

Linkage between ocean climate, post-smolt growth, and survival of Atlantic salmon (*Salmo salar* L.) in the North Sea area

Kevin D. Friedland, Lars P. Hansen,
David A. Dunkley, and Julian C. MacLean



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We examined two long-term tagging studies with wild salmon stocks in the North Sea area. The salmon stocks, the Figgo in southern Norway and the North Esk in eastern Scotland, reside in relatively un-impacted rivers that continue to sustain healthy runs of salmon. The return rates for one seawinter fish (1SW), the predominant age at maturity for both stocks, were highly correlated. An analysis of sea surface temperature distributions for periods of high versus low return rate showed that when low sea surface temperatures dominate the North Sea and southern coast of Norway during May, salmon survival has been poor. Conversely, when high sea surface temperatures extend northward along the Norwegian coast during May, survival has been good. Ocean conditions can be further related to the recruitment process through growth studies for the North Esk stock. Post-smolt growth increments for returning 1SW fish showed that enhanced growth was associated with years during which temperature conditions were favorable, which in turn resulted in higher survival rates. The implicit linkage between growth and survival suggests that growth-mediated predation is the dominant source of recruitment variability. Mechanisms by which ocean climate may affect post-smolt growth are discussed.

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Key words: Atlantic salmon, growth, post-smolt survival, recruitment, sea surface temperature, thermal habitat.

K. D. Friedland: UMass/NOAA CMER Program, Blaisdell House, University of Massachusetts, Amherst, MA 01003, USA [tel: +1 413 545 2842; fax: +1 413 545 2304; e-mail: friedlandk@forwild.umass.edu]; L. P. Hansen: Norwegian Institute for Nature Research, Dronningens gt. 13, P.O. Box 736 Sentrum, N-0105 Oslo, Norway; D. A. Dunkley: Inspector of Salmon and Freshwater Fisheries, Room 407, Pentland House, 47 Robb's Loan, Edinburgh, EH14 1TY, Scotland, UK; J. C. Maclean: SOAEFD, Freshwater Fisheries Laboratory, Field Station, 16 River Street, Montrose, Angus DD10 8DL, Scotland, UK.

Introduction

The productivity of most Atlantic salmon stocks is evaluated by the yield and escapement of just two age groups of adult fish, one seawinter (1SW) and 2SW salmon, or salmon that have been at sea for one or two winters, respectively. Salmon populations have characteristic age structures that are often geographically clustered (Saunders, 1981; Shearer, 1990; Summers, 1995). The factors affecting recruitment by age in these populations are of intense interest because of recent, unprecedented declines in stock abundance (Friedland *et al.*, 1993; ICES, 1999). We believe that analogous mechanisms are at work in the Pacific Ocean as evidenced by the regional shifts in salmon productivity observed there (Beamish and Bouillion, 1993; Mantua *et al.*, 1997).

The short ocean residence of Atlantic salmon focuses concern on natural mortality and the process of sexual maturation during the post-smolt year or the first year at sea. Post-smolt mortality is believed to be most severe during the first few months at sea (Fisher and Percy, 1988; Holtby *et al.*, 1990; Eriksson, 1994; Salminen *et al.*, 1995). During this period, mortality effects are believed to be growth-mediated via various mechanisms related to variation in ocean climate and productivity, interspecific competition, and intraspecific interactions (Ricker, 1962; Neilson and Geen, 1986; L'Abée-Lund *et al.*, 1993; Friedland *et al.*, 1996). Therefore, ocean climate variation that may impact salmon growth can also affect recruitment. Age of maturity in salmonids has largely been viewed as a genetic characteristic of a stock (Thorpe, 1994). However, variation in maturity rate has

remained largely unexplained and manifests itself in systematic patterns, suggesting that some external forcing may be important (Friedland and Haas, 1996; Friedland *et al.*, 1996).

Variation in ocean conditions can impact salmon survival and maturation in a number of different ways. Water temperature has been identified as an important factor influencing growth and maturation (Saunders *et al.*, 1983; Scarnecchia, 1983; Scarnecchia *et al.*, 1991). It has also been suggested that thermal conditions may influence maturation independently of growth by influencing migration patterns (Martin and Mitchell, 1985; Friedland *et al.*, 1998). However, some climate signals are believed to be unrelated to maturation, since they affect salmon juveniles during the first weeks at sea and are thus more likely related to natural mortality (Scarnecchia *et al.*, 1989). This is the implication of a number of studies with Pacific salmon which relate stock abundance to broadscale atmospheric systems (Johnson, 1988; Beamish and Bouillon, 1993; Francis and Hare, 1994; Mantua *et al.*, 1997) and more localized upwelling circulation (Fisher and Pearcy, 1988; Kope and Botsford, 1990). In systems like the Baltic Sea, the problem has been slightly more tractable. The Baltic Sea is a confined system that has allowed researchers to more directly relate temperature and circulation variation to growth and survival (Salminen *et al.*, 1995). In contrast, we have limited knowledge of the factors influencing the growth and survival of Atlantic salmon post-smolts from either North American or European stock complexes (Friedland *et al.*, 1993).

