# Estimating Natural Selection Acting on Stream-Dwelling Atlantic Salmon: Implications for the Restoration of Extirpated Populations

ANDREW P. HENDRY,* BENJAMIN H. LETCHER,† AND GABE GRIES†

*Redpath Museum and Department of Biology, McGill University, 859 Sherbrooke Street W., Montreal, Quebec H3A 2K6, Canada, email andrew.hendry@mcgill.ca

†U.S. Geological Survey/Biological Resources Division, S.O. Conte Anadromous Fish Research Center, P.O. Box 796, One Migratory Way, Turners Falls, MA 01376 U.S.A.

**Abstract:** *Efforts to restore populations to locations from which they have been extirpated may be hampered by maladaptation in the introduced group because they came from a different environment. Estimates of natural selection acting on the new population can be used to deduce maladaptation and tailor efforts to reduce its effects. We estimated natural selection acting on Atlantic salmon (*Salmo salar*) undergoing restoration to the Connecticut River (U.S.A.). More than 3500 mark-recapture records in a small tributary (West Brook, Massachusetts) were used to estimate selection acting on body length, body mass, condition factor, and growth. Estimates were obtained for three to four different cohorts, two age classes (second and third years of life), and two seasons (winter and summer). We found little evidence that any of the traits were subject to strong directional selection (favoring larger or smaller trait values). Interestingly, fish that were larger or had higher condition factors rarely survived at higher rates, a result conflicting with the conventional "bigger is better" expectation. We also found little evidence that any of the traits were subject to strong or consistent stabilizing selection (favoring trait values near the mean). Our results suggest that the specific traits we examined are not limiting adaptation and are probably not preventing the population from becoming self-sustaining. Future efforts should concentrate on other potentially limiting traits, such as the timing of smolt migration. Our results also suggest that any additional introductions of exogenous fish need not be concentrated on the size or growth of juveniles in potential source populations.*

Estimación de la Acción de la Selección Natural sobre el Salmón del Atlántico en Arroyos: Implicaciones para la Restauración de Poblaciones Extirpadas

**Resumen:** *Los esfuerzos para restablecer poblaciones en localidades de donde han sido extirpadas pueden obstaculizarse por la falta de adaptación del grupo introducido (porque provienen de un ambiente diferente). Se pueden usar estimaciones de la acción de la selección natural sobre las poblaciones nuevas para deducir la falta de adaptación y guiar los esfuerzos para reducir sus efectos. Estimamos la acción de la selección natural sobre el salmón del Atlántico (*Salmo salar*) bajo restauración en el Río Connecticut (EE.UU.). Se usaron más de 3500 registros de captura-recaptura en un pequeño afluente (Arroyo West, Massachussets) para estimar la acción de la selección sobre la longitud del cuerpo, masa corporal, condición corporal y crecimiento. Se obtuvieron estimaciones para tres a cuatro cohortes diferentes, dos clases de edad (segundo y tercer año de vida) y dos estaciones (invierno y verano). Encontramos poca evidencia de que alguna de las características haya sido sujeta a la selección direccional fuerte (favoreciendo valores mayores o menores). Se remarcó que los peces de mayor tamaño y con mejores condiciones corporales raramente sobrevivieron en tasas mayores, resultado que contradice la expectativa convencional de que "cuanto más grande mejor". También encontramos poca evidencia de que alguna de las características estuviera sujeta a selección estabilizante fuerte o consistente (favoreciendo valores cerca de la media). Nuestros resultados sugieren que las características específicas que examinamos no limitan la adaptación y probablemente no impidan que la po-*

---

*Paper submitted February 19, 2002; revised manuscript accepted September 19, 2002.*

Conservation Biology, Pages 795–805
Volume 17, No. 3, June 2003

*blación se vuelva auto sostenible. Los futuros esfuerzos deben concentrarse en otras características potencialmente limitantes, tales como la sincronización de la migración de juveniles. Nuestros resultados también sugieren que introducciones adicionales de peces exógenos no necesitan concentrarse en el tamaño o crecimiento de juveniles en potenciales poblaciones fuente.*

## Introduction

Conservation and management often focus on distinct population segments within species, particularly for salmon and trout (*Oncorhynchus* and *Salmo* spp.). This emphasis is warranted because local populations provide critical resources for humans and other animals that reside nearby. Moreover, the health of local populations is important for the genetic and demographic health of entire metapopulations, which are groups of populations linked by dispersal. Despite widespread recognition that distinct populations are biologically important, and despite their mandated protection under the U.S. Endangered Species Act (Waples 1991), many such populations have undergone drastic declines or been extirpated. For example, Nehlsen et al. (1991) found that "at least 106 major populations of salmon and steelhead on the West Coast have been extirpated." Cumulative losses of distinct populations, and the obvious benefits of regaining them, have led to a number of reintroduction efforts (e.g., Atlantic salmon [*Salmo salar*]; Parrish et al. 1998). Here we show how measurements of natural selection might aid such restoration efforts.

One of the major challenges facing restoration is that introduced individuals have often evolved in a different environment from that at the new site. Because of adaptation to the original environment (local adaptation is particularly strong in salmon; Taylor 1991), individuals introduced to new locations may initially be maladapted. This mismatch between existing and optimal phenotypes should reduce survival or reproductive success and cause strong natural selection to act on the new population. If the population is to become fully restored (i.e., self-sustaining), it must respond to this selection by adapting to the new environment (Gomulkiewicz & Holt 1995; Boulding & Hay 2001). Indeed, "contemporary" adaptation appears to be a common component of successful introductions (Reznick & Ghalambor 2001).

Information about the strength and form of selection could prove useful in several ways. First, estimates of directional selection—favoring individuals at one end of the phenotypic distribution—will reveal the expected direction of evolution (Endler 1986; Kingsolver et al. 2001). If, for example, selection favors large individuals, a self-sustaining population would likely have larger body sizes. Restoration could thus focus on facilitating the evolution of larger size, perhaps through selective breeding or the introduction of larger individuals. Second, estimates of stabilizing selection, which favors individuals in the center of the distribution, or disruptive selection, which favors individuals at both extremes of the distribution, reveal expected changes in phenotypic variation (Endler 1986; Kingsolver et al. 2001). When stabilizing selection is strong, the introduction of additional phenotypes may depress population fitness and should be avoided. Third, estimates of selection can be combined with estimates of genetic variation to make predictions about the speed and direction of evolutionary change (Lande & Arnold 1983; Schluter 2000). Such information could prove useful in long-term planning.

Natural selection has never, to our knowledge, been measured in a restoration program. We performed this task for Atlantic salmon undergoing restoration to the Connecticut River (U.S.A.). Our analysis was intensive but was limited to a few traits, a few time intervals of moderate duration, a few replicates, and one component of fitness (survival). Our work should thus be viewed as a preliminary example of the direction such research might take.

