

Monthly indices of the post-smolt growth of Atlantic salmon from the Drammen River, Norway

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Indices of the monthly post-smolt growth of three maturity groups of Atlantic salmon *Salmo salar* from the Drammen River in Norway were examined. Scale samples were collected from 1983 to 2003, providing a retrospective growth history for 2854 individuals. Overall post-smolt growth of all three maturity groups decreased throughout the study period. When the post-smolt year was segmented into 8 monthly indices, there was a significant decline in growth during the fourth and fifth month, typically months of maximum growth. The pre-fishery abundance of one and two sea-winter fish from Norway also showed a decline throughout the study period and was positively correlated to the post-smolt growth of fish returning to the Drammen River. Freshwater growth was negatively correlated to the pre-fishery abundance, thus indicating that factors affecting post-smolt growth during the fourth and fifth months at sea may be responsible for declining return numbers in Norway.

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Key words: Atlantic salmon; growth; post-smolt; survival.

INTRODUCTION

In recent decades there has been an unprecedented decline in numbers of Atlantic salmon *Salmo salar* L. in the North Atlantic (Jonsson *et al.*, 2003), this despite efforts to restore stocks by fishery closures and other conservation measures (Friedland *et al.*, 1993; Youngson *et al.*, 2002). As abundance has continued to decline to levels at which widespread extirpation is possible, it has become imperative to identify the causes of recruitment failure, and in particular to identify the life-history stage responsible for any recruitment bottlenecks. Evaluations of populations in the marine stage are complicated since the fish are widely dispersed and difficult to sample. It is necessary to rely on other methods to understand the factors affecting recruitment as it appears that a majority of the mortality is occurring during marine residency (Friedland *et al.*,

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1993; Salminen *et al.*, 1995; Friedland, 1998; Youngson *et al.*, 2002; Jonsson *et al.*, 2003). The preponderance of marine mortality seems to occur during critical periods, which differ between European and North American stocks of Atlantic salmon. North American stocks have exhibited some correlation between survival and thermal conditions during spring and the first winter (Ritter, 1989; Friedland *et al.*, 1993, 2003), while the survival of European stocks appears to be mediated by growth sometime during the post-smolt period (Friedland *et al.*, 2000). It is the post-smolt mortality of European stocks that is the focus of the present study.

The post-smolt year is a time of increased energetic demand to support rapid growth and development. Smolting is physiologically stressful for Atlantic salmon as they adjust to the marine environment (Handeland *et al.*, 1996). Subsequent to smolting, Atlantic salmon are energy deficient and continue to mobilize energy stores during the first weeks at sea (Stefansson *et al.*, 2003). Laboratory studies also indicate low growth rates, low food consumption and low food conversion efficiency that continue through the first months in sea water (Handeland *et al.*, 2003). The increased energetic demand and subsequent decreased growth and metabolic efficiency contribute to high mortality rates immediately subsequent to smolting, and there are indications that post-smolts maintain heightened susceptibility throughout the rest of the post-smolt year. Tagging studies in the Baltic Sea show that the mortality rate for post-smolts throughout the year is higher than that observed for adults (Eriksson, 1994). Friedland *et al.* (1998) assessed the survival rates of Atlantic salmon from two European rivers, the Figgjo and the North Esk. It was assumed that fish from these rivers were exploiting the same areas as they both utilize the marine environment on a similar temporal and spatial scale. A correlation of return rates between cohorts of fish maturing at different ages indicated a high proportion of mortality occurred during the post-smolt year and suggested this mortality may be related to a large-scale process, such as climate variability, that affects both stocks (Friedland *et al.*, 1998).

Through altered thermal regimes, climate variability may have a direct effect on the growth rate of many fish species (Reddin *et al.*, 1997; Niva & Jokela, 2000; Ottersen *et al.*, 2004), while the survival and growth of Atlantic salmon is also affected by several indirect mechanisms (Ottersen *et al.*, 2004). In addition to alteration of migratory pathways, climatic variability affects the conditions experienced by post-smolts before they have the opportunity to actively seek a preferred habitat. As smolts move down the river to enter the marine environment, their movement depends largely on the speed and direction of currents, although active movement out into the main current of the river to avoid backwaters and sloughs has been suggested (Hansen & Jonsson, 1985; McCormick *et al.*, 1998). As post-smolts, their distributions continue to be regulated by passive transport mechanisms and limited by swimming ability (Friedland & Reddin, 1993; Friedland *et al.*, 1999; Holm *et al.*, 2000). During this time, post-smolts are exposed to the prevailing climatic conditions and it is not until some point later in the post-smolt year that the swimming ability of the Atlantic salmon begins to exceed current velocities and they are able to actively seek a preferred habitat (Friedland *et al.*, 1998, 1999). Climate variability has also been associated with alterations in the predator-prey relationship

for Atlantic salmon. In the north-west Atlantic there was an increase of post-smolts in the diet of gannets *Morus bassanus* on Funk Island, associated with a shift in prevalence of warm water to cold water pelagic prey (Montevecchi *et al.*, 2002). It is not likely that increases in predator density alone are responsible for the declining numbers of Atlantic salmon (Friedland *et al.*, 2000), but predation is difficult to quantify owing to relatively low densities of Atlantic salmon in the marine environment (Jonsson & Jonsson, 2004) and growth-mediated predation has long been considered a likely source of survival variance.