We develop three lines of evidence to address one aspect of age-specific recruitment patterns in Atlantic salmon. First, we compute age disaggregated return rates for two stocks of wild run salmon from the North Sea area. Second, we describe variation in sea surface temperature (SST) distribution for the Northeast Atlantic Ocean. Finally, we report on the post-smolt growth history for one of the North Sea stocks. These three lines of evidence are then compared, focusing on the time period when juvenile salmon first enter the marine environment. We then discuss how ocean climate conditions can affect the early marine survival of juvenile salmon.

Material and methods

Return rates

The rivers Figgjo and North Esk are small, relatively un-impacted, salmon rivers that empty into the North Sea. The Figgjo is located in southern Norway and supports a stock mainly comprising 1SW fish (Fig. 1). A wild-smolt tagging program has been conducted since 1965 (with the exception of 1982) with annual releases ranging from as few as 154 to as many as 5000 fish

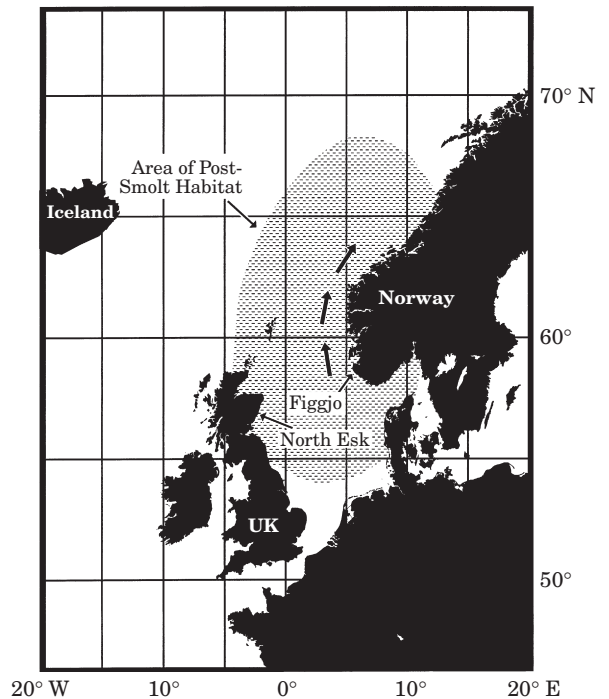


Figure 1. Map of Northeast Atlantic area with rivers Figgjo and North Esk indicated and general area of post-smolt habitat marked with hatching. Large arrows show general direction of Norwegian coastal current.

(Table 1). Pre-smolt juveniles were captured by electrofishing 2–4 weeks before the smolt migration and tagged with individually numbered Carlin tags (Carlin, 1955) to the dorsal side of the fish under MS222 anesthesia. Fish were held in a net pen located at the capture site for a few hours before being released back into the same area of the river. Fishers reported adult recaptures of tagged fish.

The North Esk is a river of similar size to the Figgjo on the eastern coast of Scotland (Fig. 1). Migrating smolts were intercepted in a trap situated just above the head of tide (Shearer, 1992). All trapped smolts were tagged with individually numbered external tags under MS222 anesthesia. During 1965–1967, diamond-shaped silver plates were attached to the anterior end of the dorsal fin using a silver wire. Since then, Carlin tags affixed using polyethylene threads were applied. The fish were allowed to recover from the effects of the anesthetic for a few hours, after which they were released back into the river. The number of smolts tagged each year varied from 1124 to 17 445 (Table 1), due to variations in trap efficiency caused by differences in spring discharge levels.

Return rates in both rivers were based on the number of tag returns by sea-age and the number of tagged fish released by smolt cohort. Return rates were interpreted as survival rates since the observed changes in abundance exceeded the range of what could be reasonably

Table 1. Number of wild smolts tagged in the rivers Figgjo and North Esk.

Smolt year	Number tagged	
	Figgjo	North Esk
1965	454	9474
1966	322	5783
1967	154	8825
1968	459	5323
1969	1278	1312
1970	2439	11 539
1971	3542	7240
1972	2723	5791
1973	5000	13 391
1974	2000	11 762
1975	1000	7627
1976	1649	5882
1977	1176	2505
1978	999	2111
1979	173	1760
1980	993	11 475
1981	982	10 371
1982		11 848
1983	919	1456
1984	944	6527
1985	994	6210
1986	976	1124
1987	994	4976
1988	997	3874
1989	1000	4967
1990	1000	17 445
1991	962	8721
1992	997	2941
1993	1000	2964

produced by changes in fishing mortality alone. Recaptures of 1SW salmon at the Faroe Islands were included on the 2SW recapture lists, since they would not be expected to return to homewaters in the same year.

