

The relationship between smolt and postsmolt growth for Atlantic salmon (*Salmo salar*) in the Gulf of St. Lawrence

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The interaction of ocean climate and growth conditions during the postsmolt phase is emerging as the primary hypothesis to explain patterns of adult recruitment for individual stocks and stock complexes of Atlantic salmon (*Salmo salar*). Friedland et al. (1993) first reported that contrast in sea surface temperature (SST) conditions during spring appeared to be related to recruitment of the European stock complex. This hypothesis was further supported by the relationship between cohort specific patterns of recruitment for two index stocks and regional scale SST (Friedland et al., 1998). One of the index stocks, the North Esk of Scotland, was shown to have a pattern of postsmolt growth that was positively correlated with survival,

indicating that growth during the postsmolt year controls survival and recruitment (Friedland et al., 2000). A similar scenario is emerging for the North American stock complex where contrast in ocean conditions during spring in the postsmolt migration corridors was associated with the recruitment pattern of the stock complex (Friedland et al., 2003a, 2003b). The accumulation of additional data on the postsmolt growth response of both stock complexes will contribute to a better understanding of the recruitment process in Atlantic salmon.

Anadromous salmonids produce cohorts of juvenile smolts that migrate over a short period of time at a nearly uniform size; however, the variability that occurs in migration timing and

the size spectra of smolts is of potential interest in the study of recruitment (Hoar, 1976; Wedemeyer et al., 1980). Enhancement and restoration programs provide data on the effect of smolt size on return rate where hatchery practices both intentionally and unintentionally produce fish of varying size and quality. There are many case studies that show positive correlations between smolt size and return rate in salmonids, but non-significant relationships have also been observed, which underscore the fact that the contrast in size that can be achieved in hatcheries is often outside ecologically relevant limits (Farmer, 1994; Salminen et al., 1994). The functional relationship between smolt size and return rate is probably more accurately described as nonlinear and as having some optimality within the range of hatchery releases (Bilton et al., 1982; Henderson and Cass, 1991).

Researchers have also considered the effect of smolt size at ocean entry and the effect of smolt size on the ensuing growth patterns of postsmolts. Ward and Slaney (1988) described a positive relationship between return rate and smolt size for rainbow trout (*Salmo gairdneri*), suggesting that the recruitment rate of a year class was mediated by the mortality that occurred when the fish migrated to sea. When new data were added to that relationship, the original conclusions were no longer supported, indicating that factors other than smolt size at ocean entry contribute to recruitment (Ward, 2000). Although size at ocean entry may contribute to mortality risk, postsmolt growth, and the biotic and abiotic factors affecting postsmolt growth, often play a dominant role (Salminen et al., 1995). However, what has remained obscure is whether size at ocean entry influences postsmolt growth. Skilbrei (1989) and Nicieza and Branña (1993) reported negative relationships between smolt size and

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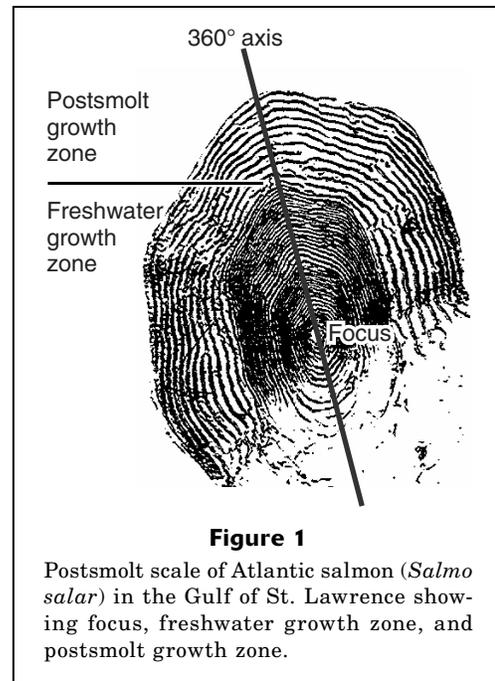
marine growth in Atlantic salmon, whereas Lundquist et al. (1988) and Salminen (1997) reported positive relationships. Einum et al. (2002) reported an inverse relationship between pre- and postsmolt growth of Atlantic salmon and suggested that phenotypic characteristics favoring growth in one environment may not necessarily favor growth in another. The body of mixed results sheds little light on whether smolt size confers a growth advantage to postsmolts. It also leaves in doubt the importance of freshwater experience on postsmolt survival. Common to this body of work is the dependence on samples coming from river returns and fishery catches that may not be representative of the full range of growth signatures in postsmolt populations because they do not include data from mortalities and often do not include data from some return age groups.

