

# Longitudinal gradients in threshold sizes for alternative male life history tactics in a population of Atlantic salmon (*Salmo salar*)

Nadia Aubin-Horth, Jean-Francois Bourque, Gaetan Daigle, Richard Hedger, and Julian J. Dodson

**Abstract:** Atlantic salmon (*Salmo salar*) males may mature early in life in freshwater, rather than maturing after a migration to sea, if their size is above a threshold value. We analyzed the spatiotemporal variation in size and incidence of the early maturity tactic among males over an 8-year period in six subpopulations on two branches of a river and collected environmental data on each site and across the river scape. A positive longitudinal trend in the frequency of early maturing males that was stable over the 8-year period occurred from the mouth to the head of the river. Threshold sizes for early maturation varied among subpopulations; size thresholds for male parr to mature were higher in downstream habitats and lowest upstream. This pattern was consistent in both river branches over the 8-year period and was not related to either the density of parr or site-specific abiotic habitat characteristics. However, the cumulative incidence of habitat features that could impede migration of large individuals increased with increasing upstream distance. Migration costs may contribute to the observed variation in threshold sizes.

**Résumé :** Les mâles du saumon atlantique (*Salmo salar*) peuvent atteindre la maturité sexuelle tôt dans la vie en eau douce au stade de tacon, plutôt qu'après une migration en mer, si leur taille est supérieure à une valeur seuil. Nous avons analysé la variation spatio-temporelle de la taille et de l'incidence de la stratégie de maturité hâtive chez les tacons mâles sur une période de 8 ans dans six sous-populations de deux branches d'une rivière et récolté des données sur l'environnement à chaque site et sur le paysage fluvial. Il existe un gradient positif longitudinal stable sur la période de 8 ans dans la fréquence de tacons mâles matures de l'embouchure à la tête de la rivière. La taille seuil pour la maturation des mâles tacons variait entre les sous-populations; la taille seuil pour la maturation des tacons mâles est plus élevée dans les habitats en aval et plus basse en amont. Ce patron est uniforme dans les deux branches de la rivière durant la période de 8 ans, mais n'est pas en corrélation avec la densité des tacons, ni les caractéristiques physiques des habitats spécifiques à chaque site. Cependant, l'incidence cumulative de caractéristiques de l'habitat pouvant empêcher la migration vers l'amont des grands individus anadromes augmente avec la distance vers l'amont. Les coûts de migration contribuent possiblement aux variations de la taille seuil pour la maturation.

## Introduction

The development of alternative phenotypes is often controlled by the state of an individual at a specific moment in its life. The liability trait, which is often a continuous trait such as body size, controls a dichotomous developmental pathway at a threshold node, such that all states above a certain value develop into a given phenotype (Hazel et al. 1990; Roff 1996; Nijhout 2003). In many systems, the threshold has been proposed to be a complex trait that can evolve through natural selection and thus reflect local adaptations (invertebrates: Gotthard 1998; Moczek and Nijhout 2003;

Tomkins and Brown 2004; vertebrates: Hutchings and Myers 1994; Nicieza et al. 1994; Hazel et al. 2004).

The dichotomous reproductive tactics of male Atlantic salmon (*Salmo salar*) provide a striking example of two divergent alternative life histories that co-exist within populations. Some males are anadromous, migrating to sea after 2–4 years of residence in their natal river and returning to freshwater to reproduce after 1–3 years at sea. However, other males never leave freshwater and become sexually mature as parr at ages 1 to 3 (Jones and Orton 1940; Hutchings and Jones 1998). These males sneak reproductive opportunities and fertilize a small proportion of the eggs rather than fight with larger and older anadromous males.

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Early maturity occurs in Atlantic salmon male parr if body size exceeds a threshold value during a critical period in the spring before fall reproduction (Saunders et al. 1982; Rowe and Thorpe 1990; Juanes et al. 2000). The incidence of early maturing males is variable among rivers, and variation in the relationship between size at capture and maturation has also been reported among populations (Myers et al. 1986; Hutchings and Myers 1994).

Within a river, the incidence of early male maturity may be expected to covary with the individual growth and condition of fish, such that sites that favour the development of larger and (or) faster-growing males should also favour the development of a higher proportion of early maturing males, as a higher proportion of males would surpass the threshold. This expectation was falsified in a study of male salmon at age 1 (their first opportunity to mature) sampled in different subpopulations of a river. Aubin-Horth and Dodson (2004) observed a poor relationship between size in the spring and the probability of maturing the next fall, indirectly suggesting multiple thresholds for maturation within the same river system. In addition, variation in the relationship between size and maturation incidence observed among tributaries of the same river system and related to altitude was not the result of variation in growth rate (Baum et al. 2004).