Area of suitable thermal habitat

We used the areal coverage of various SST ranges, which we refer to as thermal habitat, to evaluate the effect of decadal scale ocean climate variation in the North Sea area on salmon post-smolts. These calculations were guided by two principles. First, post-smolt migrations from freshwater to the ocean tend to occur during similar time periods each year (Solomon, 1978; Thorpe and Morgan, 1978; Jonsson and Ruud-Hansen, 1985; Saunders, 1986; Mills, 1989; Reddin, 1988). Second, the swimming potential of post-smolts limits their migratory range and thus circumscribes the nursery habitat (Dutil and Coutu, 1987; Reddin and Short, 1991; Holst *et al.*, 1993; Jonsson *et al.*, 1993).

Thermal habitats were derived from the Comprehensive Ocean-Atmosphere Data Set (Slutz *et al.*, 1985). These data are assembled from ship reports, research

vessels, buoys, and other devices and are summarized as monthly means averaged by $2^\circ \times 2^\circ$ square latitude-longitude boxes. Their compilation provides a depiction of SST worldwide. Areal coverage of thermal habitat was computed for four 3°C temperature ranges ($5\text{--}7^\circ\text{C}$, $6\text{--}8^\circ\text{C}$, $7\text{--}9^\circ\text{C}$, $8\text{--}10^\circ\text{C}$) over a 22° longitude bracket centered at 0° . Data were examined for the months of March through July. Since Figgjo and North Esk smolts usually enter the marine environment during late April to early May, they will likely enter marine waters of $8\text{--}10^\circ\text{C}$ (Thorpe and Morgan, 1978; Jonsson and Ruud-Hansen, 1985). Therefore, this temperature range was considered to be of ecological significance to the salmon and was used to highlight trends in SST distribution. Trends were compared by computing correlation coefficients between 1SW and 2SW recapture rates and thermal habitats for each month and temperature range combination. Missing values were eliminated on a pairwise basis as opposed to listwise.

Average, monthly, SST fields were computed for two periods of contrasting post-smolt survival. The temperature fields represented periods of high and low return rate for 1971–1974 and for 1986–1988, respectively. The resultant fields were then formed into triangular irregular networks (TIN) along which 2° isothermal contours were drawn. The maximum length of any TIN face was constrained such that areas of the sea surface with missing temperature values did not influence contour drawing, and contours did not extend beyond the observed data. The geographic area between 8°C and 10°C , representative of the temperature range post-smolts enter the marine environment, was highlighted.

Post-smolt growth increment

Scale samples were collected from returning 1SW and 2SW salmon to the North Esk. Scales were removed from rows 3–5 above the lateral line on a line between the posterior end of the dorsal fin and the anterior end of the anal fin – the standard position for Atlantic salmon. Impressions of clean scales were made in cellulose acetate strips and the distance from the scale focus to the beginning of sea growth and the 1SW annuli were determined (Fig. 2). Using linear back-calculation based on size-at-capture, the post-smolt growth increment (cm) was determined by differencing the total 1SW increment and the freshwater increment. Scale sample sizes averaged 798 and 886 scales per year for the 1SW and 2SW returns, respectively; all year-age samples exceeded 225.

Results

Comparison of return rates

Return rate for 1SW salmon was higher than for 2SW fish in both stocks (Fig. 3). The 1SW rates averaged

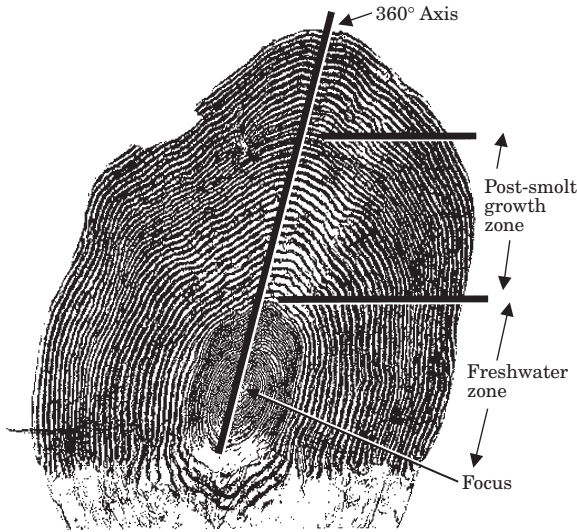


Figure 2. Atlantic salmon scale showing location of freshwater and post-smolt growth zones.