In addition to added predation pressure brought on by changes in the prevailing climatic condition, Friedland *et al.* (2000) identified the importance of examining indirect effects of climate variability on the availability and amount of Atlantic salmon prey. It is important that post-smolts obtain sufficient prey to facilitate growth, which enhances migration ability, predator avoidance and physiological fitness (Levings, 1994; Thorpe, 1994; Rikardsen *et al.*, 2004). Although Atlantic salmon exhibit some of the characteristics of opportunistic feeders, variation of zooplankton and fish larvae is highly dependent on environmental and oceanographic conditions, in particular temperature, which may have a large effect on the availability of suitable prey. Friedland *et al.* (2006) identified the possibility of the switch to piscivory as a critical stage for Atlantic salmon, emphasizing the possible effect of the piscivorous switch on the growth-mediated predation experienced by post-smolts in addition to energetic demands. While the association of a single factor or suite of factors with the recent decline in Atlantic salmon populations may be difficult to define and quantify, an examination of growth during the post-smolt year may help to identify critical periods within the post-smolt year and begin to clarify the involvement of various factors.

In the present study, retrospective growth analyses were used to gain insight into the post-smolt life of Atlantic salmon from the Drammen River in Norway. This study is a sample of survivors and thus, associated biases must be considered in the analysis. These data, however, allow the isolation of critical growth periods during the post-smolt year and an examination of the timing of post-smolt growth in association with the decline of European Atlantic salmon stocks. The possible factors involved in the decline of European Atlantic salmon stocks and implications for future studies are discussed.

MATERIALS AND METHODS

Image analysis techniques were used to characterize scale measurements representative of the freshwater and marine growth of Atlantic salmon. Samples were collected between 1983 and 2003 from fish returning to the Drammen River, located in southern Norway, 40 km south-west of Oslo (Fig. 1). Three maturity groups were represented in the sample: fish that matured after one winter at sea (1SW), fish that matured after two winters at sea (2SW) and fish that matured after three winters at sea (3SW). A total of 2854 fish were sampled, with an overall mean of 51 1SW, 44 2SW and 42 3SW fish sampled each year (Table I).

Impressions of each scale were pressed onto a cellulose acetate slide and a Nikon[©] (DXM1200X) microscope mounted digital camera was used to record an image of each scale impression (3840 × 3072 pixels). Using Image Pro 5.1[©] software, a transect was

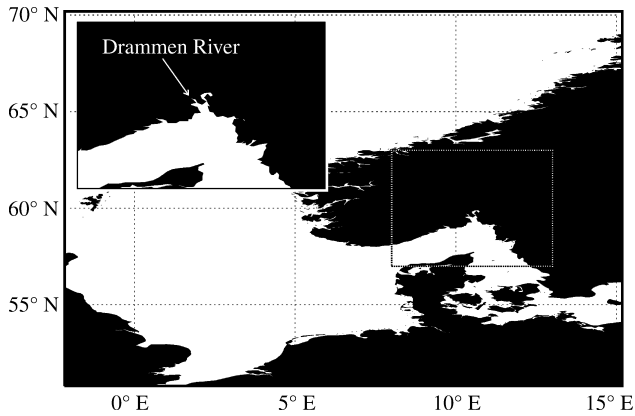


FIG. 1. Map of the north-east Atlantic area showing location of Drammen River, Norway.

drawn along the 360° axis from the foci of the scale to the edge of the freshwater growth zone. Another transect was then drawn along the 360° axis from the termination of the freshwater growth to the edge of the scale to record the marine growth zone (Fig. 2). The edge of the freshwater growth was identified by the increased circuli spacing representing sea entry. The spacing between circuli was automatically measured for

TABLE I. Number of one sea-winter (1SW), two sea-winter (2SW) and three sea-winter (3SW) samples of Atlantic salmon from the Drammen River, Norway

Smolt Year	1SW	2SW	3SW	Combined
1980			46	46
1981		37	40	77
1982	52	48	41	141
1983	54	44	35	133
1984	57	46	43	146
1985	49	40	45	134
1986	55	41	42	138
1987	53	46	47	146
1988	52	45	46	143
1989	49	48	46	143
1990	50	47	43	140
1991	46	42	36	124
1992	53	42	34	129
1993	57	48	42	147
1994	51	43	25	119
1995	51	40	48	139
1996	48	47	42	137
1997	47	43	45	135
1998	48	43	43	134
1999	47	44	40	131
2000	51	39	44	134
2001	52	45		97
2002	41			41

