

Benjamin H. Letcher

Life history dependent morphometric variation in stream-dwelling Atlantic salmon

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Abstract The time course of morphometric variation among life histories for stream-dwelling Atlantic salmon (*Salmo salar* L.) parr (age-0+ to age-2+) was analyzed. Possible life histories were combinations of parr maturity status in the autumn (mature or immature) and age at outmigration (smolt at age-2+ or later age). Actual life histories expressed with enough fish for analysis in the 1997 cohort were immature/age-2+ smolt, mature/age-2+ smolt, and mature/age-2+ non-smolt. Tagged fish were assigned to one of the three life histories and digital pictures from the field were analyzed using landmark-based geometric morphometrics. Results indicated that successful grouping of fish according to life history varied with fish age, but that fish could be grouped before the actual expression of the life histories. By March (age-1+), fish were successfully grouped using a descriptive discriminant function and successful assignment ranged from 84 to 97% for the remainder of stream residence. A jackknife of the discriminant function revealed an average life history prediction success of 67% from age-1+ summer to smolting. Low sample numbers for one of the life histories may have limited prediction success. A MANOVA on the shape descriptors (relative warps) also indicated significant differences in shape among life histories from age-1+ summer through to smolting. Across all samples, shape varied significantly with size. Within samples, shape did not vary significantly with size for samples from December (age-0+) to May (age-1+). During the age-1+ summer however, shape varied significantly with size, but the relationship between shape and size was not different among life histories. In the autumn (age-1+) and winter (age-2+), life history differences explained a significant portion of the change in shape with size. Life

history dependent morphometric variation may be useful to indicate the timing of early expressions of life history variation and as a tool to explore temporal and spatial variation in life history expression.

Keywords Geometric morphometrics · Mature parr · Shape · Smolts

Introduction

Expression of life histories of Atlantic salmon (*Salmo salar*) is quite variable during stream residence (Metcalf 1998). Depending primarily on growth opportunity, some fish will migrate from rearing streams (smolt) early and others will delay outmigration for a year or more. Also, faster growing males tend to mature as parr in streams before migrating to the sea (Whalen and Parrish 1999; Letcher and Gries 2003). The relationship between the two life histories is not simple, however, because there appears to be an interaction between maturity and smolt age (Thorpe 1986; Berglund 1995). Male parr that mature in the autumn may be less likely to smolt the following spring (Myers 1984; Whalen and Parrish 1999; Letcher et al. 2002), and high maturation rates may reduce overall smolt production (Myers 1984; Metcalfe 1998; Whalen et al. 2000).

The interaction between smolt age and parr maturation also results in a complex set of size trajectories in the field for fish with different combinations of life histories (Utrilla and Lobon-Cervia 1999; Letcher and Gries 2003). Prior to maturation in the autumn, the largest fish are those that will mature and will also smolt the following spring. On average, fish that mature but will not smolt the following spring are smaller and similar in size to immature fish that will smolt in the spring. Following maturation, sizes of the following year's smolts, whether they were mature or immature, are similar and much larger than fish that will delay smolting. At this time, there is often a clear bimodality to sizes of early versus late smolts (Thorpe et al. 1982; Heggenes and Metcalfe 1991; Nicieza

B. H. Letcher (✉)
S.O. Conte Anadromous Fish Research Center, US Geological
Survey/Leetown Science Center,
P.O. Box 796, One Migratory Way
Turners Falls, MA, 01376, USA
e-mail: bletcher@forwild.umass.edu
Tel.: +1-413-8633803
Fax: +1-413-8639810

et al. 1991, 1994), but it is often not clear whether fish in the upper or lower mode had been mature. While there are differences in size among life histories on average, size differences are not generally diagnostic for life history variation.

For organisms with dramatic ontogenetic habitat shifts, such as salmon, it is important to estimate stage-specific production to understand population dynamics. Numbers and sizes (Eriksson et al. 1987; Lundqvist et al. 1994) of Atlantic salmon smolts can play a large role in numbers of adults returning to spawn and may therefore be a critical stage in population dynamics. Smolt production has been estimated both directly (with traps) and indirectly (based on pre-smolt abundances). Direct methods are very time-intensive and are usually limited to a few streams in a basin. Indirect estimates suffer from mortality assumptions from the pre-smolt sample to the time of smolting and from assumptions about which fish will smolt. Individual smolting probability is difficult to predict before smolting, and becomes more complex when life histories interact to influence probability of smolting. Male parr maturity has been estimated to reduce smolt production directly via lower survival of mature parr (Myers 1984) or indirectly via a reduced probability of smolting for previously mature parr (Whalen et al. 2000; Letcher et al. 2002). Spatial and temporal variation in growth opportunity can also influence the expression of life histories (Metcalf and Thorpe 1990), making it difficult to predict smolt production for a particular stream even if the interactive effects of life histories on smolt production are understood.