### Atlantic Salmon

Atlantic salmon spawn in the fall, laying their eggs in the gravel of streams or rivers (Fleming 1996). The fertilized eggs hatch after several months and then remain in the gravel for several more weeks. Fry (age 0+) emerge in the spring or early summer and take up residence within streams, often defending specific territories (Keeley & Grant 1995). In their first fall, surviving juveniles ("parr") may move a short distance downstream, but most remain near their summer territory (Cunjak et al. 1989). In the winter, parr often hide under stones, particularly during the day (Cunjak 1988). In the spring, some parr (now age 1+) migrate to the ocean as "smolts," whereas others remain in fresh water for another summer and winter (Hutchings & Jones 1998). In the following spring, many of these holdovers migrate to the ocean as 2+ smolts. Some (often many) males mature in fresh water, and some of these may later smolt and migrate to the ocean (Hutchings & Jones 1998). After 1–3 years in the North Atlantic, most surviving salmon return to their natal streams to spawn.

Atlantic salmon were once common throughout the North Atlantic, with their southern limit reaching Connecticut in the United States and northern Portugal in Europe. In the last few centuries, however, salmon have been extirpated from large regions of Europe and from nearly all their native range in the United States. The last remaining wild U.S. populations were recently listed as endangered under the U.S. Endangered Species Act. Wild populations continue to decline over much of their remaining range (Parrish et al. 1998). Probable causes of the declines and extirpations include introduction of exotic species, interbreeding with domesticated salmon, pollution, dams, and fishing (Parrish et al. 1998). Conservation efforts currently emphasize hatchery supplementation, habitat protection and rehabilitation, restrictions on fishing, and reintroductions.

### Connecticut River

Atlantic salmon were extirpated from the Connecticut River at least 150 years ago, largely by dams that prevented upstream passage. Many of these dams now have fish-passage facilities, and an intensive restoration effort has been underway for 30 years. Restoration began with the introduction of large numbers of fish from a variety of rivers (18 different sources; Rideout & Stolte 1989). The primary source was the Penobscot River (Maine) and the remaining sources were in Canada (Newfoundland, Quebec, New Brunswick).

The Connecticut River is a different environment from the Penobscot River and the other sources. Not only do they enter the ocean at different latitudes (Penobscot: 44°36′N; Connecticut: 41°18′N), but most of the Connecticut watershed is at lower latitudes than most of the Penobscot watershed. The Penobscot has lower temperatures, longer winters, lower discharges, and a smaller watershed. No life-history data exist for the historical Connecticut population, but many salmonid life-history traits vary with latitude, temperature, and discharge (e.g., Jonsson & L'Abée-Lund 1993). Some variation is the result of phenotypic plasticity (Jensen et al. 2000), but some also has a genetic basis (e.g., Riddell et al. 1981; Nicieza et al. 1994; Jensen et al. 2000). For traits with a genetic basis, we would therefore expect fish introduced into the Connecticut to be maladapted and subject to directional selection. The new population might also experience some stabilizing selection because it was founded by a variety of sources and hence may have had artificially high genetic and phenotypic variation.

Since the early 1990s, the Connecticut River population has been maintained exclusively by hatchery production within the watershed. Returning adults are captured at hydroelectric dams, and 10% are released upstream to spawn naturally. The remaining 90% are held in hatcheries until they mature, at which time they are mated in a design that maintains genetic diversity (Letcher & King 2001). Approximately 90% of the fry produced by these matings are stocked into streams throughout the watershed, and the remaining fish are raised to maturity in hatcheries as "domestic broodstock." The offspring of domestic broodstock are then stocked in a similar fashion. Because survival is much higher in the hatchery than in the wild, approximately 90% of the fish released each year are the progeny of domestic broodstock. Despite the annual release of millions of juveniles (1987–1997), restoration is proceeding slowly: on average, 233 adults return each year, and this number does not appear to be increasing.

Several studies of introduced salmon have revealed adaptation to new environments (Hendry 2001; Quinn et al. 2001), but some features of the Connecticut River program may hinder such adaptation. First, most of the fish are sheltered from natural selection during breeding and incubation. Second, most of the released juveniles had parents that did not experience natural selection (the domestic broodstock). Third, fish released into different tributaries are not propagated as separate populations when they return as adults. As a result, many fish stocked into a given stream or region had parents or grandparents that experienced different environments. These factors imply that adaptation may not be complete and that the potential for natural selection in the wild remains high.

## Methods

### Study Site and Fish Sampling

Our study was conducted in the West Brook, Massachusetts (lat 42°25′N, long 72°39′W), a second-order stream in the Connecticut River watershed. The brook originates from a reservoir and is 6.3 km long. Our study site was 1 km below the reservoir and had 47 contiguous sections that averaged 20.3 m in length, 96.6 $m^2$ in area, and 2% in gradient. Average water temperatures during our study were 14.5° C in the summer (May–September; maximum, 19.7° C) and 4.4° C in the winter (October–April; minimum, −0.4° C). Average discharge was 0.22 $m^3$/second in the summer (minimum, 0.03 $m^3$/second) and 0.46 $m^3$/second in the winter (maximum, 10.7 $m^3$/second). Based on habitat surveys conducted on 30–31 July 1997, stream width averaged 4.7 m, water depth averaged 8.8 cm, and substrate size (longest axis of rocks) averaged 21.5 cm (Letcher et al. 2002). The only fish species present in the brook were brown trout (*Salmo trutta*), brook trout (*Salvelinus fontinalis*), and Atlantic salmon.

The study site did not have any obstructions to fish movement, but a waterfall 4 km downstream ensured that the only salmon present were fish we had stocked (i.e., fish stocked in other streams could not have entered our site). The waterfall may have also hindered, but probably did not prevent, access to the brook by the historical salmon population. Regardless of the historical presence of salmon, the West Brook is generally representative of Connecticut River tributaries in the region. Stocking took place on a single day during the last 2 weeks of April in each year. Fry were stocked at a density of 50 individuals per 100 $m^2$ and were 26–28 mm in fork length. Our analyses are based on fish stocked in 1996–1999.

We sampled all 47 sections 30 times between May 1997 and September 2000. Sampling involved electrofishing (500 V unpulsed DC current) and night seining, in a combination designed to balance efficiency with minimal impacts on the fish (Gries & Letcher 2002*a*; Letcher et al. 2002). Sections were sampled sequentially upstream, with two passes in each section. We also sampled 140 m above and below the site at the end of each electrofishing sample. In three of the years, a picket-weir smolt trap was constructed 3 km downstream of the study site. The trap was installed in April when water temperatures reached 5° C, and smolts did not enter the trap for another 2 weeks. A similar trap has been used to catch smolts in nearby streams (Whalen & Parrish 1999). The trap was cleaned and checked for fish twice daily.

Each captured fish was anesthetized in buffered MS-222 (100 mg/L), measured for fork length (mm), and weighed (g). The first time each fish was captured ($n$ = 3628), we removed a few scales to determine age and year of stocking and inserted an 11-mm PIT tag intraperitoneally through a small incision made between the pectoral fins (Gries & Letcher 2002*b*). Tag number, length, and mass were recorded each subsequent time a fish was captured. All fish were also squeezed gently to test for milt expression (revealing mature male parr) and then released within 1 m of their capture location. These repeated samples of individual fish formed the basis of our analyses. Additional details on the study site and sampling procedures is provided by Letcher et al. (2002).

