

# The emerging role of climate in post-smolt growth of Atlantic salmon

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Friedland, K. D., Chaput, G., and MacLean, J. C. 2005. The emerging role of climate in post-smolt growth of Atlantic salmon. — ICES Journal of Marine Science, 62: 1338–1349.

Though it is well established that mortality during the post-smolt year is critical in shaping recruitment patterns in Atlantic salmon (*Salmo salar* L.), the controlling mechanism for North Atlantic stocks remains elusive. The emerging paradigm is based on relationships between survival and ocean thermal conditions during the early marine phase. The survival of post-smolts from both Europe and North America has been correlated to sea surface temperature conditions during their first month at sea. In addition, data for European fish support the hypothesis that growth mediates survival during that time. Thus, the working model for a salmon recruitment mechanism is analogous to those proposed for other fish species. We present growth data for two stocks, the Gironck Burn, which is a tributary to the River Dee, Scotland, and the Margaree River, Canada. Circuli spacing data for Gironck Burn fish suggest post-smolt growth is negatively correlated with temperature in the migration corridors during the first months at sea, while post-smolt growth of Margaree fish appears to be positively correlated with temperature. Growth is either patterned by a physiological response to an optimal temperature, or is co-varying with some ecosystem effect on growth, and the growth response might affect mortality and maturation of the stocks.

Published by Elsevier Ltd on behalf of International Council for the Exploration of the Sea.

Keywords: Atlantic salmon, climate, growth, post-smolt.

Received 8 August 2004; accepted 25 April 2005.

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## Introduction

The selective advantage of anadromy is attributed to the protection of early life history stages provided by relatively sheltered and stable freshwater rearing habitats where spawning occurs (Gross *et al.*, 1988). Despite lower productivity than marine environments, sheltered freshwater rearing areas tend to produce stable recruitment to intermediate freshwater life stages, a phenomenon illustrated by Atlantic salmon (*Salmo salar* L.) life history (Chadwick, 1987). Hence, the freshwater portion of the life history is less commonly associated with the mechanisms that produce high or low recruitments. On the other hand, the marine phase is associated with variable survival, which in turn produces the wide swings in recruitment we observe on interannual and inter-decadal time scales (Bley and Moring, 1988; Jonsson *et al.*, 2003). Though the role of mortality

during the post-smolt year is critical in shaping recruitment patterns in Atlantic salmon, the nature of recruitment mechanisms for North Atlantic stocks has remained obscure.

A critical period for salmonids appears to be during the transition from freshwater to marine habitats. Salmon smolts are challenged by physiological stressors and exposed to a wider array of potential predators in marine habitats than in freshwater habitats (Magee *et al.*, 2003; Vehanen, 2003). The idea that this time period represents a recruitment bottleneck is supported by observations of Pacific (Fisher and Percy, 1988; Holtby *et al.*, 1990) and Baltic populations (Eriksson, 1994; Salminen *et al.*, 1995). Support for similar recruitment control in Atlantic salmon populations (McCormick *et al.*, 1998) comes from two sources, correlative analyses relating spring ocean climate conditions to recruitment and post-smolt growth analyses that relate growth to recruitment patterns.

Ocean conditions, as represented by sea surface temperature (SST) and variations in thermal habitat, show correlation with abundance and survival time-series in both North American and European stocks. Friedland *et al.* (1998a) analysed the survival time-series for two stocks from central Europe, one from southern Norway, and the other from eastern Scotland, and observed that thermal regimes during the first weeks at sea were correlated with their survival patterns. Climate mediation of survival was suggested by the environmental correlates; however, the nature of the survival mechanism was further elucidated with growth data for one of the two index stocks. In a follow-up study, Friedland *et al.* (2000) reported that post-smolt growth for the Scottish stock correlated to survival and climate conditions. Analogously similar to mechanisms hypothesized for larval and other juvenile fish, these data support the contention that recruitment patterning survival is simply a function of growth during a critical period, suggesting size-mediated predation control of salmon abundance as noted in other marine fish (Anderson, 1988; Pepin, 1991; Sogard, 1997). Environmental variation during spring has also been related to recruitment in North American fish. Friedland *et al.* (2003a, b) found that spring thermal conditions in the Gulf of St. Lawrence co-vary with recruitment time-series for North American stocks. European and North American salmon stocks appear to be responding to climate or to factors co-varying with SST. It is interesting, however, that the relationship between SST and survival appears to be negative in North America, opposite to what would be expected if temperature was directly affecting growth.

Post-smolt growth data for North American salmon are of limited utility in evaluating patterns of recruitment because of the origin of samples analysed thus far. A study comparing two hatchery stocks supports the view that survival rates between stocks can be related to post-smolt growth (Friedland *et al.*, 1996); however, no evidence is yet available for a North American stock to show that interannual variation in survival is related to post-smolt growth because of the absence of data for wild fish (Friedland, 1998).

Our goal with this investigation is to examine the early marine growth of two stocks, the Gironck Burn, which is a tributary to the River Dee, Scotland, and the Margaree River, Canada, and to relate their growth patterns to SST conditions along the putative post-smolt migration pathways of the fish.