It would be very useful to be able to assay fish in a stream and determine life histories directly. Combined with survival estimates, these data could provide a direct estimate of future smolt production because the proportion of smolts would be known for that stream in that year. Such data would also be useful for understanding mechanisms generating expression of life histories across streams and years because variation in biotic and abiotic factors and resulting growth variation could potentially be related to life history variation. There is currently no technique available to assign fish to one of the four possible combinations of life histories resulting from early/late smolting and mature/immature parr. I present a geometric morphometric approach to assessing life history

variation. Over the last decade, geometric morphometrics (Rohlf and Marcus 1993) has been replacing traditional morphometric approaches (Monteiro et al. 2002) because it (1) provides a clear mathematical definition of shape that is independent of size (Dryden and Mardia 1998), (2) can capture a description of shape in all directions not just those between pairs of landmarks, (3) describes shape with relatively low dimensionality and high power (Rohlf 2000a, 2000b), and (4) tends to be more effective in discriminating groups based on shape variation (Adams and Funk 1997; Monteiro-Filho et al. 2002).

Traditional morphometric variation has been used with Atlantic salmon for stock discrimination (MacCrimmon and Claytor 1986), tributary-specific population discrimination (Riddell et al. 1981), resident versus anadromous population discrimination (Riley et al. 1989), and discrimination of early maturity of aquaculture adults (Kadri et al. 1997) and of early versus late smolts (Nicieza 1995). Within two populations, Nicieza (1995) found no overlap in discriminant canonical score values between early and late smolts near the time of smolting. This is not necessarily surprising because morphometric differences between early and late smolts are visually apparent near the time of smolting. For interpreting mechanisms responsible for life history variation and for predicting smolt production, it would be useful to know when life history dependent morphometric variation is apparent during the freshwater life of parr. Using individually tagged, free-ranging fish with known life histories, I assessed the time course of assignment to correct life histories using geometric morphometrics.

Materials and methods

Study animals

Details of the study stream and fish capture are described briefly here; details can be found in Letcher et al. (2002) and Letcher and Gries (2003). The study stream (West Brook) is a small (~5 m wide), 3rd order stream in Massachusetts, USA (42°25'N, 72°39'W). Each spring, unfed Atlantic salmon fry (~26 mm) are stocked into the stream at a density of 50 m⁻². Other fish species present include naturally reproducing populations of brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*). Atlantic salmon from the 1997 stocking year (SY) were sampled during 10 collections

Table 1. Numbers of fish caught from the four life histories for each sample

Sample no.	Fish age	Median date	Average fork length (mm±S.D.)	Smolt		Non-smolt		Total
				Mature	Immature	Mature	Immature	
8	0+	16 December 1997	71.8±6.9	11	31	20	1	63
9	1+	24 March 1998	75.0±6.5	9	22	14	1	46
11	1+	26 May 1998	109.4±9.6	14	34	16	1	65
13	1+	17 July 1998	116.5±7.7	9	17	11	1	38
16	1+	27 October 1998	121.8±9.0	12	24	16	1	53
17	1+	6 December 1998	122.1±9.8	12	28	23	2	65
18	2+	28 March 1999	128.8±12.3	7	26	22	2	57
Smolt trap	2+	1 May 1999	152.0±9.6	13	30	0	0	43

through the study reach (1 km long), from age-0+ in December to age-2+ in early summer. Results from seven of these samples are reported (Table 1) including data from fish captured in a smolt trap designed to catch outmigrating smolts. Data from samples reported here are from a long-term study and were not renumbered (i.e., starting from one) to allow comparison with other reports from the long-term study. Results from all 10 samples were not included here for brevity (the three intervening samples showed similar results).