## Data Sets for Estimating Selection

It would be mechanistically possible to estimate selection between each pair of samples that shared individuals, but it was more appropriate to use a subset of these samples. First, we estimated selection only for starting and ending samples conducted by electroshocking, which was more efficient than night seining (Gries & Letcher 2002*a*). Second, we used intervals when fish were unlikely to emigrate because in selection analyses we assumed that missing fish had died. This criterion excluded the fall, when juvenile salmon may move downstream, and the spring, when they leave as smolts (Cunjak et al. 1989). Our smolt trap was not effective as an ending sample because it sometimes had low capture efficiency. Third, we estimated selection over intervals of roughly similar duration. As a result of these criteria, selection was estimated for 1+ fish in each of four summers (average dates: 20 May to September 30 1997; 26 May to 18 September 1998; 31 May to 30 September 1999; 25 May to 27 September 2000) and for 1+ and 2+ fish separately in each of three winters (16 December to 24 March 1998; 6 December to 28 March 1999; 14 December to 14 March 2000).

A substantial fraction of Atlantic salmon males may mature in fresh water (Hutchings & Jones 1998), and these may differ from immature males in body size, energy stores, behavior, or survival (Whalen & Parrish 1999; Arndt 2000). Our work in the West Brook has shown that a large fraction of males mature in freshwater and exhibit differences from immature fish in size but not overall survival (Letcher et al. 2002). Owing to potential differences between mature and immature fish, we performed selection analyses including all individuals ("all fish" data set) and then excluding individuals detected as mature in any sample ("immature fish" data set).

We estimated selection on four traits, all of which were calculated from measures of body size. The first two (length and mass) were measured directly at each sample. The third (relative condition factor) was calculated as $10{,}000 \cdot \text{mass} \cdot \text{length}^{-b}$ (Cone 1989), where $b$ is the slope of the regression of $\log_{10}$mass on $\log_{10}$length for the entire data set ($b = 2.965$, $r^2 = 0.99$). The fourth (growth) was calculated as [(mass at time 2) − (mass at time 1)]/days. This measure of growth was essentially uncorrelated with body mass for a given combination of stocking year, age, and season (immature fish: $r^2 = 0.00 - 0.10$). Moreover, our multiple regressions included length, which was highly correlated with mass and thus removed any effects of body size when selection on growth was estimated. Because growth could only be measured for fish that survived, it was calculated for the interval preceding that over which selection was estimated. The inclusion of growth data reduced sample sizes, so first we performed selection analyses without growth data to infer selection on length, mass, and condition factor. We then performed the analyses again with growth data to infer selection on that trait. Thus, all selection analyses were performed four times: with and without mature fish and with and without growth data.

## Estimating Selection

We used established methods to estimate selection. Trait values were standardized to a mean of zero and a standard deviation of unity within each combination of starting sample, stocking year, and data set (Lande & Arnold 1983). Fish captured in the ending sample for an interval, or in any subsequent sample, were assigned an absolute fitness of unity. Fish not captured in the ending sample, or any subsequent sample, were assigned an absolute fitness of zero. Some of these latter fish might simply have left the study site, but our choice of intervals minimized this possibility. Relative fitness was then determined for each fish as its absolute fitness divided by the mean fitness of all individuals for that combination of starting sample, stocking year, and data set (Lande & Arnold 1983).

We used four sets of linear regressions of relative fitness on standardized trait values to estimate selection during each combination of interval, stocking year, and data set (Lande & Arnold 1983). In set 1, we used simple regressions for each trait alone to estimate linear selection differentials, which represent the total strength of directional selection acting on that trait (direct selection plus indirect selection acting through the other traits). In set 2, we used multiple regressions for all traits together to estimate linear selection gradients, which represent the strength of directional selection acting directly on each trait (excluding indirect selection). Body mass was left out of the multiple regressions because it was highly correlated with body length. In set 3, we added squared values for a trait to the set 1 regression for that trait to estimate univariate quadratic (nonlinear) selection differentials, which represent the total strength of disruptive selection (when positive) or stabilizing selection (when negative). In set 4, we added squared terms for all traits and cross-product terms between all pairs of traits to the set 2 regressions to estimate univariate quadratic selection gradients (coefficients for squared terms, representing direct stabilizing or disruptive selection) and bivariate quadratic selection gradients (coefficients for cross-product terms). Bivariate gradients represent correlational selection favoring combinations of traits that are similar (when positive) or different (when negative). Brodie et al. (1995) review these types of selection and methods for their estimation.

Survival generates dichotomous outcomes, for which logistic regression is probably more appropriate than linear regression (Janzen & Stern 1998). Therefore, using logistic methods, we performed all the above regressions again. The resulting logistic regression coefficients were then converted to their linear regression equivalents (Janzen & Stern 1998). We did not adjust significance levels for multiple comparisons because the coefficients were not redundant tests of the same hypothesis. However, such adjustments can easily be made. Finally, we used univariate cubic splines (nonparametric regressions) to estimate the shape of the selection function acting on each trait (Schluter 1988). To facilitate interpretation of the splines, we used raw data (not standardized) and absolute fitness (0 or 1). For the splines, we used smoothing parameters ($\lambda$) that minimized error and provided the best compromise between sensitivity and biological reality: length, 4.0; mass, 4.0; relative condition factor, −6.0; and growth, −10.0.

## Results

Averages and variances for each trait differed among seasons (winter, summer), age classes (1+, 2+), and stock-

**Table 1. Basic information on traits, samples sizes, and survival in selection analyses for West Brook salmon.**[a]

| | *Winter intervals (stocking year/fish age*[b]*)* | | | | | | *Summer intervals (stocking year/fish age*[b]*)* | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | *1997/1+* | *1998/1+* | *1999/1+* | *1996/2+* | *1997/2+* | *1998/2+* | *1996/1+* | *1997/1+* | *1998/1+* | *1999/1+* |
| Immature fish without growth data | | | | | | | | | | |
| length (mm) | 70 (7) | 73 (6) | 71 (6) | 135 (9) | 126 (10) | 121 (10) | 117 (7) | 107 (10) | 104 (9) | 109 (9) |
| mass (g) | 3.8 (1.2) | 4.4 (1.2) | 4.0 (1.0) | 25.5 (4.9) | 21.6 (5.3) | 19.3 (4.4) | 20.8 (4.1) | 15.6 (4.0) | 14.1 (3.6) | 17.1 (3.8) |
| CF | 0.12 (0.01) | 0.13 (0.01) | 0.13 (0.01) | 0.12 (0.01) | 0.12 (0.01) | 0.13 (0.01) | 0.15 (0.01) | 0.15 (0.01) | 0.14 (0.01) | 0.15 (0.01) |
| starting *n* | 230 | 640 | 379 | 121 | 96 | 173 | 197 | 174 | 374 | 323 |
| survival (%) | 72.2 | 63.0 | 72.6 | 38.8 | 58.3 | 44.5 | 54.3 | 63.8 | 55.1 | 47.1 |
| Immature fish with growth data | | | | | | | | | | |
| growth (mg/day) | 0.01 (0.08) | 0.09 (0.12) | 0.15 (0.12) | 0.06 (0.07) | 0.30 (0.15) | 0.26 (0.14) | no data | 4.21 (0.79) | 2.86 (0.66) | 3.70 (0.72) |
| starting *n* | 107 | 177 | 196 | 105 | 64 | 142 | no data | 112 | 189 | 182 |
| survival (%) | 70.1 | 62.1 | 74.5 | 41.9 | 56.3 | 43.7 | no data | 63.4 | 52.4 | 48.9 |
| All fish without growth data | | | | | | | | | | |
| starting *n* | 306 | 751 | 469 | 191 | 174 | 242 | 282 | 267 | 508 | 444 |
| survival (%) | 79.1 | 68.4 | 77.8 | 51.3 | 63.8 | 53.7 | 66.3 | 77.2 | 64.2 | 59.0 |
| All fish with growth data | | | | | | | | | | |
| starting *n* | 142 | 210 | 251 | 153 | 115 | 188 | no data | 168 | 260 | 257 |
| survival (%) | 77.5 | 68.1 | 80.1 | 54.2 | 61.7 | 52.7 | no data | 75.0 | 62.7 | 62.3 |

