Ecology of Freshwater Fish 2005
Printed in Denmark · All rights reserved

ECOLOGY OF
FRESHWATER FISH

Assessment of winter size-selective mortality of young-of-the-year Atlantic salmon (*Salmo salar*) using otolith microstructure analysis*

Johnston P, Bergeron NE, Dodson JJ. Assessment of winter size-selective mortality of young-of-the-year Atlantic salmon (*Salmo salar*) using otolith microstructure analysis.
Ecology of Freshwater Fish 2005. © Blackwell Munksgaard, 2005

Abstract – The objectives of this study were, first, to assess the usefulness of otolith microstructure analysis to examine winter size-selective mortality of young-of-the-year (YOY) Atlantic salmon and, secondly, to validate various hypotheses relating to the dynamics of two populations with different winter survival. By examining otolith microstructure, we back-calculated body size at hatching and at emergence of YOY salmon sampled in fall 2000 and in early summer 2001 on the Petite Cascapédia River and the Bonaventure River (Québec, Canada). The results of the study did not reveal any size-selective mortality of YOY salmon in the Petite Cascapédia River, while in the Bonaventure River, size-selective mortality of the smaller individuals of the cohort was detected. This case study allowed not only a better comprehension of the population dynamics of those rivers but demonstrated the usefulness of otolith analysis to detect winter size-selective mortality under a natural environment.

P. Johnston[1], N. E. Bergeron[1], J. J. Dodson[2]

[1]INRS-Eau, Terre et Environnement, Québec, [2]Département de biologie, Université Laval, Cité universitaire, Québec, Canada

Key words: size-selective mortality; winter; Salmo salar

P. Johnston, INRS-Eau, Terre et Environnement, 490 rue de la Couronne, Québec, QC, G1K 9A9 Canada; e-mail: Patricia_Johnston@inrs-ete.uquebec.ca

*This is a contribution to the scientific program of CIRSA (Centre Interuniversitaire de Recherche sur le Saumon Atlantique).

Accepted for publication December 23, 2004

Un resumen en español se incluye detrás del texto principal de este artículo.

Introduction

The winter season is generally recognized as being a long period of harsh environmental conditions often causing a bottleneck in stream dwelling salmonid populations (Bjornn 1971; Mason 1976). Many studies have characterized this high winter mortality as having either shown size-selection against small individuals (Lindroth 1965; Hunt 1969; Smith & Griffith 1994; Meyer & Griffith 1997) or random mortality (Lund et al. 2003), whereas other studies have shown spatiotemporal and intercohort variations in the direction of the selection (Aubin-Horth 2002; Hendry et al. 2003). In these studies, a number of methods were used to characterize size-selective mortality, including controlled experiments, tracking of marked or known individuals, follow-up of length–frequency distributions through time and monitoring of the characteristics of survivors in natural populations (reviewed in Sogard 1997). The latter, however, is considered as the most concrete and relevant method of assessing size-selective mortality (Sogard 1997). This approach was employed for juvenile Atlantic salmon (*Salmo salar* L.), by Good et al. (2001) to assess summer size-selective mortality and by Aubin-Horth & Dodson (2004) to study the link between size-selective mortality and precocious maturation. Both studies used otolith-based back calculations to determine fish lengths. This method allowed the detection of size-selective mortality, which showed in both studies an interannual variability that was suggested to be related to various habitat characteristics (i.e. hydroclimatic conditions, habitat availability). Based on these insights into the interaction of populations with environmental conditions, the use of otolith microstructure analysis to assess size-selective mortality of juvenile salmon during the winter season appears promising.

The first objective of this study was to assess the usefulness of otolith microstructure analysis to

doi: 10.1111/j.1600-0633.2005.00089.x

examine winter size-selective mortality of young-of-the-year (YOY) Atlantic salmon. The second objective was to validate various hypotheses relating to the dynamics of two populations with different winter survival. The population of the Petite Cascapédia River (Québec, Canada) was selected for this study because it has been seen to experience a winter bottleneck. The relative density of YOY salmon in the Petite Cascapédia River from 1984 to 2000 was on average nine times higher than the relative density of age-1 post-young-of-the-year (PYOY) salmon (from two to 25 times more YOY than PYOY depending on the year of sampling) (Boudreau & Bourdages 2000). The second river selected for this study, the neighbouring Bonaventure River, had a relative density of YOY nearly twice that of age-1 PYOY salmon for the same period (from one to three times more YOY than PYOY depending on the year of sampling) (Bourdages & Boudreau 2001). Among the numerous hypotheses suggested to explain the low survival of YOY salmon in the Petite Cascapédia River, that of limiting habitat features is the most plausible because the availability of coarse substrate and winter habitat has been shown to be low in this river (Coulombe-Pontbriand & Lapointe 2004).