In this study we report on an analysis of scale growth indices from a collection of postsmolts from the Gulf of St. Lawrence. We measured freshwater growth signatures representative of smolt size and freshwater growth prior to migration and postsmolt growth was partitioned by season. These are samples of a life stage in an intermediate phase of marine life that is infrequently sampled and may be free of some of the assumed biases associated with samples from spawning fish.

Material and methods

We collected data on scale circuli spacing that was representative of the freshwater and postsmolt growth for juvenile salmon captured in the Gulf of St. Lawrence. These postsmolt salmon were collected in 1982–84 and were originally reported in Dutil and Coutu (1988). They were captured in experimental gill nets along the northwest shore of the Gulf during the months of August to October.

Freshwater and postsmolt growth descriptors were interpreted from circuli spacing patterns deposited on the scale. Scales were cleaned and mounted between glass slides and the spacings of scale circuli were measured with a Bioscan Optimas (Media Cybernetics, Inc., Silver Spring, MD) image processing system. Freshwater zone length (FZL) was taken as the total distance from the center of the scale focus to the transition between freshwater and postsmolt growth (Fig. 1). This transition zone is defined by the appearance of the first marine intercirculus spacing, i.e., as a wider spacing (according to the reader's judgment) than the progression of spacings in the freshwater zone. The FZL ends at the last freshwater circulus. FZL was interpreted as a proxy for smolt length at migration. The mean of the last five circuli spacings during the freshwater phase was computed for each sample (CSLF, circuli spacing during last freshwater period). This circuli spacing index was interpreted as an indication of freshwater finishing growth (the final phases of freshwater growth prior to migration). Two circuli spacing indices were extracted from the postsmolt zone, the mean spacing between intercirculi 2 through 6—an interval which



was interpreted as the growth index for the early marine period (CSFM, circuli spacing during first marine period)—and the mean intercirculi spacing of the next five pairs occurring later in the postsmolt growth—an interval interpreted as an index of summer growth (CSSM, circuli spacing during summer marine period). The total length of the postsmolt growth zone was also extracted (MZL, marine zone length), which was the distance from the freshwater-marine transition, starting at the last freshwater circulus to the outer edge of the scale. All measurements were made on a single scale from each specimen along the 360° axis of the scale.

We tested the functional relationship between freshwater and marine growth, early and late marine growth, and seasonal progression of the growth zones using linear regression. We tested the significance of the slope parameters for each relationship as an indication of variable dependency.

We also considered whether these data might contribute to our understanding of size selective mortality by constructing a time series plot of FZL and MZL against date of capture. An anticipated positive trend in MZL would reflect growth during the marine phase, but any trend in FZL would reflect size-specific removals attributable to size at ocean entry.

Results

Measurements were taken from the scales of 587 postsmolts collected during 1982–84. FZL averaged 0.67 mm (SD=0.163) for all samples. CSLF averaged 0.022 mm (SD=0.0049), reflecting the slower growth and more narrowly spaced circuli of the freshwater zone. The two

circuli spacing indices from the postsmolt growth zone were larger in magnitude than the index from the freshwater zone. CSFM averaged 0.061 mm (SD=0.0109) and reflected a threefold increase in circuli spacing between the freshwater and marine zones. CSSM averaged 0.064 mm (SD=0.0100), reflecting the increased growth occurring within the duration of marine residency. MZL increased over time from approximately 0.6 mm in early August to 1.2 mm by mid-October.

The data we examined to test the relationship between smolt size and freshwater finishing growth and postsmolt growth indicate an absence of any linkage between the two growth environments. We found no significant relationships between smolt sizes as represented by FZL and either spring (CSFM) or summer (CSSM) postsmolt growth as represented by the circuli spacing indices. The scatter between CSFM and FZL suggests there were no linear trends for any of the study years (Fig. 2A). None of the three regressions had slopes significantly different from zero (Table 1). There was also an absence of any relationship between CSSM and FZL as evidenced by a similar pattern of scatter for the coordinates (Fig. 2B) and by an absence of significant slopes.