Various hypotheses have been formulated to explain variation in the incidence of early maturation of salmon males among different habitats and to relate early maturation to biotic or abiotic characteristics of the environment. For example, the probability of early maturation has been positively correlated with parr density (Baum et al. 2004). Alternatively, the incidence of early maturation has been associated with a certain modal substrate size (Myers et al. 1986). Furthermore, environmental factors may be associated not only with variation in incidence, but also with variation in thresholds in body size for early maturation among subpopulations. For example, Tomkins and Brown (2004) showed that density was the factor driving the evolution of threshold for maturation in two male forms in different populations of European earwig (*Forficula auricularia*) insects.

In this study, we used data acquired from six sample sites in two branches of a river over 8 consecutive years to discriminate the influence of variations in absolute body size and the threshold values in body size for maturation on the incidence of early male maturity in Atlantic salmon. We also examined the influence of environmental characteristics (both the biotic characteristic of parr density and the abiotic characteristics of velocity, depth, and substrate size) in determining variation in early maturation incidence among subpopulations.

## Materials and methods

### Population studied

The Ste. Marguerite River, Saguenay, Quebec, Canada (48°20'N, 70°00'W), was used as the natural study system. This river has a mean annual discharge of  $58 \text{ m}^3 \cdot \text{s}^{-1}$  and is composed of two distinct branches of approximately equal size, referred to as the principal (PR) and the northeast (NE) branches, which converge 5 km from the outlet located on the Saguenay River. The upstream extent of salmon distribu-

tion is limited by impassable waterfalls located 83 km upstream on the principal branch and 32 km upstream on the northeast branch. The northeast branch is characterized by an initial impassable waterfall 7 km upstream, which is bypassed by a fish ladder. The salmon from both branches of the river represent one genetic population, although a significant but weak spatial genetic differentiation occurs among the subpopulations that have been studied (Garant et al. 2000).