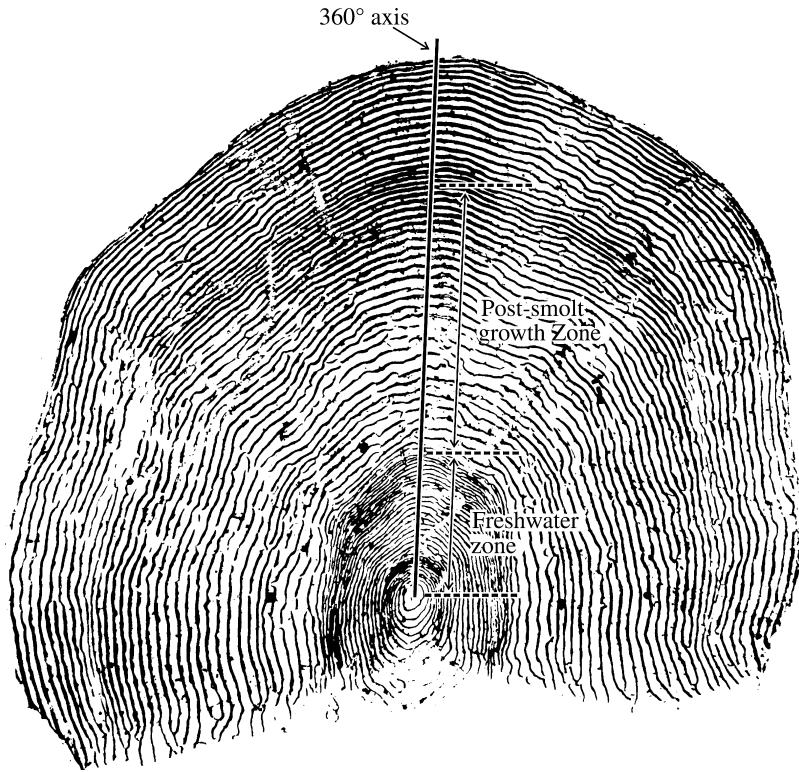


Fig. 2. Atlantic salmon scale showing axis measured and principal growth zones.

the marine zone. An aggregate length from the focus of the scale to the beginning of the marine zone was recorded for the freshwater zone.

For all analyses, individuals were grouped by smolt year rather than return year, so as to compare multiple maturity groups more effectively. This provided data from 1980 to 2002. The aggregate length of the freshwater zone was used to represent freshwater growth, with increased length representing increased freshwater growth and larger size at smolting. Circuli spacings were used to quantify marine growth, with narrow spacings indicating periods of decreased growth and wider spacings representing periods of increased growth. To extract the post-smolt growth indices for each individual, the minimum circuli spacing was identified as representative of the winter annulus for each sample. A five-point moving window was used to reduce the effect of spurious circuli values and the minimum and maximum values extracted and located by column on the data matrix. The first 10 circuli spacings of the marine zone were excluded as minimum values, owing to the propensity for small spacings during the early portion of the marine phase to be falsely identified as winter annuli. The location of the winter annulus was subsequently used to mark the end of the post-smolt growth period for each individual. A sum value of summing of all circuli spacings from the first marine circuli to the winter annulus represents the total post-smolt growth for each individual.

To examine growth more closely during the post-smolt period, the total post-smolt growth was then partitioned into putative monthly increments. European stocks of Atlantic salmon migrate to sea earlier than North American stocks, and on average experience an 8 month time period from smolting date to the first winter (Friedland & Reddin, 1993). Data gathered from tagged North American individuals captured at sea support estimates of the rate of circuli deposition and location of seasonal indices (Friedland & Reddin, 1993). The total number of circuli present in the post-smolt

period for each individual was divided by the approximate length in months of the post-smolt year, from smolting to first winter, to determine the number of circuli each individual deposits in 1 month. The sums of these circuli spacings were then tabulated for each individual to represent total growth during each putative month of the post-smolt year. This allowed the subsequent division of the post-smolt period into eight monthly increments, enabling the examination of growth during segmented time periods throughout the post-smolt stage for each individual.

To examine the relationship between changing growth patterns and survival, the pre-fishery abundance of Atlantic salmon stocks from Norway was extracted from ICES (2006). The report contained yearly abundances of 1SW and 2SW maturity groups, which were then combined to attain a total pre-fishery abundance per smolt year. The total pre-fishery abundance of Atlantic salmon from Norway was then compared to both the post-smolt and freshwater growth indices of fish from the Drammen River. The time series in this study had varying degrees of autocorrelation and to address this issue, the effective d.f. of each test were adjusted according to the procedure suggested by Pyper & Peterman (1998). The effective degree of freedom (N^*) of a correlation between two time series, in notation series X and Y , was estimated by: $N^{*-1} \approx N^{-1} 2N^{-1} \sum_{j=1}^{0.2N} (N-j) N^{-1} \rho_{xx}(j) \rho_{yy}(j)$ where N is the sample size and $\rho_{xx}(j)$ and $\rho_{yy}(j)$ are the autocorrelations of X and Y at lag j . The autocorrelation at lag j of the cross products of standardized time series of X and Y was taken according to the method suggested by Garrett & Petrie (1981). The probability associated with a correlation coefficient is designated as P and as P^* for a test with d.f. based on N^* .

RESULTS

A two factor ANOVA was conducted with freshwater growth as the response variable; smolt year and maturity as explanatory variables. There was a significant difference in freshwater growth by maturity group ($P < 0.001$), as well as by smolt year ($P < 0.001$). Freshwater growth for all maturity groups showed a positive trend during the study period [Fig. 3(a)], and linear regression indicated that the observed trend was highly significant ($P < 0.01$). Post-smolt growth was also analysed through a two factor ANOVA with smolt year and maturity group as explanatory variables. There was no significant difference between maturity groups ($P > 0.05$) and subsequent comparisons were made with the composite estimate. The mean annual post-smolt scale growth ranged from 1.653 to 2.056 mm and linear regression indicated a significant decreasing trend from 1980 to 2002 ($P < 0.01$) [Fig. 3(b)].