## Methods

The two systems, which are the focus of this study, are relatively pristine river systems supporting self-sustaining stocks of Atlantic salmon. The Gironck Burn is a tributary of the Dee River system in eastern Scotland (Figure 1). The post-smolt growth patterns of smolt cohorts emigrating

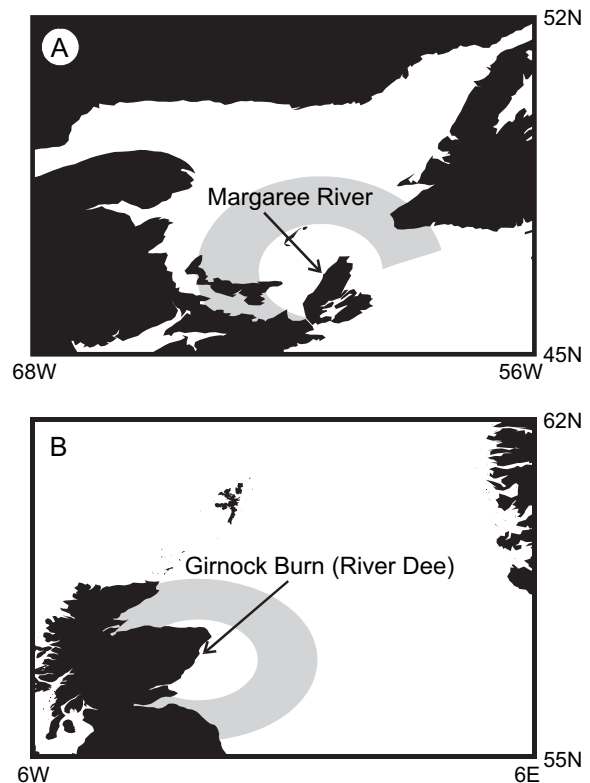


Figure 1. Maps showing location of study rivers. (A) Margaree River in eastern Canada and (B) Gironck Burn, a tributary of the River Dee in eastern Scotland. Grey area shows potential migration distance after first month at sea assuming directed migrations.

from the Gironck Burn between 1964 and 1993 were examined on scales taken from homewater adult recaptures of tagged two-sea winter (2SW) fish. Fish scales were mounted between glass slides, and spacings between successive pairs of circuli in the post-smolt zone were measured by means of an image processing system. Measurements were made on a single scale from each specimen at a pixel resolution of 0.004 mm along the 360° axis of the scale (Figure 2). Sample sizes are given in Table 1. The Margaree River is located on Cape Breton Island along the southern shore of the Gulf of St. Lawrence (Figure 1). Scales of returning wild 1SW and 2SW adults were sampled during the migration period 1986–1994. The same data collection procedure was used for both scale samples.

Growth during the post-smolt period was represented by indices derived from scale circuli spacing. The basis of representing growth with circuli spacing patterns has been demonstrated with salmonids and other fish species (Doyle *et al.*, 1987; Barber and Walker, 1988; Fisher and Percy, 1990). For the purposes of this study, we were interested in developing indices that represent growth during the first months at sea. Using an analysis of post-smolt scales from

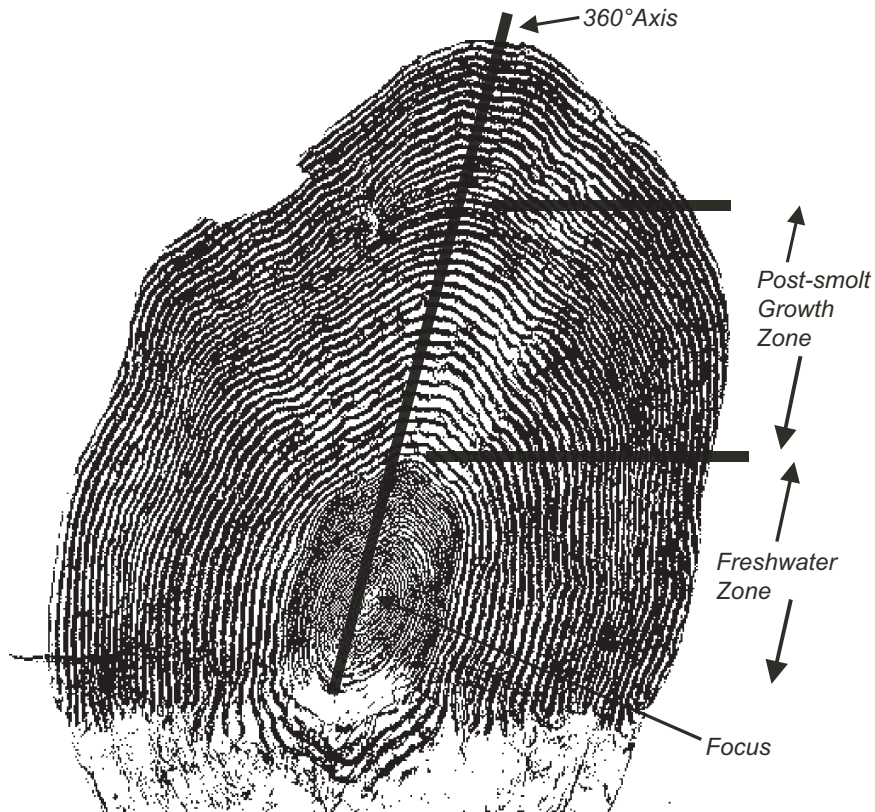


Figure 2. Atlantic salmon scale with growth zones marked.

tagged fish and ocean recaptures, Friedland *et al.* (1993) established that during the spring and summer growth seasons, circuli are laid down in salmon scales approximately every week. This period lengthens to approximately every two weeks by winter. Based on the assumption that four circuli pairs approximate a month of growth during spring and summer, we calculated a “first-4” index or the mean spacing of the first four circuli pairs meant to represent growth during the first month at sea. We similarly calculated a “second-4” index using the next four circuli pairs meant to represent the second month at sea; both first- and second-4 indices were calculated for each stock. We extended the monthly analysis of the Girnock fish by also computing a third and fourth spacing index, using the mean spacing of the next two sets of four circuli pairs, representing the third and fourth months at sea, respectively. In addition, we collected the total distance from the beginning of the marine growth zone to the first winter annulus in the Girnock fish, which represents the post-smolt growth increment or growth during the first year at sea.