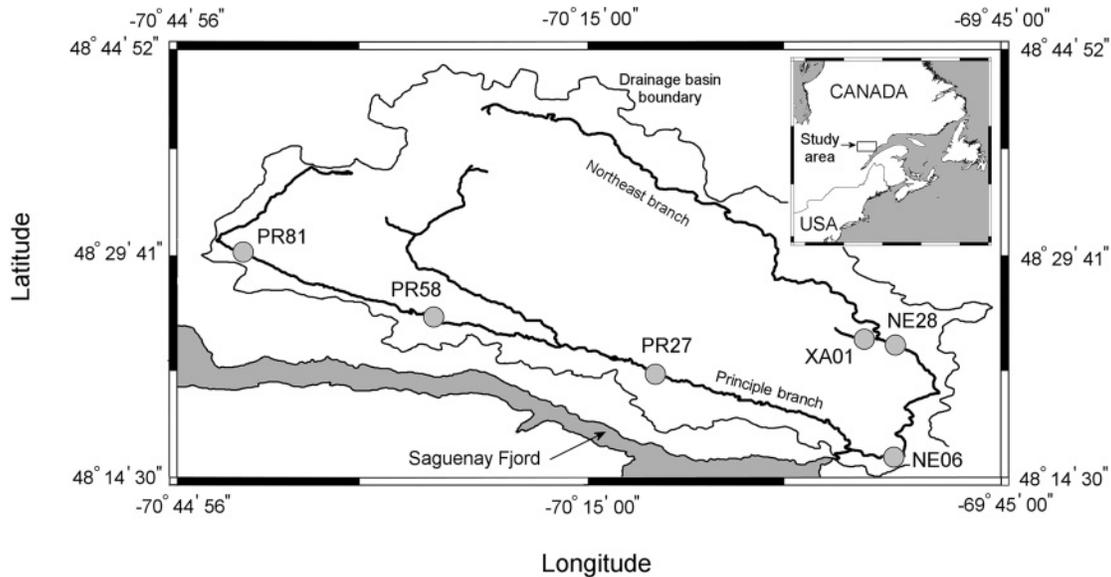
### Sampling strategy

Our sampling spanned 8 years, from 1996 to 2003. Sampling was performed once a year during the last week of August. We sampled three sites per river branch (six in total; Fig. 1). Sites were separated by 20–30 km within branches. One site (XA01) on the northeast branch was located less than 2 km upstream of another site (NE28) but was within a tributary. In choosing these sites, we took advantage of the prior knowledge that they correspond to previously determined spawning and rearing habitats and that individuals from these sites were weakly but significantly genetically differentiated at neutral markers (Garant et al. 2000). The genetic pattern was consistent among years and therefore these sites were viewed as subpopulations. Salmon offspring usually remain associated with the spawning ground of their parents, which is also suitable nursery habitat, until they migrate to marine feeding grounds. The use of specific parts of the fluvial habitat by juveniles therefore maintains the patchy distribution created by the spawning habitat preferences of their parents. Juveniles at this life stage restrain their movements to less than hundreds of metres, tens of metres in some instances, although a small fraction of older individuals may disperse over a larger area (up to 10 000 m) (Armstrong et al. 1994; Juanes et al. 2000; Webb et al. 2001). These sites also differed in distance from the mouth of the river, thus maximizing the probability of variation in environmental conditions. It has been shown that variation in local conditions linked to upstream location in a river includes width, depth, channel slope, and therefore current velocity, substrate deposition–erosion, and substrate size and arrangement, as well as cover from the banks (Vannote et al. 1980). Indeed, it was already known that the three sites sampled on the principal branch correspond to three sections that exhibit important differences in slope (19.9, 2.7, and  $0.8\text{--}6.4 \text{ m} \cdot \text{km}^{-1}$ ) from upstream to downstream sections. These differences among locations thus signalled potentially major variation in environmental conditions such as temperature, productivity, prey availability, and predation risk (Beisel et al. 1998; Folt et al. 1998; Miyake and Nakano 2002).

### Parr maturity incidence

To obtain juvenile individuals, we sampled a distance within each site of between 50 and 100 m in length. This distance incorporates a larger zone than the area covered by the territory of a typical juvenile (Armstrong et al. 1994). Electrofishing was used to sample juvenile Atlantic salmon (parr) at each sampling site. It was not possible to determine age or sex at the time of capture. Individuals were thus sacrificed for laboratory analyses.

**Fig. 1.** Location of the six sites sampled from 1996 to 2003 in the Ste. Marguerite River system (Québec, Canada).



## Environmental characteristics

### *Parr densities*

Concomitant with the mature parr sampling, an independent ground survey of juvenile Atlantic salmon density was conducted on the principal and the northeast branches of the Ste. Marguerite in August of each year from 1997 to 2004. Between 30 and 48 survey stations were sited along the length of the two branches in each year. In each parcel (5 m by 20 m), juvenile salmon density was estimated using single-pass electrofishing. Juveniles were categorized, on the basis of length, as being either fry (first summer of life) or parr (ages 1–3).

### *Abiotic environmental characteristics of sample sites*

Differences in abiotic environmental characteristics among selected sites were investigated in August 2003. At each site, a rectangular sampling area was defined (320 to 1500 m<sup>2</sup>, depending on river width) and divided into a grid of 100 sampling points. At each point, we measured water depth, water surface velocity, and substrate size (using the *b* axis, also known as the intermediate axis, defined as the shortest axis across the maximum projection plane) of a randomly selected pebble.

### *Airborne survey of the principal branch*

Abiotic environmental characteristics throughout the principal branch were determined from an airborne survey, conducted between 1000 and 1500 on 17 and 18 August 2002 using a helicopter-mounted XEOS true-colour digital camera (GENIVAR Inc., Quebec, QC G2J 1C8, Canada). The rationale to using an airborne survey was that it would show how habitat properties varied along the length of the river (the river scape), indicating areas that will impact on migration. Depth and substrate size ( $D_{50}$ ) were estimated for each pixel using the method outlined by Carbonneau et al. (2004a, 2004b). River-scape variation in depth and substrate size as a function of distance from the river mouth was determined by estimating the median depth and mean substrate size of

each image along the series of images. Images in which more than two-thirds of the channel was less than 30 cm in depth were classified as being those most likely to be subject to low flows; images in which  $D_{50}$  was greater than 20 cm were classified as those most likely to contain rapids (fast-flowing water in areas of steep gradients, characterized by the presence of cobbles and boulders).

## Analyses

### *Parr maturity incidence*

We determined age group (in years) using the annual patterns present on otoliths (Campana and Jones 1992). We determined sex and maturity state in males by dissection according to the classification of Jones (1940). Mature female parr were never observed. Parr maturity incidence was calculated as the number of males exhibiting ripe testes divided by the total number of males in a sample from a given site. We computed these ratios separately for age-1 and age-2 fish and for each year. We found no age-0 individuals (in their first year of life) to be sexually mature in this system, and older individuals ( $\geq 3$  years) are very rarely found as almost all migrate to sea at this age (J.J. Dodson, unpublished data). It is important to note that mature male parr that survive can migrate to sea and eventually become large anadromous males (Whalen and Parrish 1999). It was not possible to estimate incidence of early maturation for age-2 males in subpopulation NE06 in 1997 as only one such individual was captured at this site in 1997. Given the binomial nature of the response variable, the incidences of early maturity among male parr were compared using a logit model (Hosmer and Lemeshow 2000). In this model, the effect of branch was taken into account, as well as the effect of sites within branches, the effect of year, the effect of age, and the effect of body size. The model was fitted using the GENMOD procedure of SAS (SAS Institute Inc. 2003). A significant interaction between size and site (within branch) would suggest different threshold sizes for maturation in different subpopulations. The Hosmer–Lemeshow test was

**Table 1.** Frequency of early male maturity in each subpopulation for each year and age class, with sample sizes in parentheses.

