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Natural selection acting on body size, growth rate and compensatory growth: an empirical test in a wild trout population

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ABSTRACT

Organisms usually grow slower than their maximum potential under a given set of conditions, suggesting that fast growth carries a corresponding fitness cost. A pattern of growth that might influence such costs is compensatory (or catch-up) growth, where individuals grow faster than expected. One form of compensatory growth occurs when small individuals grow faster for their size than do large individuals, thereby decreasing (or slowing the increase in) size disparity between themselves and larger conspecifics. We tested these ideas over several seasons in wild brown trout (*Salmo trutta*) by estimating selection acting on individual size, growth and compensatory growth. We then examined population-level growth patterns to determine whether they influence individual-level selection. Selection generally did not favour large individuals or those with slow growth; indeed, the opposite was more likely. Moreover, selection did not act against small/fast-growing individuals (i.e. those expressing compensatory growth). Population-level growth was proportional (i.e. mass increases were a constant percentage of initial mass across the range of body sizes) in all seasons except for the spring and, to a lesser degree, the early summer of the second year of life. In these two intervals, small fish showed greater proportional growth than large fish and small/fast-growing fish had higher (or at least not lower) survival. An intriguing explanation for these results is that fast (and compensatory) growth is only exhibited when the costs of fast growth are low. Our study introduces a novel approach for assessing growth at the population level, as well as the survival costs associated with individual size and growth.

Keywords: brown trout, compensatory growth, correlational selection, costs of growth,
life-history trade-offs, *Salmo trutta*.

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INTRODUCTION

Large body size confers obvious fitness benefits to many organisms (Roff, 1992; Stearns, 1992). In salmonid fishes, for example, large individuals have decreased susceptibility to gape-limited predators (e.g. Parker, 1971), increased ability to defend high-quality territories (e.g. Fausch and White, 1981), earlier maturation (e.g. Rowe and Thorpe, 1990), and larger and more eggs (e.g. Hendry *et al.*, 2001). Large size can be achieved more quickly through fast growth and so we might also expect organisms to grow as fast as possible. In contrast to this expectation, ample empirical evidence suggests that organisms typically grow at rates slower than their maximum potential under a given set of conditions (Case, 1978; Conover and Present, 1990; Arendt, 1997; Blanckenhorn, 2000). To reconcile the benefits of large size with the empirical evidence for restrained growth, investigators have predicted that high growth rates carry a corresponding fitness cost (Arendt, 1997; Blanckenhorn, 2000).

Most of the research on potential costs of fast growth has been conducted in the laboratory (Ali *et al.*, 2003). This work has suggested that fast growth may increase predation risk (Lima and Dill, 1990; Werner and Anholt, 1993; Gotthard, 2000; Lankford *et al.*, 2001; Munch and Conover, 2003), reduce swimming performance (Gregory and Wood, 1998; Billerbeck *et al.*, 2001), reduce the strength of skeletal elements (Arendt and Wilson, 2000; Arendt *et al.*, 2001), compromise somatic development (Saunders *et al.*, 1992), decrease starvation endurance (Stockhoff, 1991; Gotthard *et al.*, 1994; but see Gotthard, 1998), and decrease adult longevity (Sevenster and Van Alphen, 1993; Chippindale *et al.*, 1994; but see Zwaan *et al.*, 1995a,b). These potential costs should translate into reduced survival of fast-growing individuals, and yet few studies have tested for such effects in wild populations (for reviews, see Arendt, 1997; Ali *et al.*, 2003; for an exception, see Olsson and Shine, 2002). Moreover, the costs of fast growth can be difficult to assess because the larger size attained through faster growth may itself reduce mortality (see above). We disentangle these opposing effects by measuring natural selection acting on combinations of size and growth in a wild population.

The costs and benefits of fast growth may be context-dependent, including in relation to previous growth history. In particular, the costs of fast growth may depend on how quickly individuals have grown in the past. For example, compensatory growth occurs when individuals that have undergone a period of reduced growth subsequently grow faster than expected (e.g. Weatherley and Gill, 1981; Hayward *et al.*, 1997; Nicieza and Metcalfe, 1997; Morgan and Metcalfe, 2001). One form of compensatory growth occurs when small individuals grow relatively fast, thus decreasing the expected size difference between themselves and larger individuals (e.g. Nicieza and Metcalfe, 1997). Depensatory growth has the opposite effect (e.g. Ryer and Olla, 1996). Compensatory growth may require more risky foraging strategies (Damsgård and Dill, 1998), and therefore increase the costs of fast growth for small individuals. Selection on growth may also depend on the overall pattern of growth in the population, which reflects the opportunity for growth by individuals of different sizes. We test for costs of compensatory growth by examining whether small/fast-growing individuals have the lowest survival, and whether any such effects relate to the overall pattern of growth in the population.

More precisely, compensatory growth can be a property of an individual (some small individuals grow fast in relation to other small individuals) or the population (small individuals as a whole grow fast in relation to large individuals). Quantifying compensatory growth at the individual level is relatively easy (e.g. residuals from relationships between initial size and final size). Quantifying compensatory growth at the population level is more difficult because it requires somehow specifying 'expected growth' for individuals of different sizes. We instead suggest a comparative approach that positions particular growth intervals *relative to each other* with respect to the growth of small versus large individuals. This can be accomplished by estimating the slope of the relationship between log_e *final mass* and log_e *initial mass*. The less steep the slope, the faster that small individuals are growing in relation to large individuals, with a slope of unity corresponding to proportional growth throughout the size range (i.e. individuals of different sizes grow a constant proportion of their initial size).