The relationship was further tested by considering the growth that occurs just prior to smolt migration as an indication of smolt condition at entry into the marine environment. As was the case with the bivariate relationships with FZL, CSLF was not a significant predictor of either CSFM or CSSM (Fig. 3). None of the slopes were significantly different from zero (Table 1).

Growth in the early and later part of the post-smolt season were correlated. There were significant positive linear relationships between CSSM and CSFM for all three years (Fig. 4), indicating that the postsmolts began their marine residence with rapid growth and continued to grow at a rapid rate through summer. The slopes of all three regressions were significantly different from zero (Table 1).

A time series plot of MZL, plotted by date of capture, shows an increasing trend reflecting the growth that postsmolts experience during early marine residence (Fig. 5). For the same fish, we also plotted FZL by date of capture and found a negative trend over time, indicating that FZL decreased during the period (Table 1), which would not be consistent with selective mortality of smolts of smaller initial size.

Discussion

Our main findings indicate that marine growth of post-smolt Atlantic salmon sampled from August to October in the Gulf of St. Lawrence was independent of freshwater growth history. Neither smolt size nor the last freshwater growth period of smolts prior to migration was related to postsmolt growth patterns. Furthermore,

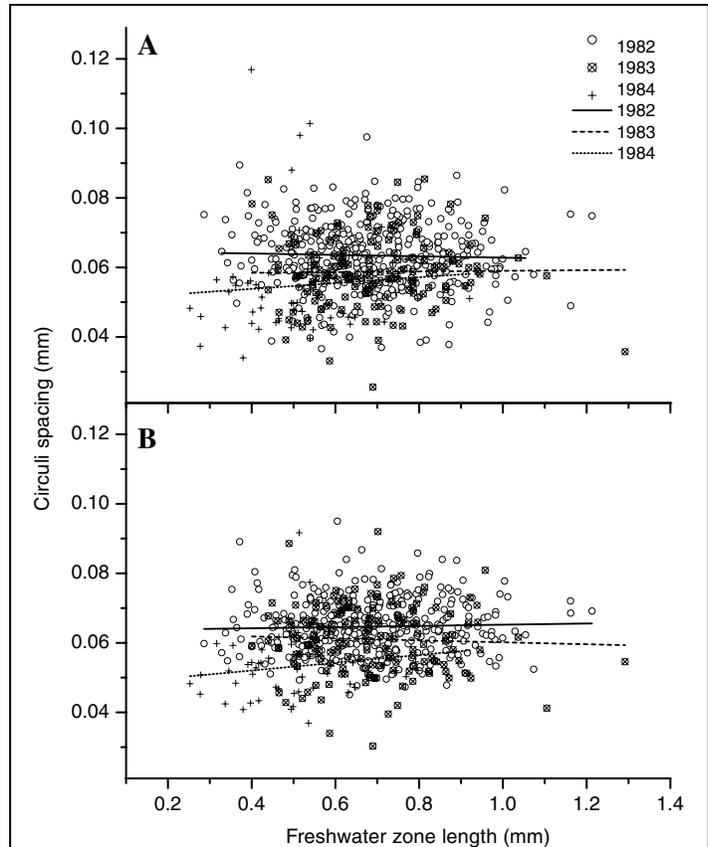


Figure 2
Relationships between circuli spacing during the early marine period (A) and circuli spacing during the summer marine period (B) and freshwater zone length for Atlantic salmon (*Salmo salar*) in the Gulf of St. Lawrence.

Table 1

Linear associations between scale growth indices and date of capture for Gulf of St. Lawrence Atlantic salmon (*Salmo salar*) postsmolts. FZL=freshwater zone length; CSLF=mean of the last five freshwater intercirculi spacings; CSFM=mean spacing of intercirculi spacings 2 through 6; CSSM=mean spacing of intercirculi spacings 7 through 11; DOC=date of capture.