	Site	1996	1997	1998	1999	2000	2001	2002	2003
Age 1	PR27	0.09 (11)	0.25 (4)	0.29 (34)	0.17 (23)	0.15 (13)	0.08 (13)	0.09 (11)	0.09 (11)
	PR58	0.11 (9)	0.20 (10)	0.47 (15)	0.69 (13)	0.50 (10)	0.22 (9)	0.17 (6)	0.27 (11)
	PR81	0.50 (10)	0.71 (7)	0.75 (8)	0.44 (9)	0.60 (10)	0.18 (11)	0.08 (12)	0.18 (11)
	NE06	0.54 (13)	0.31 (13)	0.50 (32)	0.50 (26)	0.25 (8)	0.00 (7)	0.00 (13)	0.53 (15)
	NE28	0.55 (11)	0.27 (11)	0.30 (10)	0.21 (14)	0.25 (8)	0.28 (18)	0.35 (17)	0.25 (12)
	XA01	0.50 (8)	0.55 (20)	0.73 (11)	0.67 (9)	0.83 (12)	0.38 (13)	0.00 (5)	0.50 (14)
Age 2	PR27	0.50 (12)	0.50 (4)	0.63 (8)	0.75 (4)	0.38 (8)	0.14 (7)	0.13 (8)	0.36 (14)
	PR58	0.78 (9)	0.60 (10)	1.00 (9)	0.88 (17)	0.80 (10)	1.00 (4)	0.70 (10)	0.79 (14)
	PR81	1.00 (9)	0.79 (14)	1.00 (11)	0.85 (13)	1.00 (9)	0.73 (11)	0.70 (10)	0.58 (12)
	NE06	0.55 (11)	NA	0.36 (14)	0.71 (7)	0.43 (7)	0.80 (5)	0.17 (6)	0.57 (7)
	NE28	0.75 (4)	0.70 (10)	1.00 (8)	0.75 (8)	0.78 (9)	0.22 (9)	0.63 (8)	0.56 (9)
	XA01	0.80 (10)	1.00 (7)	0.83 (6)	0.75 (20)	0.67 (3)	0.83 (6)	0.62 (13)	0.75 (8)

used to confirm the goodness of fit of the model to the data ( $\chi^2 = 5.62$ ,  $df = 8$ ,  $p = 0.6902$ ). To quantify the predictive power of the model, the area under the receiver operating characteristics (ROC) curve was calculated ( $c = 0.801$ ). This result was considered as providing excellent discrimination of the two maturity states (mature vs. nonmature). We then employed the “leave-one-out” cross-validation technique to verify the robustness of the model (Stone 1977). We systematically excluded one fish at a time and predicted its maturity state with the logit model adjusted with the remaining data set. We then computed the sensitivity (probability of correctly classifying a fish as mature) and the specificity (correctly classifying a fish as immature) for different probability levels that a fish was mature. The best compromise between sensitivity (66.9%) and specificity (67.0%) occurred at a probability level of 48.8%. Thus, a fish of given size with a predicted probability of being mature exceeding 48.8% was classified as mature. This probability level best discriminated between the two maturity states while minimizing the two errors of misclassification and corresponded to the fraction of mature fish in the total sample. Contrasts were calculated to specify the effect of different factors included in the logit model following the detection of significant sources of variation. Contrasts were conducted using the Fisher protected least significant difference (LSD) method. Additional methods were used to verify the results of multiple comparisons by using the MULTTEST procedure in SAS (SAS Institute Inc. 2003). All tests provided essentially the same results. The relationship between incidence of maturity and distance from sites to the river mouth was established by a decomposition of the sites effect into a linear and quadratic effect of distance.

#### Threshold body sizes for early maturation

We estimated the threshold body sizes (according to length) for discriminating between mature and immature fish for sites within branches. These threshold body sizes were determined using a probability level of 48.8%, the value that best discriminated between the two maturity states while minimizing errors of misclassification (see above).

#### Environmental characteristics

Parr densities data were pooled together for upstream and downstream sections of a given river branch and the mean density was compared between upstream and downstream

river sections using the Fisher protected LSD method. This was done separately for the principal and the northeast branches of the river. The relationship between mean annual parr density and the estimated incidence of early male maturity was established using Kendall rank correlation.

Univariate analyses of variances (ANOVA) were performed on individual abiotic environmental characteristics to identify whether significant differences in mean properties existed among the sites. For those characteristics exhibiting significant differences among sites, Kendall rank correlations were used to explore their relationship with the estimated incidence of early male maturity.

