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The morphological plastic response to water current velocity varies with age and sexual state in juvenile Atlantic salmon, *Salmo salar*

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SUMMARY

1. Salmonids, like many other fish species, exhibit morphological plasticity to variations in water current velocity. However, little is known about how this response varies with age and alternative sexual tactics that usually coexist in the same area. We therefore sampled immature 1- and 2-year-old and sexually mature *Salmo salar* parr to determine how the morphological response to slow and rapid water currents varies across these groups.
2. Both 1- and 2-year-old immature parr in rapid habitats can be distinguished from individuals in slow habitats using a combination of fin measurements. In contrast, body shape measurements were useful only to distinguish 2-year-old individuals in the different habitat types. We also showed that mature parr are notably robust, irrespective of habitat type. For these individuals, only their body length differed between slow and rapid water currents, being bigger in slow water currents.
3. Our results imply that fins are the first structures to respond to water current velocity, followed by changes in body shape as individuals grow bigger. The robust phenotype observed for mature parr is likely to pose extra limitations on movement due to an increase in drag forces, thus contributing to their smaller size in rapid water currents.

Keywords: drag, mature parr, phenotypic plasticity, shape, swimming

Introduction

Continuous exposure to the physical and biotic properties of an individual's habitat usually induces a phenotypic response in that individual. Such responses, which arise through phenotypic plasticity, are considered adaptive if they increase the likelihood of survival or the efficiency with which available resources are exploited (Stearns, 1989; Day & McPhail, 1996). Changes in behaviour and physiology are the most conspicuous responses to variation in environmental conditions (West-Eberhard, 2003 p. 180). However, external morphological changes are also widely documented, usually in feeding structures such as jaws and beaks, and are correlated with the level of mechanical stress needed to exploit a particular resource (Grant *et al.*, 1976; Wimberger, 1991; Day & McPhail, 1996; Lecomte & Dodson, 2005).

Variation in water current velocity induces phenotypic changes in many fish species (Weihs, 1989; Sagnes, Champagne & Morel, 2000; Svanback & Eklov, 2003; Ohlberger, Staaks & Holker, 2006). Specifically, water current velocity has been found to affect intrinsic physiological processes such as metabolic activity (Boily & Magnan, 2002), and also influence body size and shape. This is because water currents affect (i) the movement of fish through passive displacement (Videler, 1993) and (ii) the prey encounter rate (Wankowski & Thorpe, 1979; Fausch, 1984; Grant &

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Noakes, 1987; Hill & Grossman, 1993; Nislow, Folt & Seandel, 1998).

The interaction between water and an individual's phenotype determines the extent to which water influences locomotion. An increase in water current velocity increases drag forces and consequently the energetic demands to swim against the direction of water flow (Blake, 1983; Videler, 1993). Drag is overcome by thrust, which is produced by the lateral undulations of the posterior end of the body. During the generation of thrust, the caudal peduncle and the caudal fin act as the main propeller while the other fins help to control propulsion and stabilize the body (Drucker & Lauder, 2002; Webb, 1988; Weihs, 1989).

Although drag can be reduced by avoiding rapid flowing water, there is a strong positive linear relationship between current velocity and food abundance (Nislow *et al.*, 1998). Thus, phenotypic strategies that minimize swimming costs in rapid currents should increase the total energetic gains that can be obtained in these energetically rich habitats. In general, such strategies have been found to include changes in behaviour (Godin & Rangeley, 1989; Enders *et al.*, 2005) and the development of higher propulsion capacities or other modifications in body shape towards a more hydrodynamic form (Pettersson & Hedenstrom, 2000).

Many north Atlantic freshwater river systems harbour immature and mature juvenile Atlantic salmon (*Salmo salar* L.), generally referred to as parr (although large variation exists for age-at-maturity across the demography of this species; see Myers, Hutchings & Gibson, 1986; Metcalfe & Thorpe, 1990; Letcher & Gries, 2003). Sexually mature male parr, while still juvenile, invest heavily in gonad development and spermatogenesis to participate in spawning in late autumn and early winter. The hyperextention of the ventral cavity, due to the disproportionate enlargement of the testes, gives rise to the common observation that their body shape is prominently robust. In addition, the high metabolic expenditure required in this developmental trajectory results in low growth efficiencies (i.e. half of that of immature fish) (Tucker & Rasmussen, 1999; Jonsson & Jonsson, 2003), so that by the end of autumn mature parr are the same size or even smaller than their immature counterparts (Saunders, Henderson & Glebe, 1982).

