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When bigger is not better: selection against large size, high condition and fast growth in juvenile lemon sharks

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Abstract

Selection acting on large marine vertebrates may be qualitatively different from that acting on terrestrial or freshwater organisms, but logistical constraints have thus far precluded selection estimates for the former. We overcame these constraints by exhaustively sampling and repeatedly recapturing individuals in six cohorts of juvenile lemon sharks (450 age-0 and 255 age-1 fish) at an enclosed nursery site (Bimini, Bahamas). Data on individual size, condition factor, growth rate and inter-annual survival were used to test the 'bigger is better', 'fatter is better' and 'faster is better' hypotheses of life-history theory. For age-0 sharks, selection on all measured traits was weak, and generally acted against large size and high condition. For age-1 sharks, selection was much stronger, and consistently acted against large size and fast growth. These results suggest that selective pressures at Bimini may be constraining the evolution of large size and fast growth, an observation that fits well with the observed small size and low growth rate of juveniles at this site. Our results support those of some other recent studies in suggesting that bigger/fatter/faster is not always better, and may often be worse.

Introduction

Studies estimating selection on quantitative traits have provided valuable insights into natural selection in the wild (reviews: Endler, 1986; Kingsolver *et al.*, 2001; Hereford *et al.*, 2004; Kingsolver & Pfennig, 2004). Nearly all such studies, however, have focused on terrestrial systems, and none of the above reviews includes a single study of a strictly marine species. Moreover, we are not aware of any study measuring selection on a large marine vertebrate – presumably because of the difficulty of obtaining replicated, large samples of individuals that can be tracked over long periods of time. And yet selection on such organisms may be qualitatively different, a point we consider in more detail below. The aim of our study was to estimate the strength and direction of natural selection acting on life history and morphology in a large marine vertebrate. We overcame the usual logistic constraints by intensively studying a localized, insular population of juvenile lemon sharks (*Negaprion brevirostris*).

We can see several reasons why selection in a marine environment might be qualitatively different from that in terrestrial or freshwater environments. First, the extensive three-dimensional nature of the ocean, as well as the often unpredictable distribution of resources (De Troch *et al.*, 2006), may increase spatio-temporal variation in selection. Secondly, high gene flow in the ocean (Hare *et al.*, 2005; Cowen *et al.*, 2006) may increase maladaptation and thereby maintain strong local selection. This may be particularly true when juveniles reside at local nurseries for extended periods (Castro, 1993), allowing strong local selection despite highly vagile adults. This last prediction, however, may not hold for large marine vertebrates that exhibit strong philopatry, for example cetaceans, some elasmobranchs and pinnipeds (Palsbøll *et al.*, 1995; Goodman, 1998; Feldheim *et al.*, 2004; Hueter *et al.*, 2005). Addressing these suppositions requires selection estimates for marine organisms.

Lemon sharks and the Bimini nursery site

The lemon shark is a large (maximum length: 3.4 m), placentally viviparous coastal species. It is found in the western Atlantic from New Jersey to Brazil, with relict

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populations along the West African coast as well as in the eastern Pacific between Baja California and Columbia (Compagno, 1984). In the western Atlantic, females give birth on a biennial reproductive cycle to between four and 18 juveniles (Feldheim *et al.*, 2002). Adults provide no direct parental care (Pratt & Casey, 1990), and so juveniles forage independently in shallow, inshore nursery sites. At our study site, juveniles are highly site attached for at least 3 years and have daily home ranges of no more than a few hundred square metres (Morrissey & Gruber, 1993).

The lemon shark population at Bimini, Bahamas, has been intensively studied since 1995, when a yearly tagging and recapture programme was first implemented. The enclosed nature of the nursery lagoon allows for a remarkable sampling efficiency; with approximately 99% of newborn sharks captured each year, and a high proportion of these recaptured in subsequent years (Gruber *et al.*, 2001). This exhaustive sampling allows the estimation of recapture probabilities, survivorship, and natural selection. Here, we estimate selection acting on body size, condition and growth rate.

Selection on size, condition and growth

Large body size confers some obvious fitness benefits (Roff, 1992; Blanckenhorn, 2000). In particular, larger individuals may have (1) decreased susceptibility to gape-limited predators (Parker, 1971), (2) access to a greater range of food types (Juanes & Conover, 1994), (3) greater competitive ability (Fausch & White, 1981), (4) increased resistance to extreme conditions (Henderson *et al.*, 1988) or disease (West & Larkin, 1987), (5) earlier maturation (Rowe & Thorpe, 1990) and (6) greater reproductive output (Hendry *et al.*, 2001). These expected benefits underpin the 'bigger is better' hypothesis of life history theory, which has received broad support in the form of a general trend toward selection for large size in many taxa (Sogard, 1997; Blanckenhorn, 2000; Kingsolver & Pfennig, 2004). And yet, a number of recent studies have failed to find selection favouring large size (e.g. Quinn *et al.*, 2001; Sinclair *et al.*, 2002; Carlson *et al.*, 2004), reviving interest in testing this hypothesis.

Body condition (e.g. mass for a given length) is thought to be positively related to fitness; a hypothesis that might be called 'fatter is better'. In particular, an animal in good condition should have more energy reserves, which should increase survival and reproductive output. This hypothesis is so widely accepted that measures of condition are commonly used as surrogates for fitness in studies of selection. And yet, the condition of an individual can be determined by a combination of environmental factors that include resource availability, habitat quality, and the abundance of predators (for review see Begon *et al.*, 1996). Moreover, achieving high condition may involve many of the same constraints as achieving fast growth (see below). It therefore seems profitable to measure selection on body condition in natural populations.

Fast growing individuals are generally thought to accrue the benefits of large size more rapidly (reviews: Arendt, 1997; Sogard, 1997). To the extent that bigger is better, we might therefore also expect that 'faster is better'. Indeed, and even more so than for body condition, growth rates are often used as surrogates for fitness in studies of selection. And yet, a growing body of work indicates that fast growth may have attendant fitness costs (Arendt, 1997; Lankford *et al.*, 2001; Biro *et al.*, 2004; Sundström *et al.*, 2005). As one example, the increased foraging effort required to achieve fast growth may increase the risk of predation (Biro *et al.*, 2004; Sundström *et al.*, 2005). As another, the consumption of a large meal may be detrimental to swimming ability and thus predator avoidance (Lankford *et al.*, 2001). Other possible costs of fast growth include trade-offs with defence allocation, developmental stability, energy storage and immune system function (Arendt, 1997; Sogard, 1997). Direct estimates of selection on growth rate are needed to determine whether these costs are manifested in nature, and yet such estimates have been rare until recently (Hendry *et al.*, 2003; McAdam & Boutin, 2003; Carlson *et al.*, 2004).

We perform formal selection analyses using 705 juvenile lemon sharks in six cohorts (1995–2000), each of which was tracked for at least 4 years. From these data, we estimate the strength and direction of selection acting on size, condition and growth. Our findings are then interpreted with respect to the conventional 'bigger is better', 'fatter is better' and 'faster is better' hypotheses. We are reasonably confident that our results will reflect natural (rather than anthropogenic) selection because the population was not subject to heavy fishing pressure during the study period.