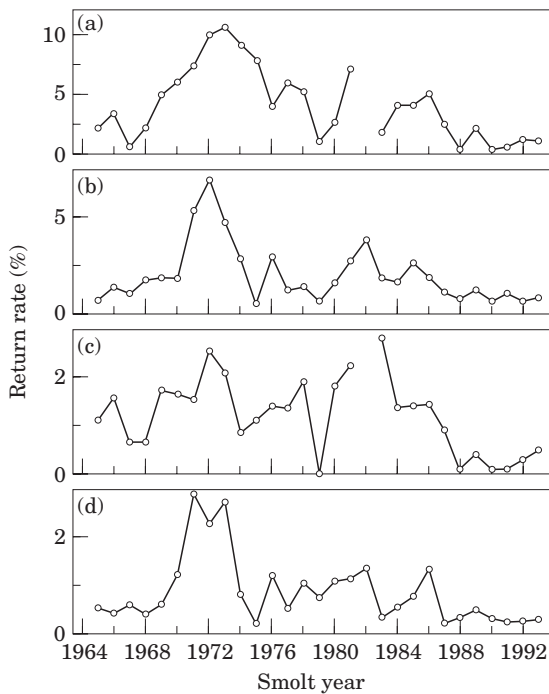


Figure 3. Tag recovery rate versus smolt year for (a) 1SW salmon to the river Figgjo, (b) 1SW salmon to the North Esk, (c) 2SW salmon to the river Figgjo, and (d) 2SW salmon to the North Esk.

4.1% and 2.0% for the Figgjo and North Esk stocks, respectively. Both stocks experienced 1SW recovery rates as low as 0.5%. The Figgjo had the highest rate observed of 10.6% for the 1973 smolt cohort, whereas the maximum for the North Esk was 6.9% for the 1972

cohort. The 2SW recovery rates averaged 1.2% (29% of the 1SW average) and 0.9% (43% of the 1SW average), respectively. From these return rate data, it appears that at least 76% of the Figgjo stock and 70% North Esk stock mature at 1SW; these are minimum estimates without exact knowledge of fishery removals. Therefore, both stocks are comprised mostly of 1SW fish and have shown wide contrast in return rate over the past three decades.

Time series of 1SW return rate for the two rivers were similar. Rates peaked during the early 1970s, and then declined to levels less than 1% by the late 1980s (Fig. 3a, b). Both series were significantly autocorrelated at a lag of 1 year. The similarity in the structure is also reflected in the strong positive correlation between the two sets (Fig. 4(a); $p < 0.001$).

Both stocks had high 2SW recovery rates during the early 1970s, followed by marked declines in the mid-1970s (Fig. 3c, d). However, where the North Esk 2SW rate continued its decline through the 1980s, the Figgjo stock 2SW rates peaked again around 1983. Since 1985, recovery rates in both stocks have declined to record low levels. The time series for 2SW return rates of the two stocks are not as well correlated between stocks (Fig. 4b; $p < 0.005$) and show varying degrees of correlation to their counterpart 1SW rates (Fig. 4c, d). The difference in return rate by age is reflected in the correlation between 1SW and 2SW recovery rates by smolt years within stock (for both Figgjo and North Esk, $p < 0.001$).

Comparison of thermal habitat to return rate

A reciprocal relationship emerged in the correlation analysis of thermal habitat trends and salmon return rates. The survival of both Figgjo and North Esk 1SW fish was negatively correlated with the area of 5–7°C SST in May (Fig. 5a). In contrast, for both stocks there is a positive relationship between survival of 1SW fish and the area of 8–10°C SST in May (Fig. 5d). The regime shift between warm and cool conditions resulted in an inverse relationship between the extent of warm and cool thermal habitat. We attribute greater significance to the 8–10°C thermal habitat, since these are the water masses post-smolts enter after migrating from fresh water. The negative correlations observed for the 5–7°C habitat data were weakly echoed in the 6–8°C data (Fig. 5b); and only Figgjo data showed any significant correlation to 7–9°C thermal habitat data (in July; Fig. 5c).

Correlation between 2SW return rates and thermal habitat differed between the two stocks. For the Figgjo stock, the only significant correlation was a positive one for the area of 7–9°C thermal habitat in May (Fig. 5g). For the North Esk stock, correlations between 2SW recovery rate and thermal habitats showed similar patterns to those observed for the 1SW data. Significant 2SW correlations of opposite sign were found with