Linear associations		Probability H_0 : slope = 0		
Predictor (X)	Dependent (Y)	1982	1983	1984
FZL	CSFM	0.53	0.87	0.57
FZL	CSSM	0.50	0.61	0.22
CSLF	CSFM	0.27	0.70	0.22
CSLF	CSSM	0.33	0.57	0.27
CSFM	CSSM	<0.01	<0.01	<0.01
DOC	FZL	<0.01		
DOC	MZL	<0.01		
Sample size		374	158	55

there was no evidence that size at the smolt stage of postsmolts captured later in the season was larger than those captured earlier in the season, indicating that there was no size-selective attrition on smaller smolts during August to October. The strength of these data is that the samples were derived from collections of postsmolts, not river returns or fishery catches, and thus it is less biased and more representative of natural mortality factors. It will take considerably more data to fully test this hypothesis, but the highest priority should be given to similar sample collections, especially those collected earlier in the year (Holm et al., 2000). These data will be pivotal in interpreting the relative impact of size at ocean entry versus postsmolt growth for determining postsmolt survival.

Understanding survival during the postsmolt period is of great importance in the face of declining stock abundance and possible stock extirpations over portions of the range of Atlantic salmon (Anderson et al., 2000). With evidence showing the success of conservation efforts to increase freshwater populations (Swansburg et al., 2002), the range of potential life stages

and habitats causing recruitment failure is reduced. Evidence at the population level showing coherence between early marine growth and survival at sea is still a long way from providing sufficient evidence to fully describe survival mechanisms or climate linkages. The hypothesized climate forcing appears to be related to a mismatch between ocean entry time for smolts and the thermal regime they find during their transition to marine life (Friedland et al., 2003b). The concept is supported by the growth response of postsmolts over a range of temperatures that they would likely encounter during that period of time. Atlantic salmon postsmolts follow a nonlinear growth response to temperature and optimum growth occurs at 13°C (Handeland et al., 2003). Variations in migration timing could result in fish encountering ocean conditions that are too warm or cool; these variations could explain the different associations of North American and European stocks to ocean temperatures. It would also be interesting to know if the thermal growth optimum is robust to varying feeding rations, which may be an issue for regional stock groups in the North Atlantic.

The transition period from freshwater to marine life is characterized by a number of dynamic changes in growth and predation. The highest mortality rates for postsmolts occur during the first weeks at sea (Eriksson, 1994). As a consequence, even a minimal variation in these rates will have a large impact on adult recruitment. Size-selective mortality on juveniles has been demonstrated for other salmonids such as sockeye salmon (*Oncorhynchus nerka*) and has been shown to be seasonally concentrated (West and Larkin, 1987). Size-specific predation often occurs but predators, such as adult bird species, are not likely to grow at corresponding rates to those of the fish (Dieperink et al., 2002). Thus, size at ocean entry and the ability to grow out of the size range vulnerable to specific predators must affect the dynamics of predation rate. The period of predation vulnerability is mediated by growth rate; therefore the argument returns to what confers faster growth on postsmolts in some years?

One dynamic that challenges all stocks is the transition from predominantly invertebrate to piscivorous prey. Some authors suggest it is the success in making this transition, or the time it takes to make the transition, that dictates the amount of time the postsmolts take to grow out of the predation-vulnerable size range (Dutil and Coutu, 1988; Andreassen et al., 2001; Salminen et al., 2001). Depending on prevailing foraging conditions, this transition may be promoted by increased smolt size, as was the case in the northern Baltic Sea in 1990–93 (Salminen et al., 2001). One potential explanation for the contradictory views on the relationship between pre- and postsmolt growth in