To allow identification of individual fish, all fish were tagged with PIT tags (11 mm) on first capture. Upon each capture, fish were measured for length (± 1 mm) and wet mass (± 0.1 mg) after anesthetizing in MS-222 ($100 \text{ mg} \cdot \text{l}^{-1}$). A digital picture of the left side of each fish was also taken. The camera was placed a fixed distance from the fish and fish were aligned on a straight line. Fish were returned live to the location of capture in the stream following workup.

Morphometric analyses using pictures from the subset of captured fish that survived to express one of three life histories (Table 1) were performed. Because fish were individually tagged and eventual life histories could be identified for each fish, pictures of fish before, during, and after the expression of life history characteristics could be examined. The possible life histories result from the combination of variation in male parr maturity and smolt age. In the autumn (age-1+) a portion of the males mature as parr and fish either will or will not smolt at age-2+. Very few fish from the 1997 stock year were immature/age-2+ non-smolts (Table 1); this life history was not included in the present analysis.

Morphometric and statistical analyses

I used 12 landmarks to characterize shape variation (Fig. 1). All landmarks except no. 12 (center of the eye) were placed on the outline of the body, with pairs of points perpendicular to the horizontal plane of the body midline. A set of four landmarks defined the rostral (nos. 2 and 3) and caudal (nos. 4 and 5) edges of the eye and a set of six landmarks were placed at the rostral (nos. 6 and 7) caudal (nos. 10 and 11) and midpoint (nos. 8 and 9) of the length of the pectoral fin (Fig. 1). Landmarks were digitized directly from digital pictures taken in the field using the TPSDIG program (see Rohlf et al. 1996).

For each sample (Table 1), relative warp scores for all fish using the TPSRELW program (see Rohlf et al. 1996) were generated. Relative warp scores are a multivariate description of shape variation. Due to the nature of the field sampling, it was not possible to capture all individuals on all samples for a complete repeat measures design, nor was it possible to sample unique individuals across samples for complete independence among samples. Overall, 421 pictures were analyzed from 106 individuals which resulted in each individual being represented in an average of four out of eight samples. Thus, because individuals can reappear in multiple samples, comparisons among samples must be viewed with caution because samples were not independent.

To test for variation among life histories for each sample, I ran a MANOVA using the 20 relative warp scores [two dimensions: (12 landmarks - 2)] as the dependent variables and the three life histories as the independent variable. I then conducted a canonical variate analysis to examine group ordination along canonical roots for fish from each sample. I report the *P*-value for the discriminant function and the percentage of fish assigned to the correct life

history. To test whether the discriminant function could be useful for predicting life history of unknown fish, a cross-validation jackknife procedure was also run for each sample.

Because shape can change with size as fish grow, I conducted three analyses to evaluate the extent and nature of shape change among samples. First, I tested whether shape changed with size for fish from all samples by regressing landmark data on centroid size (the TPSREGR program). Centroid size is a measure of geometric size of each fish (Bookstein 1991). Second, I conducted a similar regression for fish from each sample separately. Third, I tested whether life history differences in shape persisted after accounting for size variation by running an ANCOVA with life history as the independent variable and centroid size as the covariate. I performed initial ANCOVAs for each sample to assess differences in slopes. If there were no differences in slopes among life histories, I then evaluated variation in intercepts. I used the TPSREGR program for this analysis. Variation in intercepts but not slopes indicates that shape varies consistently across size for fish with different life histories.

Results

Both the MANOVA (Table 2) and discriminant function (Table 3) indicated that future life histories could not be separated based on shape for age-0+ fish in December (sample 8). The first two canonical roots also demonstrated substantial overlap among life histories for fish from sample eight (data not shown). Three months later, in March (age-1+, sample 9), there was less overlap among life histories (Fig. 2), assignment success was higher (84%), the *P*-value of the discriminant function was less than 0.05 (Table 3), but the MANOVA did not uncover significant differences ($P > 0.05$) among life histories (Table 2). By sample 13 (age-1+, July), there was little overlap among life histories, assignment success was 97% and *P*-values for both the MANOVA and discriminant function were less than 0.05. This pattern continued through age-2+ March, with a range of assignment success of 84%–92% (Table 3).