Many variables influence the presence of juvenile salmon in an area (Armstrong *et al.*, 2003; Hedger *et al.*, 2005). Parr can be found utilizing habitats that range in mean water column velocities from 0 to 80 cm s^{-1} (Hedger *et al.*, 2005). Although few studies have assessed the impact of water current velocity on the morphology of immature or mature juvenile Atlantic salmon (but see Pakkasmaa & Piironen, 2001), it has been well documented for other salmonids, particularly the genus *Salvelinus* (Mclaughlin & Grant, 1994; Boily & Magnan, 2002; Peres-Neto & Magnan, 2004). Most of these studies have found the expected association of robust body outlines with slow flowing water and streamlined shapes with rapid flowing water. However, these studies have usually focused on a single age cohort in the laboratory and have never considered whether the alternative reproductive phenotypes, coexisting with immature fish, may also exhibit a plastic response to this environmental variable. Thus, even though these studies highlight how morphology is shaped by water current velocity, they fail to document the potential variation in this response across different ages and sexual states.

We used traditional morphometrics to test the association between rapid and slow water currents and the morphology of 1- and 2-year-old (hereafter referred to as 1+ and 2+) immature and mature parr. Our first objective was to identify the phenotypic traits that differ between immature fish (1+ and 2+) sampled in the two habitats to determine if the plastic response is similar between the two age groups. For this, we tested the null hypotheses of (i) no shape differences between individuals sampled in slow and rapid water currents and (ii) no difference in the plastic response between the two age groups. Our second objective was to describe the shape of mature parr to identify the principal morphological traits that contribute to their robust appearance. As mentioned above, fish developing this sexual tactic require a high intake of food to meet their metabolic demands (Tucker & Rasmussen, 1999). Therefore, if the robust shape of these fish does not impose locomotory restrictions, we hypothesized that they should be found more often in rapid water currents, profiting from the higher levels of food provided by these habitats. However, if overcoming drag is more costly than the energetic gains obtained in these habitats, mature parr can be predicted to be found more often in slower water currents. Finally, mature parr may also exhibit plasticity for other traits which would permit exploitation of their habitat at lower costs. We thus tested the null hypothesis of no differences in morphology between rapid and slow current habitats.

Methods

Study site and sampling protocol

The Sainte-Marguerite River (48°20′N, 70°00′W), Quebec, Canada, has a mean annual water discharge of 58 $m^3 s^{-1}$ to the Saguenay Fjord. Its two major tributaries, the Principal and North Eastern branches, provide suitable habitats for Atlantic salmon within the first 82 and 32 km, respectively, with further upstream movement prevented by waterfalls. The salmon subpopulations of the North Eastern branch were colonized in the mid 1980s following the construction of a migratory ladder which provided spawners access to previously unoccupied habitats (Fig. 1). A stretch of 200–500 m along this river was sampled at seven stations (Fig. 1). These stations were high parr density regions previously identified using data gathered by the Centre Interuniversitaire de Recherche sur le Saumon Atlantique (CIRSA) over a 10-year period. In addition, along the Principal Branch, each station was located at a distinct sedimentary link (as described in Davey & Lapointe, 2007) so that similar physical features (i.e. substrate size) were shared by all stations. For the North Eastern Branch, only estimates of parr density were available for selecting sampling stations. However, we ensured that the substrate features were similar to those at the Principal Branch stations. Furthermore, Garant, Dodson & Bernatchez (2000) sampled recently emerged individuals to determine the magnitude of genetic structuring on spatial and temporal scales within and between these river branches. They reported a non-significant net *F*st value between branches of 0.0014 so that no genetic groupings by river branches could be formed. Although some significant variation in allele frequencies was explained by spatial variation among sampling sites (only 0.9%), no relationships between geographic and genetic distances were found in the 2 years sampled. In fact, they found that one of their sites in the North Eastern branch (NE 28, which in our study is the same geographic position as NE3) harboured salmon that were most similar in their genetic polymorphisms to salmon from any other site irrespective of river branch.

At each station, six 22 × 7 m quadrats were placed in areas characterized by either slow or rapid water currents, that is, three quadrats per habitat type. Although the habitat occupied by a juvenile salmon may include an area as large as 100 m^2 (Okland, Thorstad & Naesje, 2004), salmon usually spend 90% of their time in relatively small territories, depending on age and size. For example, a 10-cm-long fish will use an area of 1–2 m^2 (Grant & Kramer, 1990; Steingrimsson & Grant, 2003). Even so, fish are probably exposed to a variety of water current velocities. Thus, the quadrats we used, each with an