Methods

Study area and sampling

Bimini, Bahamas, is a mangrove-fringed chain of islands located 85 km directly east of Miami, Florida. The Bimini islands enclose a 21 km^2 lagoon that is 0–120 cm deep at low tide and serves as a nursery for approximately 300 juvenile and sub-adult lemon sharks (Morrissey & Gruber, 1993). Each year since 1995, approximately 99% of the juveniles have been captured in two adjacent areas of the Bimini lagoon: North Sound and Sharkland (Gruber *et al.*, 2001). Sampling always takes place between 23 May and 11 June (Table 1), just after pupping by adult females (S. Gruber, personal observation). During this time, newborn and juvenile sharks are captured in 180-m long and 2-m deep gill nets (Manire & Gruber, 1991). All sharks are weighed (kg), measured for precaudal length (PCL, tip of snout to precaudal pit in cm; Compagno, 1984), and tagged intramuscularly with an individually-coded passive integrated transponder tag. Tag number, PCL, and

Table 1 Sample sizes, sample dates, and mean trait values for age-0 and age-1 juvenile lemon sharks at the start (all fish) and end (surviving fish) of each selection interval*.

Sampling interval						
Data sets and traits	1995 (2–11 June)	1996 (23 May–10 June)	1997 (26 May–11 June)	1998 (26 May–10 June)	1999 (25 May–6 June)	2000 (21 May–8 June)
All age-0 fish†						
Length (cm)	48.25 ± 1.7	48.73 ± 1.66	48.36 ± 1.60	48.78 ± 2.03	48.21 ± 1.67	48.31 ± 2.15
Mass (kg)	1.28 ± 0.28	1.38 ± 0.17	1.35 ± 0.17	1.43 ± 0.21	1.32 ± 0.17	1.27 ± 0.17
Condition factor	1.14 ± 0.21	1.19 ± 0.086	1.19 ± 0.087	1.23 ± 0.095	1.18 ± 0.092	1.13 ± 0.086
Starting (*n*)	82	42	97	66	95	68
Survival (%)	58.5	64.3	55.7	56.0	61.1	48.5
Surviving age-0 fish						
Length (cm)	48.31 ± 1.86	48.46 ± 1.39	48.15 ± 1.70	48.96 ± 1.89	48.14 ± 1.64	48.38 ± 2.17
Mass (kg)	1.27 ± 0.26	1.34 ± 0.16	1.33 ± 0.18	1.42 ± 0.20	1.32 ± 0.16	1.27 ± 0.14
Condition factor	1.13 ± 0.20	1.18 ± 0.090	1.19 ± 0.085	1.22 ± 0.096	1.19 ± 0.098	1.12 ± 0.095
All age-1 fish without growth data						
Length (cm)	n/a	54.24 ± 3.33	54.02 ± 3.31	53.83 ± 3.25	56.25 ± 2.45	54.19 ± 2.63
Mass (kg)	n/a	1.77 ± 0.39	1.79 ± 0.41	1.80 ± 0.41	2.02 ± 0.31	1.68 ± 0.29
Condition factor	n/a	1.095 ± 0.088	1.12 ± 0.10	1.14 ± 0.11	1.14 ± 0.089	1.055 ± 0.12
Starting (*n*)	n/a	51	35	58	41	70
Survival (%)	n/a	62.7	54.3	53.4	41.5	41.4
Surviving age-1 fish without growth data						
Length (cm)	n/a	53.95 ± 3.42	52.74 ± 1.87	52.59 ± 2.26	55.58 ± 2.12	53.30 ± 2.78
Mass (kg)	n/a	1.74 ± 0.40	1.64 ± 0.27	1.65 ± 0.29	1.96 ± 0.27	1.60 ± 0.29
Condition factor	n/a	1.10 ± 0.095	1.12 ± 0.12	1.13 ± 0.097	1.14 ± 0.10	1.054 ± 0.086
All age-1 fish with growth data						
Growth (cm per year)	n/a	6.18 ± 2.88	5.59 ± 2.72	6.25 ± 3.12	7.33 ± 2.19	6.11 ± 2.72
Starting (*n*)	n/a	34	25	49	32	48
Survival (%)	n/a	64.7	52.0	51.0	40.6	43.8
Surviving age-1 fish with growth data						
Growth (cm per year)	n/a	5.94 ± 2.95	4.80 ± 2.22	4.90 ± 1.64	6.89 ± 2.32	5.067 ± 1.95

*Data are numbers of tagged fish in each of the three data sets at the start of each selection interval (starting *n*), the proportion of those fish that survived to age-1 or age-2, and trait means (mean ± 1 SEM) for fish at the start and end of each selection interval for one data set.

†Fish ages are the first year of life (age-0) and the second year of life (age-1).

mass are recorded each subsequent time a shark is captured. A small piece of fin (2 mm^2) is taken from every shark for subsequent DNA extraction. Genetic analyses of these samples have been used to characterize population genetics (Feldheim *et al.*, 2001) and mating systems (Feldheim *et al.*, 2002), and are used here to aid in determining the age of juveniles (see below).

Age determination

The following methods allowed us to confidently assign ages to 91% of the sharks caught between 1995 and 2000; the remainder were excluded from analyses.

Umbilical status has been used to identify newborns (age-0 or 'young of the year') since 1997. The umbilical scar is open at birth and then slowly closes during the first few months of life, enabling age-0 sharks to be unambiguously identified at the time of sampling. Age-0 sharks identified in this way were always <52 cm in body length (PCL), and so any shark smaller than this size in the other years (1995 and 1996) was also considered to be of this age (Barker *et al.*, 2005). A few sharks were not caught at age-0 but rather at age-1 or age-2. For these, we determined the year of birth (and therefore age) based on length measurements and an average annual growth range at Bimini of 5.2–7.1 cm (Barker *et al.*, 2005). This method allowed us to narrow the year of birth for a given shark to at most two different years, which we then discriminated between based on microsatellite analyses of family relationships. Specifically, we matched individuals of unknown age to their siblings of known age (for more details see Feldheim *et al.*, 2004).

Recapture probabilities, emigration and survival

Like most other studies, our estimates of selection during a particular interval (one year to the next) were based on whether individuals were recaptured (assumed to have survived: absolute fitness = 1) or not recaptured (assumed to have died: absolute fitness = 0). The reliability of this approach depends on recapturing most of the individuals that were indeed still alive (Letcher *et al.*, 2005). We therefore needed to ensure that we had a high probability of recapturing fish that remained in the study area and that emigration was relatively rare and unbiased with respect to phenotype.

The first of these properties was assessed by using the program MARK (White & Burnham, 1999), to estimate annual probabilities of recapture (P, probability of catching individuals that were alive and present in the study area) and apparent survival (ϕ, probability that individuals were alive and present in the study area). Individual capture histories (captured = 1 or not captured = 0, in each year) were generated for each tagged shark over a 4-year period following its initial capture. Data for age-0 and age-1 juveniles were analysed separately, but all cohorts from each age class were included in the same analysis.

The Cormack–Jolly–Seber model was used as a global starting point for the survival analyses (Lebreton *et al.*, 1992), and four discrete models were tested: (1) survival varies with both age and cohort, (2) survival varies with age but not cohort, (3) survival varies with cohort but not age and (4) survival does not vary with age or cohort. For all of these models, we followed the general convention of allowing recapture probabilities to vary in the most complex way; among all ages and cohorts (e.g. Carlson & Letcher, 2003). Akaike's Information Criterion (*AIC*) was used to compare the four candidate models, with the best model being that with the lowest *AIC* score and therefore the highest *AIC* weight (Burnham & Anderson, 2002). If the best model had an *AIC* weight >0.8, it alone was used to estimate the probability of recapture and apparent survival. If no single model had an *AIC* weight >0.8, estimates were averaged across the set of models that had the highest weights (Burnham & Anderson, 2002).

The second property of concern (emigration) was addressed in two ways. First, we performed the above MARK analyses including or excluding the few sharks (22 age-0 and 15 age-1) that were initially tagged in the nursery area but later recaptured during opportunistic sampling at other sites around the island. Secondly, we determined whether these emigrants differed phenotypically from non-emigrants by comparing their size and condition when captured earlier at the same age in the nursery site.