The jackknife assignment rates (Table 3) indicated that the discriminant functions could be used to predict life histories of fish with unknown life histories about two-thirds of the time. This test is sensitive to the sample size of the group with the fewest individuals. In most cases, the number of mature/age-2+ smolts was close to ten (Table 1), which may have limited classification success

Table 2. MANOVA results for each sample with the 20 principle relative warps as the dependent variable and life history as the independent variable

Sample no.	<i>F</i>	Error <i>df</i>	<i>P</i> value
8	0.80	80	0.77
9	1.32	46	0.18
11	0.58	84	0.97
13	1.98	30	0.027
16	3.20	60	0.000023
17	2.35	82	0.00056
18	1.81	66	0.016
19	0.84	22	0.65

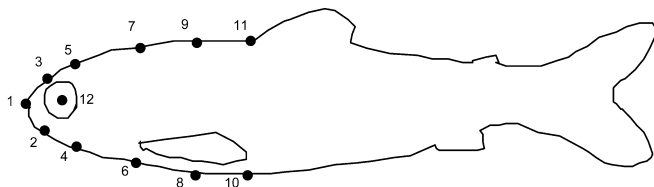


Fig. 1 Landmarks used to analyze shape variation in Atlantic salmon parr

Table 3. Percentage of fish assigned to correct life history, the *P* value, and the jackknife assignment success from the discriminant function from each sample

Sample no.	Discriminant function classification		Jackknife classification
	Percentage correctly assigned	<i>P</i> value	Percentage correctly assigned
8	59.0	0.45	53.2
9	84.4	0.023	55.6
11	64.1	0.87	54.7
13	97.3	0.005	62.2
16	92.3	<0.0001	67.3
17	84.1	0.0002	68.2
18	89.1	0.0003	69.1
19	82.6	0.026	62.8

of the jackknife compared to assignment success of the discriminant function.

There were few incorrect assignments for immature/age-2+ smolts; most of the incorrect assignments were due

to misclassification of mature fish into either the smolt or non-smolt categories (Fig. 3). Immature fish also tended to occupy distinct areas on the canonical root plots and there was more overlap between mature/age-2+ smolts and mature/age-2+ non-smolts (Fig. 2). Further, means of canonical variables were significantly different ($P < 0.05$) for the immature to mature (smolt or non-smolt) comparisons, but rarely for the smolt to non-smolt comparison for mature fish.

While the immature fish tended to occupy a distinct and separate region of the canonical roots plot (Fig. 2), the locations of the mature smolts and non-smolts shifted in different directions at different times of the year. Early in the sampling series (sample 9), root one values of the mature/age-2+ non-smolts were intermediate between the mature/age-2+ smolts and the immature/age-2+ non-smolts. By sample 13 (July), the position of the mature/age-2+ non-smolts had shifted away from the immature fish towards the mature/age-2+ smolts. By sample 18 (March, age-2+), the position of the mature/age-2+ smolts had shifted away from the mature/age-2+ non-smolts towards the immature/age-2+ smolts (Fig. 2). Thus, during

