitive hierarchy among females in which the largest females in the group have greater access to the nest (e.g. McCormick, 2006). Because larger females deposit larger egg masses (Cole & Sadovy, 1995; Johnson *et al.*, 2010), such patterns may help explain why larger males receive more eggs. Finally, large size may be positively associated with frequency of courtship behav-

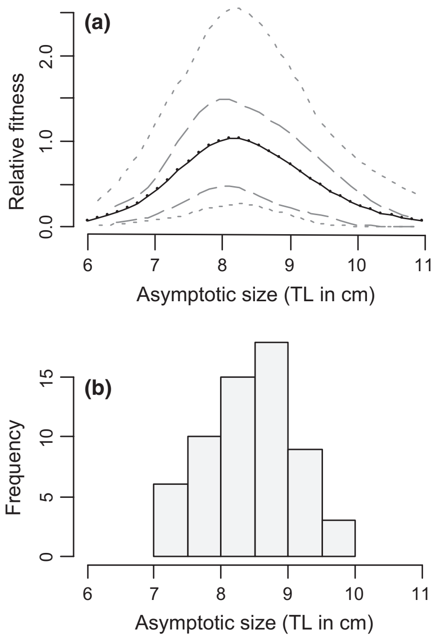

Fig. 5 Lifetime selection on asymptotic size. Panel (a) illustrates the relationship between relative value of fitness (net reproductive rate, R_0) and male asymptotic size (L_∞). Solid curve illustrates the mean value of R_0 associated with each value of L_∞. Dashed lines illustrate the 2.5th, 15th, 85th and 97.5th percentiles of the resampled R_0 values. Panel (b) displays the observed distribution of male asymptotic sizes within the population ($n = 61$).

iour – a major factor influencing female choice and male mating success (Knapp & Kovach, 1991; Knapp & Warner, 1991). Surplus energy is likely to be reflected in both larger body size and increased courtship rate (Knapp, 1995), suggesting that an indirect, positive association between these two traits is plausible, although the relationship may be weak (Schmale, 1981).

For male *S. partitus*, there appears to be a clear reproductive advantage associated with large body size. Although there are many reasons why one might expect a trait to remain evolutionarily stable despite sustained, directional selection (reviewed by Merila *et al.*, 2001), examination of lifetime fitness suggested that total lifetime selection on male asymptotic size was strongly stabilizing and only weakly directional. Moreover, we found multiple life-history trade-offs that mediated the relationship between male size and lifetime reproduction. Importantly, asymptotic size was positively correlated with age at first reproduction, generating a trade-off between reproduction and survivorship. Large individuals matured at relatively large sizes, but by maturing at later ages, more individuals that *would have* grown to a large size in fact died before reaching maturity (when reproduction could be measured). This is an example of the 'invisible fraction' (i.e. the portion of the population that died before traits of interest could be measured; Grafen, 1988) being systematically different from the surviving individuals included in the correlative analysis of phenotypic selection. In cases such as these, selection measurements on fitness components do not accurately reflect total selection experienced up to that point in the life cycle (see Hadfield, 2008 for a thoughtful review).

Lifetime selection on asymptotic size was also influenced by a decrease in survival for the largest size classes of fish observed (Fig. 4). These size classes represent males that were between 6.5 and 9.3 cm TL when tagged. This subset includes all males in the reproductive selection analyses but also includes males whose reproduction was not quantified (the first 2 years of the study did not measure fecundity). Overall, the data suggest that mortality for reproductively active males is elevated. This pattern is consistent with the idea that breeding is associated with costs that affect current, and possibly future, survival. Predation is the proximate source of mortality for most reef fishes (reviews by Hixon, 1991; Hixon & Jones, 2005), including bicolour damselfish (Carr *et al.*, 2002). For male bicolours, reproductive behaviour (e.g. courtship displays, copulation and nest defence) are both energetically costly (Knapp, 1995) and incur a greater risk of predation (Emery, 1968). Regardless of the direct mechanism responsible, increased mortality of the largest males was a selective force that counteracted the increase in reproductive output associated with large male sizes (cf. Fig. 3) and contributed to stabilizing selection on asymptotic size. However, this contribution may not be particularly strong. Modelling the relationship between mortality and body size as a power function (i.e. mortality continually decreased with size) resulted in a lifetime fitness surface that was unimodal and similar to the pattern in Fig. 5, except that the peak of the fitness function occurred at 8.55 rather than 8.35 cm TL.

Although this study highlights the importance of using a complete measure of fitness in selection analyses, our estimate of net reproductive rate could still be improved with direct information on survival and growth during the planktonic, presettlement phase of the life cycle. Because asymptotic size of *S. partitus* is correlated with body size during the larval phase (Johnson *et al.*, in press) and because mortality during the presettlement phase is often size-dependent (reviews by Morse, 1989; Pepin, 1991; Perez & Munch, 2010), individuals that survive to the post-settlement phase are probably not a random sample with respect to L_∞. Not estimating selection during this phase may therefore lead to problems associated with ignoring this 'invisible fraction' of the population (Grafen, 1988). In our analyses, we assumed that survival during the presettlement phase was size selective and increased with size at a rate similar to the size dependence observed in post-settlement survival. Similarly, we assumed that presettlement growth could be inferred from post-settlement growth. Although we made an effort to estimate what we believe is the most likely pattern of selection during the presettlement phase, direct measurements of survival and growth during the planktonic phase would certainly improve our estimates of lifetime selection on asymptotic size.

Size and age at maturity and optimal body size in fishes

In this study, the major trade-off constraining optimal body size was the positive relationship between asymptotic length and age at maturity. Delaying maturity decreases cumulative survival during the juvenile phase. Such relationships may constrain body size for many species, although the overall effect of size and age-at-maturity trade-offs will depend on how strong these trade-offs are relative to other determinants of fitness (e.g. Stearns & Koella, 1986; Roff *et al.*, 2006). All else being equal, steeper relationships between size and age at maturity would result in smaller optimal sizes and vice versa.

In general, a positive relationship between size and age at maturity may represent variation in reproductive allocation; individuals that devote relatively high amounts of energy to reproduction are likely to mature earlier, at the expense of future growth (reviews by Kozlowski, 1992; Heino & Kaitala, 1999). The steepness of such relationships and the resulting constraint on optimal body size may depend strongly on a species' reproductive biology. For species with little to no parental care of offspring (e.g. broadcast spawners), size and age-at-maturity trade-offs are likely to be driven mainly by costs of gamete production and are likely to be relatively weak. In contrast, for species with extensive parental care (e.g. bicolour damselfish), the relationship between asymptotic size and age at maturity is likely to be especially strong. For male bicolour damselfish, reproduction entails not only the costs of gamete production, but also extensive energetic costs associated with courtship and vigorous defence against egg predators (Myrberg, 1972b; Knapp, 1995). Once a male matures, it is likely that little energy is devoted to further growth. These energetic constraints may result in a steep, positive relationship between asymptotic size and age at maturity, which in turn strongly constrains optimal asymptotic size. Such relationships may be common for species in which males exhibit costly parental care. We suggest that the life-history trade-off that results from such energetic constraints may be a feature that contributes to the generally small size of fishes with costly male parental care, although the effects of these trade-offs must be considered in the light of other determinants of lifetime fitness.

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