Natural selection

We estimated selection acting on four traits: body length, body mass, relative condition factor and growth rate. Body length (PCL) and body mass were measured directly on individual fish at the time of capture. Relative condition factor was calculated as $10\,000 \times \text{mass} \times \text{PCL}^{-b}$, where b is the slope of the regression line of $\log_{10}$ mass on $\log_{10}$ PCL for the entire data set ($b = 2.999$, $r = 0.99$). Fish that are heavier (lighter) than expected for their length have a higher (lower) relative condition factor (Schulte-Hostedde *et al.*, 2005). Growth rate was calculated as the change in body length between subsequent years so as to consider changes in structural size.

Selection on length, mass, and condition factor was estimated by relating these traits for individuals at the start of an interval (year i) to whether or not they survived to the end of that interval (year $i + 1$). Growth rate, however, can only be estimated for fish captured at both the beginning and end of an interval (i.e. those that survive). Selection on growth was therefore estimated by relating the change in length between year i and year $i + 1$ (here age-0 to age-1) to survival between year $i + 1$ and year $i + 2$ (here age-1 to age-2). Because growth rate data were only available for a subset of the fish, estimates of selection on all other traits excluded data for growth rate, thereby maximizing sample size. Selection on growth rate was then estimated by adding this trait to the analyses. These approaches parallel those used by Hendry *et al.* (2003).

Selection analyses benefit from standardization of both phenotypic trait values and fitness (Lande & Arnold, 1983; Janzen & Stern, 1998). Our trait values were standardized to a mean of zero and a standard deviation of unity (based on fish at the start of each selection interval) within each combination of cohort and age class (Lande & Arnold, 1983; Janzen & Stern, 1998). Fitness was then estimated as survival across the interval (i.e. from age-0 to age-1 or from age-1 to age-2). Any tagged sharks that were captured at the end of a given interval, or in any subsequent year, were known to have survived through that interval (absolute fitness = 1). Any tagged sharks not recaptured at the end of a given interval, or in any subsequent year, were assumed to have died (absolute fitness = 0). Further justification for this latter assumption is provided below. Relative fitness was then determined for each shark by dividing its absolute fitness over an interval (0 or 1), by the mean fitness of all individuals for that combination of cohort/age/interval.

Selection was estimated using standard procedures (Lande & Arnold, 1983; Schluter, 1988; Brodie *et al.*, 1995; Janzen & Stern, 1998; Hereford *et al.*, 2004). First, simple regressions of relative fitness on each trait alone were used to estimate selection differentials (i). Secondly, multiple regressions that included all traits were used to estimate selection gradients (β), which represent selection acting on each trait independent of correlations with the other traits. These regressions excluded body mass because it was too highly correlated with body length ($r = 0.99$; see Mitchell-Olds & Shaw, 1987). Thirdly, multiple regressions that included two variables (a trait and its squared values) were used to estimate univariate quadratic (nonlinear) selection differentials. Fourthly, multiple regressions that included all traits, as well as all squared and cross-product terms for those traits, were used to estimate univariate and bivariate quadratic selection gradients.

All regressions were logistic in form because of the binary response variable (i.e. fitness = 0 or 1), but here we present coefficients after conversion to their linear equivalents (Janzen & Stern, 1998). The resulting variance-standardized selection coefficients represent the number of standard deviations that selection changes the mean trait value within a generation (Kingsolver *et al.*, 2001). We also calculated mean-standardized selection coefficients (Hereford *et al.*, 2004), which represent the increase in relative fitness for a proportional change in the trait mean (with a coefficient of one theoretically indicative of selection on fitness itself). Thus, a mean-standardized coefficient of 0.50 indicates that a 100% change in the mean of a trait would lead to a 50% increase in fitness.

Our six cohorts allowed a combined analysis that can (1) evaluate temporal variation in selection for a given age and; (2) generate more precise estimates of average selection on a given trait. Specifically, we re-ran the above regressions after including 'cohort' as a random factor. Interactions between cohort and coefficients for a given trait reveal the amount of temporal variation in selection on that trait. Coefficients for a given trait without the interaction term in the model, then provide the best estimate of selection on a trait averaged over the six cohorts.

Finally, we used univariate cubic splines (Schluter, 1988; GLMSWIN1.0 spline program, Schluter, 2000) to visualize the form of selection acting on each trait for each combination of cohort and age. To facilitate the interpretation of these fitness surfaces, we used raw trait data and absolute fitness rather than standardized values. We used a binomial model, as well as smoothing parameters (λ) that minimized prediction error and best revealed the general trends: length, $\lambda = 2$; mass, $\lambda = -2$; relative condition factor, $\lambda = -2$; and growth, $\lambda = 2$. Multivariate visualizations were not necessary because few traits were considered and these were not strongly correlated (after excluding mass). Further, nearly all bivariate quadratic coefficients were nonsignificant and univariate interpretations were straightforward.

Results

We followed the fates of 450 age-0 and 255 age-1 sharks for at least 4 years after their birth. Although yearly sample sizes (Table 1) are less than ideal for estimating selection (Hersch & Phillips, 2004), these are the first estimates for a large marine vertebrate. Further, they will not be strongly influenced by sampling error because we captured nearly 99% of all newborn sharks (Gruber *et al.*, 2001) and essentially all of the subsequent survivors (see below). Moreover, we were able to combine the six cohorts and thereby estimate selection coefficients with much larger sample sizes.

Recapture and survival probabilities

Each cohort was sampled in five separate years, allowing an analysis of recapture and apparent survival probabilities across four different ages (Fig. 1a,b). Only the first three of these yielded informative estimates, however, because few fish were captured after age-4 (Fig. 1a,b). Yearly recapture probabilities were generally high up to age-3 (0.67–0.85; Fig. 1a,b), but dropped at age-4 (0.20–0.48), presumably because older juveniles were finally leaving the nursery site (B. Franks, unpublished data). Of the four possible survival models starting at age-0 (Table 2), two received much stronger support than the others: one in which survival varied with age but not cohort (*AIC* weight = 0.3903) and one in which survival varied with age and cohort (*AIC* weight = 0.3543). Averaging parameter estimates for these two models yielded survival estimates that ranged from 48% to 70%

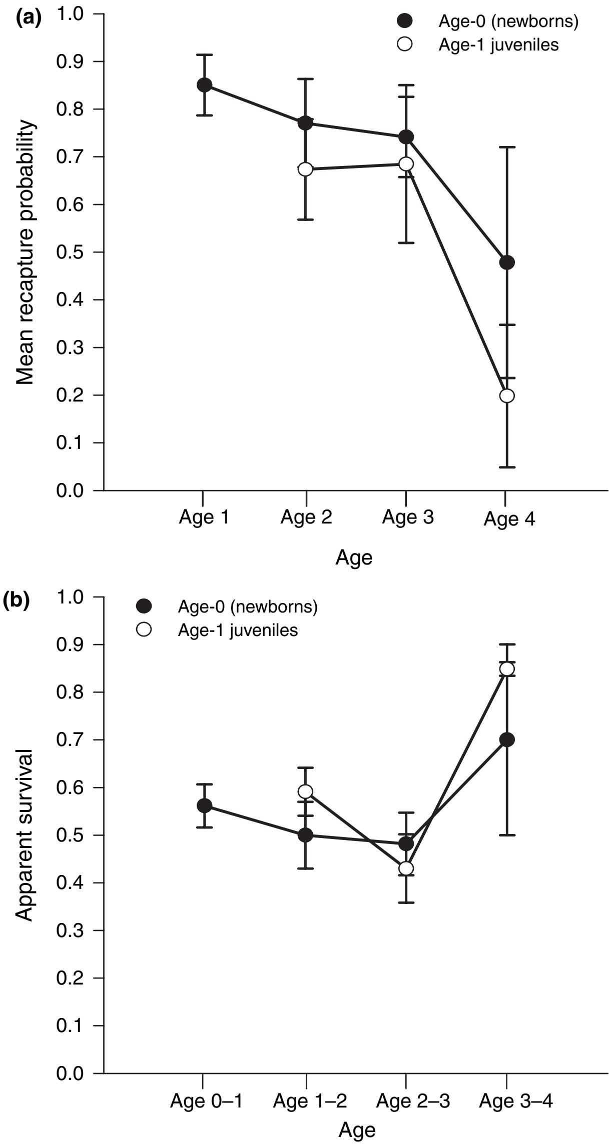

Fig. 1 Mean recapture probabilities (a) and apparent survival estimates (b) (±SE) for age-0 and age-1 juvenile lemon sharks at Bimini, Bahamas. Estimates from all cohorts were averaged over each age to facilitate comparison between age-0 and age-1 sharks.