[a] *Data are numbers of tagged fish in each of the four data sets at the start of each selection interval (starting* n*), the percentage of those fish captured at the end of the interval or in any sample thereafter (survival), and trait means (SD in parentheses) for fish at the start of each interval for one data set (values were similar for the other data sets); CF, relative condition factor.*

[b] *Fish ages are the second year of life (1+) and the third year of life (2+).*

ing years (1996, 1997, 1998, 1999; Table 1), but were similar across data sets (results not shown). Coefficients of variation were large enough that selection should have considerable potential to act on the population (immature fish: length, 6.2–10.1%; mass, 19.1–30.9%; CF, 12.0–15.4%; growth, 18.7–1236.3%). Survival varied substantially, and several general trends emerged (Table 1). First, survival was generally highest for winter 1+ fish, lowest for winter 2+ fish, and intermediate for summer 1+ fish. Second, survival was always higher for the data set including all fish than for the data set with immature fish only. Third, survival was similar for the data sets with and without growth rate. These survival rates and our sample sizes are sufficient for robust analyses of selection (Kingsolver et al. 2001). Although we used linear and logistic regressions to estimate selection, results based on the two methods were nearly identical (not shown). We therefore report only logistic coefficients converted to their linear form, along with significance levels from logistic regressions (Janzen & Stern 1998). Directional selection varied among seasons, age classes, and stocking years (Table 2; Figs. 1–4). For winter 1+ fish, directional selection did not appear to be acting on any of the traits. Of the 54 coefficients (differentials and gradients), 27 were positive, 27 were negative, and all were $p > 0.1$. For summer 1+ fish, selection favored larger individuals in 3 years (significant in 1 year, generally weaker for all fish than for immature fish) and was neutral in the other year (coefficients were small). Selection also favored summer 1+ fish with lower condition factors in the data set with immature fish (differentials significant in 2 years; Fig. 3) and was neutral in the data set with all fish. Selection on growth for summer 1+ fish was variable in direction and never significant. For winter 2+ fish, several generalizations are possible. First, selection favored smaller fish (Fig. 2): all coefficients for length and mass were negative, and a few were large and significant. Second, selection on condition factor varied dramatically among year classes (Fig. 3): it was sometimes positive, sometimes negative, and sometimes significant. Third, selection generally favored fast-growing fish (not significant) in the data set with immature fish (Fig. 4) but slow-growing fish (sometimes significant) in the data set with all fish. For most traits and intervals, differentials were similar to gradients, showing that the traits were not phenotypically correlated and that selection could act on them independently.

Stabilizing or disruptive selection did not appear to be acting strongly on any of the traits (univariate quadratic coefficients in Table 3; Figs. 1–4). For winter 1+ fish, all coefficients for length and mass were negative

**Table 2. Directional selection acting on the length, mass, relative condition factor (CF), and growth of West Brook salmon.**[a]

| | *Winter intervals (stocking year/fish age*[b]*)* | | | | | | *Summer intervals (stocking year/fish age*[b]*)* | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | *1997/1+* | *1998/1+* | 1999/1+ | 1996/2+ | 1997/2+ | 1998/2+ | 1996/1+ | 1997/1+ | 1998/1+ | 1999/1+ |
| Differentials: immature fish | | | | | | | | | | |
| length | 0.02 | −0.01 | 0.01 | −0.05 | −0.12 | −0.27*** | −0.01 | 0.14** | 0.06 | 0.04 |
| mass | 0.01 | −0.02 | −0.00 | −0.01 | −0.14 | −0.27*** | −0.03 | 0.10* | 0.04 | 0.02 |
| CF | −0.01 | −0.01 | −0.04 | 0.20* | −0.02 | −0.13 | −0.04 | −0.18*** | −0.09** | −0.05 |
| growth$^c$ | 0.02 | 0.04 | −0.06 | 0.10 | 0.00 | 0.04 | no data | −0.07 | −0.06 | 0.11 |
| Gradients: immature fish | | | | | | | | | | |
| length | 0.03 | −0.01 | 0.00 | −0.08 | −0.12 | −0.27 | −0.01 | 0.13** | 0.05 | 0.02 |
| CF | −0.03 | −0.01 | −0.04 | 0.21* | −0.01 | −0.14 | −0.04 | −0.18*** | −0.08 | −0.04 |
| length$^c$ | 0.05 | 0.08 | 0.01 | −0.09 | −0.08 | −0.26*** | no data | 0.20*** | 0.09 | −0.02 |
| CF$^c$ | −0.08 | −0.11 | −0.05 | 0.20 | −0.13 | −0.17* | no data | −0.19*** | −0.42 | −0.13 |
| growth$^c$ | 0.05 | 0.19 | −0.04 | 0.04 | 0.10 | 0.13 | no data | 0.01 | −0.06 | 0.12 |
| Differentials: all fish | | | | | | | | | | |
| length | 0.02 | −0.01 | 0.01 | −0.19*** | −0.05 | −0.28**** | −0.03 | 0.09*** | 0.01 | 0.01 |
| mass | 0.02 | −0.01 | 0.00 | −0.15** | −0.07 | −0.27**** | −0.03 | 0.08** | 0.01 | 0.00 |
| CF | 0.00 | 0.00 | −0.03 | 0.15* | 0.00 | 0.04 | 0.00 | −0.03 | 0.00 | −0.03 |
| growth$^c$ | 0.04 | −0.06 | −0.05 | −0.13* | −0.08 | −0.13* | no data | −0.03 | −0.05 | 0.07 |
| Gradients: all fish | | | | | | | | | | |
| length | 0.03 | −0.01 | 0.00 | −0.20*** | −0.06 | −0.28**** | −0.03 | 0.09** | 0.01 | 0.01 |
| CF | −0.01 | 0.00 | −0.03 | 0.18* | −0.02 | −0.02 | 0.00 | −0.02 | 0.00 | −0.02 |
| length$^c$ | 0.04 | 0.04 | 0.00 | −0.19** | 0.03 | −0.28**** | no data | 0.13*** | 0.04 | −0.02 |
| CF$^c$ | −0.06 | 0.06 | −0.03 | 0.28*** | −0.02 | 0.02 | no data | −0.05 | 0.06 | −0.06 |
| growth$^c$ | 0.07 | −0.09 | −0.04 | −0.08 | −0.09 | −0.04 | no data | 0.00 | −0.05 | 0.07 |

[a] *Selection differentials (total selection, slope coefficients from simple regressions of each trait on relative fitness) and gradients (direct selection, partial coefficients from multiple regressions of all traits on relative fitness) are standardized linear coefficients converted from logistic coefficients (Janzen & Stern 1998). Results are shown for analyses based on immature fish and for all fish (immature and mature). Probability:* *$p < 0.10$; **$p < 0.05$; ***$p < 0.01$; ****$p < 0.001$.

