

# The recruitment of Atlantic salmon in Europe

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The stock complex of Atlantic salmon, *Salmo salar*, in Europe has experienced a multidecadal decline in recruitment, resulting in the lowest stock abundances observed since 1970. Here, physical forcing, biological interactions, and the resultant growth response of post-smolt salmon are examined with a view to understanding the mechanism controlling recruitment. Sea surface temperature (SST) has increased in the Northeast Atlantic, with the pattern and seasonal change in SST negatively correlated with post-smolt survival during summer and in a region that spatially matches the post-smolt nursery. Constituents of the pelagic foodweb, including potential post-smolt food and plankton that may affect post-smolt forage, have changed on a decadal scale and correlate with salmon survival. Retrospective growth analyses of eight stock/sea age components show that post-smolt growth during summer is positively correlated with salmon survival and recruitment. The Atlantic Multidecadal Oscillation appears to be a more closely aligned climate forcing index than the North Atlantic Oscillation with respect to salmon recruitment. European Atlantic salmon recruitment appears to be governed by factors that affect the growth of post-smolts during their first summer at sea, including SST and forage abundances; growth appears to mediate survival by the functional relationship between post-smolts and their predators.

**Keywords:** Atlantic Multidecadal Oscillation, Atlantic salmon, ocean climate, recruitment.

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## Introduction

Despite dramatic reductions in fishing pressure and measures to protect critical habitats, the European Atlantic salmon (*Salmo salar*) stock complex continues to decline in abundance as a result of recruitment failure associated with the marine phase of its anadromous life cycle. This marine phase of Atlantic salmon has been difficult to study because of the habits of juvenile salmon when they leave the rivers and begin their ocean migrations. They forage mostly in the upper surface layer of the ocean and migrate away from land, so they have always been an enigma because they were rarely caught in fishing gear either as directed catch or bycatch. It was not until the development of surface fishing techniques for salmon post-smolts that a synoptic characterization of their post-smolt ocean distribution emerged (Reddin and Short, 1991; Holm *et al.*, 2000). We now know that European salmon are influenced by the North Atlantic Drift and Norwegian Currents, resulting in a transport of smolts to the north, but the ocean currents alone do not explain their distribution patterns, suggesting that early in the marine phase, salmon post-smolts use a migration orientation to guide them to the west and into the Norwegian Sea (Booker *et al.*, 2008). When researchers began to relate ocean climate conditions to recruitment patterns, they limited their hypotheses to tests

associated with the areas salmon post-smolts would inhabit during the first months at sea, because the habitats used increasingly later in the post-smolt year were unknown.

The first attempt to relate ocean climate variation to European salmon recruitment focused on the relationship between recruitment and the spatial distribution of sea surface temperature (SST), or the quantity of thermal habitats. These analyses were limited to spring, so that inferences could be related to habitats that were likely used by the post-smolts. Friedland *et al.* (1993) reported that a catch-based index of recruitment for the European salmon stock complex was correlated with a thermal habitat index of the area of the sea surface between 7 and 13°C during spring. As this habitat index covered such a broad area, it was not clear whether the variation represented a direct effect of temperature on post-smolts or simply reflected some level of climate variation co-varying with the recruitment pattern. In an attempt to refine this analysis, Friedland *et al.* (1998) used an age-disaggregated set of survival indices instead of a catch index and examined a range of thermal habitat indices. Those analyses supported the conclusion that ocean climate variation in the Northeast Atlantic appeared to be related to the recruitment pattern, but the analyses also offered limited insight on the possible mechanisms of recruitment control.

The biological component of growth was added to the analysis of salmon recruitment mechanisms with the introduction of retrospective growth analyses. Friedland *et al.* (2000) introduced a time-series of post-smolt growth increments for an index stock from Scotland, the North Esk. The growth increment analysis showed that the post-smolt growth for North Esk salmon was positively correlated with the survival pattern of the stock, and by association with the recruitment pattern of the European stock complex, because the two resembled each other. The data suggested that growth at some time during the post-smolt season, between ocean entry and the formation of the winter annulus, was influencing survival. This hypothesis is further supported by data for another stock, the Burrishoole, which showed a multidecadal pattern of post-smolt growth similar to that seen with the North Esk fish (Peyronnet *et al.*, 2007). However, neither analysis was able temporally to limit the growth effect to a subseason within the 8-month period represented by the post-smolt growth increment. McCarthy *et al.* (2008) reported an analysis of post-smolt growth for salmon in the Drammen River in Norway and addressed the issue by introducing a technique of proportionally allocating circuli spacing increments to putative months during the post-smolt season. Their findings suggest that the correlation between post-smolt growth and survival is driven by the growth during summer, principally during the fourth and fifth months of life in the ocean. The Drammen data do not cover the full range of recruitment variation for the stock or the stock complex, but the data clearly indicate that summer growth is pivotal to salmon post-smolt survival. The data offer additional support for the growth-survival hypothesis, and further suggest a season-specificity to growth-mediated survival, as has been seen elsewhere in salmonids (Beamish *et al.*, 2004; Moss *et al.*, 2005; Ruggerone *et al.*, 2005, 2007).