Table 2 Model selection for estimating apparent survival in age-0 and age-1 juvenile lemon sharks.

Model	*AIC*	Delta *AIC*	*AIC* weight	Model likelihood	Number of parameters
All age-0 fish					
$phi_{(.)}$	1199.499	1.805	0.1583	0.406	25
$phi_{(\text{cohort})}$	1200.474	2.781	0.0972	0.249	30
$phi_{(\text{age})}^{*}$	1197.694	0.000	0.390	1.000	28
$phi_{(\text{age+cohort})}^{*}$	1197.887	0.193	0.354	0.908	48
All age-1 fish					
$phi_{(.)}^{*}$	624.513	1.332	0.30394	0.5138	21
$phi_{(\text{cohort})}$	626.998	3.817	0.0877	0.1483	25
$phi_{(\text{age})}^{*}$	623.181	0.000	0.592	1.000	24
$phi_{(\text{age+cohort})}$	630.311	7.130	0.0167	0.0283	40

Four discrete survival models were tested: (1) survival does not vary with age or cohort ($phi_{(.)}$), (2) survival varies with cohort but not age ($phi_{(\text{cohort})}$), (3) survival varies with age but not cohort ($phi_{(\text{age})}$) and (4) survival varies with age and cohort ($phi_{(\text{age+cohort})}$).

*Indicates these models were used for inference.

(Fig. 1b). Of the four possible survival models starting at age-1, two models again received much stronger support than the others: one in which survival varied with age but not cohort (*AIC* weight = 0.59159) and one in which survival did not vary with age or cohort (*AIC* weight = 0.30394). Averaging parameter estimates for these two models yielded survival estimates that ranged from 43% to 85% (Fig. 1b).

Our selection estimates were likely robust to some potential biases. First, we had a very high probability of recapturing a tagged fish that was alive and present at the study site. Combining the yearly recapture probabilities of the four sampling events for each cohort, we calculate that the probability of subsequently recapturing an age-0 fish that was alive and present at the site when it reached age-1 was 0.99 (0.92 for an age-1 fish that reached age-2). Secondly, emigration did not confound our selection estimates. Only 22 age-0 and 15 age-1 fish initially tagged in the nursery area were later recaptured in opportunistic sampling at other sites around the island (3.3–7.6 km from the main nursery). Yearly survival and recapture probabilities did not differ between analyses that included or excluded these fish (paired sample *t*-test comparing estimates with and without emigrants, $P > 0.17$). When sampled at age-0, future emigrants and residents did not differ in size or condition (Student's *t*-test: length, $P = 0.162$; mass, $P = 0.181$; relative condition factor, $P = 0.745$). When sampled at age-1, future emigrants and residents did not differ in condition (Student's *t*-test: $P = 0.066$) or mass (Student's *t*-test: $P = 0.175$), but emigrants were slightly smaller (PCL = 53.02 ± 0.81 mm) than residents (54.51 ± 0.20 mm; student's t-test, $P = 0.044$).Thus, the only observed difference between residents and emigrants would act in *opposition* to our inferred selection (see below).

Natural selection

Selection differentials and gradients were closely correlated ($r = 0.931$, $P < 0.001$) across trait/age/cohort combinations and were always of the same sign (save one, Table 3). We therefore do not separately discuss differentials and gradients, but rather refer to them collectively as 'selection coefficients'.

Linear (directional) selection was variable across cohorts and ages, but some clear patterns emerged (Table 3). For age-0 sharks, selection coefficients for mass and relative condition factor were negative in five of six cohorts (Table 3), whereas the coefficients for length showed no consistency (Table 3; Fig. 2a). When cohorts were analysed together in a single ANOVA model, temporal variation in selection was not significant for length ($F_{5,431} = 0.885$, $P = 0.491$), mass ($F_{5,431} = 0.757$, $P = 0.581$), or condition factor ($F_{5,431} = 1.139$, $P = 0.339$). However, all combined selection coefficients were negative in sign, although none were significant (i.e. $P > 0.05$, see Table 3). Selection, thus, generally (but not always) favoured lighter fish, both in an absolute sense (mass) and relative to body length (condition factor), a conclusion supported by the cubic splines (Fig. 2c,e). However, the variation associated with many of the cohort-specific and overall selection estimates was so large that they were almost never significant at $\alpha = 0.05$ (Table 3). The safest interpretation then may simply be that selection does not favour larger fish.

Selection on age-1 sharks was roughly similar to that on age-0 sharks, but much stronger. Length, mass, and growth rate showed negative coefficients in all cohorts, and 10 of the 25 estimates were significant at $\alpha = 0.05$. Cubic splines confirm the interpretation that selection strongly and consistently favoured small size (Fig. 2b,d) and slow growth (Fig. 2g). Selection on relative condition factor varied dramatically in both sign and magnitude for age-1 sharks, and was never significant (Table 3; Fig. 2f). When all cohorts were analysed together in a single ANOVA model, temporal variation was not significant for any trait (length: $F_{4,240} = 0.936$, $P = 0.444$; mass: $F_{4,240} = 0.905$, $P = 0.461$; condition factor: $F_{4,240} = 0.274$, $P = 0.895$; growth: $F_{4,168} = 0.221$, $P = 0.926$), whereas combined selection coefficients were significant for all traits (save condition factor, see Table 3).

Quadratic (nonlinear) selection did not act in a consistent fashion on any of the traits. Univariate quadratic coefficients were variable in both sign and magnitude (Table A1), but all of the significant ones were negative. This suggests that selection may be stabilizing overall and is at least not disruptive, a pattern confirmed by the cubic splines (Fig. 2). Bivariate quadratic coefficients were also variable and rarely significant (Table A1).

Table 3 Linear (directional) selection coefficients acting on the length, mass, relative condition factor and growth rate of age-0 and age-1 juvenile lemon sharks.