We have limited knowledge of the post-smolt migration of Atlantic salmon, but what we do know provides a rationale for defining putative migration corridors for the studied stocks. Atlantic salmon smolts are surface

orientated animals and are not always capable of out-swimming ocean currents when they first go to sea (Jonsson *et al.*, 1993). Post-smolt salmon are, in part, passively transported during their first months at sea; thus, a combination of swimming potential and current transport vectors will circumscribe an area relevant to a specific stock. After a few months at sea, post-smolts attain sufficient size to outswim currents and will distribute according to other behaviours, such as foraging and open ocean migration. Hypothetically, if smolts achieved highly directed swimming and were constrained to speeds between 0.5 and 1.0 body lengths per second, a band of potential migration distance after one month can be posited (Figure 1). A further observation can help constrain the likely migration routes of North American smolts. Dutil and Coutu (1988) observed that post-smolts could stay resident in the Gulf of St. Lawrence through the summer, suggesting inshore waters may be part of the post-smolt nursery. These data suggest that Margaree fish are likely to be in the Gulf of St. Lawrence during their first month at sea and that they could be resident in the Gulf during their second month at sea as well. How rapidly the fish might leave the Gulf would also depend on the direction of surface currents, which would vary by year. Holm *et al.* (2000) provide data

Table 1. Number of scale samples analysed by smolt year, stock, and sea age.

Smolt year	Girnock 2SW	Margaree	
		1SW	2SW
1964	20		
1965	20		
1966	19		
1967	18		
1968	17		
1969	20		
1970	17		
1971	20		
1972	10		
1973	20		
1974	17		
1975	20		
1976	13		
1977	19		
1978	19		
1979	20		
1980	20		
1981	15		
1982	20		
1983	33		
1984	20		
1985	17		
1986	16		32
1987	17	47	36
1988	18	48	31
1989	19	43	34
1990	18	39	34
1991	35	46	38
1992	15	43	40
1993	40	40	35
1994		40	

on the summer distribution of European post-smolts. Their data show that currents and directed swimming result in a migration to the northwest, so Girnock Burn fish would be in the North Sea during their first month at sea and most likely migrating to the southern Norwegian Sea during the following months (Figure 1). Finally, smolt migration to the sea takes place over a multi-week period usually triggered by environmental cues (Whalen *et al.*, 1999). From observations of the subject stocks, enumeration facilities indicate that Margaree fish migrate at the end of May to the beginning of June and Girnock fish migrate at the end of April to the beginning of May.

Post-smolt growth data were compared with SST fields extracted from version 2 of the optimum interpolation (OI) sea surface temperature (SST) analysis by Reynolds *et al.* (2002). These data are produced weekly on a 1° grid and used *in situ* and satellite SST plus SST simulated for sea-ice

covered areas. Before analysis, satellite data are adjusted for biases using the methods of Reynolds (1988) and Reynolds and Marsico (1993). Pearson product-moment correlations were computed between the scale circuli spacing indices and the mean monthly temperature fields most likely associated with the growth pattern. For the Margaree analysis, we only examined the first two months at sea, assuming that swimming ability and point of origin of the post-smolts would constrain the potential distance they could achieve from their river of origin. The analysis was extended to the first four months at sea for the Girnock fish because of accessory findings on their growth and the nature of the ocean habitats they have to cross to reach their known summer distributions. The analysis was limited to years where both growth data and SST data were available, which begins in 1982. Correlation fields were displayed as contour plots in a geographic context. There is always the concern that time-series data used in correlation analysis might not be independent. For representative bi-variate plots of significant spatial correlation trends, we applied the effective number of degrees of freedom criteria to judge correlation significance (Pyper and Peterman, 1998).

Into the analysis, we introduced an accessory data set from a neighbouring river, the North Esk, for comparative purposes. The Esk is 60 km to the south of the Dee/Girnock system. Post-smolt growth increments collected from returns to the North Esk (Friedland *et al.*, 2000) were compared with the related scale increments from the Girnock fish. The post-smolt growth increments were from scale back-calculation data from North Esk 2SW fish.

## Results

Circuli spacing patterns of Atlantic salmon scales from the Girnock Burn and the Margaree River salmon reflect the increased growth that occurs when smolts first go to sea. The annual mean first-4 growth index for Margaree 1SW and 2SW fish ranged from approximately 0.045 mm to 0.055 mm showing a pattern of increasing growth during the study period (Figure 3A). There were significant differences in the growth for 1SW and 2SW fish, in particular, the growth for smolt year 1989. The second-4 index for Margaree fish was significantly higher than for the first-4 index. This index also suggests that growth increased during the study period and that there were significant differences between 1SW and 2SW fish; the largest differences can be seen for the data from smolt years 1990 and 1993.

Growth indices for Girnock Burn fish were slightly higher than indices for the Margaree fish. Annual means of the first-4 index for Girnock fish ranged from approximately 0.05 mm to 0.07 mm and suggest that early marine growth declined during the study period (Figure 3B). The second-4 index ranged from 0.065 mm to 0.075 mm and followed a similar time-series pattern as the first-4 index.