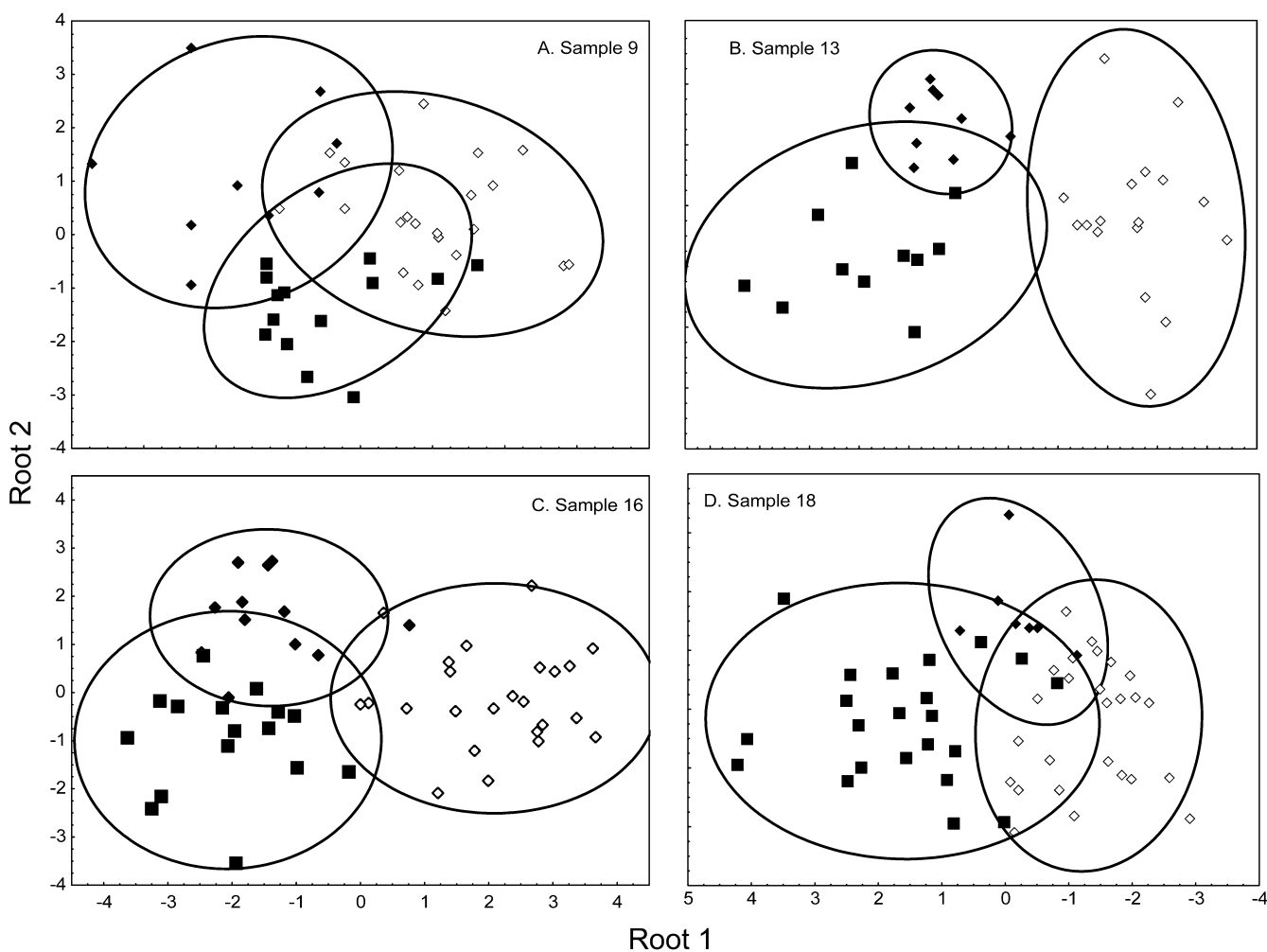


Fig. 2A–D Canonical roots from the discriminant function classified by known life histories (*open diamonds* immature/age-2+ smolt; *filled diamonds* mature/age-2+ smolt; *filled squares*

mature/age-2+ non-smolts) for four samples. Points are surrounded by 80% confidence interval ellipses to help show patterns