There was an overall decreasing trend from 1982 to 2002 in the pre-fishery abundance of 1SW and 2SW fish from Norway (Fig. 4). A corresponding decrease was evident in the post-smolt growth indices of the three maturity groups and the composite index, all of which were found to be significantly correlated with abundance. There was no relationship indicated between abundance and the freshwater growth index (Table II).

The annual post-smolt growth was segmented into 8 monthly indices for each individual. The mean monthly value of each maturity group for each smolt year was analysed. The mean annual values for months 1, 2 and 3 were slightly lower for the 1SW maturity group and a two factor ANOVA showed statistically significant difference between the maturity groups for these monthly indices ($P < 0.05$). Months 4, 5, 6, 7 and 8 showed no significant difference between maturity groups ($P > 0.05$). For subsequent analyses, all putative months were analysed by maturity group as well as by composite indices.

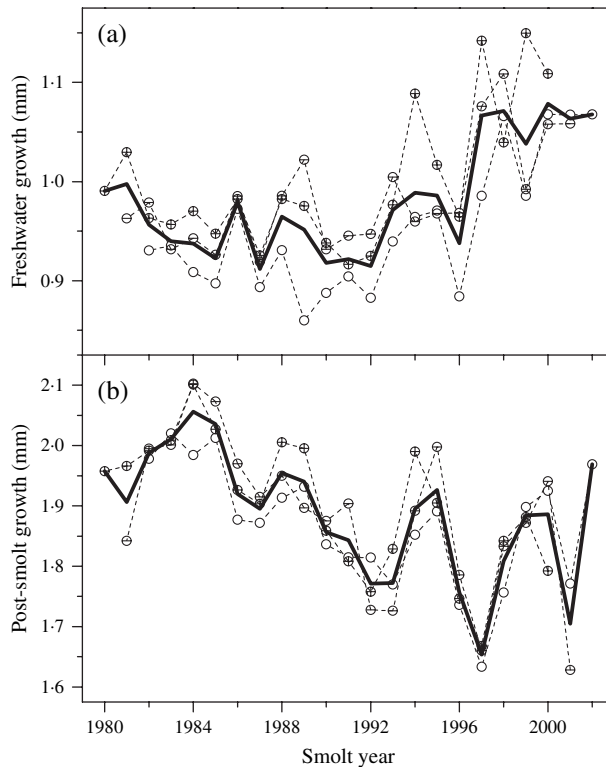


FIG. 3. Yearly means of (a) freshwater growth increment and (b) post-smolt growth increment of Atlantic salmon scales from the Drammen River [matured at one (---○---), two (---□---) and three (---△---) sea winters and combined (—)].

For all years, the overall mean annual indices showed a consistent non-linear trend, with growth gradually increasing to a maximum near the third month at sea and then decreasing to a minimum at month 8 (Fig. 5). The maximum growth increment also exhibited a declining trend over the study period ($P < 0.01$), ranging from 0.075 to 0.089 mm [Fig. 6(a)]. The maximum growth most often centred around the third month at sea (putatively identified as July) and there was some indication that the maximum growth may be shifting to earlier months throughout the course of the study period [Fig. 6(b)]. The minimum winter growth always occurred in the eighth month at sea or what was putatively identified as December; linear regression of minimum growth showed no significant change over time ($P > 0.05$), although 1995 and 1996 showed relatively high growth [Fig. (c)].

Graphs of normalized circuli spacing from each of the eight putative monthly indices (Fig. 7) show that there are some inconsistent signs of decline in months 1 and 2 ($P > 0.05$ and $P = 0.001$, respectively). Significant declines in growth over time were noted during months 3, 4, 5 and 6 ($P < 0.001$), with the greatest decrease over time noted during months 4 and 5. Months 7 and 8 changed little over time (both $P > 0.05$).

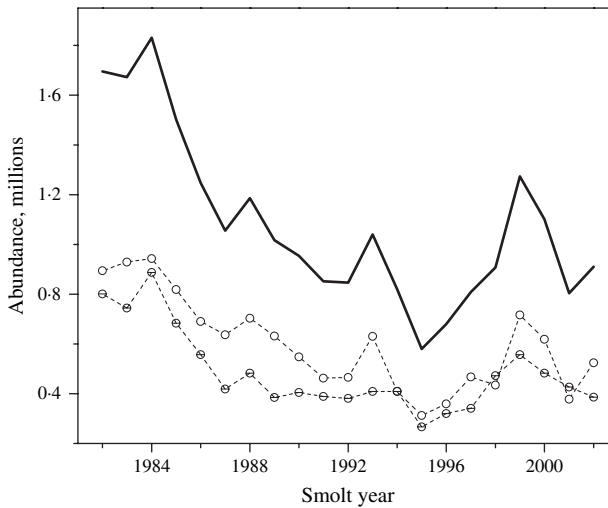


FIG. 4. Pre-fishery abundance of Norwegian Atlantic salmon stocks (ICES, 2006) [matured at one (---○---) and two (---○---) sea-winters and combined (—)].