Salmonid fishes

Stream-dwelling salmonids present an excellent system for examining selection on size and growth. First, substantial variation in size occurs among similar-aged individuals within populations. Factors influencing this variation include variable dates of emergence from the gravel (e.g. Einum and Fleming, 2000), the formation of dominance hierarchies (e.g. Jenkins, 1969; Fausch, 1984), life history (e.g. Letcher and Gries, 2003) and genetic variation (e.g. Smoker *et al.*, 1994; Silverstein and Hershberger, 1995). Second, individual growth rates vary through time. Factors influencing this variation include temperature (e.g. Elliott, 1975a,b, 1981), flow (e.g. Fausch and White, 1981; Fausch, 1984), life-history transitions (e.g. Letcher and Gries, 2003) and, presumably, genetic variation. While growth rate has been shown to be heritable in salmonids (e.g. Nilsson, 1992; Gjerde *et al.*, 1994; Pante *et al.*, 2002), no study has shown, to our knowledge, whether growth trajectories have a heritable component. Third, salmonids sometimes demonstrate strong compensatory growth, wherein individuals that have been growing slowly dramatically increase their growth rate (e.g. Mortensen and Damsgård, 1993; Hayward *et al.*, 1997; Damsgård and Dill, 1998; Maclean and Metcalfe, 2001). Fourth, stream-dwelling salmonids are exposed to many environmental factors that have a strong influence on survival (e.g. Huntsman, 1942; Cowx *et al.*, 1984; Dill and Fraser, 1984; Elliott *et al.*, 1997), probably in ways that depend on size and growth (Good *et al.*, 2001; Björklund *et al.*, 2003; Wilson *et al.*, 2003).

In this paper, we estimate natural selection acting on size and growth and then quantify population-level growth patterns in a wild population of stream-dwelling brown trout (*Salmo trutta*). Brown trout typically lay their eggs in the gravel of streams in the late fall (November–December). The eggs then incubate for several months before hatching, after which embryos remain in the gravel for an additional 5–6 weeks (Elliott, 1994). Fry (age-0^+) emerge from the gravel in late February through March and establish feeding territories (Elliott, 1994). After a few weeks, they develop vertical stripes on their sides and are henceforth referred to as 'parr'. Stream-dwelling brown trout remain highly territorial through the first few years of life (Jenkins, 1969), which makes them particularly amenable to the repeat sampling of individuals. This last property is a critical benefit for assessing the survival costs associated with particular combinations of individual size and growth. In the West Brook, maturation usually occurs during the second or third autumn of life (age-1^+ or age-2^+), and no individuals migrate to the ocean (i.e. the population is entirely non-anadromous).

MATERIALS AND METHODS

Study area

The West Brook is a 6.3 km long, third-order stream in the Connecticut River basin, Massachusetts, USA (42°25′, 72°40′). Our study site was located approximately 1 km below a small reservoir and consisted of 47 contiguous sections that averaged 20.3 m in length and 101.7 m^2 in area. The West Brook contains self-sustaining populations of brown trout and brook trout (*Salvelinus fontinalis*), and is artificially stocked each spring with juvenile Atlantic salmon (*Salmo salar*). Apart from an occasional black-nosed dace (*Rhinichthys atratulus*), these three salmonids are the only fish species present. Our study site is described further in several recent papers (Gries and Letcher, 2002a; Carlson and Letcher, 2003; Hendry *et al.*, 2003; Letcher and Gries, 2003).

Data collection

We sampled the entire study site 11 times between March 2000 and December 2001, and here report data for six sets of consecutive samples (i.e. six 'intervals'; Table 1). Three sampling techniques were used: (1) standard daytime electroshocking with unpulsed direct current at 400 V; (2) night seining (Gries and Letcher, 2002a); and (3) flashlights and aquarium nets to capture individual fish during night seining. For all techniques, we enclosed each stream section with blocking nets at the upstream and downstream ends, performed a two-pass removal, and sampled in an upstream direction. Each of the 11 samples took 7–11 days or nights to complete.

Each captured brown trout was anaesthetized (clove oil: $30\ \mathrm{mg \cdot l^{-1}}$), weighed (±0.1 g) and scale-sampled for age determination. Each of these fish larger than 60 mm fork length and 2.0 g wet weight was tagged intraperitoneally (Gries and Letcher, 2002b) with an individually coded passive integrated transponder (PIT) tag (Prentice *et al.*, 1990). A small piece of tissue was then clipped from the anal fin of each fish to serve as a secondary mark. Each time a tagged fish was recaptured, its tag number was recorded and it was weighed as before. During the course of the study, only 1% of captured brown trout had an anal fin clip but no detectable PIT tag, indicating that nearly all fish retained their tag. In this manner, we collected data on 374 brown trout that emerged from the gravel in the spring of 2000, and were then monitored for up to six intervals between August 2000 and December 2001 (corresponding to the age-0^+ to age-1^+ period).