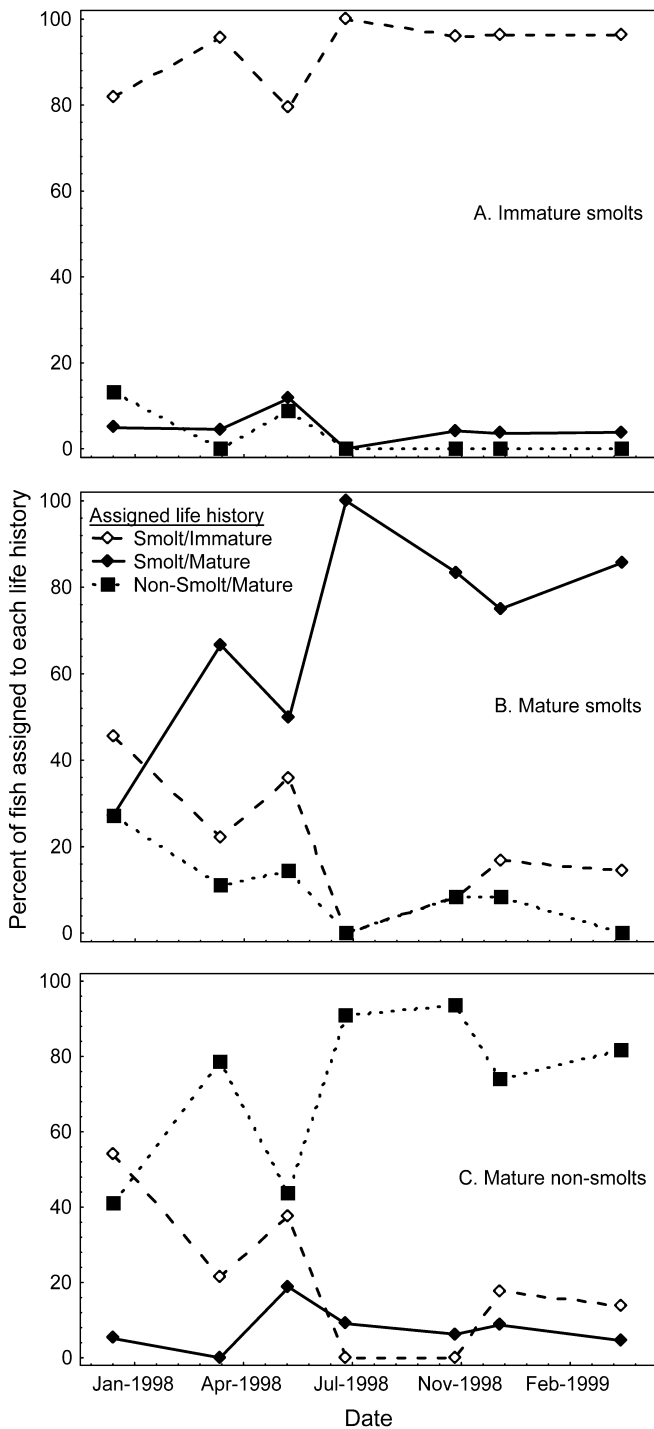


Fig. 3 Percentage of fish with known life histories (A immature smolts, B mature smolts, C mature non-smolts) assigned to one of the three possible life histories using the discriminant function. Actual life history is indicated on each panel

the time of milt expression (samples 13 and 16), canonical root values of mature fish were similar to each other and a few months before smolting the values of the age-2+ smolts were becoming more similar to each other.

Previous maturity of smolts

Maturity assignment success (previously mature or previously immature) of age-2+ smolts was 82.6% (discriminant function: Wilks' $\lambda=0.54$, $F_{12,33}=2.36$, $P=0.026$), the jackknife classification was 63% correct (Table 3), and the MANOVA was insignificant ($P=0.65$, Table 2). Assignment success was higher for previously mature (90%) than for previously immature (68.8%) fish, possibly due to the larger samples size of immature fish. The average (\pm S.D.) value of canonical root one was -0.66 ± 1.0 for previously immature parr and 1.24 ± 0.98 for previously mature parr (Fig. 4).

Shape variation with size

Combining all samples and life histories, shape varied significantly with size (Goodall F -test: $F=46.33$, $df=20,7600$, $P<0.00001$). Larger (generally older) fish tended to be deeper bodied with the eye positioned relatively closer to the tip of the snout compared to smaller fish. Among samples, there was no significant variation in shape with size for the first three samples (Table 4). For samples 13 and 16, shape varied as a function of size but life history did not explain a significant amount of the variance (ANCOVA results, Table 4). In samples 17 and 18, there was no variation among life histories in the slope of the relation between shape and size, but intercepts did vary among life histories (Table 4). This suggests a common shape relation across sizes for different life histories, but differences in shape among life histories for a particular size. Overall, shape varied significantly with size for samples 13 to 18 with size alone explaining shape variation in the earlier samples and size and life history together explaining variation in the later samples.

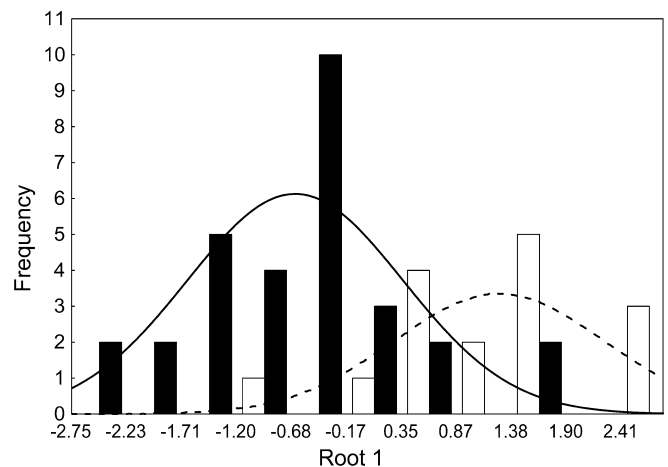


Fig. 4 Canonical root from the discriminant function for the smolt sample classified by previously mature (white columns) and immature (black columns) parr