Other data suggest that the environment impacts post-smolt growth in a way beyond the broad-scale forcing represented by analyses that track changes in thermal habitat. In an analysis of circuli spacing for another Scottish river, the Girnock Burn, Friedland *et al.* (2005) reported that post-smolt growth during the first months at sea was negatively correlated with SST, noting that the analysis was initially constrained to May and June data, for which there was greater confidence that environmental data matched the distribution of the fish. When the analysis was extended deeper into summer, and hence further along the migration of the post-smolts, the negative correlation between growth and SST was strengthened, and it showed a pattern that resembled the distribution of post-smolts revealed in trawl survey data (Holm *et al.*, 2000). A negative growth response for salmon related to increasing temperature was also detected by Todd *et al.* (2008). Collectively, these two studies suggest that warming conditions in the Northeast Atlantic are associated with decreased growth of salmon. Whether temperature is the primary agent of this change in growth is not known, however, because increasing temperature may lower growth via increased metabolic demands (Brett, 1979), but salmon are capable of moderating their temperature by migrating.

Concomitant with the observed change in SST in the Northeast Atlantic has been a change in the components of the ecosystem. Change in the area has been observed in the level of primary production (Richardson and Schoeman, 2004), secondary production (Beaugrand *et al.*, 2002; Beaugrand and Ibanez, 2004), and the distribution of marine fish (Perry *et al.*, 2005). Beaugrand and Reid (2003) correlated change in the plankton community with the

recruitment of European salmon, which suggests a specific linkage between diet and growth, although the linkage would most likely be related to conditions influencing the preferred forage of salmon post-smolts (Haugland *et al.*, 2006).

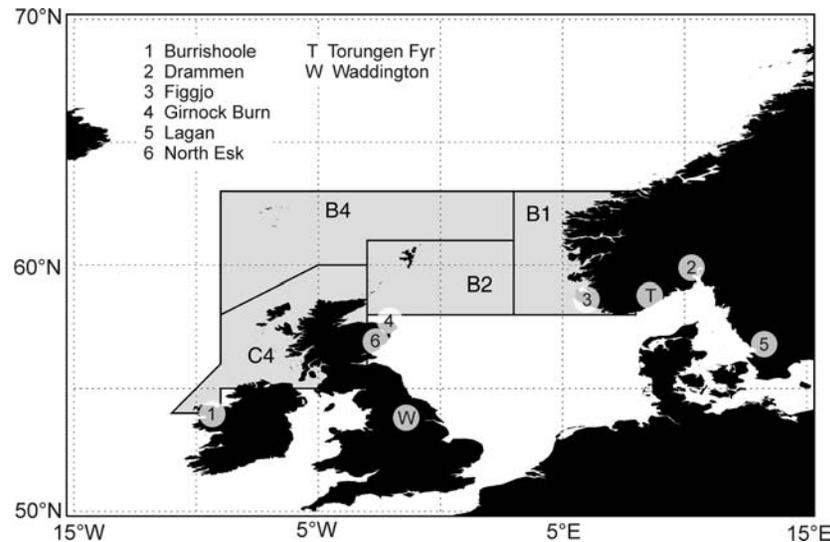
Our goal in this investigation was to approach the mechanism of European salmon recruitment holistically, by examining physical forcing and biological response. We analysed the SST fields in the Northeast Atlantic to determine whether spatial and temporal variations in the fields were related to the pattern of recruitment and whether broad-scale climate forcing was related to the pattern of recruitment variation. We reanalysed previously reported retrospective growth time-series, increasing the length of some of the series, and introduced time-series previously unreported. Finally, we analysed the abundance data for potential food and other foodweb indicators that potentially may be influencing salmon post-smolt growth and survival.

## Methods

### Recruitment of salmon

The recruitment of salmon can be assessed by examining trends in stock size, which represent the cumulative effects of mortality factors affecting multiple life stages, or by focusing on survival indices associated with key life stages responsible for the variation in recruitment. For European salmon, we can examine recruitment through both forms of data. The stock complex of European salmon has been assessed with a modified virtual population analysis, or run reconstruction analysis, that estimates the size of the stock, referred to as pre-fishery abundance, at a point in time before the first fisheries are executed (Potter *et al.*, 2004). These estimates are disaggregated by sea age of return, focusing on the two dominant sea ages of 1-sea-winter (1SW) and 2SW, and by geographic groupings, splitting the stock complex into groupings of national stocks from northern and southern Europe. The set of estimates we used were from the 2007 stock assessment (ICES, 2007), augmented with earlier estimates for Norway during the smolt years 1970–1981 (ICES, 2001) that the assessment group deemed unreliable. We do not take issue with the conclusion of the assessment of the working group that the early part of the Norwegian time-series is problematic, but we feel it is representative enough of stock size to use the data in a qualitative context, as treated here.

The survival of post-smolts, the key life stage for Atlantic salmon, can be assessed by tagging data for the stocks of two rivers. The rivers Figgjo and North Esk are small, relatively unimpacted, salmon rivers that empty into the North Sea. The River Figgjo is located in southern Norway and supports a stock of salmon mainly comprising 1SW fish (Figure 1). A wild smolt-tagging programme has been conducted in the river since 1965 and annual releases average ~1200 fish, except 1982, when no tags were applied (Table 1). Pre-smolt juvenile salmon were captured by electro-fishing 2–4 weeks before the smolt migration and tagged with individually numbered Carlin tags (Carlin, 1955) attached to the dorsal side of the fish under MS222 anaesthesia. 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 larger river than the Figgjo located on the east coast of Scotland (Figure 1). Smolt tagging has also been conducted in the North Esk, but in that tagging programme, migrating smolts were intercepted in a trap situated just above the head of tide



**Figure 1.** Map of the Northeast Atlantic Ocean, with Sir Alister Hardy Foundation for Ocean Science (SAHFOS) standard areas B1, B2, B4, and C4 highlighted in grey. These areas are used to characterize CPR (Continuous Plankton Recorder) data. Locations of river of origin of six salmon index stocks given by numbered key and climate monitoring station by lettered key.