Data analysis

Estimating selection

We used standard procedures (Lande and Arnold, 1983; Schluter, 1988; Brodie *et al.*, 1995; Janzen and Stern, 1998) to estimate the strength and form of selection acting on mass and growth in each of the six intervals. Growth was estimated for each fish in each interval as the residual from the OLS regression of $\log_e M_2$ on $\log_e M_1$, where M_1 was the mass at the first sample and M_2 was the mass at the second sample. Positive residuals indicate faster growth than expected for an individual's initial mass (hereafter 'mass'), whereas negative residuals indicated slower growth than expected. Both traits (mass and growth) were then standard-

Table 1. Intervals during which selection was estimated. 'Starting sample' and 'Ending sample' numbers correspond to those reported in Carlson and Letcher (2003)

Interval (age designation)	Starting sample	Ending sample	Average starting date (range)	Average ending date (range)	Average # of days in interval
Late summer 2000 (age-0^+)	0	1	24 August (20–29 Aug)	27 September (22 Sept–2 Oct)	34
Fall 2000 (age-0^+)	1	2	27 September (22 Sept–2 Oct)	8 December (1–15 Dec)	72
Winter 2000 (age-0^+)	2	3	8 December (1–15 Dec)	13 March (8–19 March)	96
Spring 2001 (age-1^+)	3	4	13 March (8–19 March)	9 June (5–14 June)	88
Early summer 2001 (age-1^+)	4	5	9 June (5–14 June)	25 July (20–30 July)	46
Late summer 2001 (age-1^+)	5	6	25 July (20–30 July)	9 September (4–14 Sept)	46
Fall 2001 (age-1^+)	6	7	9 September (4–14 Sept)	6 December (3–10 Dec)	89

ized to a mean of zero and a standard deviation of unity at the start of each interval. Mass and growth for each fish in a given interval were then related to the survival of that fish to the end of the next interval. For example, the mass of each fish in the 24 August sample and the growth of each fish from 24 August to 27 September were related to whether or not each fish survived until 8 December (Table 1). Similar results were obtained if selection analyses used growth rate (e.g. 24 August to 27 September) and *final* mass (e.g. 27 September) in a particular interval to predict survival in the next interval (27 September to 8 December).

A fish was assumed to have survived through an interval (absolute fitness = 1) if it was captured at the end of that interval or in any subsequent sample. A fish was assumed to have died during an interval (absolute fitness = 0) if it was not captured at the end of that interval or in any subsequent sample. It is therefore possible that some of the fish we assigned a fitness of zero had not died but instead moved out of the study site. We minimized this possibility by also sampling 140 m of stream both above and below our study site, and by examining fish caught in an Atlantic salmon smolt trap 3 km downstream. Any trout captured outside of our site were excluded from the analysis (3.1% of the tagged brown trout were captured outside of our site at least once). Table 2 provides details on the numbers of fish with data for initial mass and growth in each interval, as well as the number of those fish surviving to the end of the next interval. Absolute fitness for each fish in each interval was converted to relative fitness (Lande and Arnold, 1983; Janzen and Stern, 1998).

We used the Program MARK (White and Burnham, 1999) to estimate the probability (P) of recapturing an individual if it was alive and present in the study site at the time of sampling. The estimates and corresponding confidence intervals for each of the intervals are provided in Carlson and Letcher (2003). The average of these estimates is $P = 0.48$

Table 2. Numbers of fish caught at the start of each selection interval (Starting N), and the number of those fish captured at the end of the next interval or in any subsequent sample (Ending N)

Interval:	Late summer 2000	Fall 2000	Winter 2000	Spring 2001	Early summer 2001	Late summer 2001
Fish age:	age-0^+	age-0^+	age-0^+	age-1^+	age-1^+	age-1^+
Starting N	58	128	62	67	101	136
Ending N	34	55	29	36	68	66
Survival (%)	58.6	43.0	46.8	53.7	67.3	48.5

Note: Age designations during each interval are also reported.

(range 0.31–0.67), suggesting that we had a reasonable chance of detecting mortality. Multiple sampling events and a reasonable recapture probability had the combined effect of decreasing the chance of incorrectly assigning an individual a fitness of zero when it was actually alive.

We estimated the opportunity for selection (I) in each interval as the variance of relative fitness during that interval (Brodie *et al.*, 1995). We then estimated selection in each interval by performing four sets of regressions of relative fitness on standardized mass and standardized growth. In each case, we used logistic regressions and then converted the resulting coefficients to their linear equivalents (Janzen and Stern, 1998). First, we used simple regressions of relative fitness on each trait. Coefficients from these regressions estimate *linear selection differentials*, which represent the total strength of selection acting on each trait (i.e. direct selection on the trait plus indirect selection acting through any correlation with the other trait). Second, we used multiple regressions that included both traits. Partial coefficients from these regressions estimate *linear selection gradients*, which represent the strength of selection acting 'directly' on each trait (i.e. independent of any correlation with the other trait). Third, we used multiple regressions for each trait and squared values for that trait. Coefficients for the squared terms estimate *quadratic* (*non-linear*) *selection differentials*, which are often interpreted as the total strength of disruptive (when positive) or stabilizing (when negative) selection. Fourth, we used multiple regressions that included both traits, squared values for both traits, and the cross-product between the traits. Partial coefficients from these regressions estimate *univariate quadratic selection gradients* (squared term coefficients multiplied by two; see Blanckenhorn *et al.*, 1999) and the *bivariate quadratic selection gradient* (cross-product term), the latter representing correlational selection, which is often interpreted as favouring similar (when positive) or dissimilar (when negative) combinations of traits.

The interpretation of selection acting on size and growth is straightforward, but no study has yet attempted to infer selection acting on compensatory growth. We consider the strongest evidence for selection favouring compensatory growth to occur when directional coefficients are negative for mass and positive for growth, and when correlation coefficients between size and growth are negative. This combination would occur when small/fast-growing individuals have the highest fitness. The strongest evidence for selection favouring depensatory growth would be when the coefficients are positive for mass and growth, and when the correlation coefficients are positive.