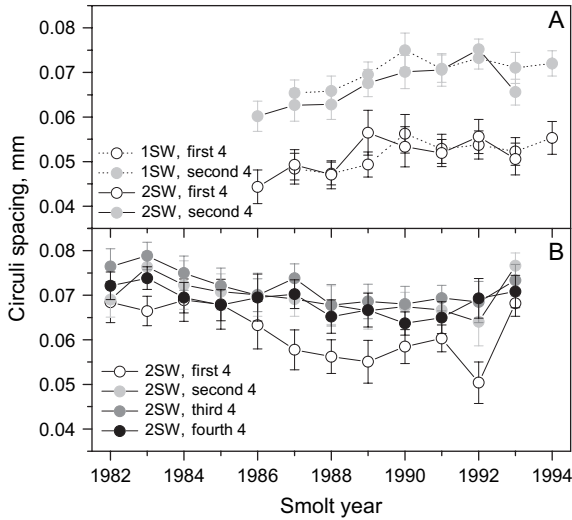


Figure 3. Circuli spacing by year for Margaree River 1SW and 2SW fish (A) and for Girnock Burn 2SW fish (B). Error bars show 95% confidence intervals around the mean.

The third- and fourth-4 indices for the Girnock ranged from 0.068 mm to 0.079 mm and 0.064 mm to 0.074 mm, respectively, and suggest that the later indices show similar interannual growth patterns (Figure 3B).

Correlation fields between Margaree scale growth indices and SST revealed environmental correlates with early marine growth that would appear to represent direct and indirect effects on the fish because not all of them were over ecologically relevant temperature ranges. Correlation between the Margaree 1SW first-4 growth index and May and June SST data are shown in Figure 4A and B, respectively. The number of observations for the Margaree data is eight, so a significant correlation coefficient is  $>0.71$  at a 95% confidence level and  $>0.83$  at a 99% confidence level. A significant negative correlation is observed in the May data. Correlation between the second-4 growth index and June and July SST are shown in Figure 4C and D, respectively. None of these correlations were significant. The same analysis was repeated for the growth indices derived from the scales of Margaree 2SW fish. Correlation between the Margaree 2SW first-4 growth index and May and June SST data is shown in Figure 5A and B, respectively. A significant negative correlation was observed in the May data and a significant positive correlation was observed in the June data.

Representative bi-variate plots of significant correlations eliminated the concern that the scatters were influenced by outlier data and suggest that some correlations are likely to represent indirect effects on the fish. Significant correlation of May SSTs with the first-4 index for 1SW fish is bracketed over a temperature range of 3–4°C, which is outside the temperature range experienced by smolts

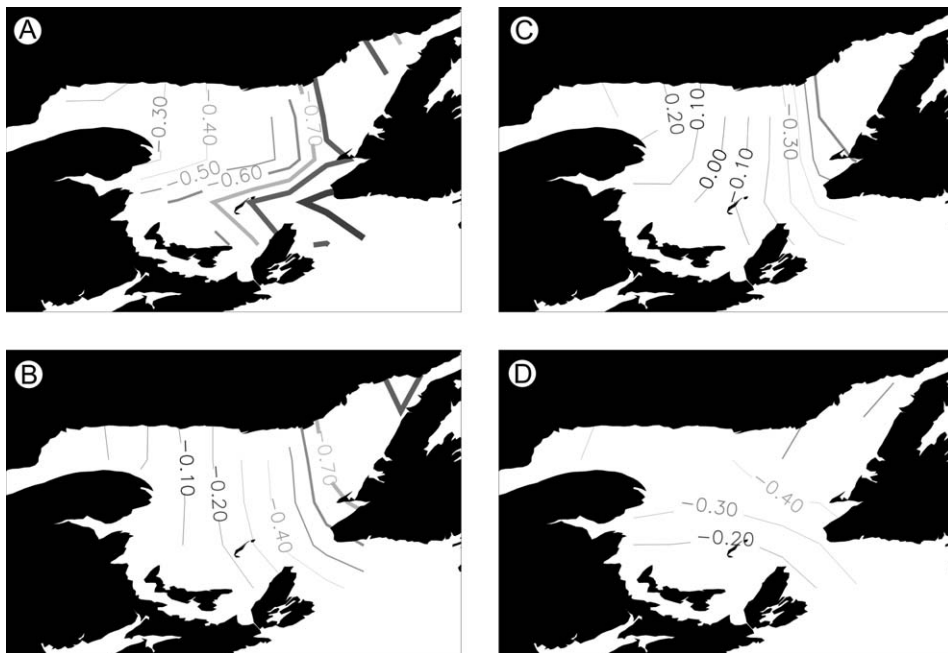


Figure 4. Contour maps showing correlation between circuli spacing indices from Margaree 1SW fish and SST. Correlations between first-4 circuli pair indices and May and June SST are in panels A and B, respectively. Correlations between second-4 circuli pair indices and June and July SST are in panels C and D, respectively. Contours of increasing thickness and shading intensity are indicative of a stronger correlation.