Table 4. Variation in shape as a function of size (centroid) among samples and results from ANCOVA testing for life history dependent shape variation with centroid size as the covariate

Size-dependent shape variation					ANCOVA results									
Sample no.	<i>F</i>	<i>df</i> ₁	<i>df</i> ₂	<i>P</i>	Different slopes?					Different intercepts?				
					Wilks'	Lambda	<i>df</i> ₁	<i>df</i> ₂	<i>P</i>	Wilks'	Lambda	<i>df</i> ₁	<i>df</i> ₂	<i>P</i>
8	0.5162	20	1,160	0.96	0.41		40	70	0.53	0.55		40	74	0.93
9	0.5349	20	860	0.95	0.11		40	40	0.01	0.22		40	44	0.23
11	0.7944	20	1,240	0.72	0.46		40	78	0.60	0.61		40	82	0.98
13	2.4318	20	720	0.00050	0.18		40	26	0.64	0.10		40	30	0.074
16	3.5328	20	1,020	0.00000	0.32		40	56	0.41	0.39		40	60	0.64
17	1.1389	20	1,260	0.30	0.45		40	80	0.51	0.24		40	84	0.0017
18	0.7471	20	1,100	0.78	0.40		40	64	0.57	0.23		40	68	0.013

Discussion

Overall, shape changed significantly as fish grew, but a large part of the variation in shape was related to life history variation. Early in stream life, when the fish were approximately 70 mm (December), there were no differences in shape among fish that would express life history differences in the future. In their second summer, however, the discriminant function, the MANOVA, and the analysis of shape variation as a function of size indicated that shape varied among life histories. There are two areas of investigation in which the this life history dependent morphometric variation may be particularly useful: (1) as an indication of the timing of early expression of life histories, and (2) as a tool for exploring variation in spatial and temporal expression of life histories.

In Atlantic salmon, parr maturation and smolting occur during fairly discrete times of the year, but the processes leading to their expression are initiated long before their actual expression (Metcalf 1998). Smolting may be triggered many months before migration (Kristinsson et al. 1985; Metcalf 1986); although they are not diagnostic for life history variation, average mass differences in the field between future age-2+ smolts and non-smolts were evident as early as age-0+ December (Letcher and Gries 2003) and it is even possible that inherent metabolic differences among individuals at hatching could influence age of smolting (Metcalf and Thorpe 1992; McCarthy 2000). Within a smolt age, there is also a correlation between parr maturation and early size; fish that are relatively large up to a year prior to maturation tend to be the fish that mature (Rowe and Thorpe 1990; Berglund 1992; Simpson 1992). For the same cohort of fish examined in the present paper, Letcher and Gries (2003) found that differences in mass between future smolts and non-smolts were evident about 5 months earlier (age-0+ December) than differences between future mature and immature fish (age-1+ June). Although there was reasonable discrimination among life histories based on shape in the current analysis in March (age-1+), there were not consistent shape differences among life histories until July (age-1+). This time of year corresponds with the onset of the timing of significant mass differences between maturing and immature fish, and corresponds with the shift in canonical root values of mature/age-2+ non-smolts

towards those of mature/age-2+ smolts. Thus, it appears that the early size (mass) differences in the field associated with smolt age alone do not correspond with shape differences, but that the later mass differences associated with both smolt age and parr maturation (or at least their timing) are related to variation in shape. This notion is reinforced by the observation that there was no shape variation across sizes within early samples but there was significant variation in shape with size or life history in later samples.

The morphometric variation among life histories reported here was assessed using a conservative set of landmarks. Because photographs were taken in the field and the fish were not always aligned perfectly straight, early analysis indicated that results could be dominated by slight body bends and that the bending obscured any subtle shape variation due to life histories. This led to use of a limited set of landmarks on the rostral half of the body and may have resulted in a greater likelihood of uncovering shape variation resulting from parr maturation compared to smolt age. Parr maturation typically results in a deepening of the body near the pectoral fins, while smolting is accompanied by a general lengthening of the body and a stretching and narrowing of the caudal peduncle. Because most of the landmarks used here were associated with the outline of the fish, it may be useful in the future to work with landmarks in combination with outlines (Bookstein 1997; Jensen et al. 2002). An enhanced set of landmarks may improve assignment success overall and for smolt/non-smolt discrimination in particular.

