

**NATURAL SELECTION ON JUVENILE BODY SIZE
IN AN ATLANTIC SALMON RESTORATION PROJECT**

Andrew P. Hendry
Organismic and Evolutionary Biology Program
University of Massachusetts Amherst
Amherst, MA 01003-5810 USA
ahendry@bio.umass.edu

Michael T. Kinnison
Department of Biological Sciences
Dartmouth College, Gilman Hall
Hanover, NH 03755 USA
michael.kinnison@dartmouth.edu

Benjamin H. Letcher
Conte Anadromous Fish Research Center
US Geological Survey, Biological Resources Division
One Migratory Way, PO Box 796
Turners Falls, MA USA 01376
bletcher@forwild.umass.edu

EXTENDED ABSTRACT ONLY – DO NOT CITE

Transplants of non-native fish are often used when attempting to reintroduce salmon into river systems from which they have been extirpated. Immediate success in restoration efforts is rarely achieved, in part because introduced fish are not well adapted to the new system. When maladaptation is strong, the introduced population should be subject to strong selection for traits that improve survival in the new environment. Our goal was to quantify the strength and form of natural selection acting on juvenile body length and mass in an Atlantic salmon population recently introduced to the Connecticut River basin, Massachusetts.

Un-fed fry (progeny of wild adults returning to the Connecticut River) were stocked into a 1 km section of the Westbrook, a Connecticut River tributary, in

spring 1996, 1997, and 1998. All fish in the section were collected by electroshocking and night-seining during the summer of their stocking year, measured for length and mass, and PIT-tagged. At monthly (summer) or tri-monthly (winter) intervals thereafter, all fish were recaptured and measured for length and mass. A smolt trap was used to collect fish leaving the section each spring. Additional information on the study is provided by Letcher et al. (this volume).

We analyzed selection on body length and mass over three-month intervals, including two winters and two summers. For each fish captured at the start of each interval, we determined whether it survived to the end of the interval (captured in the ending sample, or any sample thereafter) or died before the end of the interval (not captured in the ending sample, or thereafter). Fish that matured as parr were excluded from analyses.

Body length and mass (cube-root) were standardized (mean = 0 and SD = 1), and relative fitness was calculated by dividing each individual's absolute fitness (survived = 0, died = 1) by average absolute fitness during an interval. Selection was quantified using Lande and Arnold's (1983) linear regression methods and visualized using Schluter's (1988) cubic spline analysis.

Linear selection differentials represent combined effects of direct and indirect (i.e., total) selection acting to increase (when positive) or decrease (when negative) mean trait value. Linear differentials can be interpreted as the change in mean trait value owing to selection. Non-linear (*quadratic*) selection *differentials* represent total selection acting to increase (when positive) or decrease (when negative) trait variance. *Linear selection gradients* represent direct effects of selection acting to increase (when positive) or decrease (when negative) mean trait value. Gradients can be interpreted as the change in relative fitness with a given change in the trait, holding effects of other traits constant. Non-linear (*quadratic*) selection *gradients* represent direct effects of selection acting to increase (when positive) or decrease (when negative) trait variance. Brodie et al. (1995) further describes these measures of selection.

The strength and direction of selection on body length and mass varied between seasons (summer, winter), among cohorts (1996, 1997, 1998), and between age classes (1+, 2+). The only consistent pattern for total effects of selection (i.e., differentials and splines) was that larger individuals did not survive better than smaller individuals during the winter (Table 1; Fig. 1). Some interesting patterns were evident when considering direct effects of selection (i.e.,

gradients, which hold effects of the other trait constant). In most cases, gradients for length and mass were of opposite sign (Table 1), indicating that either longer/lighter or shorter/heavier individuals survived at higher rates. The most striking pattern was that length gradients were positive and mass gradients negative for all four samples of 1+ fish (highly significant during summers). This result indicates that longer/lighter fish survived at higher rates during their second year of life. Stabilizing selection acted on length and mass of 1+ fish during summers (highly significant in 1996). When differentials and gradients were non-significant, it was because of small effect sizes rather than small sample sizes (Table 1).