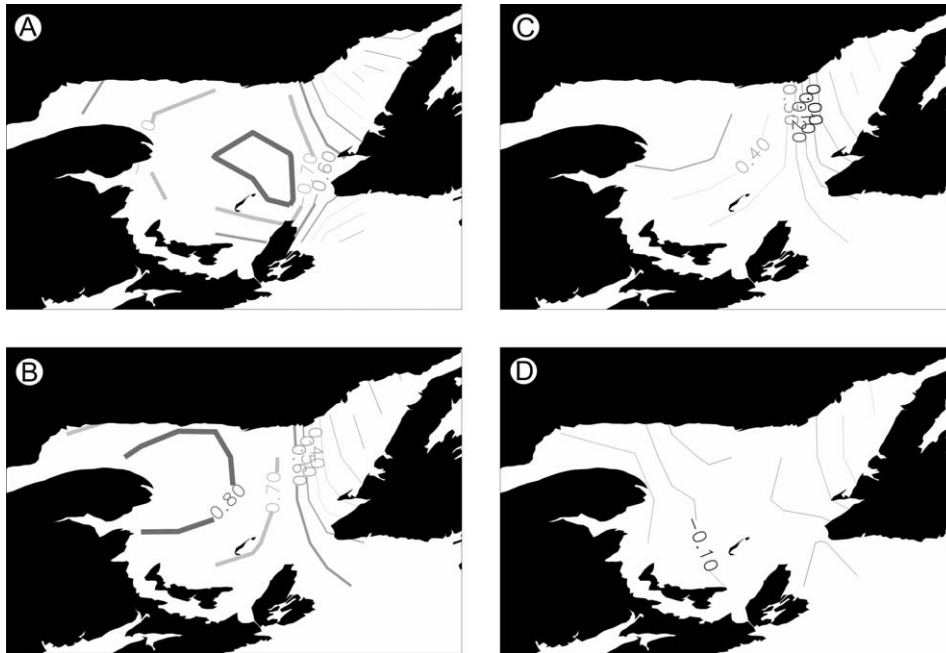


Figure 5. Contour maps showing correlation between circuli spacing indices from Margaree 2SW fish and SST. Correlations between first-4 circuli pair indices and May and June SST are in panels A and B, respectively. Correlations between second-4 circuli pair indices and June and July SST are in panels C and D, respectively. Contours of increasing thickness and shading intensity are indicative of stronger correlation.

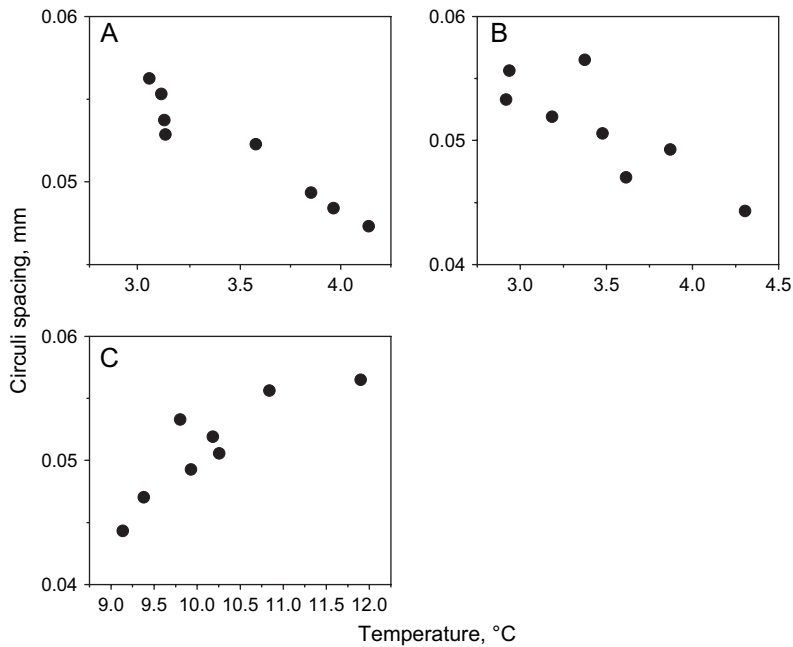


Figure 6. Key bi-variate relationships between circuli spacing indices and SST for Margaree 1SW first-4 indices and May SST (A), Margaree 2SW first-4 indices and May SST (B), and Margaree 2SW first-4 indices and June SST (C).



entering the marine environment and cooler than temperatures post-smolts are believed to utilize during early marine residence (Figure 6A). Likewise, the significant May-first-4 correlation with May SSTs for 2SW fish is over a range of 3–4°C (Figure 6B). Both of the correlations also occur in an area of the Gulf of St. Lawrence that is outside the area where smolts are expected to be found at that time. The significant correlation between June SST and the first-4 index for 2SW fish is over a more ecologically relevant range of temperatures, 9–12°C, with respect to the temperature of first ocean entry and post-smolt distribution (Figure 6C). None of the plots indicate that outliers influenced the relationships. Furthermore, analysis of the effective number of degrees of freedom did not suggest that any change to the significance criteria was needed.

Correlation fields between Girmock Burn scale growth indices and SST reveal environmental correlates with early marine growth that would appear to represent direct effects on the fish since they are over ecologically relevant ranges. Correlation between the Girmock 2SW first-4 growth index and April and May SST data is shown in Figure 7A and B, respectively. The number of observations for the Girmock data is 12, so a significant correlation coefficient is  $>0.58$  at a 95% confidence level and  $>0.71$  at a 99% confidence level. A significant negative correlation was observed in the April data. The correlation between the Girmock 2SW second-4 growth index and May and June SST data is

shown in Figure 7C and D, respectively. A significant negative correlation was observed in the June data. The significant first-4 correlation with April SSTs for 2SW fish was bracketed over a temperature range of 6–8°C, which is close to temperatures associated with first ocean entry and post-smolt distribution (Figure 8A). The significant second-4 correlation with June SSTs for 2SW fish was bracketed over a temperature range of 10–12°C, which is well within the range of temperatures associated with first ocean entry and post-smolt distribution (Figure 8B). Analysis of the effective number of degrees of freedom did not suggest that any change to the significance criteria was needed for these correlations.