The following hypotheses are based on the assumption that the presence and direction of size-selective mortality reflect certain features of the environment affecting the fish population in a given location. From the available data describing the two populations under study (Boudreau & Bourdages 2000; Bourdages & Boudreau 2001), we first hypothesized an increased mortality of the smallest individuals in the Petite Cascapédia River. This could indicate an intraspecific competition for scarce shelters (Armstrong & Griffith 2001; Harwood et al. 2002) that favour the biggest, more competitive fish. Secondly, a random mortality was expected for the YOY salmon of the Bonaventure River because the habitat in this river is not considered as limiting. The characteristics of the survivors were monitored in these two populations. Fish size was back-calculated using otoliths of salmon cohort sampled repeatedly through time with shifts in size distributions between a pre- and a postwinter sample used as evidence that the cohort had undergone selective mortality (West & Larkin 1987; Meekan et al. 1998a,b; Good et al. 2001; Aubin-Horth 2002; N. Aubin-Horth, A.J. Ryan, S.P. Good & J.J. Dodson, submitted).

Material and methods

Study sites and sample collection

The study was conducted on the Petite Cascapédia River (48° 12′N, 65° 50′W) and on the Bonaventure River (48°02′N, 65°28′W), located on the Gaspe Peninsula, Québec, Canada (Fig. 1). The Petite Cascapédia River and the Bonaventure River drain a similar area of approximately 2000 km^2 and both have a mean annual discharge of approximately 35 m^{3}s^{-1} [Water survey of Canada (National Water Data Archive, Government of Canada) gauge 010902 and 010802, 1996–2002]. The dominant fish populations are Atlantic salmon (*S. salar*), brook charr *Salvelinus fontinalis* (Mitchell), cyprinids (*Rhinichtys* sp., *Notropis* sp.) and catostomids (*Catostomus* sp.). Slimy sculpin *Cottus cognatus* (Richardson) is very abundant in the Petite Cascapédia River but completely absent in the Bonaventure River. Water temperature is generally relatively low, with mean monthly water temperature ranging from 0.1 to 11.1 °C from October 2000 to June 2001 on both rivers, depending on the position within the drainage basin [Société de la Faune et des Parcs (Québec), unpublished data]. The Petite Cascapédia River is generally 2–3 °C cooler than the Bonaventure River in summer while the temperature is similar during winter.

One site was selected on each river in order to be representative of the average density of YOY salmon. Fish densities were estimated almost every year by electrofishing at different stations of 100 m^2 distributed along the main stem of each river (the river managers are in charge of the monitoring of the fish populations). For the site of the Petite Cascapédia (P.C.) and Bonaventure River (Bon.) (Fig. 1), the relative density was estimated at 15 and 22 YOY salmon per 100 m^2 respectively for the year 2000 (Boudreau & Bourdages 2000; Bourdages & Boudreau 2001). Mean overall density was 13.7 YOY salmon per 100 m^2 for the Petite Cascapédia River (from three to 35 individuals per 100 m^2 depending on the fishing station) and 14.2 YOY salmon per 100 m^2 for the Bonaventure River (from 1 to 30 individuals per 100 m^2 depending on the fishing station) for the year 2000 (Boudreau & Bourdages 2000; Bourdages & Boudreau 2001). In order to detect winter size-selective mortality, we sampled repeatedly fish from the cohort of year 2000, i.e. before and after winter. The specimens from both sites were collected by electrofishing on October 26 and November 2 (prewinter samples) and on 26 and 27 June (postwinter samples). We attempted to take the postwinter samples at the end of April but the water level was high, making electrofishing difficult. We therefore waited for conditions allowing efficient sampling, which occurred only at the end of June. For every sample, the first 50 individuals belonging to the cohort of year 2000 were killed. All specimens were measured and weighed prior to otolith removal.

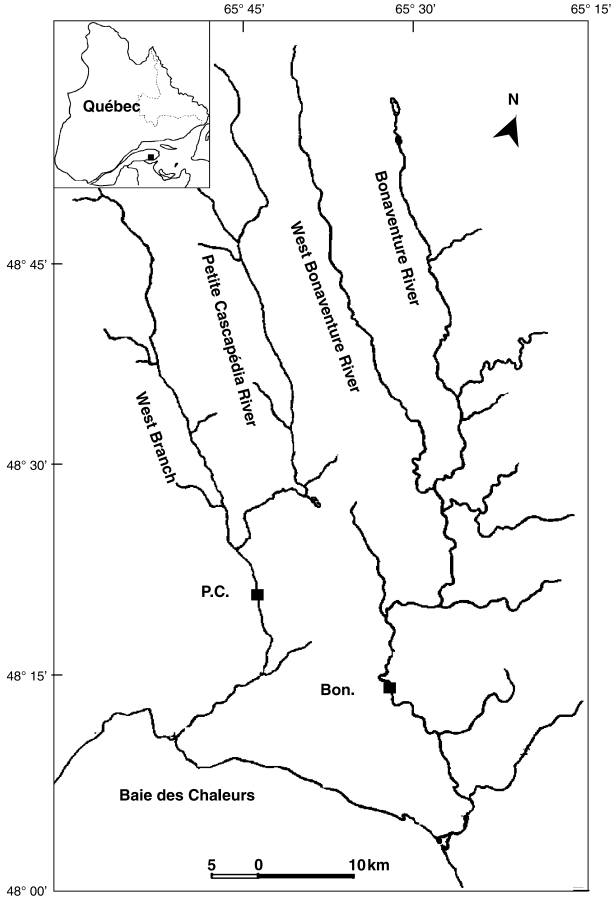

Fig. 1. Location of study sites Petite Cascapédia (P.C.) and Bonaventure River (Bon.), respectively, on the Petite Cascapédia and Bonaventure River (Québec, Canada). [Map was kindly provided by D. Bourdages & É. Boudreau, Gestionnaires de rivières à saumon du Québec (GRSQ)].