	Year of sampling						
	1995	1996	1997	1998	1999	2000	Overall (1995–2000)§
Differentials: age-0 fish†							
Length	0.036/1.76	−0.17/−8.29	−0.13/−6.054	0.078/3.80	−0.053/−2.54	0.030/1.43	−0.019/−0.91
Mass	−0.017/−0.018	−0.23*/−0.26	−0.094/−0.10	−0.027/−0.030	0.022/0.024	−0.0083/−0.0089	−0.030/−0.032
Condition factor	−0.053/−0.060	−0.16/−0.19	−0.012/−0.015	−0.17/−0.21	0.11/0.13	−0.015/−0.0162	−0.023/−0.027
Gradients: age-0 fish							
Length	0.040/1.95	−0.18/−8.89	−0.13/−6.10	0.073/3.56	−0.047/−2.24	0.029/1.38	−0.021/−0.99
Condition factor	−0.057/−0.065	−0.16/−0.20	−0.013/−0.015	−0.17/−0.21	0.11/0.13	−0.0082/−0.0092	−0.023/−0.027
Differentials: age-1 fish							
Length	n/a	−0.081/−4.41	−0.39*/−21.05	−0.39*/−21.038	−0.25/−14.16	−0.36*/−19.33	−0.29**/−15.76
Mass	n/a	−0.063/−0.075	−0.32*/−0.39	−0.36/−0.44	−0.18/−0.23	−0.27*/−0.32	−0.23**/−0.28
Condition factor	n/a	0.028/0.03	−0.033/−0.037	−0.11/−0.12	0.072/0.082	−0.0087/−0.0092	−0.0082/−0.0091
Growth‡	n/a	−0.074/−0.46	−0.30/−1.67	−0.44*/−2.72	−0.19/−1.36	−0.42*/−2.58	−0.30**/−1.89
Gradients: age-1 fish							
Length	n/a	−0.095/−5.14	−0.41*/−22.24	−0.40**/−21.43	−0.27/−15.08	−0.35*/−19.16	−0.29**/−15.90
Condition factor	n/a	0.0512/0.056	0.11/0.12	−0.047/−0.054	0.099/0.12	−0.033/−0.035	0.030/0.033
Length‡	n/a	0.024/1.30	0.027/1.46	−0.13/−7.00	−0.20/−11.25	−0.28/−15.17	−0.093/−5.06
Condition factor‡	n/a	0.13/0.14	0.014/0.016	−0.026/−0.030	−0.045/−0.051	−0.0050/−0.0053	0.052/0.058
Growth‡	n/a	−0.16/−0.96	−0.33/−1.84	−0.35/−2.18	−0.0017/−0.012	−0.26/−1.57	−0.25*/−1.57

Coefficients to the left of the slash are variance-standardized, those to the right are mean-standardized.

*$P < 0.05$, **$P < 0.01$.

†Fish ages are the first year of life (age-0) and the second year of life (age-1).

‡Regressions include growth-rate data.

§Coefficients in this column are summary estimates of overall selection (i.e. all cohorts combined).

Discussion

General patterns

We examined selection acting on juveniles of a large marine vertebrate. No study has previously accomplished this task, presumably because of the difficulty in finding populations where adequate numbers of site-attached individuals can be tagged and recaptured over multiple years. We overcame these limitations through a long-term mark-recapture study of a lemon shark population, where essentially all newborns could be captured, and where nearly all then remained resident for at least 3 years. Analyses using the program MARK showed that we would rarely fail to recapture individuals who remained alive in the study site. We also confirmed that emigration from the site did not drive the inferred patterns of selection. Survival probabilities for the first two years of life ranged from 50% to 59%, similar to estimates based on mark–depletion methods at this site (Gruber *et al.*, 2001). This nontrivial mortality rate, which may be the result of predation, starvation, or disease, suggests that significant viability selection could act on this population.

Our first major conclusion is that bigger is not better for juvenile lemon sharks at Bimini. Instead, selection generally favours smaller size, particularly between age-1 and age-2 (Table 3; Fig. 2b,d). This finding conflicts with the conventional wisdom that large size confers considerable fitness benefits (Sogard, 1997; Blanckenhorn, 2000; Kingsolver & Pfennig, 2004). And yet, a growing number of recent studies have documented selection *against* large size and fast growth (Quinn *et al.*, 2001; Sinclair *et al.*, 2002; Carlson *et al.*, 2004). Moreover, a number of plausible hypotheses can be advanced for why bigger may not be better. We will later consider these hypotheses in relation to our study population (see below).

Our second major conclusion is that 'fatter' is not better; directional selection does not act in a consistent fashion on the relative condition factor of juvenile lemon sharks at Bimini. This variation may be the result of between-year fluctuations in environmental conditions, which are known to occur at this site (S. Gruber, personal observation). Indeed, selection was also somewhat variable on size and growth, albeit to a lesser degree. This variation could conceivably reflect the stochastic nature of selection, which is unlikely to be constant in space or time (e.g. Blanckenhorn *et al.*, 1999; Jann *et al.*, 2000; Przybylo *et al.*, 2000; Kinnison & Hendry, 2001), although a temporal analysis of our selection estimates does not support this idea. Thus, although recent studies suggest that bursts of strong directional selection are often separated by periods of reversal or stasis (Hoekstra *et al.*, 2001; Grant & Grant, 2002), it remains to be seen whether year-to-year variability in selection is the rule rather than the exception.