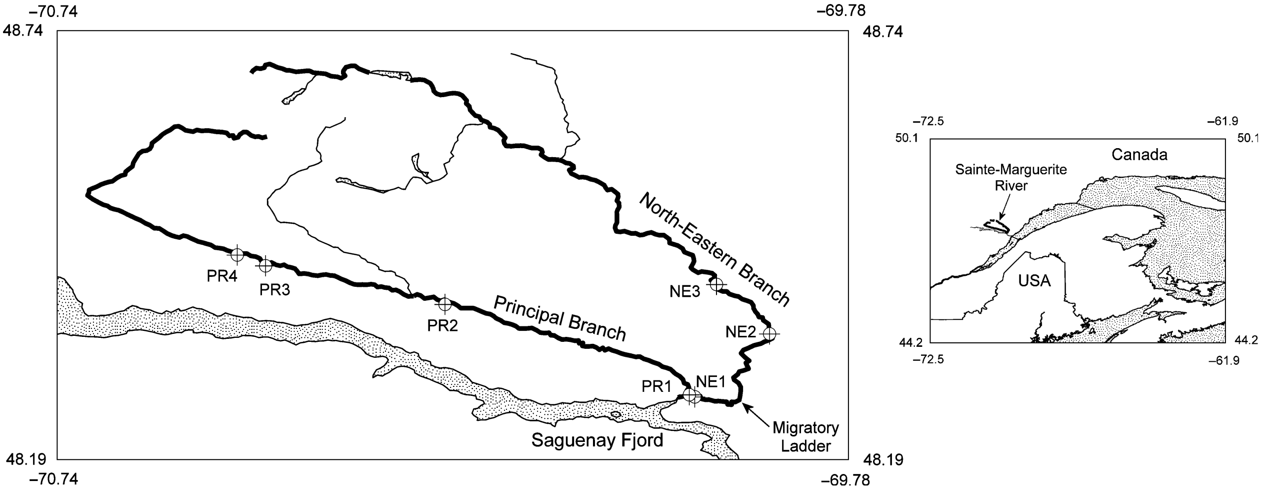

Fig. 1 The Sainte-Marguerite River. PR1-PR4: the four sampling sites located on the Principal branch. NE1-NE3: the three sampling sites located on the North-eastern branch.

area of 154 m^2, comprised an adequate sampling method because they most likely covered the range of water velocities to which the sampled fish were exposed. In addition, juvenile salmon disperse rapidly early in life and kin-related groups are fragmented shortly after emergence (Fontaine & Dodson, 1999). As such, we did not expect to sample within quadrats kin groups that could represent a potential genetic bias in our sampling method.

Once the six quadrats were in place, we left them undisturbed overnight. Early the next morning, we began two-pass electro-fishing with a team of three experienced fishermen. For the first pass, we started fishing at the downstream end of each quadrat, with a fourth person following the fishermen to measure water depth to the nearest cm. Once all six quadrats were sampled, we returned to the first quadrat to start the second pass. The electro-fishing was finished by early afternoon after which we measured the mean surface water velocity for each quadrat. Our objective was to differentiate between habitats which differed greatly in current velocity, rather than determine small variations in speed. Therefore, we used the float method to estimate current speed as it provided sufficient accuracy to categorize each habitat. Five wooden drifters were released at the upstream end of each quadrat, from which a mean velocity was estimated for each quadrat. All sites were sampled between 4 and 17 August 2007.

The captured fish were sacrificed and pinned next to a ruler on a white polystyrene board. A digital photograph of their right side was then taken. Calipers were used to measure body width to the nearest 0.1 mm. From each image, 22 other morphometric traits were measured, using the distances between specified reference points (Fig. 2). Each sample was then dissected to determine sex, and scales were removed from the body area between the pelvic fin and the posterior end of the head, above the ventral mid-line. The scales were immersed in a solution of 1% NaOH and left to soak overnight, and the following day 5–10 scales were selected and fixed on plastic slides to determine age according to Fukuwaka & Kaeriyama (1997).

Statistical analyses

The lack of genetic structuring between river branches and the non-significant relationship between genetic and geographic distances reported by Garant *et al.* (2000) justified the pooling of individuals sampled from both branches for the subsequent analyses. Overall, within the Principal and North Eastern branches we sampled 99 1+, 89 2+ and 32 mature parr, and 91 1+, 103 2+ and 26 mature parr respectively. Differences in abundance between rapid and slow-current habitats were determined using a chi-square test. Differences in size for 1+, 2+ and