A comparison with accessory data for the salmon stock in the North Esk was made to illustrate the potential importance of late season post-smolt growth in the Girmock stock. In comparing the post-smolt growth increments for North Esk and Girmock 2SW returns, we see evidence of coherence in post-smolt growth pattern between the two stocks (Figure 9). In particular there was a cluster of higher growth years in the early 1970s that is outside the time-series analysed in relation to SST data (limited to 1982 and onwards). Finally, when we compare the first-4 and second-4 growth indices to the post-smolt growth increments in Girmock fish, we see that the early marine growth is a poor predictor of the later season growth that occurred in the 1970s (Figure 10A and B, respectively). However, the

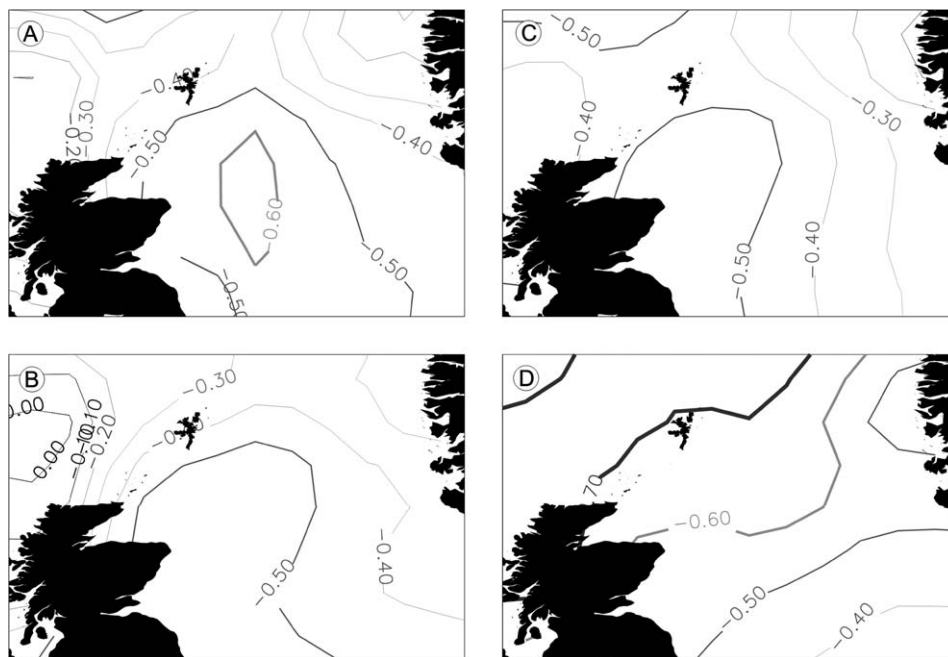


Figure 7. Contour maps showing correlation between circuli spacing indices from Girmock Burn 2SW fish and SST. Correlations between first-4 circuli pair indices and April and May SST are in panels A and B, respectively. Correlations between second-4 circuli pair indices and May and June SST are in panels C and D, respectively. Contours of increasing thickness and shading intensity are indicative of stronger correlation.

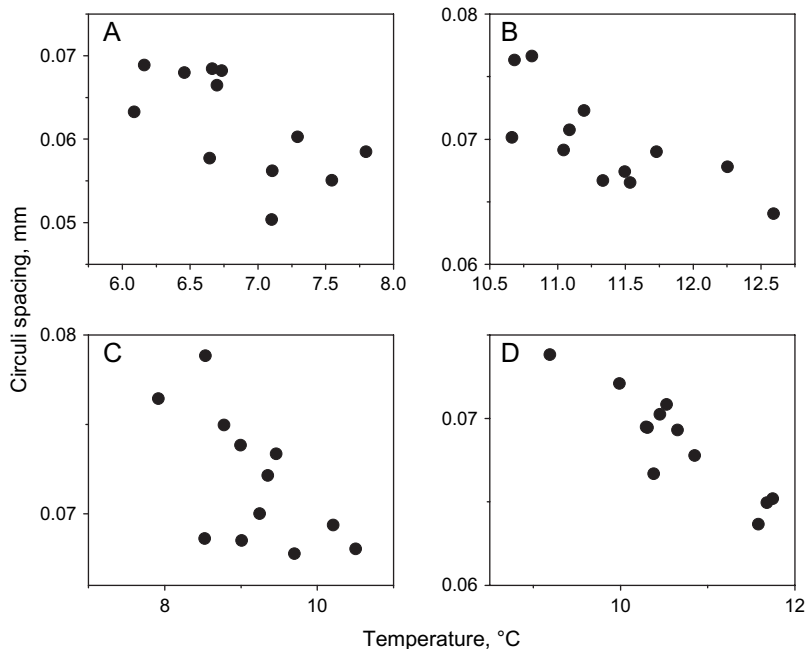


Figure 8. Key bi-variate relationships between circuli spacing indices and SST for Girnock 2SW first-4 indices and April SST (A), Girnock 2SW second-4 indices and June SST (B), Girnock 2SW third-4 indices and July SST, and Girnock fourth-4 indices and August SST, Girnock 2SW third-4 indices and July SST (C), and Girnock 2SW fourth-4 indices and August SST (D).

third-4 and fourth-4 indices are much better predictors of the post-smolt growth increment, suggesting that late season growth, i.e. growth likely occurring during July and August, may be the growth mainly influencing the recruitment pattern (Figure 10C and D). This observation provides the rationale to extend the analysis of correlation fields between Girnock scale growth indices and SST to July and August growth and to extend the spatial range of the area examined for correlation further to the north, where the nursery is located. The correlation between the Girnock

2SW third-4 growth index and June and July SST data is shown in Figure 11A and B, respectively. A significant negative correlation is observed in both months. Correlation between the Girnock 2SW second-4 growth index and July and August SST data is shown in Figure 11C and D, respectively. Significant negative correlations were observed in both months. The significant third-4 correlation with July SSTs for 2SW fish was bracketed over a temperature range of 8–10.5°C, and the fourth-4 correlation with August SSTs over a range of 9–12°C, both of which are reasonable ranges for post-smolts (Figure 8C and D). Analysis of the effective number of degrees of freedom did not suggest that any change to the significance criteria was needed for these correlations.