Otolith preparation and analysis

We followed broadly the steps described in Stevenson & Campana (1992) for otolith preparation and more precisely the procedures for otoliths of Atlantic salmon described by Aubin-Horth & Dodson (2002). Sagittal otoliths were extracted, cleaned and mounted (with sulcus face up) on microscope slides with thermoplastic glue. They were lightly ground on fine abrasive paper to the level of the core in order to improve the visibility of the increments. The preparations were viewed in light microscopy at magnifications of 200 and 400×. The microscope was coupled to a frame grabber and a calibrated image analysis system (Scion Image for Windows 2.0, Frederick, MD, USA). Otolith total radius length, radius length at hatching and radius length at emergence were measured along a constant axis using a digitized and calibrated image of the otolith (Fig. 2). A line starting in the central nucleus and forming a 45-degree angle with the posterior axis in the ventral region defined this constant axis (Fig. 2).

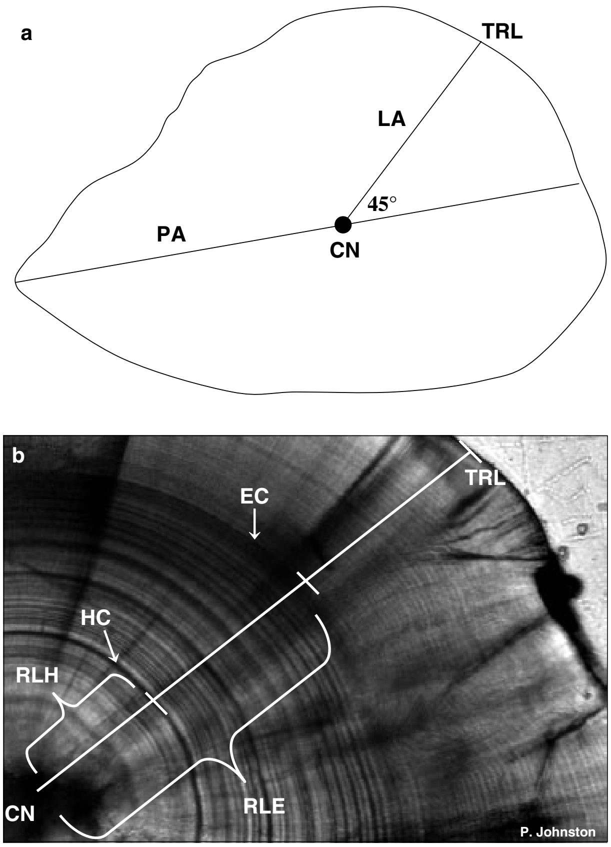

Fig. 2. (a) Schematic view of an otolith showing the different axes of measurement. PA, posterior axis; CN, central nucleus; LA, longitudinal axis; TRL, total radius length. (b) Otolith of a YOY salmon at 400× magnification. CN, central nucleus; HC, hatching check; RLH, radius length at hatching; EC, emergence check; RLE, radius length at emergence; TRL, total radius length.

Data analysis

The somatic lengths of salmon at hatching and at emergence were back calculated for pre- and postwinter samples using the biological intercept technique (Campana & Jones 1992). Assumptions of the back-calculation technique, such as daily increment formation and proportionality between the otolith and somatic growth, have previously been validated for YOY Atlantic salmon. These assumptions have been shown to be valid at hatching to emergence from the substrate, from this stage until they are aged about 300 days and also for precocious males (Wright et al. 1990; Meekan et al. 1998a; Aubin-Horth & Dodson 2002). Meekan et al. (1998a) also demonstrated that distinctive marks are laid down on the otoliths at hatching and at emergence, allowing for the identification of these events on the otoliths. The somatic–otolith size relationship was assessed with Pearson's linear correlation and a simple regression approach. An analysis of covariance was also performed to determine if regression lines for the two rivers were different. In order to detect size-selective mortality, a one-factor analysis of variance (ANOVA) was used to test the null hypothesis that back-calculated lengths at hatching and at emergence were similar between sampling occasions. Shifts in distribution of size at hatching and emergence between the pre- and postwinter samples were used as evidence to show that the cohort had undergone selective mortality (West & Larkin 1987; Meekan et al. 1998a,b; Good et al. 2001). The analysis of the size distribution of survivors implies typically a back calculation of sizes at the time of the initial sampling but, in this study, size at hatching and emergence were back-calculated for all individuals. In fact, identification of the increment corresponding to the first sampling time (prewinter) was impossible on otoliths of fish collected in summer 2001 (postwinter) because the increments deposited during winter formed a large dark zone on the otolith from which single increments could not be discerned. Therefore, we assumed that large-sized individuals at hatching and emergence have maintained their advantage in size throughout the year, which has been previously observed (Aubin-Horth & Dodson 2004). Using the Kolmogorov–Smirnov test, a length distributions analysis was performed to compare the size of collected salmon for the pre- and postwinter samples of each river as well as between the rivers for each sampling occasion.