Correlations between the post-smolt growth and the total pre-fishery abundance from Norway were adjusted for autocorrelation and compared for the three maturity groups as well as for the composite index. Some variation between maturity groups was evident, with early growth showing increased importance to the 1SW maturity group, although months 3, 4 and 5 also showed a significant positive correlation [Fig. 8(a)]. The 2SW maturity group showed a significant positive correlation for months 4 and 5 [Fig. 8(b)], while the 3SW maturity group showed a significant positive correlation for month 5 only [Fig. 8(c)]. The overall pattern of high positive correlation during months 3, 4 and 5 was evident for all maturity groups, with the composite index

TABLE II. Correlation (r) between freshwater and post-smolt growth increments from one sea-winter (SW), 2SW and 3SW Atlantic salmon, and a mean increment for a combined sample of all available ages

Growth factor	Maturity group	r	N	P	N^*	P^*
Fresh water	1SW	-0.198	21	0.389	11	0.559
	2SW	-0.306	20	0.190	9	0.424
	3SW	-0.172	19	0.481	12	0.593
	Combined	-0.266	21	0.244	9	0.489
Post-smolt	1SW	0.704	21	0.000	12	0.011
	2SW	0.651	20	0.002	11	0.030
	3SW	0.692	19	0.001	12	0.013
	Combined	0.705	21	<0.001	12	0.010

N , sample size; P , probability of correlation; N^* , the effective sample size corrected for autocorrelation; P^* , probability of correlation, also corrected for autocorrelation.

P and P^* values < 0.05 are shown in bold.

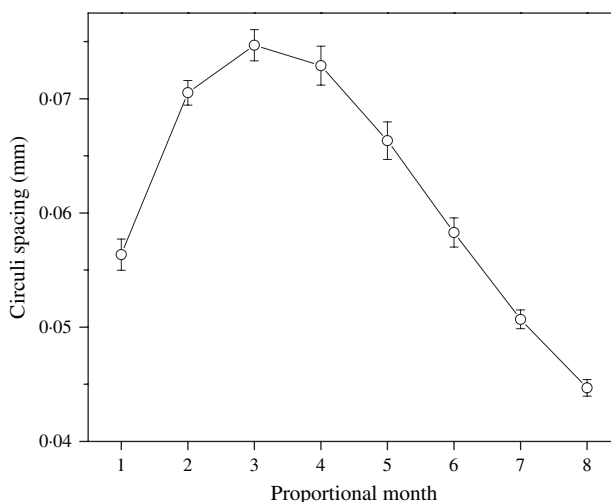


FIG. 5. Mean circuli spacing for putative monthly segments of the Atlantic salmon post-smolt growth increment with 95% CI.

indicating a significant positive correlation between the pre-fishery abundance of Norway and growth during months 3, 4 and 5 [Fig. 8(d)]. Months 2, 6, 7 and 8 showed no significant correlation, indicating that decreasing growth during the middle months was driving the overall decrease in post-smolt growth and was correlated to survival of Atlantic salmon stocks in Norway.

DISCUSSION

A positive correlation between the post-smolt growth of Atlantic salmon from the Drammen River and the pre-fishery abundance of Atlantic salmon in Norway indicates that growth during the post-smolt period is critical to survival of the cohort. Many previous studies have focused on the weeks immediately subsequent to smolting as a period of high mortality during which a recruitment bottleneck may exist for Atlantic salmon in the North Atlantic. Friedland *et al.* (2006) emphasized the high mortality rate for post-smolts during the first weeks at sea and asserted that a minimal variation in mortality at this time will have a sizable result on subsequent adult recruitment. Handeland *et al.* (1996) reported a decrease in predator avoidance abilities of post-smolts as osmotic stress increases in association with the transition to the marine environment. Although studies indicate a high mortality during the first few weeks at sea for both Atlantic and Pacific salmon (*Oncorhynchus* sp.) stocks (Eriksson, 1994; Friedland & Reddin, 2000; Fukuwaka & Suzuki, 2002) and imply that the first few weeks at sea are critical to the survival of the cohort, samples from the present study showed no consistently significant change in growth over the study period during the first two marine months. These data instead indicate a decrease in growth from 1980 to 2002 during the third, fourth, fifth and sixth months at sea, with the greatest decrease in post-smolt growth occurring during the fourth and fifth month. This indicates that the Atlantic salmon are experiencing