Basing interpretations only on linear and quadratic coefficients may obscure more complicated relationships between traits and fitness (Brodie *et al.*, 1995). For example, growth rate might influence survival for small individuals but not large individuals. We evaluated such possibilities through the use of univariate (Schluter, 1988) and bivariate (Schluter and Nychka, 1994) cubic splines (i.e. non-parametric regressions). To facilitate interpretation of these splines, we used raw mass and raw growth residuals (as opposed to standardized data). Smoothing parameters, λ, were chosen to minimize prediction error: $\lambda_{\text{mass}} = 1$ and $\lambda_{\text{growth}} = 2$ in all intervals for the univariate splines; and $\lambda = 0$ in all intervals, except the fall and winter ($\lambda = 2$), for the bivariate splines.

Population-level growth patterns

For each interval, we took the subset of fish caught in both the starting and ending samples and regressed $\log_e M_2$ on $\log_e M_1$. As noted above, a linear slope not different from unity would indicate proportional growth that remained constant across the range of body sizes (i.e. the change in mass is a constant percentage of initial mass). When this condition is satisfied, $e^{\text{intercept}}$ indicates the percentage mass increase/decrease. Slopes that differ significantly from unity indicate that proportional growth varies with body size. Slopes less than unity indicate that small fish grow proportionally more than large fish, whereas slopes greater than unity indicate the converse. We do not attempt to infer compensatory or depensatory growth from these slopes, but this might be done if it was known that 'expected' growth was a constant proportion of body size. Although this appears to be the case in at least some salmonids (Atlantic salmon: B.H. Letcher, unpublished data), we simply use these slopes in a comparative sense to address the influence of growth patterns in the population as a whole (intercepts and slopes) on selection acting on individual size and growth (from the above selection analyses).

RESULTS

Selection

Survival varied across intervals and was highest in the age-1^+ early summer (67.3%) and lowest in the age-0^+ fall (43.0%; Table 2). Similarly, the opportunity for selection (I) differed substantially across intervals (range 0.490–1.338; Table 3).

Directional selection varied across intervals (Table 3), with differentials and gradients showing almost perfect correspondence – as expected because size and our measure of growth (residuals from initial *vs* final mass regressions) were uncorrelated. Selection coefficients for mass were negative in five of the six intervals (Table 3), suggesting that selection generally favoured small fish (see also Fig. 1). However, these coefficients were significant at $\alpha = 0.05$ in only one interval (age-1^+ early summer) and at $\alpha = 0.10$ in only one other interval (age-1^+ spring). Selection coefficients for growth were essentially zero in one interval (age-1^+ late summer) and positive in three of the other five intervals (Table 3; Fig. 2). These positive coefficients were significant at $\alpha = 0.05$ in one interval (age-0^+ late summer) and at $\alpha = 0.10$ in one other interval (age-0^+ winter). None of the negative coefficients for growth were significant at $\alpha = 0.10$.

Non-linear selection did not act in a consistent fashion on mass or growth: univariate quadratic coefficients were variable in both sign and magnitude (Table 3; see also Figs. 1 and 2). For mass, quadratic terms were positive in four of the six intervals, suggesting disruptive selection, but were only significant at $\alpha = 0.10$ in one interval (age-0^+ late summer).

Table 3. Directional selection acting on initial mass and growth; univariate quadratic selection acting on initial mass (initial mass^2) and growth (growth^2); and bivariate quadratic selection acting on trait combinations (initial mass × growth) in West Brook brown trout

Interval:	Late summer	Fall	Winter	Spring	Early summer	Late summer
Fish age:	age-0^+	age-0^+	age-0^+	age-1^+	age-1^+	age-1^+
Opportunity for selection (*I*)	0.718	1.338	1.157	0.874	0.490	1.068
Linear selection differentials						
initial mass	−0.12	−0.11	−0.21	−0.22*	−0.15**	0.01
growth	0.23**	−0.16	0.23*	−0.04	0.10	0.00
Linear selection gradients						
initial mass	−0.12	−0.11	−0.21	−0.21*	−0.15**	0.01
growth	0.23**	−0.16	0.23*	−0.04	0.09	0.00
Quadratic selection differentials						
(initial mass)^2	4.77*	−2.11	0.43	2.05	−1.97	1.35
(growth)^2	0.25	0.11	−0.02	−0.29	−0.28**	0.19
Quadratic selection gradients						
(initial mass)^2	4.93**	−2.18	1.15	2.13	−1.89	1.41
(growth)^2	0.32	0.07	−0.11	−0.23	−0.24**	0.19
initial mass × growth	−0.61	0.12	0.42	0.61	−0.51	0.44

Note: Selection differentials and gradients are standardized linear coefficients converted from logistic coefficients (Janzen and Stern, 1998). Probability: $^*P < 0.10$, $^{**}P < 0.05$. *P*-values are for the logistic regressions but the coefficients themselves are converted to their linear equivalents.

Univariate cubic splines suggested slightly more complex patterns, particularly during the age-1^+ early and late summer (Fig. 1). None of the negative quadratic coefficients for mass were significant at $\alpha = 0.10$. For growth, quadratic terms were negative in three of the six intervals, suggesting stabilizing selection, but were only significant in one interval (age-1^+ early summer). Cubic splines confirmed the presence of stabilizing selection in this interval and the lack of stabilizing selection in the other intervals (Fig. 2). None of the positive quadratic coefficients for growth were significant at $\alpha = 0.10$.