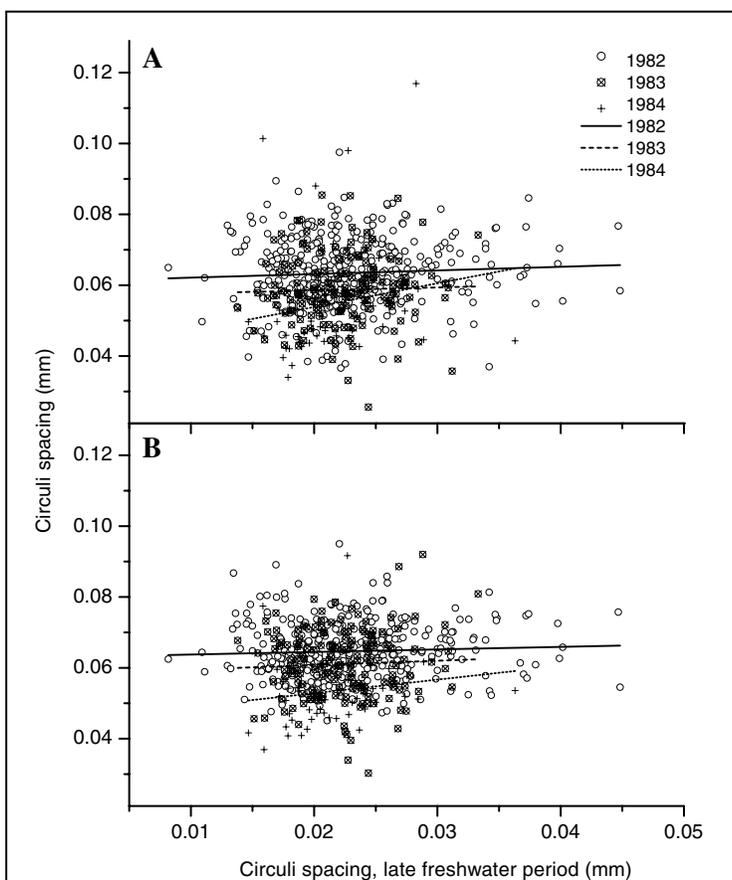


Figure 3

Relationships between circuli spacing during the early marine period (A) and circuli spacing during the summer marine period (B) and circuli spacing during the late freshwater period for Atlantic salmon (*Salmo salar*) in the Gulf of St. Lawrence.

Atlantic salmon may arise from geographical differences or year-to-year changes (or both) in prey regimes during the critical diet-transition period. In lake-run brown trout, Niva and Jokela (2000) found a positive correlation between hatchery growth rate and postsmolt growth in a lake with small fish as the main prey. In contrast, hatchery growth did not predict growth in a lake where the fish had to prey on bottom-dwelling invertebrates. This finding may indicate that assessment of individual performance may be highly specific to environments in migratory salmonids.

Size of postsmolts at ocean entry in salmonids also manifests itself in predictable patterns of life history variation. In sea trout (*Salmo trutta*) there is a close correspondence between size of juvenile stage and adult size, which is believed to have an impact on recruitment through size variation at critical life stages (Elliott, 1985). Hutchings and Jones (1998) found that smolt age and size had a small effect on the growth-rate threshold for maturity in Atlantic salmon. Smolt-size variation in sea trout has been associated with latitude, indicating that for this species recruitment strategies are likely adapted to local physical conditions, predators, and prey regimes (L'Abée-Lund et al., 1989). Wild smolts are often smaller than hatchery smolts for the same or allied strains, yet they consistently survive at higher rates (Poole et al., 2003). Obviously there are other cofactors that can explain why the wild fish overcome any advantage conferred on hatchery fish by their larger size at migration. The wild versus hatchery comparison is a relatively weak piece of evidence to use to dismiss the idea that smolt size is an important survival factor. However, a recent study of size at ocean entry in a Quebec stock of wild fish may provide more useful evidence (Dodson¹, Caron²). The investigators found that the size spectra of smolts were not different from the size spectra of back-calculated smolt sizes for returning adults, suggesting some factor other than size at ocean entry was controlling survival. It should be noted that postsmolts collected in the present study were of unknown origin, but the scale pattern for the freshwater zone clearly indicates that they were of wild origin.

The growth response of postsmolts may be governed by a simple response to temperature optima occurring in coastal marine waters, but it may also be more complex than that. The surface waters in the Gulf of St. Lawrence circulate in wide-scale