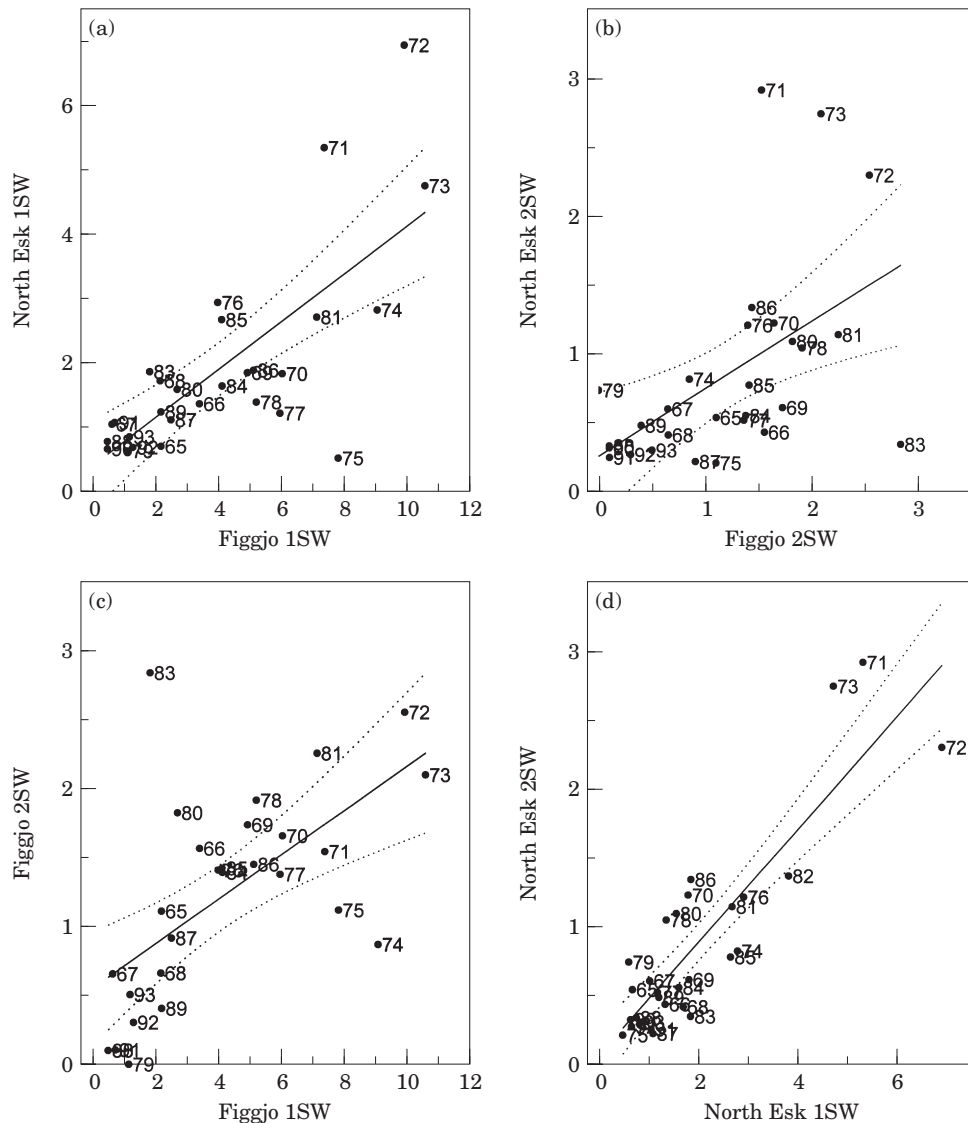


Figure 4. Scattergrams illustrating coherence between stocks and correlation between ages within stocks (labels refer to smolt year): (a) North Esk versus Figgjo 1SW return rate ($r=0.73$; $p<0.001$); (b) North Esk versus Figgjo 2SW return rate ($r=0.52$; $p<0.005$); (c) 2SW versus 1SW return rate in the Figgjo ($r=0.62$; $p<0.001$); and (d) 2SW versus 1SW return rate in the North Esk ($r=0.88$; $p<0.001$). Broken line represents 95% confidence interval.

May 5–7°C and 8–10°C thermal habitats (Fig. 5e, h), lower correlations with 6–8°C habitat (Fig. 5f), and no correlation with the 7–9°C habitat data (Fig. 5g).

Contrast in thermal habitat

Spring thermal conditions in the Northeast Atlantic were different during the period of high return rates versus the more recent period of lower return rates. These differences were easily traced by following the geographical extent of 8–10°C surface water through the spring period (Fig. 6). In March, there

are few differences in the distribution of 8–10°C water between the two survival periods. However, by April there is a divergence in the SST distributions with 8–10°C water distributed further to the north and east during the period of high survival. This trend continues into May when all North Sea and southern Norwegian coastal waters were in excess of 8°C during the period of high survival, while during the period of low survival a large part along the Norwegian coast was colder. By June, the bands of 8–10°C are separated by different latitude distributions.