The number of increments between hatching and emergence marks was counted on the otoliths in order to evaluate the growth, growth rate and duration of the pre-emergence period. The absolute growth during this period was calculated by subtracting back-calculated somatic length at emergence from the back-calculated length at hatching. The growth rate was obtained from the ratio between absolute growth and the number of increments (days) between hatching and emergence. A one-factor ANOVA was used to compare the pre-emergence growth, duration and growth rate between sampling occasions for fish of each river. All statistical analyses were performed using STATISTICA, StatSoft, Inc. (1997).

Results

Although 50 individuals were collected from each river on each of the two sampling occasions, the effective sample sizes are smaller because of chipped and fissured otoliths created during sample preparation, and of vateritic otoliths (Campana & Jones 1992) which cannot be used for analysis. Two independent readers first identified the hatch and emergence checks before the size-selective mortality analysis. Only the otoliths where the same checks were identified by the two readers were kept. Nevertheless, measurements of total radius were possible with most of the otoliths so they were almost all included in the analysis of the somatic–otolith size relationship.

Length distribution of YOY salmon of pre- and postwinter samples

The length distribution of YOY salmon was compared between rivers for both the pre- and postwinter samples. For the prewinter samples we observed that length distribution of YOY salmon of the Petite Cascapédia River was significantly different than that of the Bonaventure River (Kolmogorov–Smirnov test, $P < 0.001$) (Fig. 3a). YOY salmon of the Petite Cascapédia River were larger than those of the Bonaventure River [mean: P.C. = 53.7 mm ($N = 34$); Bon. = 48.9 mm ($N = 38$)]. However, comparison of the postwinter samples did not show significant length distribution differences between the Petite Cascapédia and the Bonaventure River (Kolmogorov–Smirnov test, $P > 0.10$) (Fig. 3b). The mean length for the YOY of the Petite Cascapédia River was 57.2 mm ($N = 31$) and 60.1 mm ($N = 42$) for those of the Bonaventure River. For both rivers, YOY salmon increased in length between the pre- and the postwinter samples (Kolmogorov–Smirnov test: P.C. $P < 0.03$, Bon. $P < 0.001$; Fig. 3).

Somatic–otolith size relationship

In both rivers, there was a significant linear correlation between otolith radius and somatic length of YOY salmon [P.C. $R = 0.54$, $P < 0.05$ ($N = 65$); Bon. $R = 0.75$, $P < 0.05$ ($N = 80$)] and the regression lines were significantly different (ANCOVA: $F_{1,142} = 19.31$, $P < 0.001$) (P.C. $y = 86.94x + 21.68$; Bon. $y = 111.55x + 8.58$), justifying the nongrouping of the data. This difference in regression parameters does not however affect the accuracy of back-calculations using the biological intercept technique because the fish-otolith slope is calculated independently for each fish (Campana & Jones 1992). Nonlinearity in the somatic–otolith size relationship causes higher bias in back-calculations than variations around the intercept value (Campana & Jones 1992).

Assessment of size-selective mortality

Lengths at hatching and at emergence were back-calculated for fish of the pre- and the postwinter samples. For YOY salmon of the Petite Cascapédia River, no significant shifts were recorded for the length at hatching or the length at emergence between the pre- and the postwinter samples (ANOVA, hatching: $F_{1,58} = 0.62$, $P = 0.44$; emergence: $F_{1,53} = 0.06$, $P = 0.81$; Fig. 4a,b). The mean size at hatching of

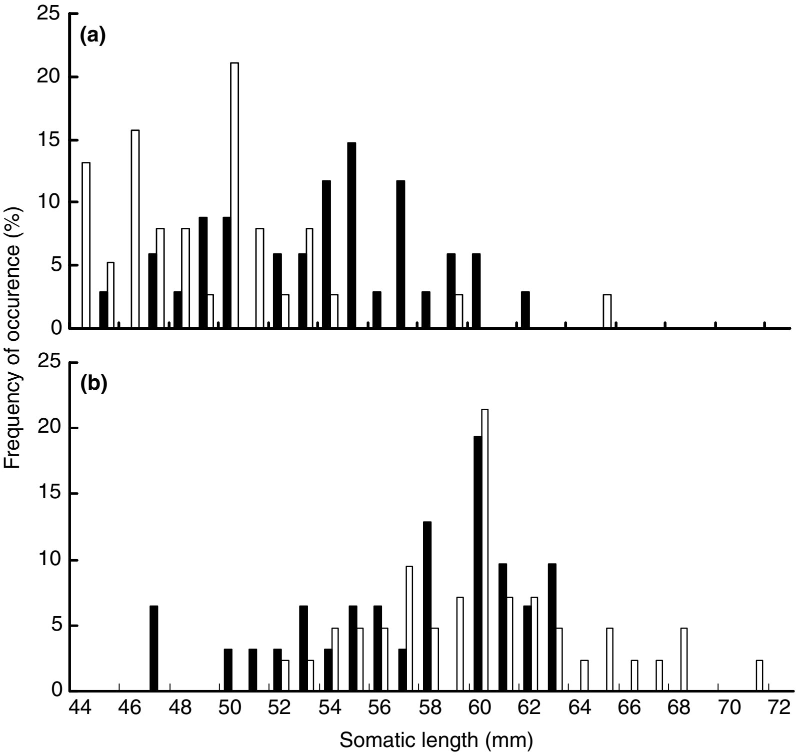

Fig. 3. Size distributions of YOY salmon (a) in prewinter sample and, (b) in postwinter sample of the Petite Cascapédia (solid bars) and Bonaventure (open bars) rivers.