## Results

### Variation in parr maturity incidence

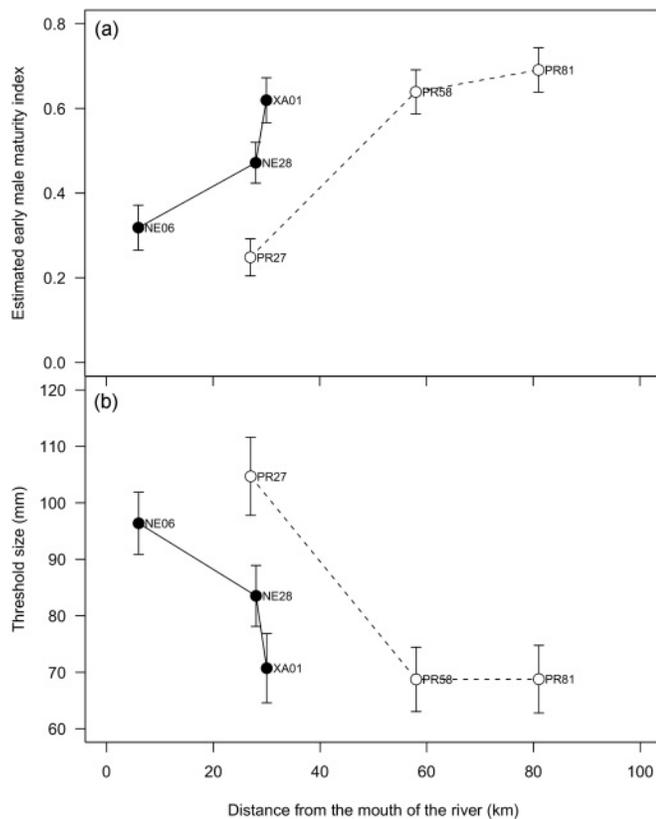
The incidence of early maturity was highly variable among years (Table 1). The logit model revealed a significant effect of fish length on the incidence of early male maturity with significant contributions of sites within branches, year, and age (Table 2). After controlling for the effect of size, there was a significant longitudinal gradient in the incidence of early maturing males (Table 2). The incidence of early maturity increased upstream in a linear fashion in both branches of the river (northeast,  $p = 0.0003$ ; principal,  $p < 0.0001$ ). The quadratic function was also significant in the principal branch ( $p = 0.0366$ ), indicating a tendency for the incidence of early maturity to reach an asymptote in this branch (Fig. 2a). This positive longitudinal gradient was temporally stable with no year by site (within branches) interaction ( $p = 0.27$ ; Table 2). This stability persisted for almost a decade despite the large variation in the incidence of early maturity among years. Therefore, although the incidence of early maturity changed over time, the ranking according to the incidence of mature male parr within a branch stayed the same, and the gradient from the mouth to the head of the river was conserved. Finally, there was a significant branch by age effect on early male maturity ( $p = 0.0096$ ; Table 2). Two-year-old males from the principal branch showed a significantly higher incidence of maturity than 1-year-old males (65% vs. 39%, respectively,  $p = 0.0025$ ). This was not observed in the northeast branch (48% vs. 46%, respectively,  $p = 0.8101$ ). As a result, the incidence of early male maturity of age-2 males in the principal branch

**Table 2.** Logistic regression (logit function) model using the GENMOD procedure of SAS (SAS Institute Inc. 2003) to establish the relationship between the incidence of early male maturity as a function of body size (length) and the influence of river branch, sampling sites within branches, age of parr, and year of sampling.

Source	df	F value	Pr > F	$\chi^2$	Pr > $\chi^2$
<b>Length</b>	<b>1</b>	<b>22.8</b>	<b>&lt;0.0001</b>	<b>22.8</b>	<b>&lt;0.0001</b>
Branch	1	1.21	0.2723	1.21	0.272
<b>Site (branch)</b>	<b>4</b>	<b>16.24</b>	<b>&lt;0.0001</b>	<b>64.97</b>	<b>&lt;0.0001</b>
<b>Year</b>	<b>7</b>	<b>6.93</b>	<b>&lt;0.0001</b>	<b>48.54</b>	<b>&lt;0.0001</b>
Year × branch	7	1.05	0.3965	7.33	0.3954
Year × site (branch)	28	1.14	0.2802	31.98	0.2752
Age	1	3.7	0.0547	3.7	0.0543
<b>Branch × age</b>	<b>1</b>	<b>6.7</b>	<b>0.0098</b>	<b>6.7</b>	<b>0.0096</b>
Site × age (branch)	4	1.36	0.2463	5.44	0.2452
Year × age	7	0.2	0.985	1.41	0.9851
Year × branch × age	7	0.69	0.6769	4.86	0.6769

**Note:** Significant sources of variation are indicated in bold.

**Fig. 2.** (a) Early male parr maturity frequency among all males and (b) threshold sizes (body length at which the probability of maturity is 48.8%) as a function of distance upstream from the river mouth. Solid circles represent the mean of each site of the northeast branch; open circles represent the mean of each site of the principal branch. Vertical bars indicate  $\pm 1$  standard error.



was greater than that of age-2 males in the northeast branch ( $p = 0.0194$ ).