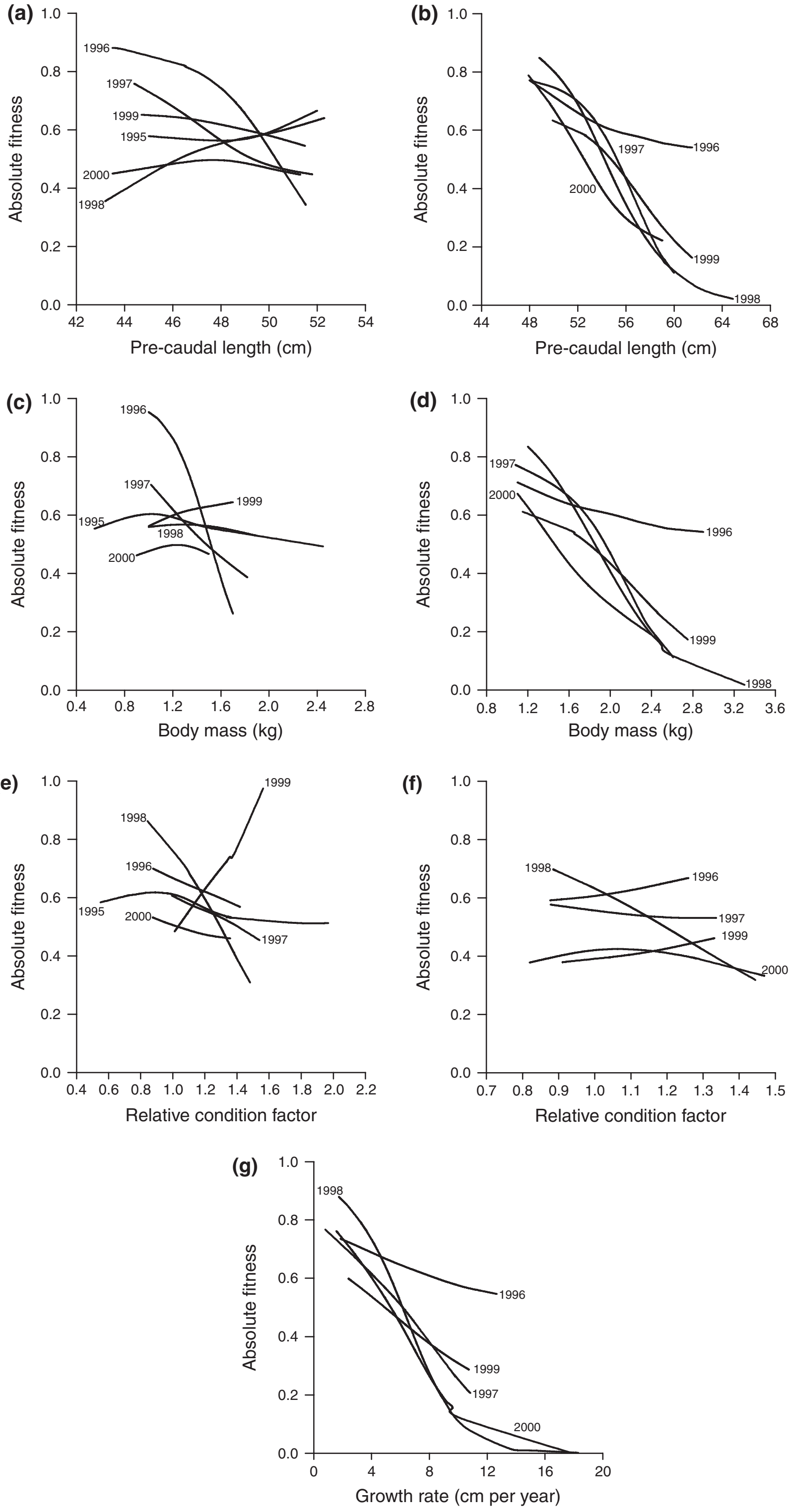

Fig. 2 Relationship between initial precaudal length (a,b), body mass (c,d), relative condition factor (e,f), or growth rate (g) and an individual's absolute fitness for each cohort of age-0 (a,c,e) and age-1 (b,d,f,g) juvenile lemon sharks. The lines are univariate cubic splines (Schluter, 1988; PCL, $\lambda = 2$; mass, $\lambda = -2$; relative condition factor, $\lambda = -2$ and growth, $\lambda = 2$, see Methods). Growth was calculated for the interval preceding that (i.e. age-0 to age-1) over which selection was estimated (i.e. age-1 to age-2) and thus only available for age-1 juveniles.

Our third major conclusion is that 'faster' is not better for juvenile lemon sharks at Bimini. Indeed, selection on age-1 fish strongly favoured slower growth in all cohorts (Fig. 2g), a result that again conflicts with conventional wisdom (see Introduction). Instead, our results parallel more recent work showing fitness costs associated with fast growth (Billerbeck *et al.*, 2001; Lankford *et al.*, 2001; Mangel & Stamps, 2001; Biro *et al.*, 2004; Brown & Braithwaite, 2004). Proposed reasons for these costs include increased predation risk (Billerbeck *et al.*, 2001; Lankford *et al.*, 2001; Biro *et al.*, 2004; Brown & Braithwaite, 2004), reduced swimming performance (Billerbeck *et al.*, 2001; Lankford *et al.*, 2001), decreased foraging ability (Biro *et al.*, 2004), as well as decreased immunological competence and starvation endurance (Mangel & Stamps, 2001). These specific hypotheses have typically been investigated in laboratory studies, but our work suggests the importance of also doing so in nature.

Strong selection against large size and fast growth should cause the evolution of smaller size and slower growth. Lemon sharks are too long lived (i.e. >25 years) for us to see if this sort of evolutionary change is indeed taking place at Bimini. We can, however, examine the outcome of this selection by comparison with another surveyed population (Marquesas Key, Florida; Barker *et al.*, 2005). Compared with Marquesas, Bimini sharks are smaller at age (length: 54 cm vs. 74 cm at age-1) and grow much slower (6 cm vs. 20 cm between age-0 and age-1). Although we cannot be certain that this difference is genetic, the observed selection against large size and fast growth is at least consistent with the apparent evolution of small size and slow growth of Bimini sharks.

Selection in a large marine vertebrate

Nearly all previous estimates of selection have been for terrestrial or freshwater organisms, and yet it may be qualitatively different for large marine vertebrates. Here we compare strengths of selection in our study to those documented in other taxa (from Kingsolver *et al.*, 2001) and to theoretical predictions (Hereford *et al.*, 2004). Based on variance-standardized coefficients, selection acting on size-related traits for age-0 lemon sharks is weak (median absolute value = 0.08) in relation to other taxa (median = 0.16). For age-1 sharks, however, selection acting on length (median = 0.31) and growth (median = 0.22) was relatively strong. Indeed, these latter values fall into the 77th and 65th percentile for all taxa combined (Kingsolver *et al.*, 2001). These differences are even greater when comparisons were restricted to estimates based on viability selection (86th and 77th percentile).

For mean-standardized coefficients, a suggested benchmark for strong selection is unity, because this value should correspond to the strength of selection on fitness itself (Hereford *et al.*, 2004). Our mean-standardized coefficients have a median absolute value of 0.32 (range = 0.0089–22.24), suggesting that the typical strength of selection acting on Bimini sharks was at least a third as strong as selection on fitness itself, and comparable with other taxa (Hereford *et al.*, 2004). Some of our estimates, however, are so much greater than unity that they call into question the utility of such comparisons. One problem is that absolute values are biased upward because of sampling error (Hereford *et al.*, 2004). Other possible explanations include: (1) a bias caused by considering only one component of fitness or; (2) environmentally induced covariance between traits and fitness (Hereford *et al.*, 2004).

Thus, the only available estimates for a large marine vertebrate suggest that selection is not weaker than for other taxa, and may even be stronger. We suggest that high dispersal in the marine realm maintains strong selection by preventing full adaptation to local conditions. Indeed, dispersal rates appear to be high for lemon sharks, as population structure at neutral markers is generally lacking on the scale of thousands of kilometres (Feldheim *et al.*, 2001). The juveniles, however, remain in their local nursery sites for several years (Morrissey & Gruber, 1993). Selection may therefore be fine-grained, whereas evolutionary responses are coarse-grained.

Mechanisms of selection

Regression coefficients in and of themselves do not provide guidance as to the specific cause of apparent selection (e.g. sampling bias, emigration, predation, starvation, or disease). So much is known about our study site, however, that we can at least make some informed speculations. One possibility is that selection may not be acting at all, but that our estimates are biased because of preferential capture of particular individuals during sampling. Gillnets can be selective for smaller sharks (Carlson & Cortés, 2003), which may cause apparent selection on size-related traits. This seems unlikely at Bimini, however, because we catch nearly all of the fish within the nursery (Gruber *et al.*, 2001), and because we routinely catch larger sharks using the same nets at a different nursery site (Marquesas Key, Florida).

A second possibility is size-selective emigration (Kingsolver & Smith, 1995; Letcher *et al.*, 2005); larger, faster-growing sharks may be more likely to emigrate from our study site. This potential bias seems unlikely in our study because emigration by age-0 or age-1 sharks is rare at Bimini: (1) telemetry reveals high site fidelity and limited movement (Morrissey & Gruber, 1993); (2) displaced lemon sharks return to their original home ranges (Edrén & Gruber, 2005) and; (3) age-0 sharks are rarely captured outside of the nursery area (Gruber *et al.*, 2001). Moreover, age-1 emigrants were actually *smaller* than residents, a difference that would act in opposition to our inference of selection against large size.

A third possibility is that selection for small size and slow growth at Bimini is a function of low resource availability. On the one hand, this seems unlikely because the Bimini lagoon is not resource limited, especially with respect to the primary prey item of the lemon shark (i.e. yellowfin mojarra, *Gerres cinereus*; Newman & Gruber, 2002). Moreover, we find no relationship across years between shark density (range: 70–105 individuals km^{-2}) and selection coefficients for any trait (all $r^2 < 0.544$; all $P > 0.155$). We have also never witnessed aggressive interactions among sharks in the Bimini nursery area (Gruber, 1982), suggesting a lack of interference competition. On the other hand, the nursery area does suffer from wide swings in ecological conditions, with exceedingly high and variable temperatures (due to shallow water and frequent rain showers), low nutrients and wide salinity fluctuations (S. Gruber, personal observation). Selection for small size and slow growth may be related to episodic variation in resource availability driven by these ecological factors.