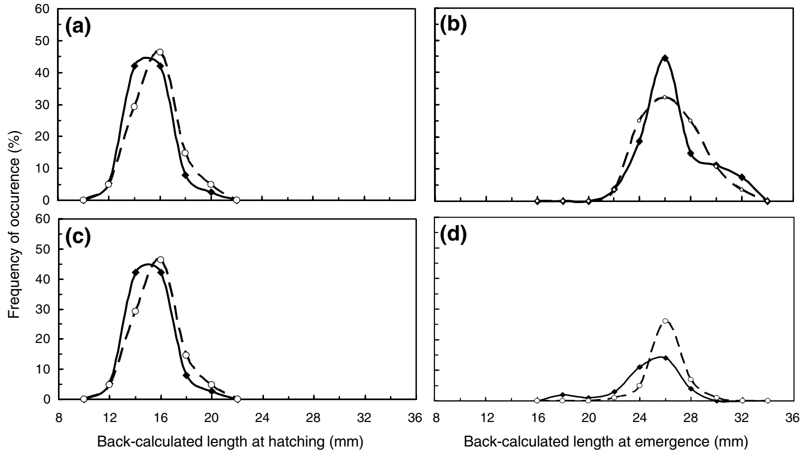

Fig. 4. Back-calculated length (a) at hatching and, (b) at emergence for YOY salmon of the Petite Cascapédia and back-calculated length (c) at hatching and, (d) at emergence for YOY salmon of Bonaventure River. Solid lines with squares represent prewinter samples and dashed lines with open circles represent postwinter samples.

fish collected in pre- and postwinter samples were 15.1 mm (SD ±1.68, $N = 34$) and 15.5 mm (SD ±2.07, $N = 26$), respectively, while mean size at emergence for fish of the prewinter sample was 25.8 mm (SD ±2.33, $N = 27$) and 25.5 mm (SD ±2.34, $N = 28$) for salmon of the postwinter sample.

For the Bonaventure River, no significant shift in back-calculated length at hatching was observed between the pre- and postwinter samples (ANOVA, $F_{1,77} = 1.28$, $P = 0.25$) (Fig. 4c). Mean size at hatching for fish collected in prewinter was 14.3 mm (S.D. ±1.55, $N = 38$) while fish caught in the postwinter sample had a mean size at hatching of 14.7 mm (SD ±1.79, $N = 41$). Back-calculation results of the size at emergence revealed however significant differences between the size of salmon sampled in prewinter (mean = 23.6 mm, SD ±2.28, $N = 35$) and postwinter (mean = 25.2 mm, SD ±1.47, $N = 40$) (ANOVA, $F_{1,73} = 13.06$, $P < 0.001$) (Fig. 4d).

Pre-emergence absolute growth, duration and growth rate

The pre-emergence absolute growth, duration and growth rate were calculated for fish of all samples. For the Petite Cascapédia River, no significant differences were found between the pre- and the postwinter samples for absolute growth, number of days spent in the substrate and growth rate of pre-emergent salmon

Table 1. Mean values, standard deviations and statistics (one-way ANOVA) for pre-emergence absolute growth, duration and growth rate for the Petite Cascapédia River and the Bonaventure River.

	Mean prewinter	Mean postwinter	SD prewinter	SD postwinter	*F*	*P*-value
Petite Cascapédia						
Absolute growth†	10.59 mm ($N = 27$)	10.04 mm ($N = 23$)	±2.25	±2.17	0.75	0.39
Duration‡	22.60 days ($N = 5$)	20.00 days ($N = 12$)	±3.36	±3.84	1.73	0.21
Growth rate§	0.39 mm·day^{-1} ($N = 5$)	0.53 mm·day^{-1} ($N = 12$)	±0.14	±0.15	2.96	0.11
Bonaventure						
Absolute growth†	9.17 mm ($N = 35$)	10.49 mm ($N = 39$)	±2.26	±1.88	7.58	0.007*
Duration‡	19.47 days ($N = 28$)	26.58 days ($N = 24$)	±6.42	±6.08	16.68	0.001*
Growth rate§	0.50 mm·day^{-1} ($N = 28$)	0.42 mm·day^{-1} ($N = 24$)	±0.13	±0.08	7.54	0.008*

*indicates significant statistics.

†Absolute growth was calculated by subtracting back-calculated somatic length at emergence from the back-calculated length at hatching.

‡Duration of the pre-emergence period corresponds to the number of increments (days) between hatching and emergence checks on the otoliths.

§Growth rate was obtained by the ratio between absolute growth and the number of increments between hatching and emergence.

(Table 1). As otoliths from the prewinter sample were very opaque, accurate counting of daily increments was very difficult. Consequently, almost all otoliths of this sample were eliminated from this analysis, reducing the sample size from 27 to five specimens. Thus, only the pre- and postwinter comparison of pre-emergence growth could be considered for this river. For the Bonaventure River absolute growth and the number of days spent in the substrate were significantly higher for individuals of the postwinter sample, while the growth rate was lower for individuals of this sample (Table 1). Unlike the otoliths of the Petite Cascapédia samples, those of the Bonaventure River were clear so we consider that the counting of the increments was accurate.