(Shearer, 1990). All smolts trapped were tagged with individually numbered external tags under MS222 anaesthesia. During the years 1965–1967, smolts were tagged with diamond-shaped silver plates attached to the anterior end of the dorsal fin using a silver wire. Since then, smolts have been tagged with Carlin tags affixed using polyethylene threads. Smolts were allowed to recover from the effects of the anaesthetic for a few hours, then released back into the river. The number of smolts tagged each year has averaged ~5900 fish (Table 1), with the numbers of fish tagged varying as a result of 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, because the observed changes in abundance exceeded the range of what could be produced reasonably by changes in fishing mortality alone. For the purposes of this study, recaptures of 1SW salmon at the Faroe Islands were included on the 2SW recapture lists because they would not be expected to return to home waters in the same year. Principal component analysis of the pre-fishery abundance and return rate time-series was carried out to represent the general trend suggested by the component signals.

### Size of smolts at ocean entry

The size of smolts as a factor affecting post-smolt survival and resultant recruitment was evaluated by examining time-series from the two index stocks used in the recruitment evaluation. The smolts used in the Figgjo and North Esk tagging studies were measured. A subsample of 50 fish per year was used to estimate smolt size of the Figgjo stock (Table 1). For the North Esk stock, the sample size of lengths measured is nearly the same as the number of fish tagged through the year 2000; since then, the number of fish tagged has been a subsample of the number of fish measured. The adequacy of the length of samples was evaluated by calculating 95% confidence intervals to assess graphically if smolt lengths were different between years. Mean smolt sizes

were correlated with the first principal component of the return rate time-series.

### Climate change in fresh-water habitats

There are a multitude of factors that can affect the size of Atlantic salmon smolts, many of which are beyond the scope of this study. However, climate factors affecting fresh-water rearing conditions can be assembled and compared with smolt size and parallel events in the marine environment. Temperature and rainfall patterns for the UK and southern Norway were extracted from the dataset of climate parameters assembled by the European Climate Assessment and Dataset project (Klein Tank *et al.*, 2002). Fresh-water climate conditions were represented by temperature and rainfall patterns at the Waddington and Torungen Fyr stations, for the UK and southern Norway, respectively (Figure 1).

### Trends in SST

Trends in SST across the Northeast Atlantic Ocean were characterized using the extended reconstructed SST dataset (ERSST, version 2), a dataset based on an SST compilation of the International Comprehensive Ocean–Atmosphere Data Set (ICOADS) and representing interpolation procedures that reconstruct SST fields in regions with sparse data (Smith and Reynolds, 2003, 2004). The spatial resolution of the data is bins of 2° longitude by 2° latitude, and the temporal resolution is monthly; we extracted data from the area 60–80°N and 10°W–20°E over the period 1965–2005. These temperature fields were correlated with the first principal component of the return rate time-series.

### Plankton food resources in the post-smolt nursery

The abundance of plankton food items, those that may aggregate salmon prey, or plankton that provides forage for the prey of Atlantic salmon post-smolts, was extracted from the Continuous Plankton Recorder (CPR) database hosted by the Sir Alister Hardy Foundation for Ocean Science. The CPR survey is an upper-layer plankton monitoring programme that has collected

**Table 1.** Sample sizes used in tagging experiments and estimates of mean smolt length for fish in the Figgjo and North Esk rivers.

Smolt year	Tagging		Lengths	
	Figgjo	North Esk	Figgjo	North Esk
1965	454	9 474	50	9 446
1966	322	5 783	50	5 783
1967	154	8 825	50	8 825
1968	459	5 323	50	5 308
1969	1 278	1 312	50	1 313
1970	2 439	11 539	50	11 535
1971	3 542	7 240	50	7 240
1972	2 723	5 791	50	5 791
1973	5 000	13 391	50	1 3391
1974	2 000	11 762	50	11 762
1975	1 000	7 627	50	7 627
1976	1 649	5 882	50	5 882
1977	1 176	2 505	50	2 505
1978	999	2 111	50	2 111
1979	173	1 760	50	1 760
1980	993	11 475	50	11 537
1981	982	10 371	50	10 371
1982		11 848		12 002
1983	919	1 456	50	1 456
1984	944	6 527	50	6 571
1985	994	6 210	50	6 216
1986	976	1 124	50	1 131
1987	994	4 976	50	1 131
1988	997	3 874	50	3 874
1989	1 000	4 967	50	3 874
1990	1 000	17 445	50	17 494
1991	962	8 721	50	8 807
1992	997	2 941	50	2 992
1993	1 000	2 964	50	2 966
1994	305	6 606	50	6 629
1995	998	5 847	50	5 914
1996	899	4 121	50	4 123
1997	1 000	4 054	50	4 472
1998	999	4 377	50	4 593
1999	1 000	2 520	50	2 524
2000	997	3 400	50	3 557
2001	864	4 744	50	9 905
2002	1 000	4 941	50	11 097
2003	1 000	1 561	50	4 260
2004	1 000	349	50	2 309
2005	1 000		50	2 310
2006			50	2 608