A fourth possibility is predation pressure. Individual fish that achieve large size and fast growth presumably forage more frequently and in riskier situations, which increases predation risk (Martel & Dill, 1995; Mangel & Stamps, 2001; Biro *et al.*, 2003; Biro *et al.*, 2004; Brown & Braithwaite, 2004). Juvenile lemon sharks are susceptible to both inter- and intra-specific predation (S. Gruber, unpublished data), particularly from larger, sub-adult lemon sharks. Most feeding by juvenile lemon sharks takes place in or near the mangrove roots, which afford protection from predation (S. Gruber, personal observation). Fast growth, however, may also require foraging away from the mangroves. In fact, some juveniles stray outside the nursery area from time to time (Morrissey & Gruber, 1993), which will increase their exposure to predators. Predation may also favour smaller size and slower growth if faster growing fish are less adept at escaping predators (Billerbeck *et al.*, 2001; Lankford *et al.*, 2001) or if larger prey are preferred by predators (see Sogard, 1997).

A fifth possibility is that selection favouring small size and slow growth may be offset by selection favouring large size and fast growth at some other life stage (see Schluter *et al.*, 1991). Indeed, selection is known to vary with age in other fish species (Hendry *et al.*, 2003; Carlson *et al.*, 2004; Zabel & Achord, 2004), and this was also the case in our study (Table 3). Opposing selection seems inevitable at some point; otherwise this population would be forever evolving a smaller size. We suggest that size and growth in Bimini sharks reflects a balance between opposing selection pressures acting during different life history stages – and that this balance is different from other populations. In particular, selection against large size and fast growth in young juveniles may be stronger at Bimini than elsewhere, leading to a smaller equilibrium body size. Indeed, we have already noted that size-at-age and growth rates are lower at Bimini than at Marquesas (Barker *et al.*, 2005), the only other site where lemon sharks have been intensively studied.

Conclusion

Although studies of natural selection are logistically difficult for large marine organisms, we were able to generate robust estimates through an intensive, long-term, mark–recapture study of a lemon shark nursery site at Bimini, Bahamas. Our results suggest that selection at this site may play an important role in the evolution of size-related traits. We found strong directional selection against large size and fast growth, which fits with the small size and slow growth of sharks at this site. And yet, body size and growth in this population may still be greater than the optimum – otherwise selection should largely be absent. Partial maladaptation that maintains selection could be the result of high gene flow from other nursery sites where selection favours different phenotypes (i.e. larger size and faster growth). The specific selection pressures at Bimini have not been confirmed but may relate to increased predation on individuals that take more risks during foraging, or to other environmental characteristics at this site.

Our findings further challenge the conventional 'bigger is better', 'fatter is better' and 'faster is better' hypotheses. This conclusion is particularly interesting given that lemon sharks are large in general. We suggest that this paradox may be partly resolved by considering opposing selection pressures, which could theoretically favour larger size and faster growth later in life. Monitoring a population through only a portion of their life history can give an incomplete picture of selection, and so future work should aim to study selection at other life stages. Only then can we confirm whether selection on large marine vertebrates differs qualitatively from that for other organisms.

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References

Arendt, J.D. 1997. Adaptive intrinsic growth rates: an integration across taxa. *Q. Rev. Biol.* **72**: 149–177.

Barker, M.J., Gruber, S.H., Newman, S.P. & Schluessel, V. 2005. Spatial and ontogenetic variation in growth of nursery-bound juvenile lemon sharks, *Negaprion brevirostris*: a comparison of two age-assigning techniques. *Env. Biol. Fishes* **72**: 343–355.

Begon, M., Mortimer, M. & Thompson, D.J. 1996. *Population Ecology, a Unified Study of Animals and Plants*, 3rd edn. Blackwell Science, Oxford.

Billerbeck, J.M., Lankford, T.E. Jr & 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., Post, J.R. & Parkinson, E.A. 2003. From individuals to populations: Prey fish risk-taking mediates mortality in whole-system experiments. *Ecology* **84**: 2419–2431.

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* **271**: 2233–2237.

Blanckenhorn, W.U. 2000. The evolution of body size: what keeps organisms small? *Q. Rev. Biol.* **75**: 385–407.

Blanckenhorn, W.U., Morf, C., Mühlhäuser, C. & Reusch, T. 1999. Spatiotemporal variation in selection on body size in the dung fly *Sepsis cynipsea*. *J. Evol. Biol.* **12**: 563–576.

Brodie, E.D. III, Moore, A.J. & Janzen, F.J. 1995. Visualizing and quantifying natural selection. *TREE* **10**: 313–318.

Brown, C. & Braithwaite, V.A. 2004. Size matters: a test of boldness in eight populations of the poeciliid *Brachyraphis episcopi*. *Anim. Behav.* **68**: 1325–1329.

Burnham, K.P. & Anderson, D.R. 2002. *Model Selection and Multimodel Inference: A Practical Information-theoretic Approach*. Springer-Verlag, New York.

Carlson, J.K. & Cortés, E. 2003. Gillnet selectivity of small coastal sharks off the southeastern United States. *Fish. Res.* **60**: 405–414.

Carlson, S.M. & Letcher, B.H. 2003. Variation in brook and brown trout survival within and among seasons, species, and age classes. *J. Fish Biol.* **63**: 780–794.

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.

Castro, J.I. 1993. The shark nursery of Bulls Bay, South Carolina, with a review of the shark nurseries of the southeastern coast of the United States. *Env. Biol. Fishes* **38**: 37–48.

Compagno, L.J.V. 1984. *FAO Species Catalogue: Sharks of the World*. Food and Agriculture Organization of the United Nations, Rome.

Cowen, R.K., Paris, C.B. & Srinivasan, A. 2006. Scaling of connectivity in marine populations. *Science* **311**: 522–527.

De Troch, M., Van Gansbeke, D. & Vincx, M. 2006. Resource availability and meiofauna in sediment of tropical seagrass beds: local versus global trends. *Mar. Env. Res.* **61**: 59–73.

Edrén, S.M.C. & Gruber, S.H. 2005. Homing ability of young lemon sharks, *Negaprion brevirostris*. *Env. Biol. Fishes* **72**: 267–281.

Endler, J.A. 1986. *Natural Selection in the Wild*. Princeton University Press, Princeton.

Fausch, K.D. & White, R.J. 1981. Competition between brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) for positions in a Michigan stream. *Can. J. Fish. Aquat. Sci.* **38**: 1220–1227.

Feldheim, K.A., Gruber, S.H. & Ashley, M.V. 2001. Population genetic structure of the lemon shark (*Negaprion brevirostris*) in the western Atlantic: DNA microsatellite variation. *Mol. Ecol.* **10**: 295–303.

Feldheim, K.A., Gruber, S.H. & Ashley, M.V. 2002. The breeding biology of lemon sharks at a tropical nursery lagoon. *Proc. R. Soc. Lond. B* **269**: 1655–1661.

Feldheim, K.A., Gruber, S.H. & Ashley, M.V. 2004. Reconstruction of parental microsatellite genotypes reveals female polyandry and philopatry in the lemon shark, *Negaprion brevirostris*. *Evolution* **58**: 2332–2342.

Goodman, S.J. 1998. Patterns of extensive genetic differentiation and variation among European harbor seals (*Phoca vitulina vitulina*) revealed using microsatellite DNA polymorphisms. *Mol. Biol. Evol.* **15**: 104–118.

Grant, P.R. & Grant, B.R. 2002. Unpredictable evolution in a 30-year study of Darwin's finches. *Science* **296**: 707–711.

Gruber, S.H. 1982. Role of the lemon shark as predator in the tropical marine environment: a multidisciplinary study. *Fla. Scient.* **45**: 46–75.

Gruber, S.H., De Marignac, J.R.C. & Hoenig, J.M. 2001. Survival of juvenile lemon sharks at Bimini, Bahamas, estimated by mark-depletion experiments. *Trans. Am. Fish. Soc.* **130**: 376–384.

Hare, M.P., Guenther, C. & Fagan, W.F. 2005. Nonrandom marine dispersal can steepen marine clines. *Evolution* **59**: 2509–2517.