Compensatory growth appeared to be *favoured* by selection in three intervals. First, age-0^+ late summer fish were characterized by negative (non-significant) selection on mass, positive (significant at $\alpha = 0.05$) selection on growth, and negative (non-significant) correlational selection (Table 3). Bivariate cubic splines further revealed that selection favoured the small/fast-growing individuals (i.e. a steep slope of increasing fitness towards the upper left of Fig. 3A) but was essentially neutral for large/slow-growing individuals (i.e. a relatively flat slope towards the lower right of Fig. 3A). Second, age-0^+ winter fish were characterized by negative (non-significant) selection on mass and positive (significant at $\alpha = 0.10$) selection on growth (Table 3). The correlational coefficient was not negative but bivariate cubic splines revealed that selection favoured smaller/faster-growing fish over the entire phenotypic range (i.e. a relatively constant slope of increasing fitness from the lower right to the upper left of Fig. 3C). Third, age-1^+ early summer fish were characterized by negative

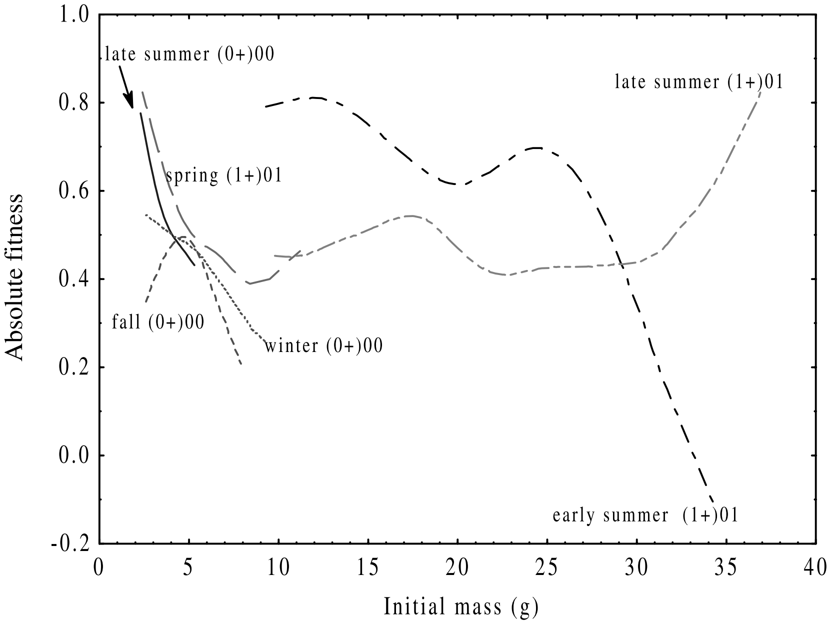

Fig. 1. Relationships between initial mass and an individual's absolute fitness (survived = 1; died = 0) during each season. The lines are cubic splines (Schluter, 1988) generated from the middle 95% of the data; $\lambda = 1$ (see Methods).

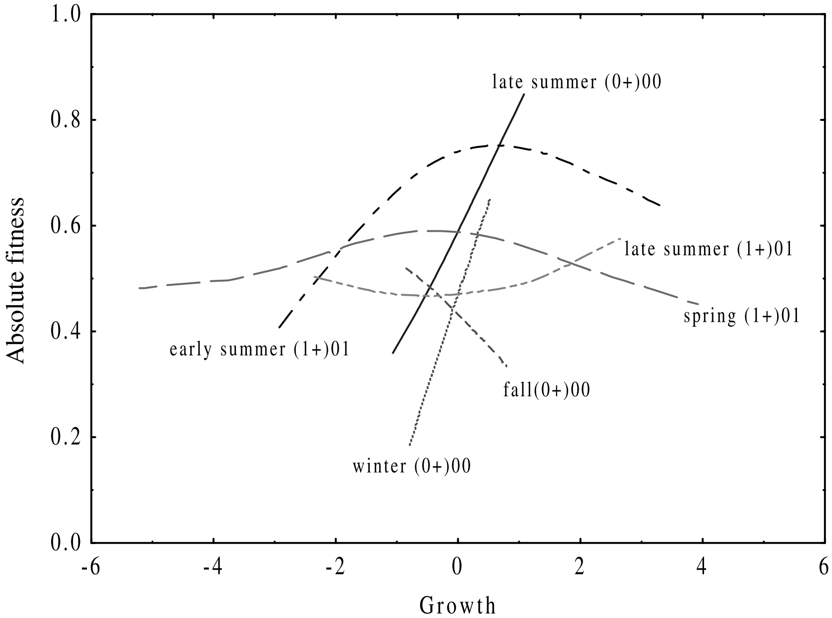

Fig. 2. Relationships between growth and an individual's absolute fitness (survived = 1; died = 0) during each season. The lines are cubic splines (Schluter, 1988) generated from the middle 95% of the data; $\lambda = 2$ (see Methods).