In the future, we intend to add data for additional stocking years, examine selection on growth rate, and evaluate likely evolutionary responses in the population. Assuming a heritability of juvenile body length of 0.11 and mass of 0.13 with a genetic correlation of 0.98 (Gjedrem, 1983; Jónasson, 1993), and considering only selection during summers (Table 1), evolutionary responses predicted by equation 5.14 in Roff (1997) are slight per-generation decreases in length (0.008 SD) and mass (0.010 SD). Quantifying natural selection and the genetic basis for phenotypic traits allows prediction of evolutionary responses during restoration. This predictive ability may facilitate consideration of alternative restoration strategies, and suggest time frames needed for recovery.

References

- Brodie III, E.D., A.J. Moore, and F.J. Janzen. 1995. Visualizing and quantifying natural selection. *Trends Ecol. Evol.* 10:313-318.
- Gjedrem, T. 1983. Genetic variation in quantitative traits and selective breeding in fish and shellfish. *Aquaculture* 33:51-72.
- Jónasson, J. 1993. Selection experiments in salmon ranching. I. Genetic and environmental sources of variation in survival and growth in freshwater. *Aquaculture* 109:225-236.
- Lande, R., and S.J. Arnold. 1983. The measurement of selection on correlated characters. *Evolution* 37:1210-1226.
- Roff, D.A. 1997. *Evolutionary quantitative genetics*. Chapman & Hall, New York.

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

Acknowledgements

We thank personnel of the Conte Anadromous Fish Research Center (USGS-BRD) for their help in the field, especially Gabe Gries and Todd Dubreuil. The USDA Northeast Forest Experimental Station contributed partial funding. Travel support was provided by US Department of Agriculture and US Geological Survey.

Table 1. Results of tests for selection on body length and mass, including total selection (differentials) and direct selection (gradients), as well as directional selection (linear) and stabilizing or disruptive selection (quadratic). Positive linear differentials and gradients indicate directional selection for larger trait values. Negative quadratic differentials and gradients indicate stabilizing selection (a reduction of trait variance). ^a $P < 0.10$, ^b $P < 0.05$, ^c $P < 0.01$, ^d $P < 0.001$

Stock year	Winter				Summer	
	1997	1998	1996	1997	1996	1997
Fish age	1+	1+	2+	2+	1+	1+
Start day	Dec 10	Dec 01	Dec 10	Dec 01	Jun 17	Jun 22
End day	Mar 17	Mar 16	Mar 17	Mar 16	Sept 23	Sept 10
Starting N	231	748	121	96	139	78
Survival (%)	67.1	61.0	38.8	57.3	64.7	70.5
	<u>Linear selection differentials</u>					
Length	-0.106	-0.010	-0.070	-0.109	-0.023	0.082
Mass	0.046	-0.015	-0.081	-0.109	-0.066	0.025
	<u>Linear selection gradients</u>					
Length	0.331	0.141	-0.931 ^a	0.023	0.835 ^d	1.627 ^d
Mass	-0.327	-0.153	0.907 ^a	-0.133	-0.881 ^d	-1.574 ^d
	<u>Quadratic selection differentials</u>					
Length	-0.015	-0.041	-0.116	-0.177	-0.044	-0.035
Mass	-0.037	-0.043	-0.101	-0.216	-0.013	-0.050
	<u>Quadratic selection gradients</u>					
Length	-0.908	0.348	-0.166	-0.854	-4.894 ^c	-1.576
Mass	-1.760	0.266	0.054 ^b	-2.154	-4.110 ^b	-1.776

Figure 1. Non-parametric cubic splines illustrating the form of total selection acting on body length in juvenile Atlantic salmon.