and enumerated plankton taxa in the North Atlantic since 1946 (Warner and Hays, 1994). Sampling is carried out by a high-speed CPR towed by merchant ships of opportunity (Hays, 1994). Seawater is filtered by the CPR onto silk screens with an effective aperture size of 270  $\mu\text{m}$ . In the laboratory, the screens are sectioned for spatially allocated counts and calibration to determine a plankton density (Warner and Hays, 1994). We considered the abundances of seven plankton categories: phytoplankton colour index (PCI), *Calanus finmarchicus*, *Calanus helgolandicus*, total amphipods, total euphausiids, total small copepods (<2 mm, traverse stage in analysis), and total large copepod (>2 mm, eye-count stage of analysis). The input data were monthly abundances for the period 1965–2005 from four of the CPR standard areas (Figure 1), areas only partially overlapping the region considered to be the post-smolt nursery for salmon in the Northeast Atlantic (Holm *et al.*, 2000). Three-month running

means of the abundances of potential post-smolt food items were correlated with the first principal component of the return rate time-series.

### Retrospective patterns of post-smolt growth

We used a combination of scale reading and image analysis to characterize scale patterns representative of marine growth during the post-smolt period of Atlantic salmon. For one stock, the North Esk, post-smolt growth is represented by a post-smolt growth increment determined from conventional scale reading. The first 29 years of this time-series were reported in Friedland *et al.* (2000); the dataserie is extended here to 40 years (Table 2). Scale samples were collected from 1SW and 2SW salmon returning to the North Esk. Scales were removed from the standard position for Atlantic salmon, namely 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. Scale impressions of clean scales were made in cellulose acetate strips. From the impressions, the distances from the scale focus to the beginning of sea growth and the 1SW annuli were determined (Figure 2). Using linear back-calculation based on size at capture, the post-smolt growth increment was determined as the difference between the total 1SW increment and the fresh-water increment. Increments are given in centimetres. Scale sample sizes averaged 871 and 731 scales per year for the 1SW and 2SW returns, respectively; all year-age samples exceeded 225 (Table 2).

The post-smolt growth increment and estimate of monthly growth during that period were measured using image analysis for four river stocks and samples from Greenland. European salmon caught at West Greenland are mostly from rivers in southern Europe and would have likely matured as 2SW fish the year following the fishery (Reddin and Friedland, 1999). The four river stocks, arrayed from west to east, are located in Ireland, Scotland, Norway, and Sweden. The Burrishoole River is located in western Ireland and has a trapping facility to sample returning fish (Figure 1). The stock is mainly 1SW fish, so the scale analysis focused on that age group (Peyronnet *et al.*, 2007). The samples were a combination of wild and hatchery-origin salmon; annual sample size averaged 46 fish (Table 2). The Girnock Burn is a sub-tributary of the River Dee, Scotland. The wild origin returns to this river are mostly 2SW, and they form the basis of the scale-analysis sample, which averaged 20 fish per year (Friedland *et al.*, 2005). The Drammen River in southern Norway was sampled between 1983 and 2003. Three maturity groups, 1SW, 2SW, and 3SW, return to the river; for this study, we focused on the 1SW and 2SW returns, which provided average sample sizes of 51 and 46, respectively. The Lagan is a river on the west coast of Sweden that empties into the North Sea; unlike east coast Swedish rivers that empty into the Baltic Sea, fish from the Lagan undertake their marine migration in the North Atlantic Ocean. The Lagan is a hatchery stock mostly composed of 1SW returns; sample sizes for that stock averaged 46 fish per year.

The post-smolt growth increment and estimates of monthly growth were drawn from measurements of circuli spacings of the marine portion of the scale. Scale samples were impressed into acetate slides, or for the Girnock Burn, the scales were mounted between glass slides. Using image processing, the spacings between successive pairs of circuli were measured along a transect on the 360° axis from the first pair of marine circuli to the edge of the scale, so measuring all circuli spacings in the marine growth

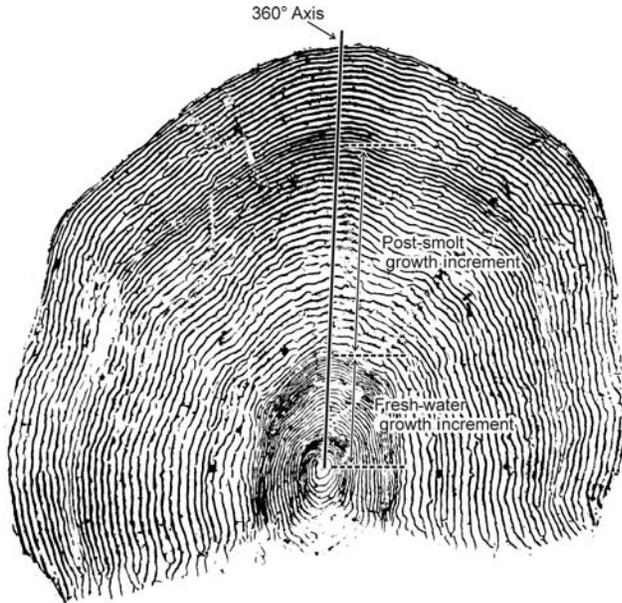
**Table 2.** Sample sizes for circuli spacing and post-smolt growth increment analysis by stock group and sea age of return.