[b] *Fish ages are the second year of life (1+) and the third year of life (2+).*

[c] *Regressions including growth-rate data.*

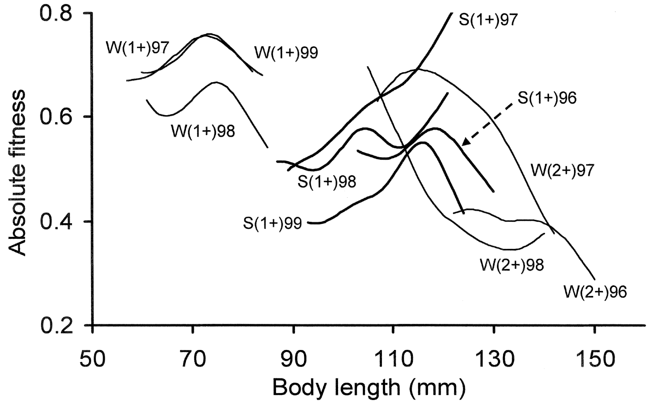

*Figure 1. Relationships between the body length of immature fish (data set without growth rate) and their absolute fitness (survived, 1; died, 0) for each combination of stocking year (1996, 1997, 1998, 1999), age class (1+, 2+; see Table 1 footnote), and season (S, summer; W, winter). Summer intervals are shown with thicker lines than winter intervals. The lines are cubic splines (Schluter 1988) and exclude the lowest 2.5% and the highest 2.5% of the trait values (to make the major trends more obvious).*

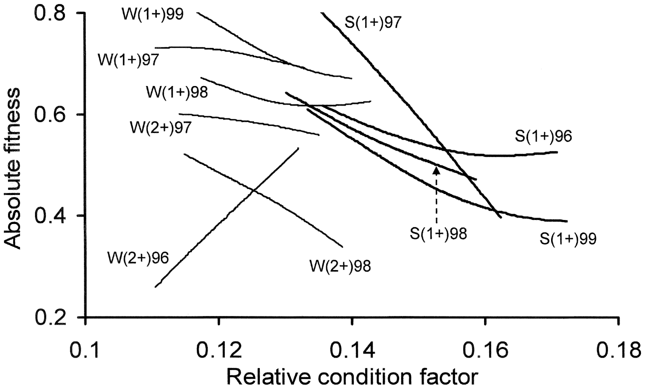

*Figure 3. Relationships between the relative condition factor of immature fish and their absolute fitness. The legend for Fig. 1 provides definitions of figure elements.*

(stabilizing) but were also very close to zero and not significant, except for length gradients in 2 years (Table 3). Coefficients for the other traits varied in sign and were significant only for condition factor in the 1999 stocking. For that cohort, the coefficient was positive (disruptive). For summer 1+ fish, coefficients for length, mass, and condition factor varied in sign among years and were rarely significant, except in the 1999 stocking (Table 3). Coefficients for growth were always negative (significant in 1 year), however, suggesting some selection against both high and low growth rates. Cubic splines suggested more complex patterns for growth in summer 1+ fish, particularly in the 1999 stocking (Fig. 4). For winter 2+ fish, coefficients varied in sign among years (Table 3) and were rarely significant. When significant (length and mass for all fish in the 1999 stocking), the coefficients were negative (stabilizing). Differentials were usually similar in sign and magnitude to gradients, suggesting that the traits were uncorrelated from the perspective of quadratic selection.

Correlational selection (favoring particular combinations of traits) was neither strong nor consistent (bivariate quadratic coefficients in Table 3). The coefficients for a trait usually varied in sign and magnitude and were rarely significant. For combinations of length and growth, however, several results are worth noting. First, coefficients were usually negative (not significant) for winter 1+ fish, suggesting that selection may act against fish with similar trait combinations, and therefore against fish with large size and fast growth and fish with small size and slow growth. Second, the other coefficients were strongly positive in some samples but strongly neg-

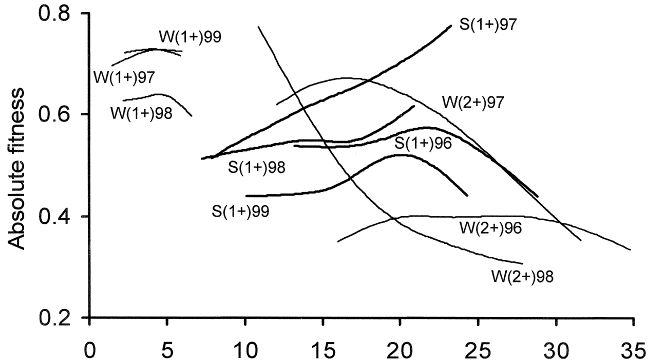

*Figure 2. Relationships between the body mass of immature fish and their absolute fitness. The legend for Fig. 1 provides definitions of figure elements.*

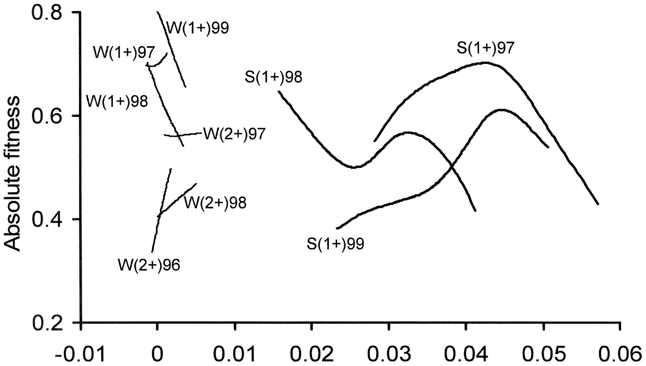

*Figure 4. Relationships between the growth of immature fish and their absolute fitness. The legend for Fig. 1 provides definitions of figure elements.*

**Table 3. Univariate quadratic selection acting on body length (length•length), body mass (mass•mass), relative condition factor (CF•CF), and growth (growth•growth); and bivariate quadratic selection acting on trait combinations (length•CF, growth•CF, growth•length) in West Brook salmon.[a]**