Henderson, P.A., Holmes, R.H.A. & Bamber, R.N. 1988. Size-selective overwintering mortality in the sand smelt, *Atherina boyeri* Risso, and its role in population regulation. *J. Fish Biol.* **33**: 221–233.

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

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. *Cons. 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.

Hersch, E.I. & Phillips, P.C. 2004. Power and potential bias in field studies of natural selection. *Evolution* **58**: 479–485.

Hoekstra, H.E., Hoekstra, J.M., Berrigan, D., Vignieri, S.N., Hoang, A., Hilt, 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.

Hueter, R., Heupel, M.R., Heist, E.J. & Keeney, D.B. 2005. Evidence of philopatry in sharks and implications for the management of shark fisheries. *J. Northwest Atl. Fish. Sci.* **35**: 239–247.

Jann, P., Blanckenhorn, W.U. & Ward, P.I. 2000. Temporal and microspatial variation in the intensities of natural and sexual selection in the yellow dung fly *Scathophaga stercoraria*. *J. Evol. Biol.* **13**: 927–938.

Janzen, F.J. & Stern, H.S. 1998. Logistic regression for empirical studies of multivariate selection. *Evolution* **52**: 1564–1571.

Juanes, F. & Conover, D.O. 1994. Piscivory and prey size selection in young-of-the-year bluefish: predator preference or size-dependent capture success? *Mar. Ecol. Prog. Ser.* **114**: 59–69.

Kingsolver, J.G. & Pfennig, D.W. 2004. Individual-level selection as a cause of Cope's rule of phyletic size increase. *Evolution* **58**: 1608–1612.

Kingsolver, J.G. & Smith, S.G. 1995. Estimating selection on quantitative traits using capture-recapture data. *Evolution* **49**: 384–388.

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.

Kinnison, M.T. & Hendry, A.P. 2001. The pace of modern life II: from rates of contemporary microevolution to pattern and process. *Genetica* **112–113**: 145–164.

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

Lankford, T.E. Jr., Billerbeck, J.M. & Conover, D.O. 2001. Evolution of intrinsic growth and energy acquisition rates. II. Trade-offs with vulnerability to predation in *Menidia menidia*. *Evolution* **55**: 1873–1881.

Lebreton, J.D., Burnham, K.P., Clobert, J. & Anderson, D.R. 1992. Modeling survival and testing biological hypotheses using marker animals – a unified approach with case studies. *Ecol. Monograph* **62**: 67–118.

Letcher, B.H., Horton, G.E., Dubreuil, T.L. & O'Donnell, M.J. 2005. A field test of the extent of bias in selection estimates after accounting for emigration. *Evol. Ecol. Res.* **7**: 643–650.

Mangel, M. & Stamps, J. 2001. Trade-offs between growth and mortality and the maintenance of individual variation in growth. *Evol. Ecol. Res.* **3**: 583–593.

Manire, C.H. & Gruber, S.H. 1991. Effect of M-type dart tags on field growth of juvenile lemon sharks. *Trans. Am. Fish. Soc.* **120**: 776–780.

Martel, G. & Dill, L.M. 1995. Influence of movement by coho salmon (*Oncorhynchus kisutch*) parr on their detection by common mergansers (*Mergus merganser*). *Ethol.* **99**: 139–149.

McAdam, A.G. & Boutin, S. 2003. Variation in viability selection among cohorts of juvenile red squirrels (*Tamiasciurus hudsonicus*). *Evolution* **57**: 1689–1697.

Mitchell-Olds, T. & Shaw, R.G. 1987. Regression analysis of natural selection: statistical inference and biological interpretation. *Evolution* **41**: 1149–1161.

Morrissey, J.F. & Gruber, S.H. 1993. Habitat selection by juvenile lemon sharks, *Negaprion brevirostris*. *Env. Biol. Fishes* **38**: 311–319.

Newman, S.P. & Gruber, S.H. 2002. Comparison of mangrove and seagrass fish and macroinvertebrate communities in Bimini. *Bahamas J. Sci.* **9**: 19–27.

Palsbøll, P.J., Clapham, P.J. & Mattila, D.K. 1995. Distribution of mtDNA haplotypes in North Atlantic humpback whales: the influence of behaviour on population structure. *Mar. Ecol. Prog. Ser.* **116**: 1–10.

Parker, R.R. 1971. Size selective predation among juvenile salmonid fishes in a British Columbia inlet. *J. Fish. Res. Board Can.* **28**: 1503–1510.

Pratt, H.L. Jr. & Casey, J.G. 1990. Shark reproductive strategies as a limiting factor in directed fisheries, with a review of Holden's method of estimating growth- parameters. In: *Elasmobranchs as Living Resources* (L. H. Pratt, S. Gruber & Y. Taniuchi, eds), NOAA Technical Report 90, pp. 97–109, U.S. Dept. Comm, Washington.

Przybylo, R., Sheldon, B.C. & Merilä, J. 2000. Patterns of natural selection on morphology of male and female collared flycatchers (*Ficedula albicollis*). *Biol. J. Linn. Soc.* **59**: 213–232.

Quinn, T.P., Hendry, A.P. & Buck, G.B. 2001. Balancing natural and sexual selection in sockeye salmon: interactions between body size, reproductive opportunity, and vulnerability to predation by bears. *Evol. Ecol. Res.* **3**: 917–937.

Roff, D.A. 1992. *The Evolution of Life Histories: Theory and Analysis*. Chapman & Hall, New York.

Rowe, D.K. & Thorpe, J.E. 1990. Differences in growth between maturing and non-maturing male Atlantic salmon, *Salmo salar* L., parr. *J. Fish Biol.* **36**: 643–658.

Schluter, D. 1988. Estimating the form of natural selection on a quantitative trait. *Evolution* **42**: 849–861.

Schluter, D. 2000. http://www.zoology.ubc.ca/~schluter/splines.html.

Schluter, D., Price, T.D. & Rowe, L. 1991. Conflicting selection pressures and life history trade-offs. *Proc. R. Soc. Lond. B* **246**: 11–17.

Schulte-Hostedde, A.I., Zinner, B., Millar, J.S. & Hickling, G.J. 2005. Restitution of mass-size residuals: validating body condition indices. *Ecology* **86**: 155–163.

Sinclair, A.F., Swain, D.P. & Hanson, J.M. 2002. Measuring changes in the direction and magnitude of size-selective mortality in a commercial fish population. *Can. J. Fish. Aquat. Sci.* **59**: 361–371.

Sogard, S.M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: A review. *Bull. Mar. Sci.* **60**: 1129–1157.

Sundström, L.F., Löhmus, M. & Devlin, R.H. 2005. Selection of increased intrinsic growth rates in coho salmon, *Oncorhynchus kisutch*. *Evolution* **59**: 1560–1569.

West, C.J. & Larkin, P.A. 1987. Evidence for size-selective mortality of juvenile sockeye salmon (*Oncorhynchus nerka*) in Babine Lake, British Columbia. *Can. J. Fish. Aquat. Sci.* **44**: 712.

White, G.C. & Burnham, K.P. 1999. Program MARK: Survival estimation form populations of marked animals. *Bird Study* **46**: 120–138.

Zabel, R.W. & Achord, S. 2004. Relating size of juveniles to survival within and among populations of chinook salmon. *Ecology* **85**: 795–806.

Supplementary Material

The following supplementary material is available for this article online:

Table S1. Univariate quadratic selection acting on length (length × length), mass (mass × mass), relative condition factor (condition factor × condition factor), and growth (growth × growth); and bivariate quadratic selection acting on trait combinations (length × condition factor, growth × condition factor, growth × length) in juvenile lemon sharks[a]

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