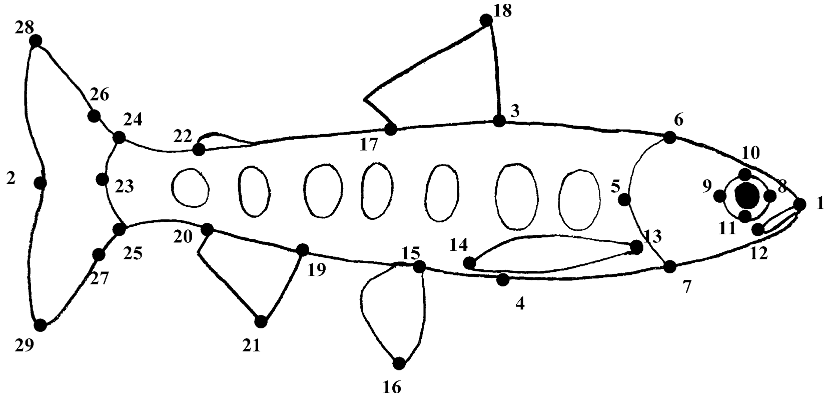

Fig. 2 Reference points used for morphometric measurements. 1–2, fork length; 3–4, body depth (B_D); 1–5, head length (H_L); 6–7, head depth (H_D); 8–9–10–11, mean orbital length (O_L); 1–12, mouth length (M_L); 1–13, predorsal length (PD_L); 1–15, prepelvic (PP_L) length; 13–14, pectoral length (PC_L); 15–16, pelvic length (PL_L); 20–23, caudal length (C_L); 24–25, caudal depth (C_D); 26–27, minimum caudal fin length ($MinC_{FL}$); 28–29, maximal caudal fin length ($MaxC_{FL}$); and width (W, not shown) . Distances between: 1–6, tip of snout and upper head (SH_L); 13–3, pectoral fin and dorsal fin origin (OPD_{FL}); 3–17, origin and insertion of dorsal fin (OID_{FL}); 3–18, origin and tip of dorsal fin (OTD_{FL}); 3–19, origin of dorsal and anal fins (ODA_{FL});19–20, origin and insertion of anal fin (OIA_{FL}); 19–21, origin and tip of anal fin (TA_{FL}); 17–19 insertions of dorsal and anal fins (DA_{FL}); 22–20, insertions of adipose and anal fins (AA_{FL}).

mature parr between habitat types were determined using *t*-tests. We used body length (from the most anterior point of the snout to the fork of the caudal fin) as a measure of overall size for each individual. Our data set was standardized and each morphological trait was size-adjusted to compensate for the dependence of allometric variation on fish size using the method proposed by Reist (1986) (see also the discussions by Fleming, Jonsson & Gross, 1994 and Peres-Neto & Magnan, 2004):

$$y_{ij} = \frac{\log x_{ij} - 1}{p \sum_i^p \log x_{ij}}$$

where, y is the size-corrected value, p is the number of morphological variables measured, and x is the value of the ith individual of the jth character.

Following size-correction, the differences in shape between mature and immature parr and between habitats for each group (i.e. 1+, 2+ and mature parr) were determined using multivariate analysis of variance (MANOVA). Our findings corroborated those of Rowe & Thorpe (1990), where no differences in length or shape were found between males and females of the 1+ and 2+ age classes. Sexes were thus also pooled for all subsequent tests. We used the canonical root of a DFA to identify the combination of variables that predicts both habitat membership (i.e. the variables that discriminate fish found in rapids from those found in slow-current habitats) and life history tactics (i.e. the variables that discriminate mature from immature parr). The relative importance of each variable for discriminating between individuals belonging to different groups was determined by correlating the canonical roots of the DFA with each variable (StatSoft, Inc., 2001). If the MANOVA was significant, we also used univariate comparisons to determine how traits differed in magnitude between our group comparisons after being adjusted for size.

Because the computation of a two-group DFA (i.e. rapid and slow currents) is identical to a MANOVA, the significance of both tests should be congruent. In this case, the significance values of the discriminant functions were obtained through a Monte-Carlo test based on 10^6 iterations (Chessel, Dufour & Thioulouse, 2004). Following this, a leave-one-out cross-validation procedure determined how useful the discriminant functions were to predict sexual tactic and habitat membership when fish were of unknown origin. We emphasize that all mature parr used in our analyses were aged 2+. Although we did find some aged 1+ and 3+, they were too poorly represented in our data set to permit meaningful conclusions. Finally, we used Fulton's condition factor (K = weight per length^3) and the fineness ratio (F = body depth per body length) (Sibbing & Nagelkerke, 2001) to consider the potential costs of drag for all fish. Fulton's condition factor has been traditionally used as an index of fish condition (Nash, Valencia & Geffen, 2006). A low fineness ratio is characteristic of a streamlined phenotype. Specific to mature parr, we used the fineness ratio to compare their robustness with that of immature fish. We also used the gonad somatic index (GSI = gonad weight per total body weight) to determine if investment in reproductive tissue was different between habitats. All differences for these ratios were calculated using *t*-tests and corrected with a Bonferroni procedure for multiple comparisons.

All statistical analyses were performed, using *R*, version 2.4.1 (R Development Core Team., 2006).

Results

Habitat features and abundance data

Current velocity in rapids was double that of slow-current habitats (rapid $\overline{u}$ = 100.5 ± 33 cm s^{-1}; slow $\overline{u}$ = 44.5 ± 22 cm s^{-1}). No significant difference in water depth existed between habitat types (rapid $\overline{u}$ = 47.3 ± 10.8 cm; slow $\overline{u}$ = 48.6 ± 10.9 cm for water depth) (*t*-test, $t_{207} = -0.8945$, $P = 0.3721$).