Smolt year	Burrishoole 1SW	Drammen 1SW	Drammen 2SW	Girnock 2SW	Greenland 2SW	Lagan 1SW	North Esk 1SW	North Esk 2SW
1961	18							
1962	36							
1963	35							
1964	41			20				
1965	46			20			973	1 940
1966	40			19		50	1 022	1 304
1967	41			18		52	669	592
1968	50			17		57	1 271	1 010
1969	50			20		57	898	1 630
1970	47			17		58	754	956
1971	49			20		52	936	956
1972	51			10		45	1 421	651
1973	33			20		48	851	1 312
1974	48			17		53	476	1 258
1975	49			20		49	1 173	578
1976	34			13		43	547	986
1977	45			19	50	49	747	1 216
1978	51			19	50	47	999	866
1979	49			20	44	53	457	1 526
1980	49			20	50	57	322	630
1981	41		37	15	49	53	589	337
1982	50	52	48	20	50	58	226	365
1983	47	54	44	33	50	60	378	611
1984	40	57	46	20	50	60	297	442
1985	50	49	40	17	51	58	972	585
1986	50	55	41	16	50	56	812	490
1987	57	53	46	17	50	55	1 345	422
1988	50	52	45	18	50	57	1 110	420
1989	50	49	48	19	50	57	592	436
1990	51	50	47	18	49	59	319	507
1991	51	46	42	35	50	58	1 039	404
1992	50	53	42	15		36	676	464
1993	50	57	48	40		22	618	380
1994	50	51	43		50	48	435	279
1995	50	51	40		49	12	1 141	527
1996	50	48	47		50	17	1 116	451
1997	51	47	43		52	2	1 590	782
1998	50	48	43		36	9	1 205	519
1999	50	47	44		50	23	1 432	470
2000		51	39		49		909	708
2001		52	45				1 417	664
2002		41					1 280	486
2003							874	367
2004							950	

zone (Figure 2). The first pair of marine circuli is identified as the first wide circuli spacing after the relatively tightly spaced circuli of the fresh-water zone. The end of the post-smolt growth increment was associated with the first winter growth annulus, which was located by computing five-point running means of circuli spacings and selecting the minimum mean. A running means averaging was done to reduce the effect of measurement error on locating the winter annulus. The sum of the circuli spacings from the beginning of the marine zone to the winter annulus was used as the post-smolt growth increment.

To examine growth more closely during the post-smolt period, the total post-smolt growth increment was partitioned into putative monthly increments. We considered the post-smolt period for European stocks of Atlantic salmon to last for a period of 8 months, based on the time when most stocks migrate to sea and assuming that the winter annulus is formed after December, or

associated with shortest photoperiod of the year (Friedland *et al.*, 1993). The total number of circuli present in the post-smolt growth increment for each salmon was divided by eight to determine the number of circuli pairs allocated to each monthly period, so the circuli pairs are proportionally allocated to monthly periods. The mean spacing of circuli for each proportionally allocated month thus becomes an index that is more reasonable to compare between individuals, with a varying number of circuli deposited in the marine zone. We recognize that it is unlikely that the same number of circuli will actually be deposited each month of the post-smolt period (Bilton, 1975), but we feel our approach is reasonable considering that we are simply attempting to compare the same relevant portion of scales from different fish. The post-smolt growth increment and estimates of monthly growth were correlated with the first principal component of the return rate time-series.



**Figure 2.** Atlantic salmon scale showing measurement axis and principal growth increments.

**Climate indices**

The pattern of recruitment for European Atlantic salmon was compared with two broad-scale indices of climate forcing known to affect the physical environment and biological populations across the North Atlantic Ocean, and the associated terrestrial habitats. The North Atlantic Oscillation (NAO) is defined as the difference in normalized sea level pressure between Lisbon, Portugal, and Stykkisholmus, Reykjavík, Iceland; we used the winter index (December through March) and view the index as the principal mode of atmospheric forcing (Hurrell *et al.*, 2001). We also used a second index known as the Atlantic Multidecadal Oscillation (AMO), which is defined as a detrended pattern of SST variability in the North Atlantic (Enfield *et al.*, 2001). The detrending is intended to remove recent global climate change effects induced by increasing greenhouse gas emissions. The AMO signal appears to have a period of 20–40 years between warm and cool conditions. These climate-forcing indices were correlated with the first principal component of the return rate time-series.

**Time-series correlation**

The time-series we compared here had varying degrees of autocorrelation. We sought to account for this autocorrelation in our correlation analyses (Pearson product-moment correlation) by adjusting the effective degrees of freedoms of each test according to the procedure suggested by Pyper and Peterman (1998). The effective degree of freedom ( $N^*$ ) of a correlation between two time-series, in notation series  $X$  and  $Y$ , was estimated from

$$\frac{1}{N^*} \approx \frac{1}{n} + \frac{2}{n} \sum_{j=1}^{n/5} \frac{(n-j)}{n} \rho_{xx}(j) \rho_{yy}(j), \quad (1)$$