| | *Winter intervals (stocking year/fish age[b])* | | | | | | *Summer intervals (stocking year/fish age[b])* | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | *1997/1+* | *1998/1+* | *1999/1+* | *1996/2+* | *1997/2+* | *1998/2+* | *1996/1+* | *1997/1+* | *1998/1+* | *1999/1+* |
| Differentials: immature fish | | | | | | | | | | |
| length•length | −0.05 | −0.06 | −0.05 | −0.13 | −0.19 | 0.21 | −0.06 | 0.02 | 0.04 | −0.06 |
| mass•mass | −0.04 | −0.07 | −0.05 | −0.13 | −0.17 | 0.27* | −0.10 | 0.03 | 0.06 | −0.11 |
| CF•CF | −0.06 | 0.05 | 0.08** | −0.01 | −0.07 | −0.08 | 0.19* | −0.04 | −0.01 | 0.12* |
| growth•growth[c] | 0.16 | 0.01 | −0.02 | −0.02 | 0.08 | 0.02 | no data | −0.20** | −0.08 | −0.07 |
| Gradients: immature fish | | | | | | | | | | |
| length•length | −0.02 | −0.06 | −0.05 | −0.12 | −0.13 | 0.26* | −0.05 | 0.02 | 0.05 | −0.13 |
| CF•CF | −0.03 | 0.05 | 0.10* | 0.01 | −0.09 | −0.09 | 0.20 | −0.01 | −0.01 | 0.30*** |
| length•CF | −0.02 | −0.01 | 0.03 | 0.02 | −0.12 | 0.03 | −0.06* | −0.09 | −0.01 | 0.14* |
| length•length[c] | −0.17 | −0.09 | −0.14* | −0.10 | −0.27 | 0.23 | no data | 0.23 | 0.20* | −0.18 |
| CF•CF[c] | −0.23 | 0.05 | 0.13 | 0.00 | −0.24 | −0.07 | no data | −0.09 | 0.00 | 0.21** |
| growth•growth[c] | 0.05 | −0.02 | −0.02 | −0.08 | 0.15 | −0.01 | no data | −0.25** | −0.07 | −0.08 |
| length•CF[c] | −0.01 | 0.02 | 0.03 | −0.02 | 0.11 | 0.08 | no data | 0.01 | −0.01 | 0.08 |
| growth•CF[c] | 0.15 | 0.07 | −0.07 | −0.06 | −0.20 | −0.09 | no data | 0.04 | 0.01 | −0.03 |
| growth•length[c] | 0.06 | −0.06 | −0.05 | 0.39** | −0.14 | 0.01 | no data | −0.16** | 0.13* | 0.11 |
| Differentials: all fish | | | | | | | | | | |
| length•length | −0.03 | −0.04 | −0.05 | −0.12 | −0.23*** | 0.03 | −0.03 | 0.03 | 0.03 | −0.09* |
| mass•mass | −0.03 | −0.04 | −0.04 | −0.04 | −0.19** | 0.11 | −0.05 | 0.03 | 0.05 | −0.12** |
| CF•CF | −0.05 | 0.04 | 0.07* | −0.10 | −0.06 | −0.06 | 0.06 | 0.01 | −0.03 | 0.04 |
| growth•growth[c] | 0.12 | 0.00 | −0.03 | 0.11 | 0.06 | 0.14 | no data | −0.15*** | −0.02 | −0.07 |
| Gradients: all fish | | | | | | | | | | |
| length•length | −0.01 | −0.04 | −0.05 | 0.03 | −0.23** | 0.05 | −0.02 | 0.03 | 0.04 | −0.13** |
| CF•CF | −0.03 | 0.04 | 0.09** | −0.14* | −0.08 | −0.07 | 0.06 | 0.01 | −0.02 | 0.14** |
| length•CF | −0.02 | 0.00 | 0.04 | 0.01 | −0.06 | 0.03 | −0.03 | −0.04 | 0.03 | 0.07 |
| length•length[c] | −0.11* | −0.08 | −0.09* | −0.08 | −0.20 | 0.04 | no data | 0.22* | 0.16* | −0.14* |
| CF•CF[c] | −0.10 | 0.05 | 0.12* | 0.04 | −0.12 | −0.03 | no data | −0.02 | 0.00 | 0.14** |
| growth•growth[c] | 0.10 | 0.00 | −0.02 | −0.04 | 0.08 | 0.07 | no data | −0.16*** | −0.03 | −0.08 |
| length•CF[c] | 0.01 | 0.05 | 0.04 | −0.06 | −0.05 | 0.06 | no data | 0.01 | 0.01 | 0.07 |
| growth•CF[c] | 0.04 | 0.02 | −0.07 | −0.09 | 0.06 | −0.21** | no data | 0.02 | 0.07 | −0.03 |
| growth•length[c] | −0.01 | −0.08 | −0.03 | 0.27** | −0.15 | 0.09 | no data | −0.06 | 0.10** | 0.09* |

[a] *Further details in Table 2. Probability:* *$p < 0.10$; **$p < 0.05$; ***$p < 0.01$.
[b] *Fish ages are the second (1+) and third year of life (2+).*
[c] *Regressions including growth-rate data.*

ative in others (Table 3). Thus, certain combinations of these two traits can influence survival but in opposing ways in different years, seasons, and age classes.

## Discussion

Our analysis of natural selection acting on Atlantic salmon in a restoration program yielded several conclusions. First, selection was variable across seasons, age classes, and cohorts (stocking years). Second, patterns of directional selection acting on body size (length and mass) varied through the course of a salmon's freshwater life. In the second winter (1+ fish), survival was not related to body size; in the second summer (1+), survival was positively related to body size; and in the third winter (2+), survival was negatively related to body size (statistical significance varied). Third, immature fish with high condition factors were not more likely to survive than those with low condition factors. Fourth, quadratic selection (stabilizing or disruptive) was weak and inconsistent. These conclusions are probably robust because we had more replicates (three to four per season and age class) and larger sample sizes (all-fish data set: $n$ = 174–751, median $n$ = 294) than most other studies of selection in nature (median $n$ = 134; Kingsolver et al. 2001).

### Variation in Selection

Studies of natural populations often document considerable variation in selection (e.g., Blanckenhorn et al. 1999; Jann et al. 2000). Such variation may occur across seasons, age classes, and years, as was the case for West Brook salmon. Some of the variation in other studies may result from small sample sizes, short intervals, or poor surrogates for fitness (Kingsolver et al. 2001). In contrast, our sample sizes were large, our intervals were at least 3 months long, and survival was our surrogate for fitness. Variation in West Brook salmon should thus have a biological basis. Variation between seasons and ages probably arises because optimal trait values differ through ontogeny and across seasons. Indeed, opposing selection pressures during different life-history stages are common in natural populations (Schluter et al. 1991).

Variation among cohorts probably arises because of interannual variation in the environment. For example, Grant and Grant (1995) found that survival and beak size in *Geospiza fortis* were positively correlated in a dry year but negatively correlated in a wet year. Selection on stream-dwelling Atlantic salmon may be similarly influenced by the environment. For example, Good et al. (2001) found that selection on 0+ salmon during the summer was weak and favored large fish in a drought year but was strong and favored small fish in a flood year. Potentially important interannual variation in the West Brook included temperature (July: 14.3–16.9° C; December: 0.1–5.3° C) and discharge (July: 0.02–0.09 $m^3$/second; December: 0.05–0.25 $m^3$/second). However, the group that experienced the strongest selection in summer (1997, 1+) did not experience exceptional discharges or temperatures. The cohort that experienced the strongest selection in winter (1998, 2+) did not experience exceptional discharges but did experience the coldest water. However, a robust analysis of interannual variation will require additional years of data.

## Directional Selection

West Brook salmon did not experience strong or consistent directional selection. Selection is usually weak in natural populations (median of absolute differentials = 0.13; Kingsolver et al. 2001), probably because they are well adapted. In contrast, introduced populations should experience strong selection because they may often be maladapted. For example, divergence of sockeye salmon (*Oncorhynchus nerka*) introduced to Lake Washington would match estimated selection differentials of at least 0.34 for female body length and 0.47 for male body depth (assuming $h^2 = 0.3$; Hendry 2001). These differentials would fall into the 81st and 90th percentiles of Kingsolver et al.'s (2001) review. Divergence of guppies (*Poecilia reticulata*) introduced into different predator environments would match estimated selection differentials of 0.172–0.220 for female age and 0.013–0.281 for female size (Reznick et al. 1997). Conversely, selection differentials in West Brook salmon had a median absolute value of only 0.04 (immature fish; Table 2), with a maximum of 0.27 (73rd percentile; Kingsolver et al. 2001).