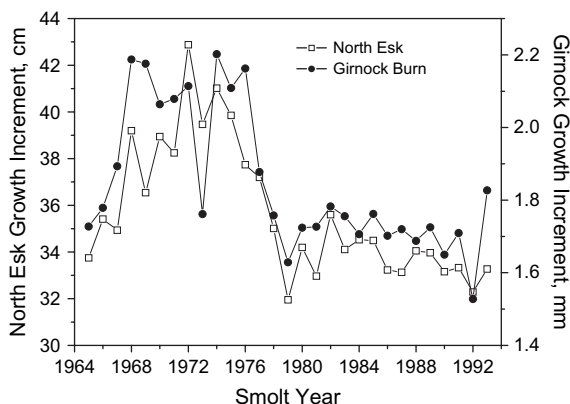


Figure 9. Post-smolt growth increment for North Esk (based on back-calculation) and Girnock (based on scale measurements) returns by smolt year.

## Discussion

Our main finding is that early marine growth of Atlantic salmon is related to ocean conditions in the putative migration corridors related to specific stocks. The nature of this relationship is still poorly understood and may not be the same amongst stocks and stock groups. Our data for the Girnock Burn suggest that growth is negatively affected by higher temperatures that may be exceeding optimal temperatures for fish from the Girnock feeding at natural rations (Handeland *et al.*, 2003). The spatial distribution of these correlations follows a northwest progression that would be consistent with the summer distribution of



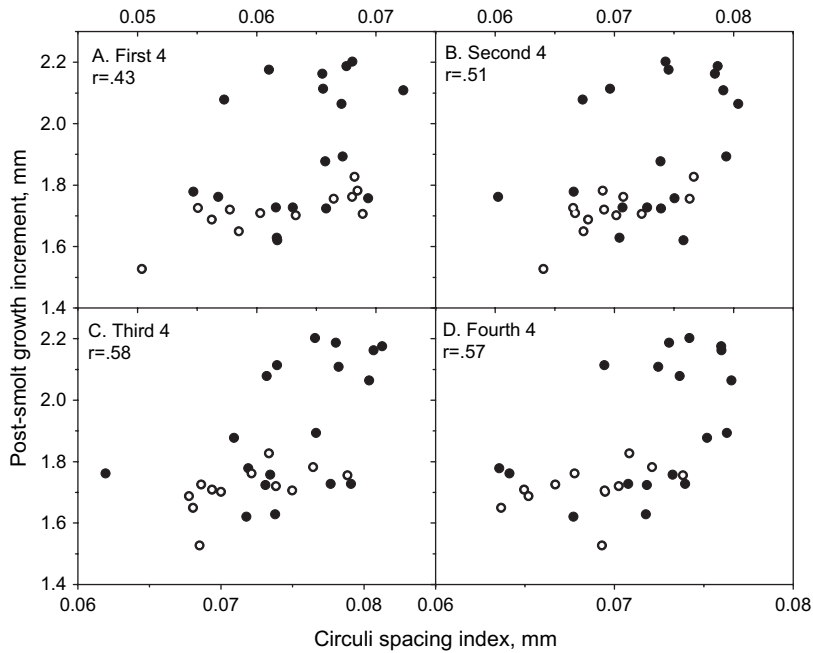


Figure 10. Post-smolt growth increment vs. first-4 (A), second-4 (B), third-4 (C), and fourth-4 (D) circuli spacing indices for Girnock 2SW fish. Open circles are years 1982–1993.

European post-smolts (Holm *et al.*, 2000). The environmental variable associated with recruitment variability in Europe is thermal habitat, which does not address the issue of whether cool or warm conditions differentially affect

post-smolts. Coherence between post-smolt growth patterns of Girnock and Esk salmon further supports the notion that post-smolt growth mediates survival in European fish (Friedland *et al.*, 2000). The questions are whether or not