Estimating smolt production of even small streams is notoriously difficult. Direct methods, using traps or weirs, are laborious, expensive, and usually limited to only a few streams. Weirs also have a tendency to wash out in high flow, often when a large portion of the smolts is migrating out of the stream. Direct smolt estimates have the distinct advantage of obtaining an actual count, after applying capture efficiency corrections, of the captured fish. Indirect methods of estimating smolt production rely on an estimate of overwinter mortality to scale autumn abundance estimates and do not usually include parr maturity as a factor that could influence smolt production. There are many assumptions included in these indirect estimates, but smolt production for a fairly large number

of streams can be estimated in a single year. The morphometric approach described here could be used as a way to add a life history component to indirect smolt estimates that rely on autumn parr densities. Additionally, in streams that could be sampled 1–3 months prior to smolt migration (e.g., southern extent of Atlantic salmon's range), the morphometric approach could provide an estimate of the number of fish that would smolt without the uncertainty of overwinter survival estimates. The results presented here, however, only indicate that there are detectable life history differences in stream-dwelling Atlantic salmon using geometric morphometrics. To actually use the approach across multiple streams and even across years in a single stream, further work will be required to increase predictive ability and to validate the transportability of discriminant functions describing life history variation.

In addition to the possibility of using morphometric variation to predict the proportion of a population that will smolt in a single year, it may also be possible to use the approach to look either forward or backward in time from some stage of the fish's life in a stream in an attempt to improve understanding of factors responsible for determining life histories. This kind of information can be obtained from streams that have extensive tagging efforts and where individuals have known life histories [such as the West Brook, see also Jones et al. (2002)], but because of the time and expense involved very few streams can be monitored extensively. In the West Brook, the life histories expressed have varied among cohorts (Letcher and Gries 2003). For the 1997 cohort examined in this paper, there were very few immature/age-2+ non-smolts, but in a subsequent cohort (1999) there were very few mature/age-2+ smolts. The distribution of life histories for the intervening cohort (1998) is unknown due to a smolt trap failure, but it may be possible to use the morphometric approach to assign individuals from particular samples to future or past life histories and thereby recreate the distribution of life histories. This information among years, combined with other biotic and abiotic data, could lead to correlations between environmental factors and the expression of life histories. Future work will determine if the discriminant functions describing life history variation are transportable across streams and whether it will be possible to assess the relationship between environmental variables and the expression of life histories on a wide spatial scale as well.

It is clear that we can use morphometric variation to discriminate among life histories, but it is less clear why there may be morphometric variation among life histories. Is there an adaptive advantage to morphometric variation among life histories or is the morphometric variation a consequence of the life history? A clear consequence of parr maturation is the enlargement of testes [gonadosomatic indices average 8% (Fleming 1998)], which could result in shape variation. A large part of the shape difference for mature parr was a body deepening in the vicinity of the testes. Mature parr body deepening could also be adaptive if it led to an advantage in fertilization

success. In masu salmon (*Oncorhynchus masou*), there was positive selection for body size (mass) but not for body height in mature parr competing for fertilizations with migratory males (Koseki and Maekawa 2000). In Atlantic salmon, the effect of body size on fertilization success is mixed and the effect of body shape is unknown. Thomaz et al. (1997) found a positive association between parr body size and fertilization success, while Jones and Hutchings (2001) and Garant et al. (2001) found no relationship between size and fertilization success. In addition to fertilization success, variation in body size/shape could also have adaptive significance if it influenced survival before or after mating. Using data from the same cohort of fish as presented here, Hendry et al. (2003) determined that there was no strong, consistent directional selection for body size. The effects of body shape on survival are unknown, but in some streams it also appears that there may be no difference in survival between mature and immature fish (Letcher et al. 2002) suggesting that shape variation among life histories may not be under strong selection. This suggestion does not exclude the possibility that subtle shape variation within life histories could influence survival. It would be very interesting to conduct a formal selection analysis on shape as described by variation in relative warps.

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