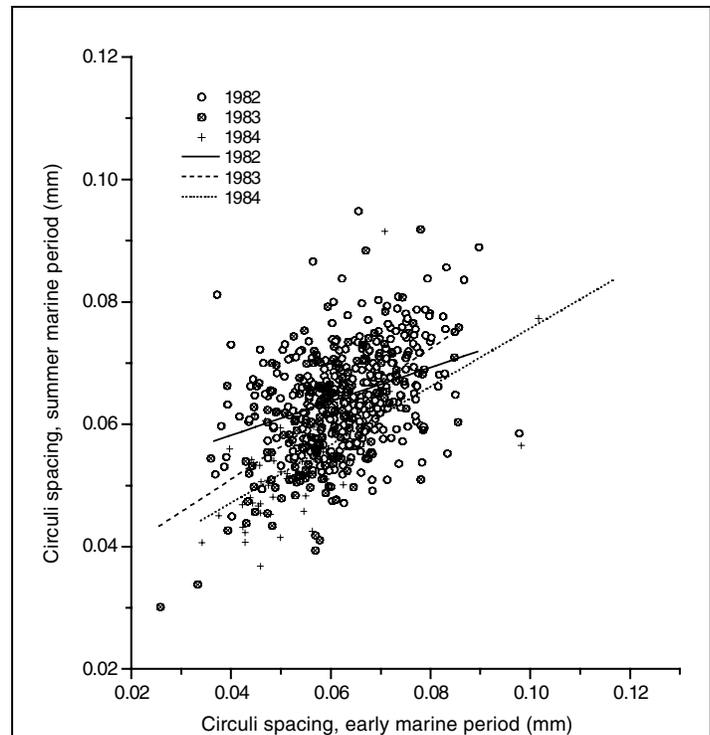


Figure 4

Relationships between circuli spacing during the summer marine period and circuli spacing during the early marine period for Atlantic salmon (*Salmo salar*) in the Gulf of St. Lawrence.

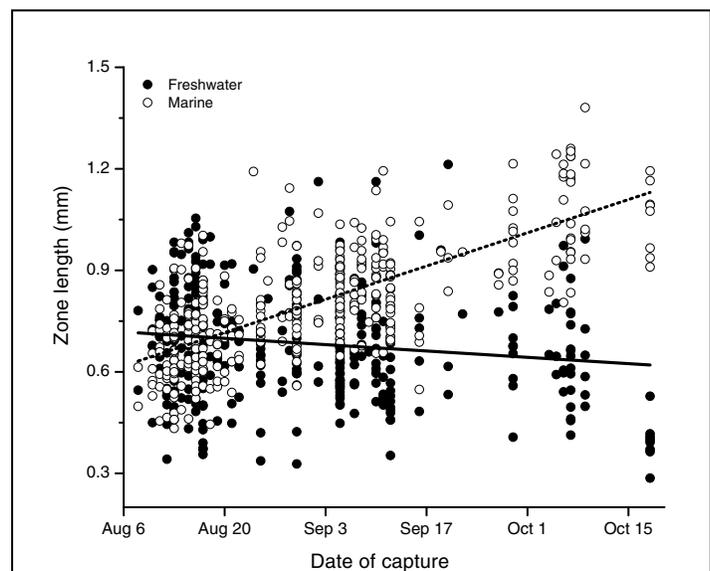


Figure 5

Freshwater zone length and marine zone length, by date of capture during the 1982 field season for Atlantic salmon (*Salmo salar*) in the Gulf of St. Lawrence.

¹ Dodson, J. 2004. Personal commun. Département de Biologie Pavillon Alexandre-Vachon, local 3058-B Université Laval, Québec, G1K 7P4, Canada.

² Caron, F. 2004. Personal commun. Direction de la Recherche Faune et Parcs Québec, 675 est, Boul. René-Lévesque Boîte 92, 11e étage, Québec, G1R 5V7, Canada.

gyres over the extremely cold waters of the cold intermediate layer (CIL), thus creating a thermally complex habitat. Strong winds periodically force cold waters from the CIL to the surface (Ouellet, 1997). Postsmolts appear to be opportunistic feeders in the ocean, and despite their predominant use of surface waters, they have been known to use benthic habitats and water column features as well (Levings, 1994; Sturlaugsson, 1994). These behaviors would distribute fish in a manner independent of surface temperatures because forage behaviors are not necessarily controlled by temperature preferences. Growth in postsmolts is also affected by other physical parameters, such as photoperiod (Forsberg, 1995), and possibly by variation in sea surface salinity as shown for chum salmon (*Oncorhynchus keta*) (Morita et al., 2001). We can predict migration timing and initial migration trajectories for postsmolts, but we are hard pressed to predict the physical nature of their habitats over time and the physiological effect of these habitats on postsmolt growth.

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