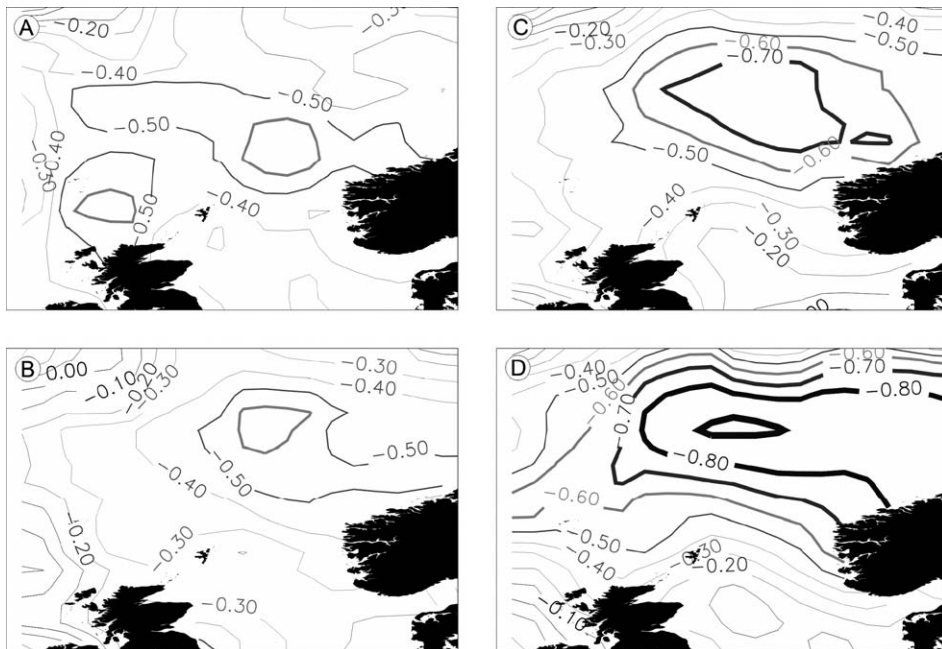


Figure 11. Contour maps showing correlation between circuli spacing indices from Girnock Burn 2SW fish and SST. Correlations between third-4 circuli pair indices and June and July SST are in panels A and B, respectively. Correlations between fourth-4 circuli pair indices and July and August SST are in panels C and D, respectively. Contours of increasing thickness and shading intensity are indicative of stronger correlation.

the mechanism is growth inhibition caused by warm conditions, and whether or not the recruitment patterning growth occurs during the first months at sea or later in the post-smolt year.

The response of Margaree fish suggests that an entirely different mechanism may be at work with North American fish. Friedland *et al.* (2003a) report that a negative correlation exists between the abundance of 2SW fish and thermal conditions in the Gulf of St. Lawrence. Our data show that temperature appears to be positively correlated with growth of 2SW fish but not for 1SW fish. Is this sensible or a conundrum? One possible explanation worth exploring is the role of maturation in shaping interannual abundance. Friedland *et al.* (2003a) reported that the thermal effect is not equivalent on age groups; the abundance of 1SW fish is not significantly correlated with thermal conditions. The positive thermal effect on post-smolt growth may reflect the contribution of maturation rate on the apparent abundance of age groups owing to the idea that rapid post-smolt growth shifts a higher proportion of the surviving post-smolts to the 1SW abundance tally (Hutchings and Jones, 1998). The immediate question that arises is, why the equivalent growth effect was not seen in the Margaree 1SW fish. Maturation is related to growth, but it also appears that other factors can differentiate the age groups, for example migration trajectory can result in changed maturity schedule (Martin and Mitchell, 1985; Friedland *et al.*, 1998b).

Temperature has primacy over ecological and physiological events affecting post-smolts during their transition to ocean life. Post-smolt metabolic rate changes dramatically with the smoltification process, increasing energy demands and actuating the need for the fish to increase their ration and make the transition to piscivorous prey (Hoar, 1988). Levings (1994) suggested that temperature might be of equal or greater importance than the type and quality of food items in the diet of post-smolts. Beaugrand and Reid (2003) observed correlation between salmon catch and time-series of ocean colour and zooplankton data, suggesting that lower trophic level production is influencing salmon post-smolts via either the abundance or quality of prey items. It is interesting that the well-known gadoid outburst, which has recently been attributed to the production pattern of zooplankton (Beaugrand *et al.*, 2003), approximates the same time period that salmon stocks were in high abundance in Europe. In studies of California Current salmonids, Brodeur *et al.* (2004) found that size and condition of post-smolts were related to oceanographic conditions in the rearing areas, with temperature being a contributing variable. It is difficult to differentiate the role of competing factors for Atlantic salmon because we have yet to replicate the California Current experiment where growth and condition were measured concurrently with conditions and resources in the rearing areas. Furthermore, growth effects can apparently propagate through the course of the post-smolt year and

impact cumulative mortality the first winter season after migration to sea (Beamish *et al.*, 2004), making measurement of the temporal progression of recruitment patterning mortality that much more important.

Our assumptions about the environmental window for post-smolts are critical to dismissing the relationships suggested for relatively cold waters ( $<4^{\circ}\text{C}$ ) of the eastern Gulf of St. Lawrence. Though we have no data demonstrating lethality of cold conditions in natural waters, Sigholt and Finstad (1990) showed that seawater temperatures of  $6\text{--}7^{\circ}\text{C}$  are lethal to salmon smolts in cage rearing settings. We must therefore assume that any correlates relating growth to transitional states of cold-water masses near the time of smolt ocean entry must reflect some covariation with conditions or factors affecting the fish at some later time and in warmer areas.

Thermal conditions have emerged as one of the most important indices of salmon productivity in both the Pacific and Atlantic (Downton and Miller, 1998; Friedland *et al.*, 2003b). In regard to the North Atlantic, there is accumulating evidence of the importance of the linkage to temperature conditions extant during the early marine stage (Sigholt and Finstad, 1990; Reddin and Friedland, 1996; Friedland *et al.*, 1999). In regard to the Pacific Ocean, Welch *et al.* (1995, 1998) demonstrated that temperature can act to restrict steelhead trout and Pacific salmon ocean distribution and may ultimately control productivity of these stocks. Other studies of Pacific salmonids suggest that ocean climate, in particular temperature, controls abundance and landings (Beamish and Bouillon, 1993; Downton and Miller, 1998), and that future productivity may be limited by global warming effects (Welch *et al.*, 1998). Understanding the mechanistic linkage between thermal conditions and growth response will undoubtedly contribute to our ability to manage these species under changing climate conditions.

## Acknowledgements

We thank M. Manning for image-processing assistance.

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