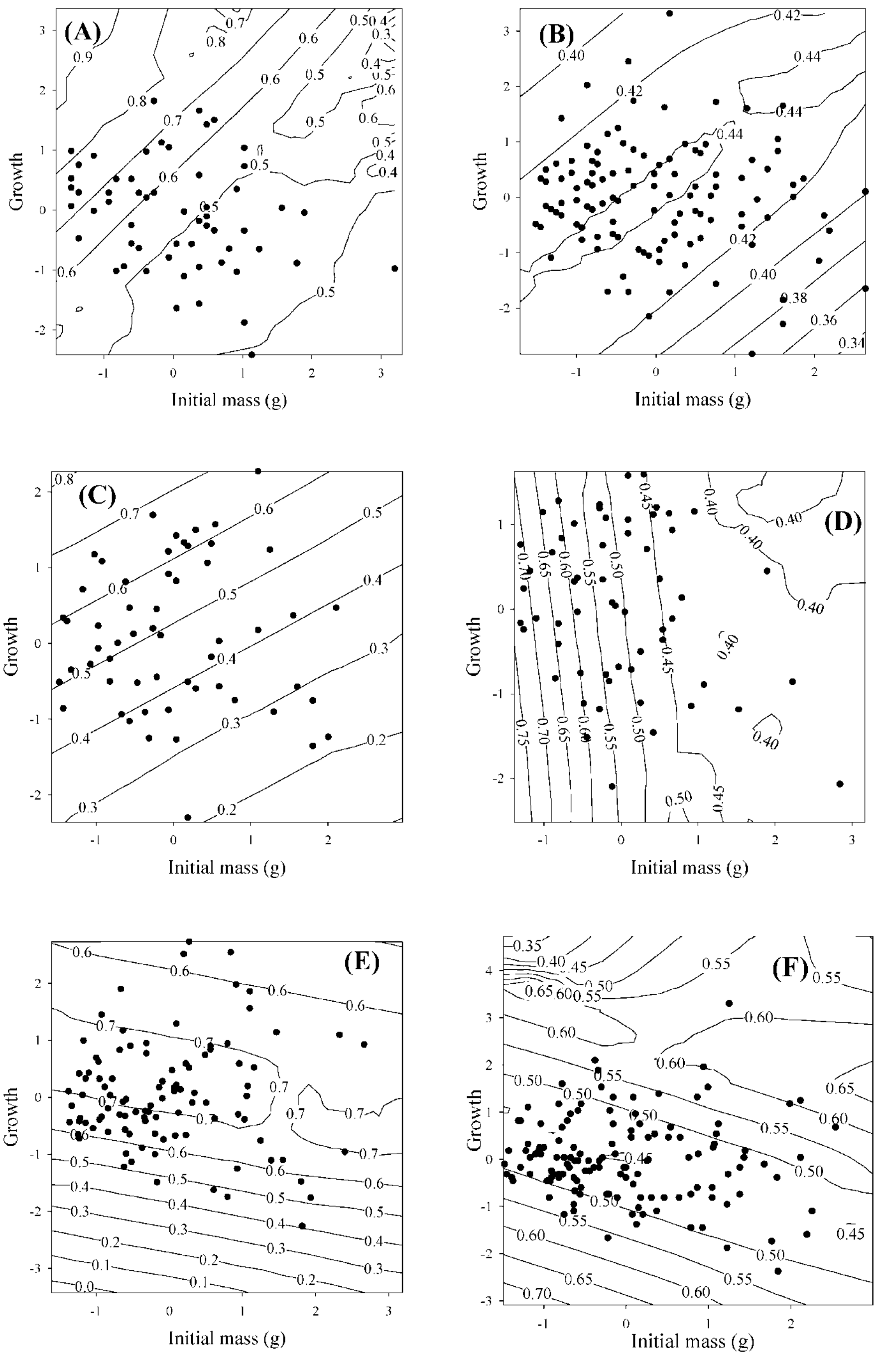

Fig. 3. Bivariate spline estimation of the fitness surface relating initial mass, growth and an individual's absolute fitness (survived = 1; died = 0) during the following intervals: age-0^+ late summer (A), age-0^+ fall (B), age-0^+ winter (C), age-1^+ spring (D), age-1^+ early summer (E) and age-1^+ late summer (F). Contour lines represent an interpolated fitness surface.

(significant at $\alpha = 0.05$) selection on mass, positive (non-significant) selection on growth, and negative (non-significant) correlational selection (Table 3). Bivariate cubic splines showed a ridge of high fitness that included small/fast-growing individuals (Fig. 3E).

Based on this combined evidence, we conclude that selection may often favour compensatory growth (i.e. small individuals growing faster than expected for their size). Moreover, we found no evidence of selection acting against compensatory growth in any interval. Specifically, selection coefficients were never positive for both mass and growth (Table 3) and bivariate cubic splines never showed that the smallest/fastest-growing individuals had the lowest fitness (Fig. 3).

Population-level growth patterns

Growth was a constant proportion of initial mass across the range of body sizes in all intervals except age-1^+ spring and age-1^+ early summer (as indicated by 95% confidence intervals for the slope; Table 4). However, the confidence interval in age-1^+ early summer nearly included unity, whereas that in the spring interval was well below unity (Table 4). These results suggest that in the spring and early summer, particularly the former, small fish grow a greater proportion of their initial size than do large fish.

Intercepts were significantly greater than zero in all six intervals, indicating positive growth throughout (Table 4). However, differences among intervals in intercepts (Table 4), as well as the elevation of the line across the entire range of body sizes (Fig. 4), suggest that growth is substantially higher in the age-1^+ spring than in any of the other intervals. Age-0^+ late summer growth also appeared slightly higher than growth in the other intervals, among which growth did not differ (Fig. 4). No relationship was evident between population-level growth patterns (slopes or intercepts from Table 4) and selection coefficients (from Table 3). However, of the four intervals showing significant selection on either size or growth, two of these (age-0^+ late summer, age-1^+ spring) were those characterized by the fastest growth (Fig. 4).