**Variation in threshold body sizes for maturation**

Threshold size that a male must reach to mature early varied among the subpopulations sampled. Estimations of the

threshold size at which the probability of early maturity equaled 48.8% indicated that the threshold sizes differed significantly among sites in both branches of the river (northeast,  $p = 0.0077$ ; principal,  $p < 0.001$ ; Fig. 2b).

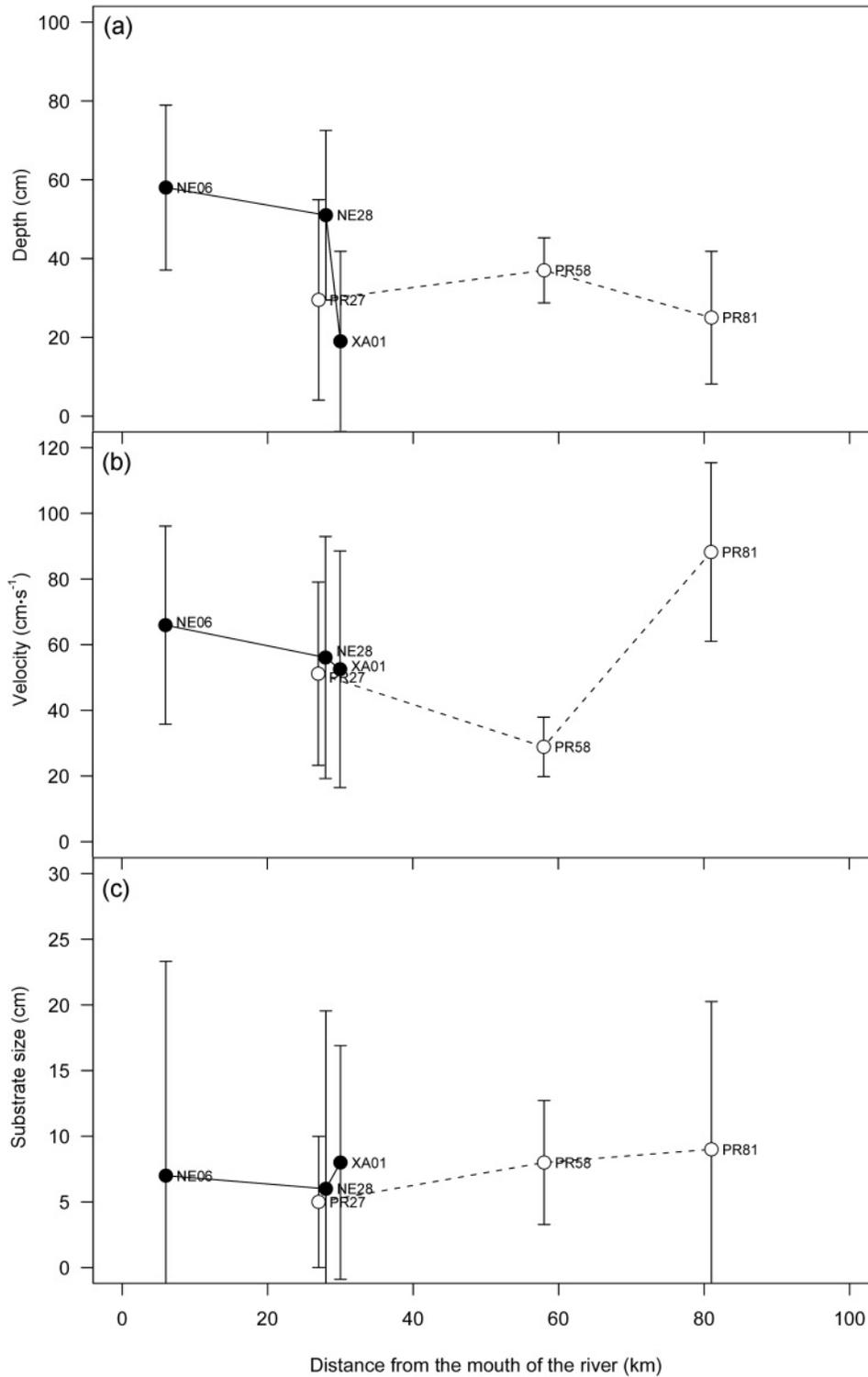
Threshold size variation was found to covary with distance from the mouth of the river of each site, and on both branches. The longitudinal gradient in incidence was linked to an interaction between the effect of the subpopulation sampled (site within branch) and size on the probability of maturing (Table 2). In the northeast branch, the threshold level estimated at NE06 was significantly greater than that estimated at the two upstream stations, whereas threshold sizes did not differ between the two most upstream stations (Fig. 2b). Similarly, in the principal branch, the threshold level estimated at the downstream station (PR27) was significantly greater than that estimated for the two upstream stations (Fig. 2b).