Overall, 1+ fish were found significantly more often in slow-current habitats (slow: 133 individuals; rapids: 57; $\chi^2_{(1)} = 30.4$, $P \leq 0.001$). However, no significant difference in abundance was found for immature 2+ (slow: 105 individuals; rapid: 88 individuals; $\chi^2_{(1)} = 1.49$; $P = 0.221$) or mature parr (slow: 36 individuals; rapid: 22 individuals; $\chi^2_{(1)} = 3.37$; $P = 0.066$), although there was a tendency to find the latter more frequently in slow habitats.

Immature fish

We found no differences in size (fork length) for all immature fish between the two habitats (*t*-test, $t_{96.4} = -0.46$, $P = 0.64$ for 1+; and *t*-test, $t_{187.2} = -1.24$, $P = 0.21$ for 2+). The MANOVA and DFA on the size-adjusted morphological variables showed that immature 2+ individuals have different shapes depending on the water current from which they were sampled (MANOVA: $F_{21,\ 171} = 3.02$, $P < 0.001$; Monte-Carlo test $P < 0.001$) (Fig. 3b). However, shape differences between immature 1+ from both habitat types were marginally significant at the conventional $\alpha = 0.05$ (MANOVA: $F_{21,168} = 1.61$; $P = 0.051$, Monte-Carlo test $P = 0.0498$) (Fig. 3a).

Further examination of the leave-one-out cross-validation classification suggests that we could use the linear combination of variables generated with the discriminant functions to correctly classify about 70% of 1+ and 2+ immature fish of unknown origin to their correct habitat type (Table 1). Overall, these results added support to the hypothesis that 1+ and 2+ immature fish from the two habitats have different shapes. Therefore, we then identified the specific variables that could be used to predict habitat membership for each age cohort (Table 2).

For 1+ individuals, we found that fin measurements were important to discriminate individuals occupying rapid water current habitats (Table 2). Particularly, after correcting for size, and using univariate comparisons, we found that the $\mathrm{MaxC_{FL}}$ was larger in individuals sampled in rapid habitats. However, no differences in other body shape variables, condition factor or the fineness ratio were found (Table 3) suggesting that body outlines are similar between habitat types for 1+ parr.

Table 1 Percentage of fish assigned to the correct habitat or sexual state*

	Classification (%)		
Group	Discriminant function	Leave-one-out cross-validation	*P*-value
1+	76	68	<0.001
2+	75	68	<0.001
Mature parr	79	60	0.1151
*Mature versus immature parr	86	83	<0.001

Similarly to 1+ fish, fin measurements were also important to discriminate 2+ individuals occupying