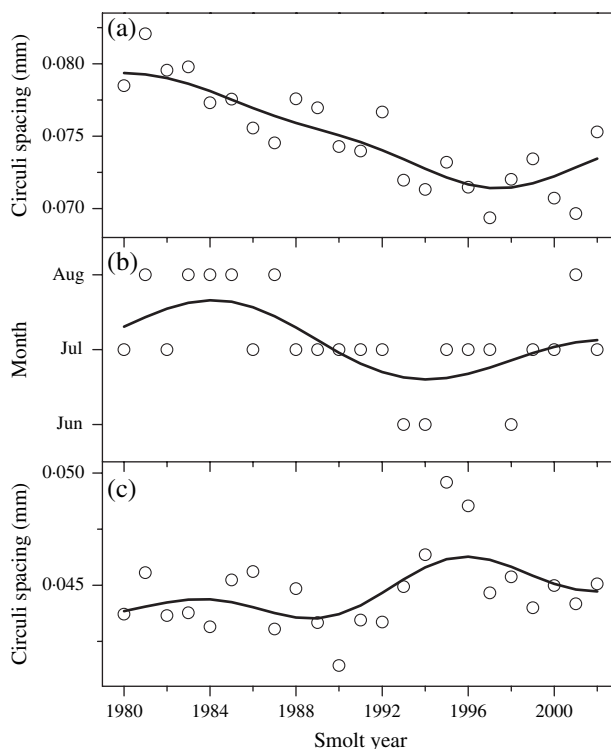


FIG. 6. Mean (a) maximum post-smolt circuli spacing, (b) month during Atlantic salmon post-smolt period that the maximum spacing occurred and (c) winter minimum spacing, with fast Fourier transform (FFT) smoothed lines.

a decrease in growth over time during the months that they are in aggregate nursery areas, rather than the period immediately subsequent to smolting (Friedland & Reddin, 1993). This decrease in the later, rather than the earlier, part of the post-smolt period may be integral to the identification of a growth-mediated recruitment bottleneck.

These data exhibit a significant positive correlation between composite post-smolt growth and the pre-fishery abundance of Norway Atlantic salmon during the third, fourth and fifth months (July, August and September) at sea, suggesting that a decrease in post-smolt growth during that time may be driving the overall decrease in pre-fishery abundance in Norway. There is some variation between maturity groups when they are disaggregated from the composite, but the overall pattern remains the same with a high correlation during the middle months. These months are historically months of largest growth during the post-smolt period for Atlantic salmon from the Drammen River, indicating that this time is a critical period of significantly accelerated growth rate. In laboratory studies, post-smolt growth and feeding increased over time with significant changes in growth between days 30 and 60, also a time when both food intake and growth rate were influenced by temperature (Handeland *et al.*, 2003). Thurow (1968) suggests that a rapid increase in growth occurs only after the diet shift to piscivory. In the Baltic, a diet shift from invertebrate prey to

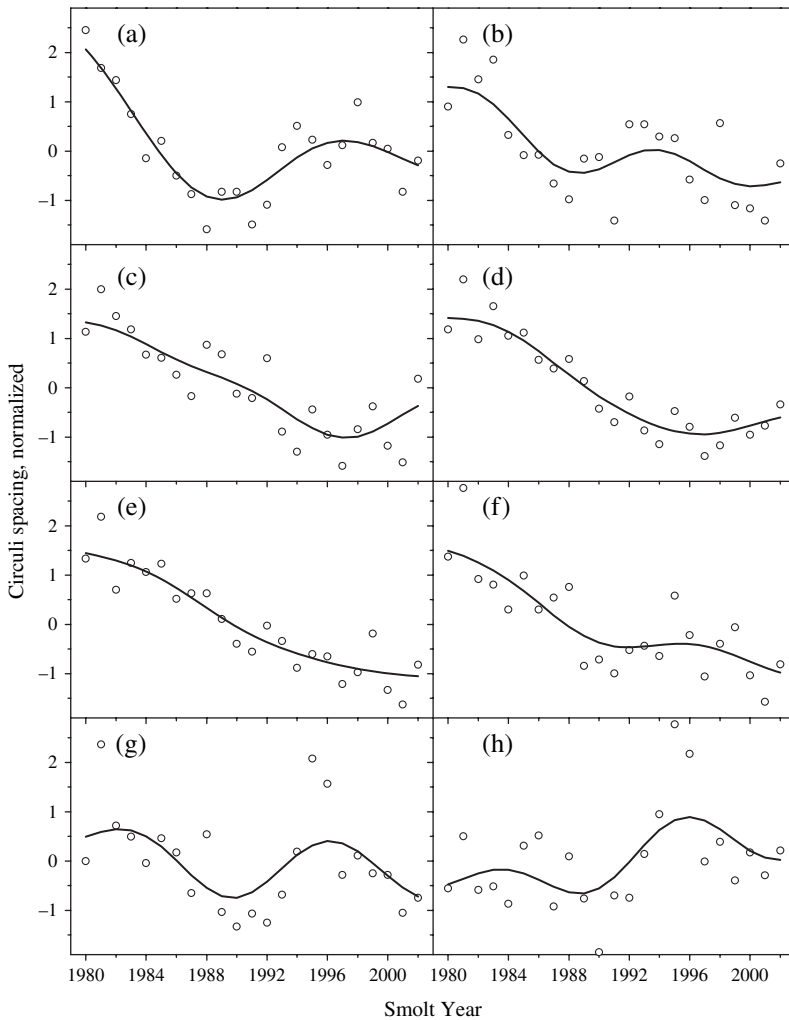


FIG. 7. (a)–(h) Mean circuli spacing for proportional month segments 1–8 by year for post-smolt Atlantic salmon, with fast Fourier transform (FFT) smoothed lines.

fish prey occurred from June to August (Salminen *et al.*, 2001). Although some studies indicate that the shift to piscivory occurs earlier in the North Atlantic (Rikardsen *et al.*, 2004), the fact that maximum growth is occurring during the third and fourth months at sea may suggest that a switch to piscivory is commencing immediately prior to these months and that a decrease in growth during this critical period may have a significant effect on survival trends of the population.