**Variation in environmental characteristics**

As revealed by a long-term study of juvenile densities conducted in both branches from 1997 to 2004, mean parr density found in the upstream ( $4.34 \text{ parr}\cdot\text{m}^{-1}$ ,  $SD = 2.90$ ) and the downstream ( $3.04 \text{ parr}\cdot\text{m}^{-1}$ ,  $SD = 2.66$ ) parts of the principal branch did not differ significantly (LSD test,  $p = 0.17$ ). Similarly, juvenile density did not differ between the upstream ( $4.92 \text{ parr}\cdot\text{m}^{-1}$ ,  $SD = 3.67$ ) and downstream ( $4.16 \text{ parr}\cdot\text{m}^{-1}$ ,  $SD = 3.49$ ) parts of the northeast branch (LSD test,  $p = 0.51$ ). On an annual basis, no significant correlation was found between the predicted incidence of early maturity and the mean annual density in both branches (Kendall rank correlation test,  $p = 0.3813$ ).

Abiotic environmental properties as measured by the ground survey showed a large amount of variation, both within individual sites and between sites (Fig. 3). Comparison by univariate analysis of variance showed that there was a statistically significant difference between the sites in terms of depth ( $p < 0.0001$ ) and velocity ( $p = 0.0064$ ) but not substrate size ( $p = 0.3147$ ). No consistent upstream trend in environmental characteristics existed. For example, median depth at PR58 was greater than that at either the downstream PR27 or the upstream PR81. Kendall rank correlation showed that there was no statistically significant relationship

**Fig. 3.** Habitat characteristics identified from the ground survey as a function of distance upstream from the river mouth: (a) depth; (b) velocity; (c) substrate size. Solid circles represent the median depth, mean velocity, and median substrate size ( $D_{50}$ ) of each site of the northeast branch; open circles represent the median depth, mean velocity, and median substrate size ( $D_{50}$ ) of each site of the principal branch. Vertical bars indicate  $\pm 1$  standard error.

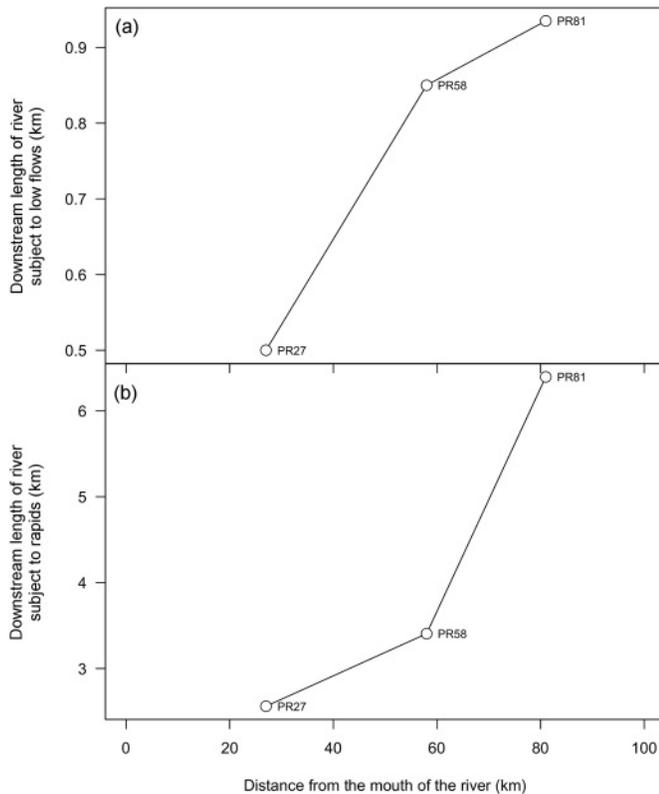


between either depth ( $p = 0.4523$ ) or velocity ( $p = 1$ ) and the estimated incidence of early male maturity.

The airborne survey showed that the cumulative incidence of habitat features that could impede the upstream migration

of adult fish, such as sections of the river subject to low flows or rapids, increased with increasing upstream distance (Fig. 4). For example, the incidence of cumulative habitat features that could impede migration was higher upstream

**Fig. 4.** Cumulative effects of downstream habitat along the principle branch as a function of distance upstream from the river mouth: (a) downstream length of river subject to low flows; (b) downstream length of river subject to rapids.



on the principal branch, such that a length of river totaling 0.85 km was subject to low flows downstream of PR81, 1.7 times the length downstream of PR 27 (0.5 km); and a length of river totaling 6.40 km was subject to rapids downstream of PR81, 1.9 times the length downstream of PR27 (2.56 km).