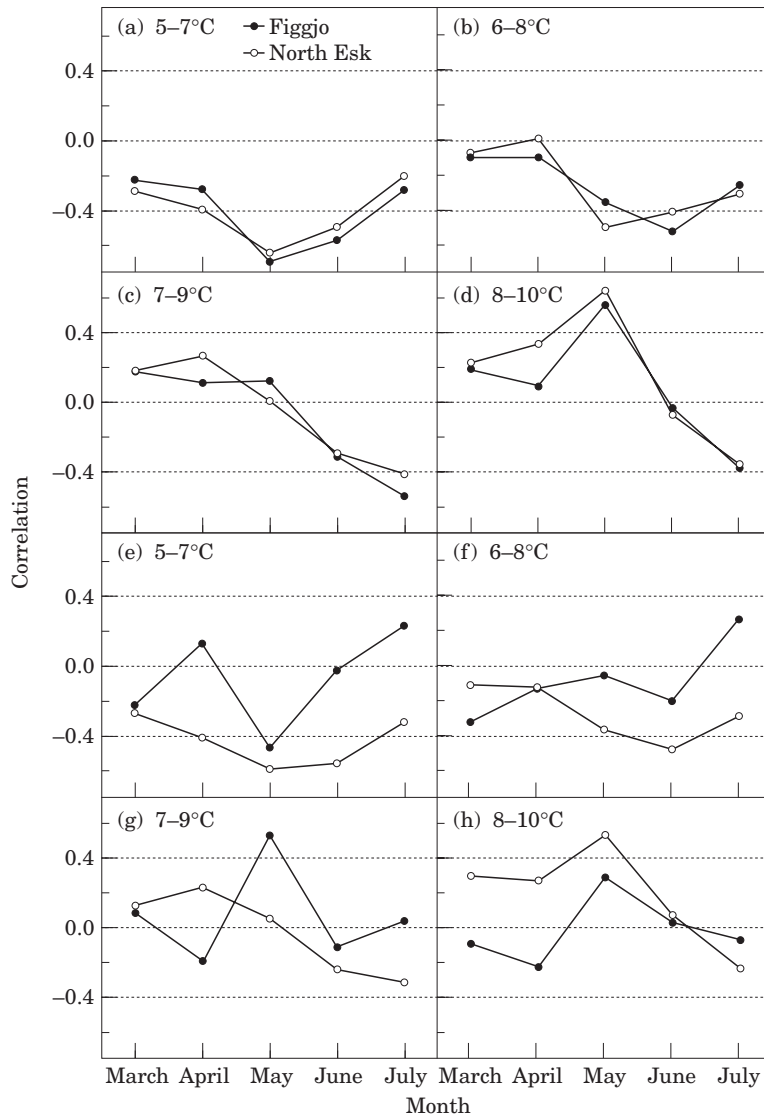


Figure 5. Correlation between return rate for Figgjo and North Esk salmon and thermal habitat versus month for 1SW salmon (a, b, c, d) and 2SW salmon (e, f, g, h). Thermal habitat computed for four thermal ranges: 5–7°C (a, e); 6–8°C (b, f); 7–9°C (c, g); and 8–10°C (d, h). Grid line at $r=0.4$ represents the approximate location of significance at $p=0.05$.

Relationship to post-smolt growth increment

Post-smolt growth increments were similar for 1SW and 2SW returns to the North Esk, and averaged 35.3 cm and 35.5 cm, respectively. Despite significant differences in some years, the time-series trends of the increment means were nearly identical for the two age groups (Fig. 7). Increments were low at the beginning of the time series, increased during the early 1970s, and declined to low levels for the remainder of the time series. This is the same general pattern observed for both North Esk and Figgjo return rate time series (Fig. 3), as demonstrated by regressing return rate on the growth increments (Fig.

8), and, by association, the same pattern as observed in the thermal habitat data.

Discussion

Our results suggest there is a link between ocean climate conditions, post-smolt growth, and post-smolt survival for salmon stocks in the North Sea area. Aspects of these relationships have been described before. Working with a combined estimate of total stock abundance for all European stocks, Friedland *et al.* (1993) reported that spring temperature conditions might influence