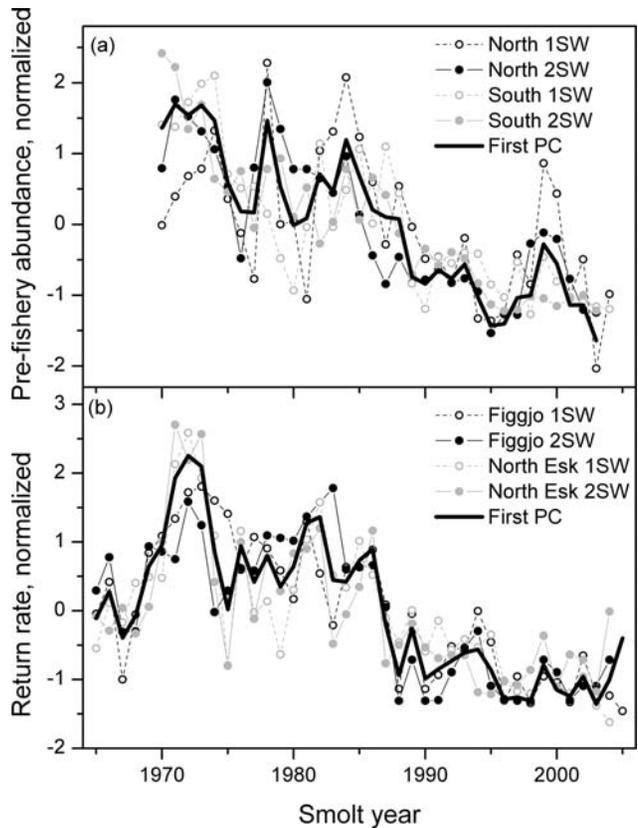
where  $n$  is the sample size, and  $\rho_{xx}(j)$  and  $\rho_{yy}(j)$  are the autocorrelations of  $X$  and  $Y$  at lag  $j$ . Following Garrett and Petrie (1981), we took the autocorrelation at lag  $j$  of the cross-products of

standardized time-series of  $X$  and  $Y$ . The probability associated with a correlation coefficient is designated as  $p$  and as  $p^*$  for a test with degrees of freedom based on  $N^*$ .

**Results**

**Recruitment of salmon**

The recruitment of salmon has been declining over the past three decades, as shown by time-series of pre-fishery abundance estimates and return rates for monitored stocks. The pre-fishery abundance of the European stock complex has averaged ~5 million salmon over the period, but the time-series shows a decline in abundance from nearly 8 million fish in the early 1970s to ~3 million fish more recently. The stock subcomponents, as partitioned by sea age and northern and southern subareas, have averaged between 1.0 and 1.8 million salmon, respectively, but the magnitude of the decline over time has not been uniform among these subcomponents. Southern subcomponents have declined more than northern components by age (Figure 3a). Within subarea components, 2SW fish have declined slightly more than 1SW fish. The first principal component of the four pre-fishery abundance time-series suggests highest recruitment during the early 1970s and lowest recruitments since the 1988 smolt year.



**Figure 3.** (a) Normalized pre-fishery abundance of European salmon partitioned by northern and southern subcomponents of the European stock complex, and sea age of return for the smolt years 1970–2004. The first PC is the first principal component of the four age-subcomponent abundances. (b) Normalized return rate of tagged salmon from the Figgio and North Esk rivers by sea age of return for the smolt years 1965–2005. The first PC is the first principal component of the four age-stock return rates.

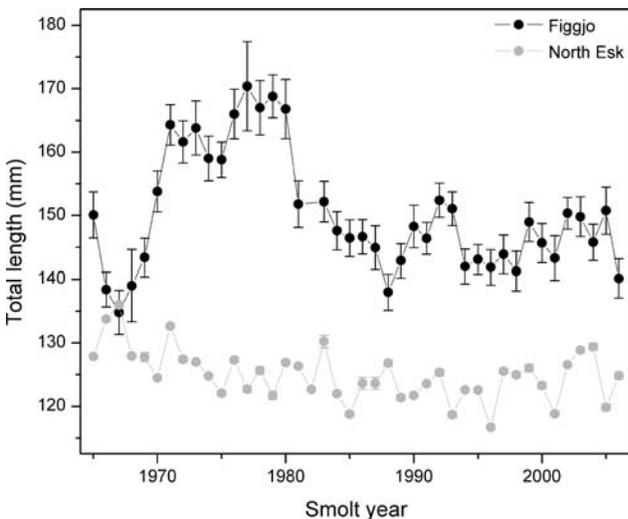
The time-series patterns of return rates for the Figgjo and North Esk stocks are similar to the patterns in pre-fishery abundances in those years that the time-series overlap. Return rates of both sea ages for the Figgjo averaged 2.0%, and for the North Esk 1.1%. We do not attach particular significance to the differences in these rates because the stocks would be expected to have different performance levels in the environment. However, the first principal component of the return rates shows striking similarities to the first principal component of the pre-fishery abundance data (Figure 3b). The two principal component time-series are significantly correlated ( $r = 0.877$ ,  $N^* = 11$ ,  $p^* < 0.001$ ). An important additional feature suggested by the return rate data is that return rates during the period 1965–1969 were lower than the peak in return rates seen in the 1970s, whereas the pre-fishery abundance data, which only start in 1970, suggest a monotonic decline in recruitment. The return rate data suggest an increasing followed by a decreasing trend in survival rates for the stocks. We suggest that the first principal component of the return rates is the best signal to represent the survival pattern of the stock complex, so it is used in correlation analyses here to represent survival and recruitment of the stock complex.

**Size of smolts at ocean entry**

The size of emigrating smolts varied by stock and over time. Smolts from the Figgjo river averaged 150 mm total length over the study period, but they showed a distinct time-series pattern of larger smolt size during the 1970s and early 1980s (Figure 4). During the 1970s, Figgjo smolts approached 170 mm. Smolts from the North Esk tended to be smaller, averaging 125 mm; there is little trend in the time-series of North Esk smolt lengths. When compared with the first principal component of the return rates, the Figgjo smolt lengths were significantly correlated with return rates, but North Esk smolt lengths were not correlated (Table 3).