The isolation of a decrease in growth during the late post-smolt period indicates changing processes in the post-smolt nursery area rather than the coastal environment. The growth of Atlantic salmon is highly responsive to thermal conditions and it is possible that there has been a dynamic change in the nursery area. Any variability in temperature within the nursery area may directly

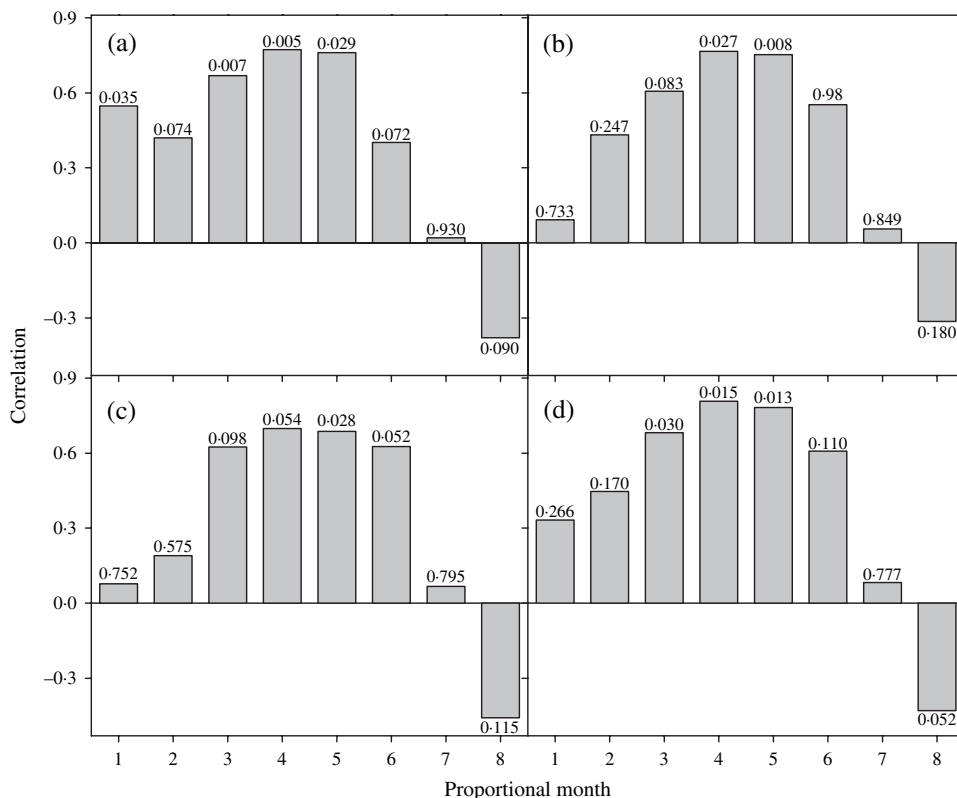


FIG. 8. Correlation between combined pre-fishery abundance of Atlantic salmon and mean circuli spacing for putative monthly segments of (a) 1SW, (b) 2SW, (c) 3SW Atlantic salmon and (d) the composite index. Columns are labelled with the probability associated with each correlation coefficient, adjusted for autocorrelation.

contribute to the declining growth rate indicated by these data, as climate variability has been identified as a factor that may significantly affect marine ecosystems through direct, indirect and integrated ecological mechanisms (Ottersen *et al.*, 2001). The North Atlantic Oscillation (NAO) is a dominating climatic feature in the North Atlantic and has shifted over the last three decades from a mostly positive to a mostly negative index and appears to account for the increasingly severe winters in the north-west Atlantic (Hurrell, 1995). As the mortality of pelagic fishes is inversely related to body size (Peterson & Wroblewski, 1995), with growth highly responsive to water temperature (Brett, 1979), cooling trends in the North Atlantic have the potential to greatly affect Atlantic salmon in aggregate nursery areas. It is possible that the depression of growth evident in this study is due to an alteration in the local temperature and this change has the possibility to contribute to increased mortality in numerous ways.

Growth rates are integrally correlated with predation risks and it is likely that predation is one of the most important sources of mortality at anytime during the post-smolt year (Hansen & Quinn, 1998). Predation pressure is believed to be greatest during the first several weeks at sea (Hansen & Quinn,

1998), as post-smolts are physiologically stressed and exhibit heightened vulnerability to predators (Handeland *et al.*, 1996). At this time, post-smolts in the Drammen River may still be in the continental shelf waters where the abundance of potential predators is higher than in oceanic areas. Numerous factors affect mortality during this time, however, especially in the presence of alternate abundant prey species that may reduce the predation pressure on Atlantic salmon (Svenning *et al.*, 2005). Instead, the mortality effect may be more dominant later in the post-smolt period. The relationship between growth and survival suggests that growth-mediated predation may be the dominant source of recruitment variability (Friedland *et al.*, 2000) and that better growth during a critical period is associated with an ability to escape predation (Anderson, 1988; Pepin, 1991). The more quickly Atlantic salmon can increase in size, the fewer predators to which they are susceptible, so the observed decrease in growth may lead to an increased window of vulnerability to predation. In addition, a change in oceanic productivity has been hypothesized to not only decrease the food available to post-smolts, but also to increase predation pressure on salmonids from other piscivorous fishes (Fisher & Percy, 1988).