Table 4. Slope and intercept coefficients, their corresponding confidence intervals, and R^2-values from OLS regression of $\log_e$ final mass on $\log_e$ initial mass

		Slope			Intercept			
Interval	Age designation	Coefficient	Lower 95% CL	Upper 95% CL	Coefficient	Lower 95% CL	Upper 95% CL	R^2
Late summer 2000	age-0^+	0.956	0.838	1.073	0.358	0.206	0.510	0.826
Fall 2000	age-0^+	1.029	0.984	1.074	0.128	0.058	0.197	0.942
Winter 2000	age-0^+	1.012	0.972	1.051	0.119	0.053	0.184	0.978
Spring 2001	age-1^+	0.797	0.728	0.867	1.591	1.471	1.711	0.890
Early summer 2001	age-1^+	0.953	0.913	0.993	0.225	0.139	0.370	0.957
Late summer 2001	age-1^+	0.973	0.945	1.001	0.098	0.015	0.181	0.972

Note: The results are reported by interval and include the age designation during that interval.

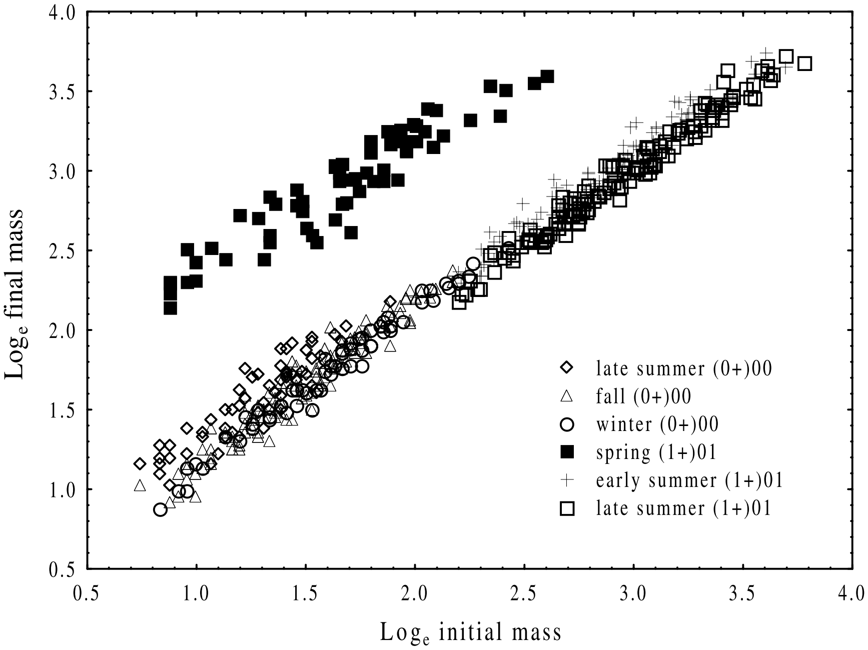

Fig. 4. Log$_e$ final mass plotted against log$_e$ initial mass grouped by season. Age designation during each season is denoted in parentheses.

DISCUSSION

Our study yielded several general conclusions, some of which contrast with conventional expectations. First, selection did not favour larger individuals and, indeed, the opposite was more likely. Second, selection did not act against individuals exhibiting fast growth and, again, the opposite was more likely. Third, selection did not act against small individuals that exhibited the fastest growth (i.e. compensatory growth). In fact, selection seemed to favour small/fast-growing individuals in half of the intervals. Fourth, growth at the population level was a constant proportion of initial mass across the range of body sizes in all intervals except for age-1$^+$ spring and, to a lesser extent, age-1$^+$ early summer. Fifth, intervals characterized by fast growth also tended to be intervals characterized by significant selection on size and/or growth.

Selection on body size

Directional selection on West Brook brown trout was generally very weak (Table 4) and roughly comparable to values reported for other natural populations. For example, selection differentials for the 749 estimates compiled by Kingsolver *et al.* (2001) have a median standardized absolute value of 0.13, which was slightly higher than that in the present study (median = 0.07). Our median differential for mass would correspond to the fifty-first percentile of Kingsolver and colleagues' (2001) data set, and our median differential for growth would correspond to the twenty-eighth percentile. It is not surprising that directional selection was weak in the West Brook because its brown trout population has been self-sustaining for a long time. In such cases, we would expect a population to be well-adapted to its environment and therefore not under strong selection. Hendry *et al.* (2003) also found little evidence of directional selection acting on size or growth in the West Brook.

Most previous work on juvenile salmonids has suggested that selection should favour large individuals (e.g. West and Larkin, 1987; Elliott, 1990; Meyer and Griffith, 1997; Einum and Fleming, 2000). This was not the case in our study: selection coefficients for mass were negative in five of six intervals and essentially zero in the sixth. Our results are thus in better agreement with several recent studies suggesting that smaller individuals may actually have higher survival (e.g. Good *et al.*, 2001; Hendry *et al.*, 2003). An alternative explanation for this result is that larger fish did not actually die but instead emigrated far enough from our study site that we did not recapture them again. If the emigration rate is biased by phenotype, estimates of selection could be biased as well (Kingsolver and Smith, 1995). To address this possibility, we simulated the effects of size-biased emigration, and found that our conclusions about selection would only be incorrect if emigration was unrealistically high and unrealistically size-biased (results not shown). Furthermore, previous work has shown that emigration from a site is often (although not always) biased towards the smaller individuals within a cohort (e.g. Cunjak and Randall, 1993; Cutts *et al.*, 1999). Another alternative is that our sampling efforts did not include some critical interval during which larger trout survive at higher rates (Elliott, 1990; Einum and Fleming, 2000). Regardless of the explanation, our study shows that larger salmonids within a cohort cannot be assumed to have a fitness advantage.