## Discussion

Variation in body size and in threshold size for maturation have both been proposed to explain among- (Hutchings and Myers 1994) and within-population variation in the incidence of alternative male reproductive phenotypes (Whalen and Parrish 1999; Aubin-Horth and Dodson 2004; Baum et al. 2004). Distinguishing the effects of these two factors has always been a major problem. In the present study, we found that when the effect of size is accounted for, distance from the mouth of the river is a significant predictor of the probability of maturing early in the life history of male salmon (interaction between size and site (within branch) on the probability of maturing). This result is in accordance with the findings by Baum et al. (2004), who found that the altitude of tributaries was a predictor of probability of maturing, independently of size. The spatial pattern found in the present study was temporally stable over almost a decade despite large variation in the absolute proportion of males maturing as parr. In addition, we estimated threshold values for each subpopulation and showed that they varied significantly.

Moreover, we showed that this variation in threshold size for development of maturation varied with distance from the mouth of the river, being highest downstream and declining upstream, a pattern found in both branches. Finally, we demonstrated that the observed variation in maturity incidence was not correlated with either parr density or abiotic environmental characteristics measured at the sampling sites.

It is possible that the estimated 20–30 mm shifts in threshold sizes between subpopulations do not translate into any fitness gain or loss. Such an option cannot be ruled out without determining the advantages or disadvantages conferred by developing as a mature parr at a given size in each of the habitats sampled. This possibility can be further examined in future experiments using common rearing environments for offspring of different subpopulations and reciprocal transplants. However, the fact that both branches showed the same trend from the mouth of the river to the most distant part of the system argues against the random variation hypothesis, especially since the trend is clinal in nature, a typical signature of adaptive variation for numerous traits (Endler 1986). Models and empirical data in different species suggest that the trade-offs between costs and benefits associated with expressing a tactic in a given environment influences the threshold that determines whether an individual will express the tactic or not (Hunt and Simmons 2001; Merckx et al. 2003; Hazel et al. 2004). In Atlantic salmon, different environmental and biological variables may modify the fitness that a male of a certain size could achieve using the sneaker tactic. If these fitness-affecting environmental conditions vary with the distance from mouth of the river, it could result in differential selection on threshold values in different subpopulations and the longitudinal pattern observed in this study.

Baum et al. (2004) showed that high parr density was associated with a high incidence of mature male parr. They proposed that higher density leads to smaller size, resulting in lower threshold levels, hence more mature parr. Although competition among mature parr cannot be excluded from playing a role in the pattern of threshold variation observed, our results do not support the Baum et al. (2004) interpretation. No statistically significant relationship was found between parr density and estimated incidence of early maturity.

The observation that the cumulative incidence of habitat features that could impede the upstream migration of adult fish increased with increasing upstream distance suggests that increasing migratory costs associated with the difficulty of upstream migration may favour residency over anadromy by a reduction in early maturity threshold size levels in male Atlantic salmon. In brown trout (*Salmo trutta*), a positive relationship was found between the cost of migration and altitude as revealed by the more rapid decline with altitude in the recruitment of migratory populations than that of resident populations (Bohlin et al. 2001). A positive relationship was also observed between cost of migration and distance in terms of female ovarian investment and male energy reserves and secondary sexual characters in Chinook salmon (*Oncorhynchus tshawytscha*) populations (Kinnison et al. 2001, 2003). We propose that the difficulty of migrating across the river scape is dependent not only on distance, but also on the existence of sections of the river that are shallow or contain rapids: the shallower the depth, the greater the

probability of interruption to flow during periods of low flows; the greater the prevalence of rapids, the greater the energy required to swim upstream. As a result, males of the upstream subpopulations would be expected to show a higher probability of maturing in fresh water for a given size, thus increasing their probability of reproducing. The energetic costs of migrating over short distances found in this river system are most probably minor. Nonetheless, the cost of upstream migration associated with the increasing probability of losing access to spawning grounds during years of low discharge and (or) high summer temperatures would favour early maturity and lower thresholds upstream, even in the absence of significant energy expenditures. The relationship between the incidence of early male maturity and the difficulty of upstream passage observed here remains anecdotal as it involves only three sites on one river. The relationship needs to be demonstrated in other river systems to adequately test the hypothesis.

In conclusion, the combination of a temporal series and spatial gradients of size and maturation incidence allowed us to determine that variation in incidence among subpopulations of Atlantic salmon was due to differences not only in size, but also in threshold values for maturation. We showed that this variation in threshold size for maturation displayed a longitudinal pattern, being highest downstream and lowest upstream on both branches of the study river. The incidence of parr maturity was not dependent on the biotic or the site-specific abiotic aspects of the environment. However, the incidence of habitat features that could impede migration of large individuals increased with increasing upstream distance. Migration costs may thus contribute to the observed variation in threshold values.

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