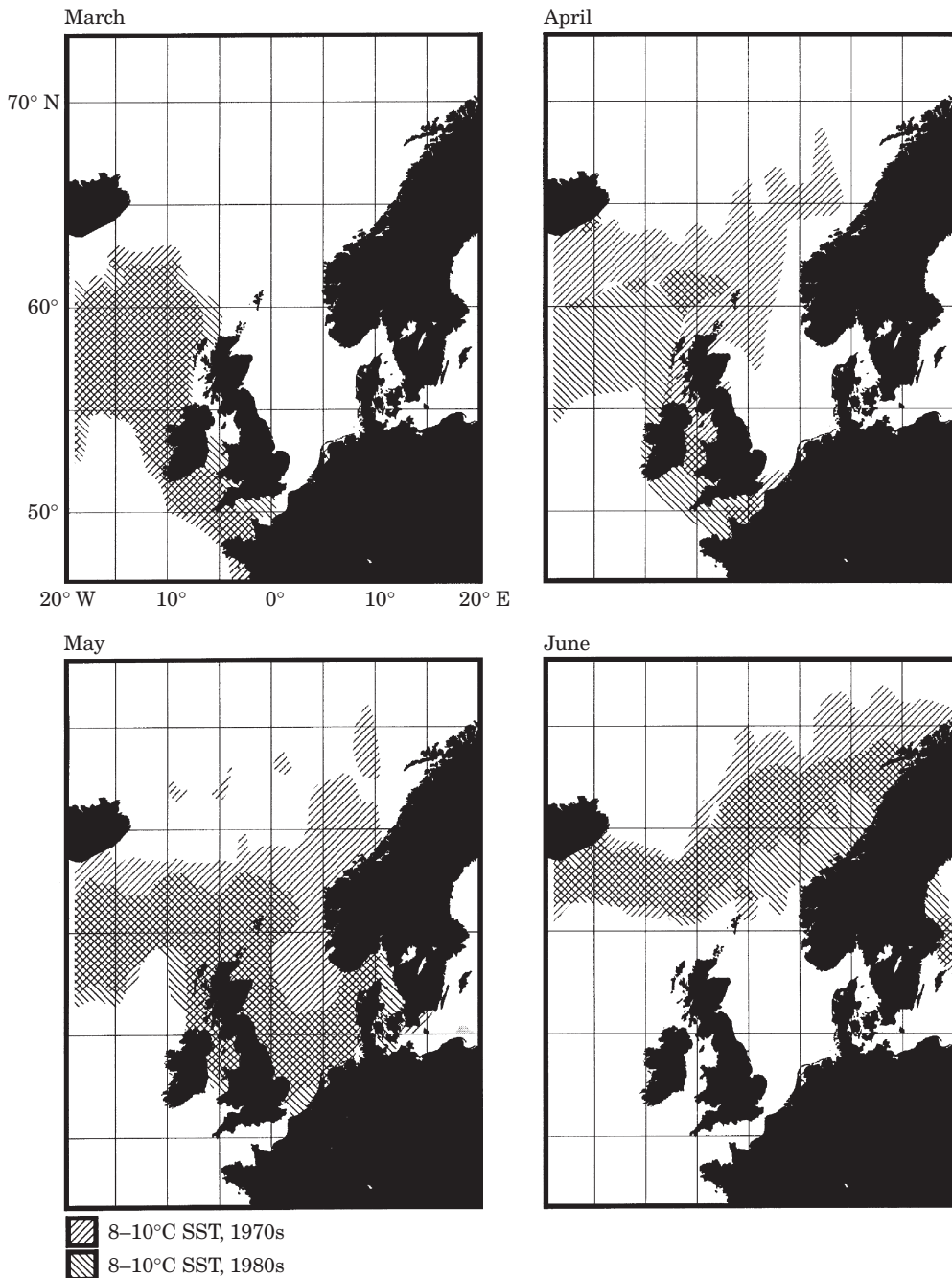


Figure 6. Sea surface temperature maps of the Northeast Atlantic area with the SST area of 8–10°C marked with hatching for two time periods, 1971–1974 and 1985–1988, over the months March, April, May, and June.

survival in some way. However, in that study both fish abundance and environmental data were smoothed in both time and space making any inference about the recruitment process impossible. The results presented here are consistent with these earlier findings, but go significantly further to elucidate the mechanism at work.

First, our analysis is discrete over time and space. We can conclude that the ocean climate variation related to the survival of salmon in the North Sea area occurs in spring when the post-smolts first enter the marine environment and occurs in the area of the North Sea and Norwegian coast. Second, because growth is correlated

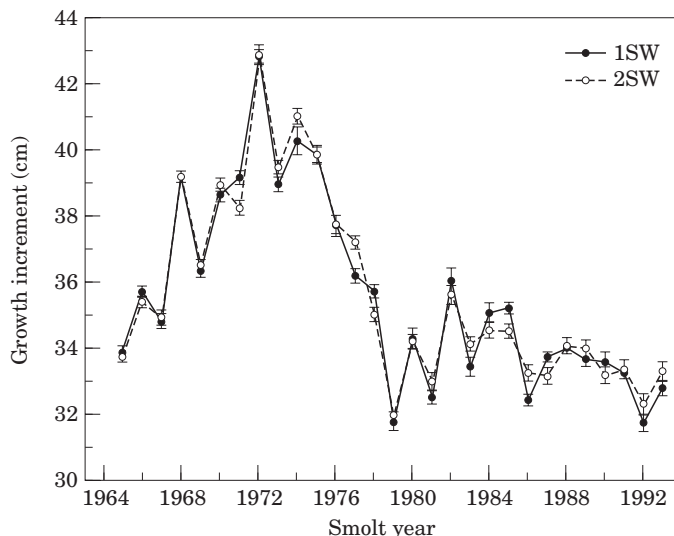


Figure 7. Post-smolt growth increment *versus* smolt year for 1SW and 2SW returns to the North Esk.

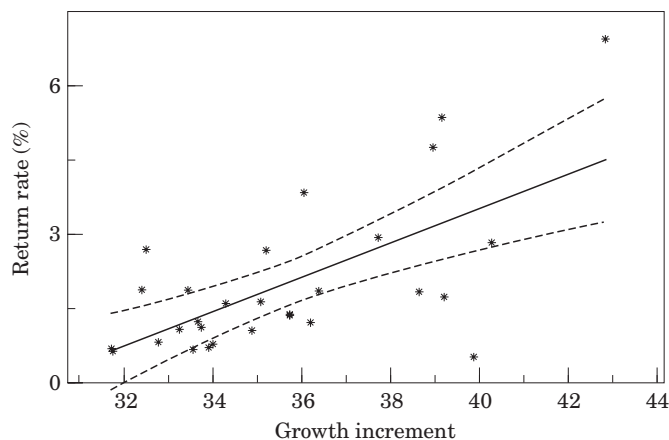


Figure 8. Scattergram and regression between 1SW return rate and post-smolt growth increment matched by smolt years for the North Esk stock ($r=0.65$; $p<0.001$). Dashed line represents 95% confidence interval.

with return rate, certain hypotheses about post-smolt survival must be rejected and others favored as more likely explanations.