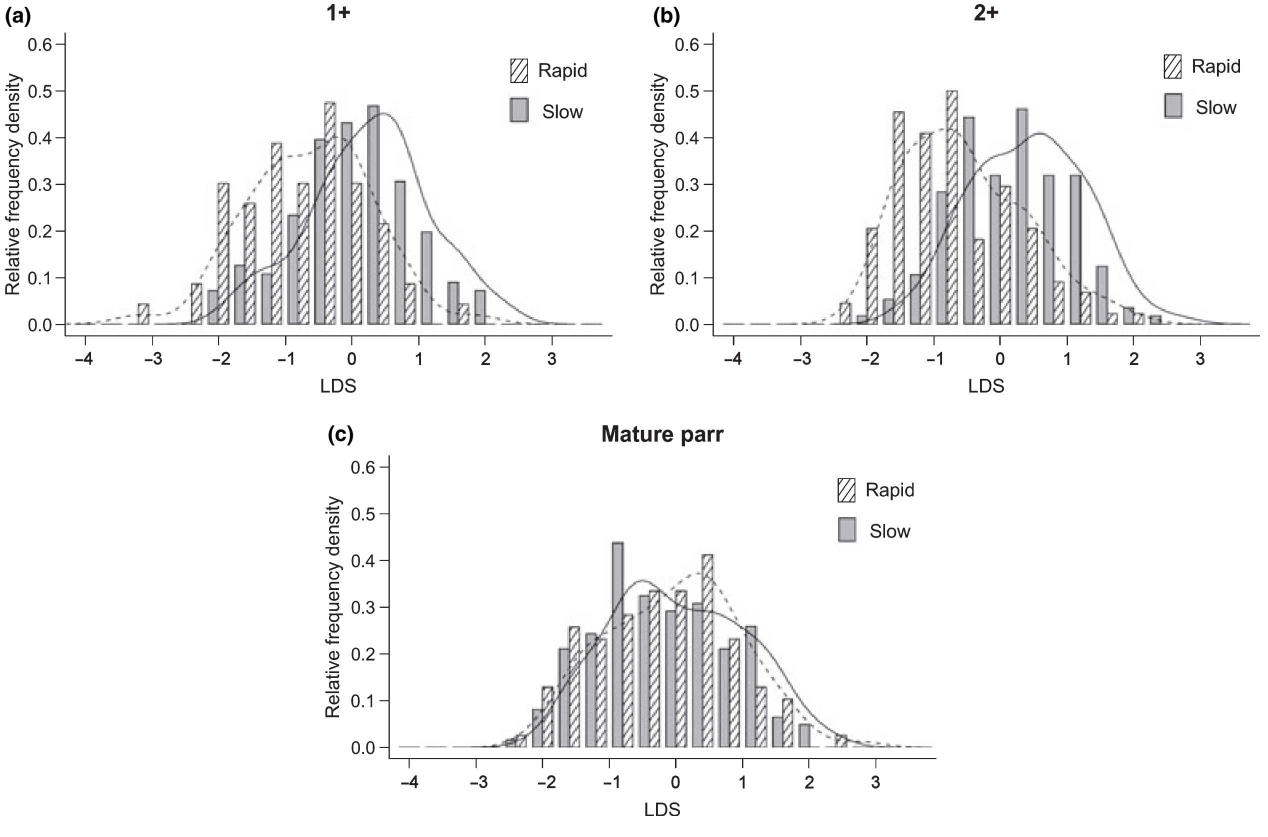

Fig. 3 Canonical scores from the discriminant function used to classify individuals from rapid and slow water current habitats for (a) 1+ (b) 2+ individuals and (c) mature parr. The broken line traces the relative frequency distribution of the canonical scores of individuals captured in rapid habitats whereas the continuous line traces scores in slow water habitats.

Table 2 Principal morphological traits that discriminate between individuals caught in rapid and slow water current velocities

	Rapid water currents				Slow water currents			
		LDA	Univariate *t*-test			LDA	Univariate *t*-test	
Age	Trait*	*r* (*P*-value)	$t_{(\mathrm{d.f.})}$	*P*-value	Trait*	*r* (*P*-value)	$t_{(\mathrm{d.f.})}$	*P*-value
1+	$\mathrm{MinC_{FL}}$	−0.61 (<0.001)	$3.6_{(109.3)}$	<0.001	$\mathrm{PP_L}$	0.46 (<0.001)	$-2.70_{(114.5)}$	<0.001
	$\mathrm{MaxC_{FL}}$	−0.49 (<0.001)	$3.2_{(144.1)}$	0.002	$\mathrm{P_L}$	0.33 (<0.001)	$-1.67_{(85.7)}$	NS
	$\mathrm{OTD_{FL}}$	−0.33 (<0.001)	$1.5_{(69.5)}$	NS	$\mathrm{O_L}$	0.32 (<0.001)	$-1.75_{(100.2)}$	NS
	W	−0.27 (<0.001)	$1.5_{(110.6)}$	NS	$\mathrm{M_L}$	0.30 (<0.001)	$-1.67_{(107.4)}$	NS
					$\mathrm{ODA_{FL}}$	0.30 (<0.001)	$-1.61_{(100.1)}$	NS
					$\mathrm{H_L}$	0.25 (<0.001)	$-1.31_{(91.4)}$	NS
2+	$\mathrm{OID_{FL}}$	−0.42 (<0.001)	$3.1_{(187.8)}$	<0.001	$\mathrm{PP_L}$	0.38 (<0.001)	$-2.8_{(190.4)}$	<0.006
	$\mathrm{MaxC_{FL}}$	−0.28 (<0.001)	$2.1_{(190.9)}$	0.04	$\mathrm{B_D}$	0.36 (<0.001)	$-2.6_{(167.7)}$	0.01
	$\mathrm{OIA_{FL}}$	−0.26 (<0.001)	$1.9_{(190.9)}$	<0.001	$\mathrm{ODA_{FL}}$	0.24 (<0.001)	$-1.7_{(180)}$	NS

The *r*-value shows the contribution of each trait to the linear combination that discriminates individuals from each habitat (here we report only $r > 0.24$). Within each water velocity group, the univariate tests show the traits that remain significantly bigger than the other group after size correction.
NS signifies that the mean trait values were not significantly different between current groups.
*See Fig. 2.