Discussion

Size-selective mortality

The results of this study did not reveal any size-selective mortality of YOY salmon in the Petite Cascapédia River, whereas, size-selective mortality against smaller individuals was detected in the Bonaventure River for the cohort of year 2000. These observations invalidate our initial hypotheses of an increased mortality of the smallest YOY salmon in the Petite Cascapédia River and that of random mortality for fish of the Bonaventure River.

The fact that no size-selective mortality was observed for YOY of the Petite Cascapédia River indicates that either size-selective mortality has not been detected or that it has not occurred. Indeed, three conditions in particular make the detection of size-selective mortality difficult (reviewed in Sogard 1997). Firstly, high mortality is necessary to allow for detection of size-selectivity as nonrandom but low mortality may not modify the size distribution of the survivors. As winter mortality of YOY salmon is considerable in the Petite Cascapédia River (Boudreau & Bourdages 2000), we should have been able to detect size-selective mortality. Secondly, physical mortality factors that are non-selective (temperature extremes, oxygen depletion, etc.) can override selective mortality factors (predation, etc.), thus masking the effects of size selection (Sogard 1997). Thirdly, the direction of selective mortality may switch across time periods, thus a single analysis at the end of this progression may indicate only random mortality. As we were unable to determine whether the latter two conditions occurred during our study, we cautiously conclude that the nondetection of size-selective mortality indicates that mortality was random for YOY salmon of the Petite Cascapédia River. The low availability of coarse substrate and winter habitat did not have a selective effect as expected. Nevertheless, a study of juvenile salmon on this river has shown an adoption of a nocturnal activity pattern throughout most of the year because of the relatively low summer water temperatures (Johnston et al. 2004). They therefore need coarse substrate to shelter under during the day, as in winter habitat, to survive. Thus, size-selective mortality associated with a low availability of suitable winter habitat (Coulombe-Pontbriand & Lapointe 2004) could have occurred prior to our prewinter sampling. In order to clarify the population dynamics in this river, the identification of significant mortality factors appears particularly important while smaller sampling intervals (i.e., months) over a longer period of time (i.e., summer and winter for a few years) would allow the identification of critical selection periods and a more accurate follow up of population abundance.

For the Bonaventure River, size-selective mortality was detected using back-calculated length at emergence but not with the back-calculated length at hatching. As larger individuals at hatching are thought to be the larger individuals at emergence as well, these results were initially difficult to explain. However, analysis of the pre-emergence absolute growth, duration and growth rate showed significant differences between the pre- and the postwinter samples. Individuals of the postwinter sample (survivors) had a higher absolute growth, stayed longer in the substrate before emerging and their growth rate was lower than for individuals of the prewinter sample. These results suggest that the individuals that emerged earlier and with a smaller body size had a lower survival than those that emerged later in the season but with a larger body size. However, the fact that survivors stayed longer in the substrate before emerging does not necessarily mean that they emerged later. In fact, a maternal effect through an earlier breeding date or a larger egg size providing more energy reserves to the offspring may have accounted for a longer stay in the substrate. According to Einum & Fleming (2000), the timing of emergence appears to be under higher selective pressure than body size. Because of the quality of the otoliths in the samples and the high density of the increments during winter, the precise date of emergence could not be back-calculated in this study. Therefore, any conclusion on the emergence date for fish sampled in this study is speculative. In addition to the maternal effect, incubation conditions (dissolved oxygen, substrate quality, etc.) play an important role in determining growth, timing of emergence and survival (reviewed in Chapman 1988). Our results suggest that size at emergence might be more determinant than size at hatching for survival, explaining why size-selective mortality was detected using back-calculated length at emergence and not with the back-calculated length at hatching.

Size-selective mortality against smaller fish of the Bonaventure River supports the widely held view that large size provides advantages in terms of competition and survival (West & Larkin 1987; Smith & Griffith 1994; Sogard 1997; Meekan et al. 1998a). It is possible that size selective mortality of smaller individuals was because of their insufficient energy stores leading to death by starvation during winter. Another possible cause of size selection might be competition between small and large individuals (including both YOY and PYOY salmon). Larger fish might occupy all available refuges or may dislodge smaller conspecifics (Harwood et al. 2002) which are subsequently more likely to be removed from the population by predation (Gregory & Griffith 1996; Armstrong & Griffith 2001). Environmental conditions might allow the survival of small individuals during the summer, while in winter, harsh conditions coupled with an increased use of interstitial refuges might induce competition constraining survival.

Size distributions

In fall 2000, YOY salmon of the Petite Cascapédia River were significantly larger at capture than those of the Bonaventure River whereas no differences were detected in the postwinter samples. Available annual electrofishing data (1989–1992, 2000) also shows a similar difference in size distributions for the early fall of three (1990–1992) of 5 years (É. Boudreau and D. Bourdages, unpublished data), which indicate that this is a recurrent trend. This difference in length distribution in fall samples may be caused by either higher growth of the Petite Cascapédia fish or by summer size-selective mortality directed towards the smaller fish of this river. In fact, summer size-dependent mortality is suspected in this river because of some limiting habitat features (discussed above) and there is also some evidence of competition and predation of YOY salmon by slimy sculpin (N.E. Bergeron and S. Heppel, unpublished data), which is very abundant in this river. Size-selective mortality can be a key determinant of mean size attained by the end of the first summer of life (Good et al. 2001). As summer size-selective mortality was not assessed in this study, the effect of growth and size-selective mortality on size distributions could not be disentangled. Similarly, the attainment of a similar body size after the winter for fish of both rivers could be explained by an earlier resumption of growth and/or higher growth rates for fish of the Bonaventure River relative to those of the Petite Cascapédia River combined with the effect of the high mortality of the smallest individuals in the population. The extent to which winter size-selective mortality played a role in displacing mean size could not however be quantified.