We suggest several explanations for the absence of strong selection in an introduced population. First, the environment may not differ appreciably between ancestral and introduced sites. If so, introduced fish will already be well adapted and should not experience strong selection. This seems unlikely in our study because the introduced fish originally came from a noticeably different environment. Second, selection on introduced populations may weaken as they approach the new optimum. Retrospective analyses of introduced populations estimate selection that has occurred in the past (Reznick et al. 1997; Hendry 2001). If current selection was measured for those same populations, it would probably be much weaker. This effect seems unlikely in our study because the population is not self-sustaining and thus probably not well adapted. Third, selection may act on traits or during intervals that we did not examine. This does seem likely because we examined only four traits, two seasons, and two age classes. It is certainly possible that we missed the critical traits or periods. For example, selection may act strongly on smolt timing (Nielsen et al. 2001) or on 0+ fish (Einum & Fleming 2000; Good et al. 2001).

Despite the general lack of strong or consistent directional selection, we did observe several subtle patterns that conflicted with conventional wisdom. For example, numerous researchers report the benefits of large size in young Atlantic salmon (e.g., Lundqvist et al. 1994; Einum & Fleming 2000) and other salmonids (e.g., Quinn & Peterson 1996). For West Brook salmon, however, large size was favored only for summer 1+ fish and strongly so only in 1 of the 4 years (Figs. 1 & 2). Winter 1+ and 2+ fish were actually more likely to survive if they were smaller, significantly so in one of the years. A similar trend occurred across ages, with winter 1+ fish being smaller and yet having higher survival than winter 2+ fish (Table 1; Letcher et al. 2002). A few other recent studies suggest that larger parr do not necessarily have higher survival (Good et al. 2001). Equally interesting was the result that immature fish with higher condition factors did not survive at higher rates (Fig. 3).

One explanation for West Brook salmon contradicting the "bigger is better" expectation is that we assumed missing fish had died, whereas some might instead have emigrated. This seems unlikely because we examined intervals for which emigration would be rare (summer and winter). Moreover, emigration should be more common for smaller fish in lower condition factors (Cutts et al. 1999). For example, Cunjak and Randall (1993) found that site fidelity during the first winter was a positive function of body size. A second possibility is that we missed the critical interval during which larger fish have higher survival. Indeed, Einum and Fleming (2000) found strong selection for large size in the first few weeks after emergence but not afterward. A third possibility is that West Brook salmon experience a qualitatively different environment from other salmon populations. For example, the West Brook is near the southern edge of the species' range. Whatever the reason, it clearly is not safe to assume that bigger is better for stream-dwelling salmonids.

### Stabilizing, Disruptive, and Correlational Selection

Selection on West Brook salmon did not usually favor individuals near the center of the phenotypic distribution (negative coefficients, stabilizing selection) or individuals near the extremes (positive coefficients, disruptive selection). In natural populations, quadratic selection coefficients center around zero and most are small (median of absolute differentials = 0.08; Kingsolver et al. 2001). This is not surprising because past selection should have eliminated most maladaptive variation from undisturbed populations. For West Brook salmon, however, strong stabilizing selection might be expected because an unnaturally diverse (and presumably variable) group of fish was originally introduced into the Connecticut River (Rideout & Stolte 1989). Instead, we found that quadratic selection was negative only 64% of the time, and few negative differentials were significant (Table 3). Moreover, quadratic differentials were nearly always small in magnitude: the median absolute differential was 0.06 (immature fish, Table 3) and the maximum was only 0.27 (83rd percentile; Kingsolver et al. 2001).

We suggest several possible reasons for West Brook salmon contradicting the expectation that strong stabilizing selection should act on an unnaturally diverse population. One possibility is that the West Brook is a forgiving environment and therefore does not select strongly for any particular phenotype. This seems unlikely because the stream is at the southern edge of the species' range. A second possibility is that selection has already weeded extreme phenotypes out of the population. This is certainly possible because few of the juveniles released each year actually return as adults. However, the range of variation in West Brook salmon remains fairly high (e.g., coefficients of variation for body mass were 19.1–30.9%). A third possibility is that selection acted most strongly on other traits or during other intervals, which is a plausible scenario as described above. Finally, quadratic selection may generally be weak on stream-dwelling Atlantic salmon, but this cannot be determined until other studies have provided comparable estimates.

For the most part, West Brook salmon did not experience strong or consistent correlational selection (favoring particular combinations of traits). Here, however, our results cannot be compared with previous work because "only a handful of studies have studied the strength of correlational selection" (Kingsolver et al. 2001). We did observe some interesting variation with respect to length and growth. In some cases, selection favored small and fast-growing individuals and large and slow-growing individuals (negative coefficients), whereas in other cases selection favored the opposite (Table 3). The former correlation suggests that selection favored compensatory growth (small individuals catching up to large individuals) and the latter that selection favored depensatory growth (large individuals becoming increasingly larger than small individuals). Interactions between these traits may be a profitable area for future research.

### Conservation

Our results may be relevant to the Connecticut River restoration program in several ways. First, if additional introductions are made, donor populations need not be targeted for particular juvenile sizes or growth rates (strong directional selection was not detected on these traits). Second, if new donor populations do vary in these traits, it will probably not severely compromise adaptation (stabilizing selection was generally weak). Third, and perhaps most important, the traits we examined do not appear to be maladapted and hence are probably not the reason the population has yet to become self-sustaining. Future studies should investigate other potentially critical traits, such as smolt timing. Of course, it is also important to remember that our inferences were drawn from only two seasons and age classes and from one tributary. Nonetheless, our analysis illustrates how measurements of selection could potentially aid restoration efforts.

## Acknowledgments

We thank everyone who helped sample the West Brook, especially T. Dubreuil. Fry for stocking were provided by the White River National Fish Hatchery. A prerelease windows version of the cubic spline program was provided by D. Schluter. Helpful comments were provided by M. Kinnison and two anonymous reviewers. Partial funding was provided by the U.S. Forest Service's Northeast Forest Experimental Station. A. Hendry was supported by the Darwin Fellowship in Organismic and Evolutionary Biology at the University of Massachusetts, Amherst.

### Literature Cited

Arndt, S. K. A. 2000. Influence of sexual maturity on feeding, growth and energy stores of wild Atlantic salmon parr. Journal of Fish Biology **57:**589–596.

Blanckenhorn, W. U., C. Morf, C. Mühlhäuser, and T. Reusch. 1999. Spatiotemporal variation in selection on body size in the dung fly *Sepsis cynipsea.* Journal of Evolutionary Biology **12:**563–576.

Boulding, E. G., and T. Hay. 2001. Genetic and demographic parameters determining population persistence after a discrete change in the environment. Heredity **86:**313–324.

Brodie, E. D., A. J. Moore, and F. J. Janzen. 1995. Visualizing and quantifying natural selection. Trends in Ecology & Evolution **10:** 313–318.