**Climate change in fresh-water habitats**

The most demonstrative change in fresh-water climate conditions has been related to the thermal regime. Decadal variations in rainfall amounts are evident in both the UK and Norway (Figure 5a),

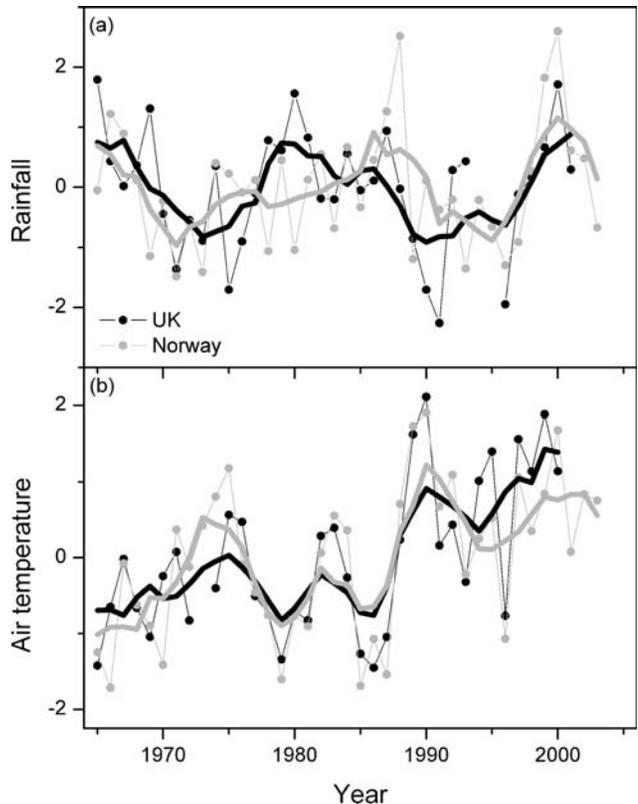


**Figure 4.** Total length of migrating smolts from the Figgjo and North Esk rivers for the smolt year period 1965–2006. Error bars are 95% confidence intervals.

**Table 3.** Correlation between smolt size and first principal component of return rates of tagged salmon.

Index	<i>r</i>	<i>n</i>	<i>p</i>	<i>N*</i>	<i>p*</i>
Figgjo	0.605	40	<b>0.001</b>	21	<b>0.004</b>
North Esk	0.242	41	0.130	41	0.130

*n*, observed sample size; *p*, probability value of correlation; *N\**, effective sample size after correction for autocorrelation; *p\**, probability of correlation after correction for autocorrelation. Significance at  $p = 0.05$  emboldened.

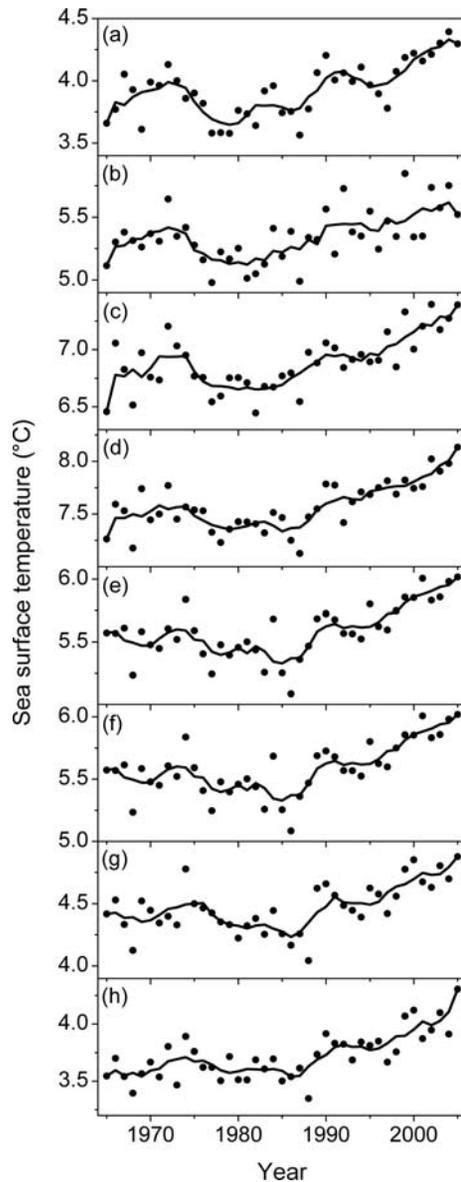


**Figure 5.** (a) Normalized precipitation and (b) air temperature observed at index sites in the UK, Waddington, and southern Norway, Torungen Fyr, with 5-year moving averages shown as heavy lines.

though these variations have not been coherent between the two areas ( $r = 0.328$ ,  $p^* = 0.062$ ). Temperatures in the nursery rearing areas, on the other hand, have trended over the study period, with the warmest conditions within the past two decades (Figure 5b). Temperatures in the UK and Norway were significantly correlated over the past four decades ( $r = 0.845$ ,  $p^* < 0.001$ ). We suspect that temperature change has contributed to the change in smolt size in the Figgjo, but we do not see a concomitant response of smolt size in the North Esk, which would have experienced similar changes in thermal regime.