Usefulness of otolith microstructure analysis

One purpose of this study was to assess the usefulness of otolith microstructure analysis to detect winter size-selective mortality of YOY Atlantic salmon. This method has proved to be a relatively simple and efficient way to gather information about the winter dynamics of juvenile salmon, allowing a better comprehension of the populations under study. However, there are inherent uncertainties and specific limitations associated with otolith analysis. Among others, unbiased sampling of the same population must be carried out (as for all field methods) (Sogard 1997), assumptions of the back-calculation technique have to be met (Stevenson & Campana 1992; Sogard 1997) and intrinsic measurement errors must be taken into consideration in the interpretation of the results (Meekan et al. 1998a). One limitation of our study design was that it did not allow the discrimination between mortality and emigration but, as densities of juvenile salmon remained relatively similar between the sampling occasions, movements were not suspected to have caused a significant bias in this study. However, obtaining an estimate of emigration–immigration processes, by marking fishes or isolating river sections, should improve future estimates of selective mortality.

The issue of fish movements should be addressed along with the question of spatial and temporal scales of sampling. In order to better understand fish dynamics in a given river, many representative sites should be sampled over relatively short time periods to ensure that critical selection periods (i.e., emergence, winter) and conditions (i.e., temperature, ice) are being documented (Sogard 1997). We found that otolith microstructure analysis is one of the most practical methods for assessing size-selective mortality during the winter season, as it is difficult to sample fish in the wild during this period. The comparison of fish length distributions alone to assess size-selective mortality entails a high potential for misinterpretation because of growth that can bias estimation of size selection (Sogard 1997; Good et al. 2001). In fact, the conclusions that could be drawn from fish length distributions or from otolith analysis were different in this study. Otolith analysis has valuable applications in population dynamics studies and constitutes a good tool for researchers or managers. Nevertheless, much research is still needed regarding the major sources of mortality and their impact on juvenile fishes and their recruitment to older life-history stages.

Resumen

1. Los objetivos de este estudio fueron, primero, evaluar la utilidad de analizar la micro-estructura de los otolitos para examinar la mortalidad invernal selectiva del tamaño en jóvenes del año (Y-O-Y) de *Salmo salar*. Segundo, validar varias hipótesis relacionadas con la dinámica de dos poblaciones con supervivencias invernales distintas.
2. Examinando la micro-estructura de los otolitos, retro-calculamos el tamaño corporal en el nacimiento y en la emergencia de Y-O-Y de *S. salar* muestreados en el otoño del año 2000 y al inicio del verano del año 2001 en los ríos Petite Cascapédia y Bonaventure (Québec, Canada).
3. Los resultados no revelaron mortalidad selectiva del tamaño en los Y-O-Y de *S. salar* del río Petite Cascapédia pero sí en el río Bonaventure donde detectamos una mortalidad selectiva del tamaño operando sobre los individuos más pequeños.
4. Este estudio ha permitido no solo una mejor comprensión de la dinámica de las poblaciones sino que demuestra la utilidad del análisis de los otolitos parta detectar mortalidad invernal selectiva del tamaño en ambientes naturales.

Acknowledgements

We would like to thank Marc-André Pouliot, Patrice Carbonneau, Antoine Morissette, Marie-Josée Gagnon, Cécile Lague for assistance in field work, Annie Ménard, Nadia Aubin-Horth and Véronique Thériault, who helped with laboratory manipulations. Thanks to partners: Société de la Faune et des Parcs du Québec (New Richmond), Z.E.C. Petite Cascapédia, Association des pêcheurs sportifs de la rivière Bonaventure. Special thanks to Martin Dorais (FAPAQ), Pascal Moreau and Gaétane Bujold (Z.E.C. Petite Cascapédia), Ronald Cormier, David Bourdages and Éric Boudreau (APSB). We would also like to thank an anonymous referee for comments on an earlier version of this manuscript. FCAR-Équipe and CIRSA funding to N.E. Bergeron supported this study. A postgraduate scholarship grant by the Fonds de recherche sur la nature et les technologies was provided to Patricia Johnston.

References

Armstrong, J.D. & Griffith, S.W. 2001. Density-dependent refuge use among over- wintering wild Atlantic salmon juveniles. Journal of Fish Biology 58: 1524–1530.

Aubin-Horth, N. 2002. Déterminisme de la variabilité à micro-échelle d'une stratégie de reproduction conditionnelle chez le saumon atlantique (*Salmo salar*) mâle. Ph.D. thesis. Québec, Québec: Université Laval.

Aubin-Horth, N. & Dodson, J.J. 2002. Impact of differential energy allocation in Atlantic salmon (*Salmo salar*) precocious males on otolith-somatic size proportionality: a longitudinal approach. Canadian Journal of Fisheries and Aquatic Sciences 59: 1575–1583.