Table 3 Comparison of Fulton's condition factor (*K*), and the fineness ratio (*F*) between individuals (1+, 2+ and mature parr) sampled in slow and rapid water currents

	K				*F*			
Body ratio	Slow	Rapid	$t\text{-test}_{(\mathrm{df})}$	*P*-value	Slow	Rapid	$t\text{-test}_{(\mathrm{df})}$	*P*-value
1+	0.867	0.871	$0.27_{(118.5)}$	0.788	0.175	0.175	$-0.054_{(91.2)}$	0.956
2+	0.917	0.861	$3.11_{(157.2)}$	0.002	0.180	0.176	$-2.4751_{(178.5)}$	0.014
Mature parr	0.962	0.956	$-0.3642_{(53.7)}$	0.717	0.190	0.192	$0.741_{(37)}$	0.463

rapid water currents. Specifically, these fish were distinguished by having larger caudal, dorsal and anal fin measurements than individuals occupying slow habitats. However, contrary to 1+ fish, 2+ individuals sampled in slow water currents had deeper bodies (Table 2) and a larger fineness ratio and a higher condition factor than fish in rapid habitats (Table 3), making them overall more robust.

Mature parr

Both the MANOVA and DFA show differences in shape between mature and immature parr (MANOVA: $F_{21,229} = 5.71$, $P < 0.001$; DFA: Monte-Carlo test $P < 0.001$) (Fig. 4). The correlation between the canonical roots and each variable shows that traits which have high canonical loadings, such as $\mathrm{B_D}$, W, and $\mathrm{OPD_{FL}}$ (Fig. 2), can be used to discriminate mature parr from immature fish, both aged 2+ (Table 4). In addition, the fineness body ratio was significantly larger for mature parr, suggesting that these individuals are less streamlined (*t*-test, $t_{85.87} = 7.93$, $P < 0.001$). The leave-one-out cross-validation suggests that the discriminant functions would correctly

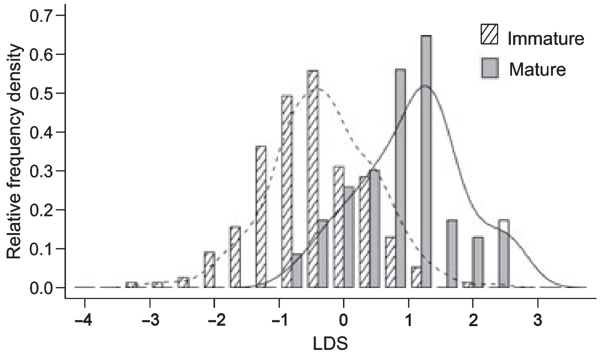

Fig. 4 Canonical scores from the discriminant function used to classify mature and immature individuals. The broken line traces the relative frequency distribution of the canonical scores of individuals captured in rapid habitats whereas the continuous line traces scores in slow water habitats.

Table 4 Principal traits that contribute to discriminating immature from mature parr

Immature parr				Mature parr			
		Univariate *t*-test				Univariate *t*-test	
Trait*	*r* (*P*-value)	$t_{(d.f.)}$	*P*-value	Trait*	*r* (*P*-value)	$t_{(d.f.)}$	*P*-value
H_L	−0.59 (<0.001)	$6.1_{(100.3)}$	<0.001	B_D	0.83 (<0.001)	$-8.4_{(87.6)}$	<0.001
O_L	−0.54 (<0.001)	$5.8_{(111.4)}$	<0.001	OPD_{FL}	0.60 (<0.001)	$-6.1_{(96.2)}$	<0.001
M_L	−0.36 (<0.001)	$3.3_{(88.8)}$	<0.001	W	0.59 (<0.001)	$-5.7_{(91.7)}$	<0.001
SH_L	−0.35 (<0.001)	$3.6_{(108.4)}$	<0.001	ODA_{FL}	0.41 (<0.001)	$-4.6_{(124.3)}$	<0.001
$MaxC_{FL}$	−0.30 (<0.001)	$2.8_{(89)}$	NS	C_D	0.31 (<0.001)	$-3.8_{(158.6)}$	<0.001
OTD_{FL}	−0.23 (0.001)	$1.9_{(80.6)}$	NS				

The *r*-value shows the contribution of each trait to the linear combination that best discriminates individuals according to their maturity state (here we report only $r > 0.20$).
*See Fig. 2.

classify unknown individuals to their sexual status 83% of the time (Table 1).

The *t*-test comparing the size of mature parr between habitats show that individuals found in slow water current were approximately 5 mm longer than those found in rapids (*t*-test, $t_{51.7} = -2.11$, $P = 0.038$), representing a weight advantage of about 1.3 g (or 15% heavier). No significant differences in shape (MANOVA: $F_{21,36} = 1.68$, $P = 0.083$; Monte-Carlo test $P = 0.081$) nor GSI (*t*-test, $t_{55.12} = -0.7715$, $P = 0.444$) were detected between the two groups. In addition, the leave-one-out cross-validation was not useful for classifying these males to either habitat, the classification being no better than what one would obtain by chance (Table 1). Thus, we conclude there are no shape differences between mature parr from the two habitat types (see Fig. 3c).