As well as greater susceptibility to growth mediated predation, decreased growth rates also influence the available prey base for Atlantic salmon. The maximum consumable prey size increases as the fish grows, but the minimum prey size remains the same. This indicates that there is a larger size range of available prey as Atlantic salmon increase in size (Salminen *et al.*, 2001). Decreasing growth rates may limit the availability of suitable prey. The situation is further complicated by the fact that a decrease in available prey may also contribute to the observed decrease in growth. Adequate and appropriate food sources for post-smolts promote growth, successful migration, predator avoidance, physiological processes and parasite resistance (Rikardsen *et al.*, 2004). In southern Norway, the prevalence of post-smolt feeding in the fjords was low compared to northern populations and crustaceans (euphausiids, pelagic shrimp and *Themisto* spp.) and marine pelagic fishes (lantern fishes, pearlshrimps, sandeel, gadids and barracudinas) constitute a majority of the marine diet (Jacobsen & Hansen, 2001; Rikardsen *et al.*, 2004; Haugland *et al.*, 2006). In a study of stomach content, crustacean species were the most common taxa, but fish species constituted a majority by mass (Jacobsen & Hansen, 2001). A change in the composition of prey items was noted during the migration from river to fjord to ocean (Andreassen *et al.*, 2001). Prey availability is integrally related to oceanographic processes, most likely varying in close association with thermal conditions (Levings, 1994; Friedland, 1998; Friedland *et al.*, 2000). In addition, Haugland *et al.* (2006) emphasized the importance of certain age 0-year groups of fish species in the post-smolt diet and suggested that the commercially expedited decline of these species may detrimentally affect Atlantic salmon post-smolts. Any variation in the abundance and availability of marine prey may affect early post-smolt survival (Friedland *et al.*, 2003; Rikardsen *et al.*, 2004), with a lack of appropriate available food reducing the growth rate and increasing vulnerability to predation (Hansen & Quinn, 1998). Jacobsen & Hansen (2001) found an increase in the mass of stomach contents from autumn to the winter in Atlantic salmon north of the Faroes, signalling a change in feeding intensity. The change in feeding intensity

was attributed to two possible causes: increased gastric evacuation owing to higher autumnal temperatures or a lack of available prey during the autumn. The present data appear to support the latter hypothesis with the possibility that decreased growth of the later post-smolt period mirrors a decreasing availability of prey during that period, although Jacobsen & Hansen (2001) reported a higher condition factor in the autumn than winter. It is possible that the decreased growth during the autumn carries over into decreased condition factor in the winter, although no decrease in growth was seen over time during the winter months in these data.

The alteration of suitable migratory pathways has been suggested as a factor in the survival of North American post-smolts (Friedland *et al.*, 1999) and should be considered for European stocks, as well. Migratory species are known to change routes in association with changing currents, temperature and salinity distributions (Minns *et al.*, 1995; Ottersen *et al.*, 2004), and habitat shifts in response to climatic alterations have already been reported for many species in the North Sea (Perry *et al.*, 2005). The nursery habitat for Atlantic salmon is dynamic and depends integrally on the abundance of primary production to support a prey base. If post-smolts are forced to swim greater distances to discover suitable thermal habitat, a growth effect may be detected. In the Baltic Sea when prey availability is unfavorable, Atlantic salmon will migrate further to locate suitable prey (Salminen *et al.*, 2001). An alteration in suitability of any of the habitats utilized will affect the population characteristics of a migratory species (Reddin *et al.*, 1997) and may contribute to an alteration of the predator-prey relationship in addition to the direct energetic cost. In North America, a period of physical and biological change on the Newfoundland and Labrador shelf initiated an increase in the prevalence of post-smolts in the diet of gannets on offshore islands (Montevecchi *et al.*, 2002). Thus, any disruption or alteration of the migratory and nursery corridor may detrimentally modify the predation pressure experienced by post-smolts in addition to increasing energy expenditure.

This sample is limited in that it consists only of survivors that have returned to the Drammen River. Although the sample consisted only of survivors, there was no evidence of a threshold effect in which uniform growth over time (Friedland *et al.*, 1993; Crozier & Kennedy, 1999) would be expected, allowing for the assumption that the sample was representative of the Atlantic salmon population from the Drammen River. Although a significant source of mortality is occurring during the first weeks of sea residence, these data suggest that mortality during this time is not growth mediated and identifies a period later in the post-smolt year as a possible recruitment bottleneck due to growth mediated processes. In the future, although difficult, it would be indispensable to sample Atlantic salmon in the nursery area to better represent both survivors and non-survivors. It is also imperative to examine more closely the nursery area for changes in thermal regime that may be directly correlated to the decrease in growth of Atlantic salmon during this time. It is possible that dynamic changes in the area are changing the prey to predator ratio and thus only the larger fish are able to obtain adequate amounts of food and escape predation.

These data suggest that the focus on critical periods during the post-smolt stage should not be solely limited to the first few weeks that the fish are at

sea. Although predation rates during this time are undeniably high and it is a time of magnified stress for Atlantic salmon, these data suggest that the late post-smolt period may be an equally important factor in explaining the increasingly variable return of Atlantic salmon to their natal rivers.

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