Aubin-Horth, N. & Dodson, J.J. 2004. Influence of individual body size and variable thresholds on the incidence of a sneaker male reproductive tactic in Atlantic salmon. Evolution 58: 136–144.

Bjornn, T.C. 1971. Trout and salmon movements in two Idaho streams as related to temperature, food, stream flow, cover, and population density. Transactions of the American Fisheries Society 100: 423–438.

Boudreau, É. & Bourdages, D. 2000. Inventaire ichtyologique par la pêche à l'électricité dans la rivière Petite Cascapédia, été 2000. Bonaventure, QC, Canada: Projet des 4 rivières, pour l'Association des Pêcheurs Sportifs de la Bonaventure.

Bourdages, D. & Boudreau, É. 2001. Inventaire ichtyologique par la pêche à l'électricité dans la rivière Bonaventure, été 2000. Bonaventure, QC, Canada: Projet des 4 rivières, pour l'Association des Pêcheurs Sportifs de la Bonaventure.

Campana, S.E. & Jones, C.M. 1992. Analysis of otolith microstructure data. In: Stevenson, D.K. & Campana, S.E., eds. Otolith microstructure examination and analysis. Canadian Special Publication of Fisheries and Aquatic Sciences, 117: 73–100.

Chapman, D.W. 1988. Critical review of variables used to define effects of fines in redds of large salmonids. Transactions of the American Fisheries Society 117: 1–21.

Coulombe-Pontbriand, M. & Lapointe, M. 2004. Landscape controls on boulder-rich, winter habitat availability and their effects on Atlantic salmon (*Salmo salar*) parr abundance in two fifth-order mountain streams. Canadian Journal of Fisheries and Aquatic Sciences 61: 648–658.

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

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

Gregory, J.S. & Griffith, J.S. 1996. Aggressive behaviour of underyearling rainbow trout in simulated winter concealment habitat. Journal of Fish Biology 49: 237–245.

Harwood, A.J., Metcalfe, N.B., Griffiths, S.W. & Armstrong, J.C. 2002. Intra- and inter-specific competition for winter concealment habitat in juvenile salmonids. Canadian Journal of Fisheries and Aquatic Sciences 59: 1515–1523.

Hendry, A.P., Letcher, B.H. & Gries, G. 2003. Estimating natural selection acting on stream-dwelling Atlantic salmon: implications for the restoration of extirpated populations. Conservation Biology 17: 795–805.

Hunt, R.L. 1969. Overwinter survival of wild fingerling brook trout in Lawrence Creek, Wisconsin. Journal of the Fisheries Research Board of Canada 26: 1473–1483.

Johnston, P., Bergeron, N.E. & Dodson, J.J. 2004. Diel activity patterns of juvenile Atlantic salmon (*Salmo salar*) in rivers with summer water temperature near the temperature-dependent suppression of diurnal activity. Journal of Fish Biology 65: 1305–1318.

Lindroth, A. 1965. First winter mortality of Atlantic salmon parr in the hatchery. Canadian Fish Culturist 36: 23–26.

Lund, E., Olsen, E.M. & Vollestad, L.A. 2003. First-year survival of brown trout in three Norvegian streams. Journal of Fish Biology 62: 323–340.

Mason, J.C. 1976. Response of underyearling coho salmon to supplement feeding in a natural stream. Journal of Wildlife Management 40: 775–778.

Meekan, M.G., Dodson, J.J., Good, S.P. & Ryan, D.A.J. 1998a. Otolith and fish size relationships, measurement error, and size-selective mortality during the early life of Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 55: 1663–1673.

Meekan, M.G., Ryan, D.A.J., Dodson, J.J. & Good, S.P. 1998b. Does mortality select size or growth potential in young sockeye salmon (*Oncorhynchus nerka*)? A simulation based on otolith-fish size relationships. Canadian Journal of Fisheries and Aquatic Sciences 55: 1674–1681.

Meyer, K.A. & Griffith, J.S. 1997. First-winter survival of rainbow trout and brook trout in the Henrys Fork of the Snake River, Idaho. Canadian Journal of Zoology 75: 59–63.

Smith, R.W. & Griffith, J.S. 1994. Survival of rainbow trout during their first winter in the Henrys Fork of the Snake River, Idaho. Transactions of the American Fisheries Society 1123: 747–756.

Sogard, S.M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bulletin of Marine Sciences 60: 1129–1157.

STATISTICA, StatSoft, Inc. 1997. STATISTICA for Windows (Computer program manual). Tulsa, OK: StatSoft, Inc. Available at: http://www.statsoft.com.

Stevenson, D.K. & Campana, S.E. (eds). 1992. Otolith microstructure examination and analysis. Canadian Special Publication of Fisheries and Aquatic Sciences 117.

West, C.J. & Larkin, P.A. 1987. Evidence for size-selective mortality of juvenile sockeye salmon (*Oncorhynchus nerka*) in Babine Lake, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 44: 712–721.

Wright, P., Metcalfe, N.B. & Thorpe, J.E. 1990. Otolith and somatic growth rates in Atlantic salmon parr, *Salmo salar* L.: evidence against coupling. Journal of Fish Biology 36: 241–249.