Discussion

Immature parr

No differences in abundance between fast and slow current habitats were found for 2+ Atlantic salmon parr. However, 1+ individuals were more often found in slow current habitats. Although this may be partly due to the difficulty of capturing small individuals in fast current velocities (e.g. Heggenes, Baglinière & Cunjak, 1999), the high sampling effort involved in our study should have minimized this effect. Thus, the difference in abundance might be related to the energetic costs associated with utilizing rapid currents for the smaller 1+ fish. Because our rapid-current habitat sites covered the range of water currents preferred by larger individuals (Hedger *et al.*, 2005) we suggest that a fraction of 1+ individuals possess sufficient energetic reserves and muscular strength to exploit such fast-current habitats.

Immature parr differed in shape but not size depending on water current velocity. Generally, these differences agree with the expectation that habitats characterized by rapid and slow water currents are occupied by individuals with streamlined and robust characteristics respectively. However, we also found some important differences in the combination of variables that classified 1+ and 2+ individuals into rapid and slow current habitats. Particularly, our results suggest that all 1+ individuals have a similar body shape, as differences related to swimming were observed only in the posterior region of the body, where thrust is generated. This result is further supported by the lack of differences in the fineness ratio and condition factor. Pakkasmaa & Piironen (2001) presented strong evidence to suggest that fin morphology (i.e. the caudal and dorsal fins) was significantly different between 0+ fish exposed to slow and rapid water currents. In our study, differences in body shape were only found for 2+ individuals. Specifically, individuals sampled in slower water currents conformed to the robust phenotype, having deeper bodies and a higher fineness ratio and condition factor than fish sampled in rapid habitats.

Overall our results imply that the plastic response to variation in water current velocity is different during the development of juvenile salmon. The consistent differences in fin morphology between current types across age cohorts imply that these structures are the first to respond to variation in water current velocities, whereas the classic streamlined and robust body outlines may only arise later in development, as seen here for 2+ individuals. Indeed, for small fish, streamlined and robust bodies may not greatly change the interactions with water currents. On the contrary, allocating resources to muscle growth and propulsion mechanisms might be more important to overcome drag. As parr grow bigger, they prefer faster water currents (Hedger *et al.*, 2005; Armstrong *et al.*, 2003). For these fish, the addition of drag-reducing mechanisms (such as slimmer shapes) may increase swimming efficiency and prey capture success (Godin & Rangeley, 1989; Ohlberger *et al.*, 2006; Rincon, Bastir & Grossman, 2007).

Mature parr

The robust phenotype of mature parr results from the developmental changes undertaken through premature sexual maturation. It is commonly observed that gonad size adds substantially to total body weight re-shaping the anterior ventral area of the body. We have shown that this results in the heavy canonical loadings of traits such as width, body height, and the length between the origins of the pectoral and dorsal fins, which strongly discriminate mature from immature individuals. In addition, we predict that these features should be more pronounced near spawning time, when maximal investment in gonad growth is achieved.

Contrary to immature fish, we found no differences in body shape between individuals sampled in the different water current velocities. However, individuals did differ in body size, such that those sampled in slow water currents were bigger than mature parr sampled in rapids. Both the elevated metabolic activity experienced through sexual maturation (Tucker & Rasmussen, 1999) and the overall robust body shape of mature parr, suggests that they are less suited for habitats featuring rapid water current velocities (Videler, 1993). Boily & Magnan (2002) using *Salvelinus fontinalis*, showed how robust fish significantly consumed more oxygen, and thus experienced higher metabolic costs, when exposed to rapid water currents. Therefore, both the tendency to find mature parr more often in slow current habitats and the size difference seen between current habitats may be related to the energetic costs associated with sustained swimming in rapid water currents. Interestingly, the lack of differences in GSI suggests that investment in gonad development in both habitats is equally high. Thus, added to the cost of producing reproductive tissue, fish in rapid habitats may also experience higher energetic demands to swim, potentially contributing to their smaller size. Given the importance of size during spawning (Thomaz, Beall & Burke, 1997), if the relationship between water current velocity and size is found to be causal, water velocity will have a direct impact on the reproductive success of mature parr.

Conclusions

In conclusion, we found shape differences for immature fish inhabiting slow and rapid water currents in both 1+ and 2+ age cohorts, as expected. Since variation in water current velocities is conspicuous in the habitat where juvenile Atlantic salmon is found, streamlined and robust shapes may be important in allowing individuals to exploit the resources found within the range of water current conditions present in their habitats. This could potentially reduce density dependent events such as competition for a common resource. In the case of mature parr, we have shown that early maturation has an important effect on body shape. In addition, mature parr captured in rapids are significantly smaller than fish found in slow-current habitats. We propose that water current velocity contributes to this size difference through the extra energetic demands experienced as body shape enlarges and movement is further limited in faster currents.

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