Post-smolts from stocks in the North Sea area distribute in a thermally dynamic area and thus experience annual variation in temperature conditions. The highest correlation between return rates and warm-water habitat (8–10°C) was restricted to May, which is also the first month in the ocean for these fish. Post-smolts are not able to outswim the ocean currents found in the North Sea and along the Norwegian coast, thus for the first months at sea they are passively transported northward (Jonsson *et al.*, 1993). This would predict that post-smolts from the Figgjo and North Esk stocks would be located in the northern part of the North Sea and along the southern coast of Norway during May and June,

which is generally confirmed by observations of tagged fish (Jonsson *et al.*, 1993). The question becomes how are the temperature changes in this area affecting the fish, or alternatively, if they are neutral to the fish, what is the actual effect with which they co-vary?

Whatever survival mechanism is explored, it would seem unwise to ignore growth as the ultimate factor controlling mortality. Growth-mediated survival of larval and juvenile life history stages has been broadly identified as critical to the recruitment process (Anderson, 1988; Pepin, 1991). The same mechanisms can be seen in salmonids (Furnell and Brett, 1986; Mathews and Ishida, 1989; Holtby *et al.*, 1990; L'Abée-Lund *et al.*, 1993; Friedland *et al.*, 1996). If we are satisfied that the variation in growth of North Esk salmon reflects the variation observed in survival of both

Figgjo and North Esk fish, we should place greater weight on growth-mediated survival mechanisms such as predation. Therefore, hypotheses that are growth-independent may be rejected or at least de-emphasized. For example, there has been speculation that survival is related to the changing abundance of predators such as marine mammals. If mortality rate were only dependent on predator density, we would not necessarily expect to see a correlation between growth and survival. Alternatively, we need to search for explanations of how climate might affect growth and in turn affect the survival rate of post-smolts.

Climate could act on fish growth directly by affecting some physiological process or indirectly by affecting change in the ecosystems. Salmonine growth increases linearly with water temperature (Brett, 1979), thus seasons with lower temperature conditions would produce slower growth. This is the most direct effect of temperature on growth we could anticipate. However, temperature may also directly stress the physiology of post-smolts by forcing additional swimming as fish try to respond to migrational cues and avoid undesirable thermal conditions (Salminen *et al.*, 1994). This assumes post-smolts have very specific thermal preferences and would try to locate optimal conditions during the first months at sea. However, we must also recognize that these effects may not produce the contrast in growth necessary to explain observed growth and survival patterns.

Indirect effects would include conditions that may impact the quantity or quality of food or other aspects of the rearing environment. Change in the temperature regime could be indicative of a number of changes that might affect primary and secondary production. Prey availability to salmonids is often related to oceanographic processes and structural features in the water column (Reddin, 1985; Pearcy *et al.*, 1988; Brodeur, 1989; St. John *et al.*, 1992; Levings, 1994; Cooney *et al.*, 1995). Change in productivity can also change the structure of food webs and thereby shift predation pressure onto post-smolts (Fisher and Pearcy, 1988). Though not yet documented for Atlantic salmon, diet composition has been shown to affect growth and is clearly implicated in the recruitment process of Pacific salmonids (Healey, 1991; Brodeur *et al.*, 1992; Perry *et al.*, 1996). It will be essential to make field observations of Atlantic salmon to distinguish between these different mechanisms.

Differences in return rate by age group varied significantly between the Figgjo and North Esk stocks, suggesting age at maturity is not a consistent feature between the two populations. Figgjo 2SW return rate was correlated with a different set of environmental factors, suggesting a divergence between the two maturity groups early in their ocean migration. Friedland *et al.* (1998) suggest maturation may depend upon

migration during the post-smolt year, and thought their work implies winter distributions are critical. The trajectory of the post-smolt migration as a whole may be decided during an earlier season.

Retrospective growth analysis may offer the means to identify which growth seasons are critical to North Sea post-smolts. Our analysis of post-smolt growth increments fails to examine the substructure within the scale that could be used to relate seasonal growth to survival. Circuli spacing patterns have been used to demonstrate relationships between post-smolt growth and survivorship in hatchery stocks (Friedland *et al.*, 1996). The detailed post-smolt growth histories for North Sea stocks would reveal any seasonal growth effects that could be related to the environmental record. Although the highest post-smolt mortality rates are associated with the first weeks at sea (Eriksson, 1994), it is not known if these rates are the most variable. Spring growth rates may set into motion size-specific mortality in the summer, which could be the source of variability that shapes annual recruitment.

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