The interpretation of selection coefficients alone may obscure more complicated relationships between traits and fitness (Schluter, 1988; Brodie *et al.*, 1995). For example, our cubic spline visualizations suggested that small size was favoured below 10 g but that size was unrelated to fitness between 10 and 25 g (Fig. 1). It is not entirely clear why the advantage to small size might only be evident for the very smallest fish but possible explanations may be found in differences in foraging behaviour and habitat choice (e.g. Jenkins, 1969; Fausch, 1984; Heggenes, 2002). For instance, larger fish may adopt behaviours and choose microhabitats that make them more conspicuous to predators. This may reduce survival until they reach a size where predators (e.g. larger trout) become gape limited. After this size, predation may have little further influence on survival.

Selection on growth

Recent theoretical and laboratory studies suggest that fast growth should carry a corresponding fitness cost (see Introduction). However, we found no evidence for such effects in West Brook brown trout: selection coefficients for growth were positive in three of five intervals (significant in one at the $\alpha = 0.05$ level and in another at the $\alpha = 0.10$ level), zero in one interval, and never significantly negative. One possible explanation for this result, as for body size (above), is that we did not measure selection during a critical interval in which fast growth is costly. A second possibility is that the costs of fast growth are manifested as it occurs, rather than during a subsequent interval (as tested in our study). Unfortunately, it is difficult to assess the instantaneous survival cost of growth rate because an individual must survive an interval if its growth is to be measured.

A third possibility for our failure to detect a survival cost of fast growth is that individuals only undertake fast growth when any survival costs are relatively low. For example, certain individuals may be in better physiological condition than others, which may keep mortality low even if they adopt risky foraging tactics. Moreover, the potential costs of fast growth may vary among times of the year in relation to the probability of mortality and the ease of achieving fast growth. In our system, growth was fastest, particularly for small individuals, in the age-1^+ spring (Fig. 4). High growth at this time followed by reduced growth thereafter is probably the result of seasonal variation in food availability and water flow. For instance, Grader (2000) found that the density of drifting food in the West Brook peaked in the spring. Additionally, the West Brook can flood in the fall, freeze over in the winter, and have very low water levels in the summer. Maximum food and intermediate flows may explain the benign conditions experienced during the spring, and suggest that this might be a time when fish can grow quickly without incurring a high cost. When organisms grow fastest during the very times when doing so is least costly, it may be difficult to detect costs of fast growth in unmanipulated natural populations.

Selection on compensatory growth

Size thresholds associated with survival (e.g. Holtby *et al.*, 1990), maturation (e.g. Rowe *et al.*, 1991) and the transition from fresh water to salt water (e.g. Wright *et al.*, 1990) have been repeatedly demonstrated in salmonids. One might therefore expect strong selection for fast growth so as to meet these size minima. However, an accelerated growth strategy in small individuals, although beneficial in terms of increased size, may be costly owing to, for example, increased foraging risk (Metcalfe and Monaghan, 2001). Despite these reasonable expectations, we found no evidence that small individuals attempting to grow fast incur a survival cost. Instead, selection actually appeared to *favour* small/fast-growing individuals during some intervals (e.g. Fig. 3A). In parallel with our above interpretations for size-independent growth, these findings suggest that: (1) compensatory growth is not costly in nature; (2) we missed the interval during which compensatory growth was costly; or (3) individuals adopt compensatory growth only when doing so is least costly. This last possibility remains particularly intriguing, especially because compensatory growth at the population level was most common during the intervals when growth was fastest (and presumably easiest).

How might small individuals achieve proportionally faster growth without incurring a survival cost? One possibility is that habitat use is size-structured with small individuals found along the edge of streams (e.g. Kennedy and Strange, 1972; LaVoie and Hubert, 1997; Heggenes, 2002) where the water may be warmer and, consequently, metabolic rate is faster (e.g. Elliott, 1976). Another possibility is that stream-dwelling salmonids reach a size threshold at which they can no longer acquire enough resources to achieve maximal growth (Hayes *et al.*, 2000). In this case, small individuals may be the only ones that can take maximal advantage of favourable growth conditions. Finally, territorial interactions that might normally suppress the growth of small fish might be less important during the spring when all fish are attempting to grow quickly.

Selection for or against compensatory growth might be interpreted as selection acting on a flexible tactic that is triggered by behavioural or physiological changes occurring at a particular time in response to some internal or external cue. However, it might also be interpreted as selection acting on particular growth trajectories. That is, a genetically based growth trajectory could include compensatory growth during a particular time. The distinction between these two scenarios is that the former views compensatory growth as a flexible, plastic response, whereas the latter views it as an inflexible, genetic response. Which of these scenarios is most likely is not clear, and yet they might have dramatic consequences for evolutionary responses to particular patterns of selection.

CONCLUSION

Selection acting on size and growth was generally weak for West Brook brown trout but some interesting subtle patterns emerged. In particular, selection did not favour larger fish or fish with slower growth for a given body size. If anything, the opposite was true. Despite its theoretical plausibility, we argue that the survival costs of fast growth have yet to be amply demonstrated in wild populations. We also found that selection did not act against compensatory growth but perhaps just the opposite: small/fast-growing individuals sometimes had higher survival. We suggest that our results could have arisen if individuals attempt to increase their relative size only when doing so is least risky. In particular, the only season during which overall growth was fast and small individuals grew proportionally more than large individuals was the age-1^+ spring, when conditions are particularly favourable for growth and survival. We suggest that it may be difficult to detect selection against fast and compensatory growth when organisms only attempt these endeavours when doing so is least costly. Nonetheless, formal analyses of selection acting on mass and growth are a promising method for assessing potential costs of fast and compensatory growth.

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