Cone, R. S. 1989. The need to reconsider the use of condition indices in fishery science. Transactions of the American Fisheries Society **118:**510–514.

Cunjak, R. A. 1988. Behaviour and microhabitat of young Atlantic salmon (*Salmo salar*) during winter. Canadian Journal of Fisheries and Aquatic Sciences **45:**2156–2160.

Cunjak, R. A., and R. G. Randall. 1993. In-stream movements of young Atlantic salmon (*Salmo salar*) during winter and early spring. Canadian Special Publication of Fisheries and Aquatic Sciences **118:** 43–51.

Cunjak, R. A., E. M. P. Chadwick, and M. Shears. 1989. Downstream movements and estuarine residence by Atlantic salmon parr (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences **46:** 1466–1471.

Cutts, C. J., N. B. Metcalfe, and A. C. Taylor. 1999. Competitive asymmetries in territorial juvenile Atlantic salmon, *Salmo salar.* Oikos **86:**479–486.

Einum, S., and I. A. Fleming. 2000. Selection against late emergence and small offspring in Atlantic salmon (*Salmo salar*). Evolution **54:** 628–639.

Endler, J. A. 1986. Natural selection in the wild. Princeton University Press, Princeton, New Jersey.

Fleming, I. A. 1996. Reproductive strategies of Atlantic salmon: ecology and evolution. Reviews in Fish Biology and Fisheries **6:**379–416.

Gomulkiewicz, R., and R. D. Holt. 1995. When does evolution by natural selection prevent extinction? Evolution **49:**201–207.

Good, S. P., J. J. Dodson, M. G. Meekan, and D. A. J. Ryan. 2001. Annual variation in size-selective mortality of Atlantic salmon (*Salmo salar*) fry. Canadian Journal of Fisheries and Aquatic Sciences **58:** 1187–1195.

Grant, P. R., and B. R. Grant. 1995. Predicting microevolutionary responses to directional selection on heritable variation. Evolution **49:**241–251.

Gries, G., and B. H. Letcher. 2002*a*. A night seining technique for sampling juvenile Atlantic salmon in streams. North American Journal of Fisheries Management **22:**595–601.

Gries, G., and B. H. Letcher. 2002*b*. Tag retention and survival of age-0 Atlantic salmon following surgical implantation with passive integrated transponder tags. North American Journal of Fisheries Management **22:**219–222.

Hendry, A. P. 2001. Adaptive divergence and the evolution of reproductive isolation in the wild: an empirical demonstration using introduced sockeye salmon. Genetica **112–113:**515–534.

Hutchings, J. A., and M. E. B. Jones. 1998. Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar.* Canadian Journal of Fisheries and Aquatic Sciences **55(supplement 1):**22–47.

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

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

Jensen, A. J., T. Forseth, and B. O. Johnsen. 2000. Latitudinal variation in growth of young brown trout *Salmo trutta.* Journal of Animal Ecology **69:**1010–1020.

Jonsson, B., and J. H. L'Abée-Lund. 1993. Latitudinal clines in life-history variables of anadromous brown trout in Europe. Journal of Fish Biology **43(supplement A):**1–16.

Keeley, E. R., and J. W. A. Grant. 1995. Allometric and environmental correlates of territory size in juvenile Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences **52:**186–196.

Kingsolver, J. G., H. E. Hoekstra, J. M. Hoekstra, D. Berrigan, S. N. Vignieri, C. E. Hill, A. Hoang, P. Gibert, and P. Beerli. 2001. The strength of phenotypic selection in natural populations. The American Naturalist **157:**245–261.

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

Letcher, B. H., and T. L. King. 2001. Parentage and grandparentage assignment with known and unknown matings: application to Connecticut River Atlantic salmon restoration. Canadian Journal of Fisheries and Aquatic Sciences **58:**1812–1821.

Letcher, B. H., G. Gries, and F. Juanes. 2002. Survival of stream-dwelling Atlantic salmon: effects of life history variation, season and age. Transactions of the American Fisheries Society **131:** 838–854.

Lundqvist, H., S. McKinnell, H. Fängstam, and I. Berglund. 1994. The effect of time, size and sex on recapture rates and yield after river releases of *Salmo salar* smolts. Aquaculture **121:**245–257.

Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. Fisheries **16(2):**4–21.

Nicieza, A. G., F. G. Reyes-Gavilán, and F. Brana. 1994. Differentiation in juvenile growth and bimodality patterns between northern and southern populations of Atlantic salmon (*Salmo salar* L.). Canadian Journal of Zoology **72:**1603–1610.

Nielsen, C., G. Holdensgaard, H. C. Petersen, B. Th. Björnsson, and S. S. Madsen. 2001. Genetic differences in physiology, growth hormone levels and migratory behaviour of Atlantic salmon smolts. Journal of Fish Biology **59:**28–44.

Parrish, D. L., R. J. Behnke, S. R. Gephard, S. D. McCormick, and G. H. Reeves. 1998. Why aren't there more Atlantic salmon (*Salmo salar*)? Canadian Journal of Fisheries and Aquatic Sciences **55(supplement 1):**281–287.

Quinn, T. P., and N. P. Peterson. 1996. The influence of habitat complexity and fish size on over-winter survival and growth of individually marked juvenile coho salmon (*Oncorhynchus kisutch*) in Big Beef Creek, Washington. Canadian Journal of Fisheries and Aquatic Sciences **53:**1555–1564.

Quinn, T. P., M. T. Kinnison, and M. J. Unwin. 2001. Evolution of chinook salmon (*Oncorhynchus tshawytscha*) populations in New Zealand: pattern, rate, and process. Genetica **112–113:**493–513.

Reznick, D. N., and C. K. Ghalambor. 2001. The population ecology of contemporary adaptations: what empirical studies reveal about the conditions that promote adaptive evolution. Genetica **112–113:** 183–198.

Reznick, D. N., F. H. Shaw, F. H. Rodd, and R. G. Shaw. 1997. Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). Science **275:**1934–1937.

Riddell, B. E., W. C. Leggett, and R. L. Saunders. 1981. Evidence of adaptive polygenic variation between two populations of Atlantic salmon (*Salmo salar*) native to tributaries of the S. W. Miramichi River, N.B. Canadian Journal of Fisheries and Aquatic Sciences **38:** 321–333.

Rideout, S. G., and L. W. Stolte. 1989. Restoration of Atlantic salmon to the Connecticut and Merrimack Rivers. Pages 67–81 in R. H. Stroud, editor. Present and future Atlantic salmon management. Marine Recreational Fisheries, Savannah, Georgia.

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

Schluter, D. 2000. The ecology of adaptive radiation. Oxford University Press, Oxford, United Kingdom.

Schluter, D., T. D. Price, and L. Rowe. 1991. Conflicting selection pressures and life history trade-offs. Proceedings of the Royal Society of London Series B **246:**11–17.

Taylor, E. B. 1991. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. Aquaculture **98:** 185–207.

Waples, R. S. 1991. Pacific salmon, *Oncorhynchus* spp., and the definition of "species" under the Endangered Species Act. Marine Fisheries Review **53:**11–22.

Whalen, K. G., and D. L. Parrish. 1999. Effect of maturation on parr growth and smolt recruitment of Atlantic salmon. Canadian Journal of Fisheries and Aquatic Sciences **56:**79–86.