**Trends in SST**

SST over the region 60–80°N and 10°W–20°E varied both spatially and temporally during the study period. The lowest temperatures were during May (Figure 6a) and December (Figure 6h), which averaged 3.9 and 3.7°C, respectively. SSTs averaged 7.6°C



**Figure 6.** Mean SST over the study area by year for the months May through December, panels (a) through (h), respectively.

during October, which had the highest monthly mean SSTs (Figure 6f). There are some features common to the time-series of monthly mean SST, with all months showing an increase in SST during the past two decades (Figure 6). For the early months of the year, there is an indication that SST was warmer at the beginning of the time-series. SST has shown distinct patterns of change on smaller spatial scales than the unit represented by our study area (Casey and Cornillon, 2001), so we correlated the first principal component of the return rates with SSTs observed in bins of  $2^\circ$  longitude by  $2^\circ$  latitude. The correlations are presented as contours plotted by map coordinates. The first principal component of the return rates is not strongly correlated with the SST fields; during the first two months, May and June (Figure 7a and b), the fish were at sea. These correlations increased over the next 5 months, July through November (Figure 7c–g), however, with the highest correlations appearing in the July and

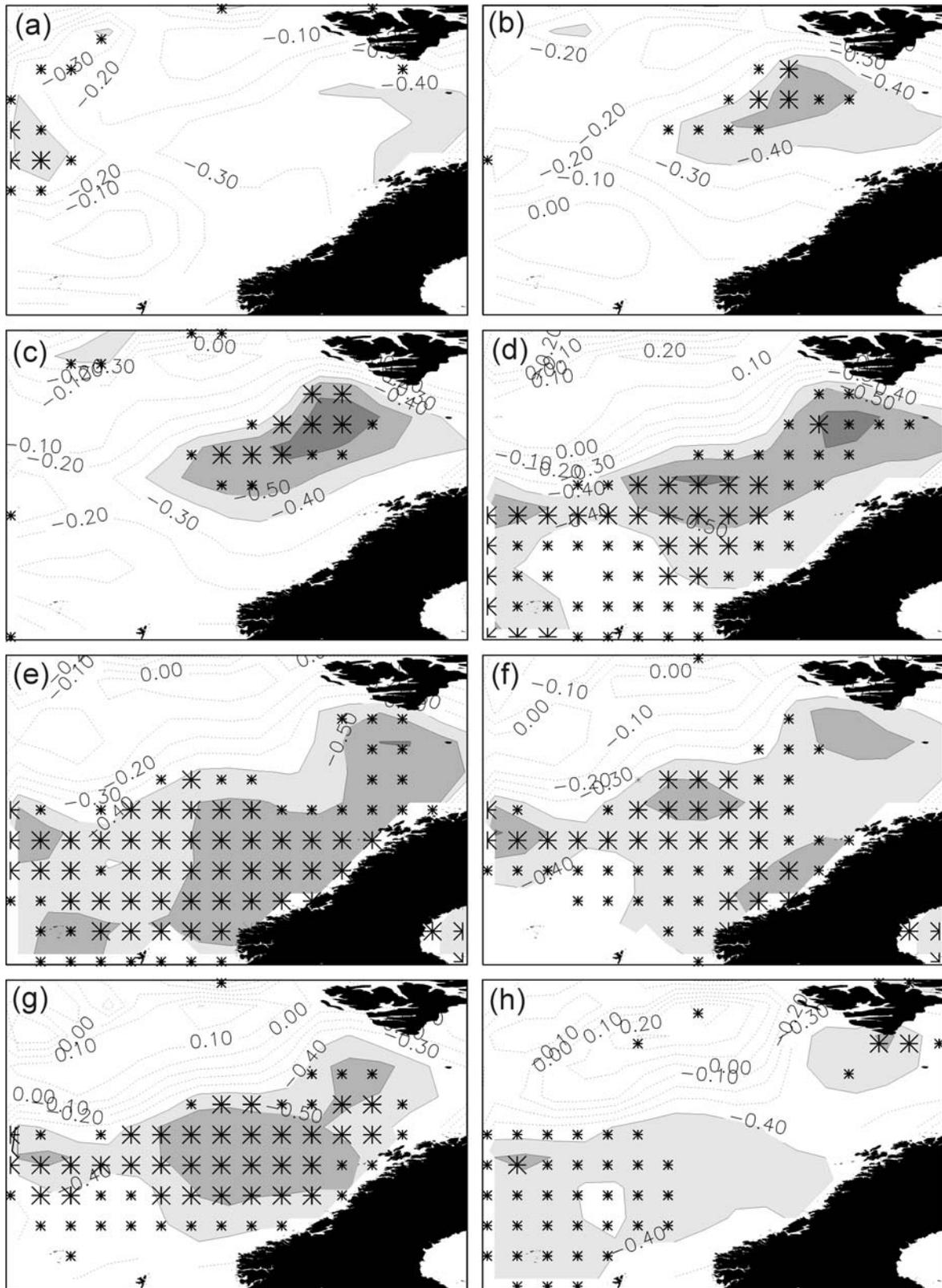
August fields. The correlations in the December SST field are much lower than the preceding fields (Figure 7h). The first principal component of the return rates was negatively correlated with SST in summer and autumn, with the strongest correlations during July and August, suggesting that warm conditions had a negative influence on recruitment.

#### Plankton food resources in the post-smolt nursery

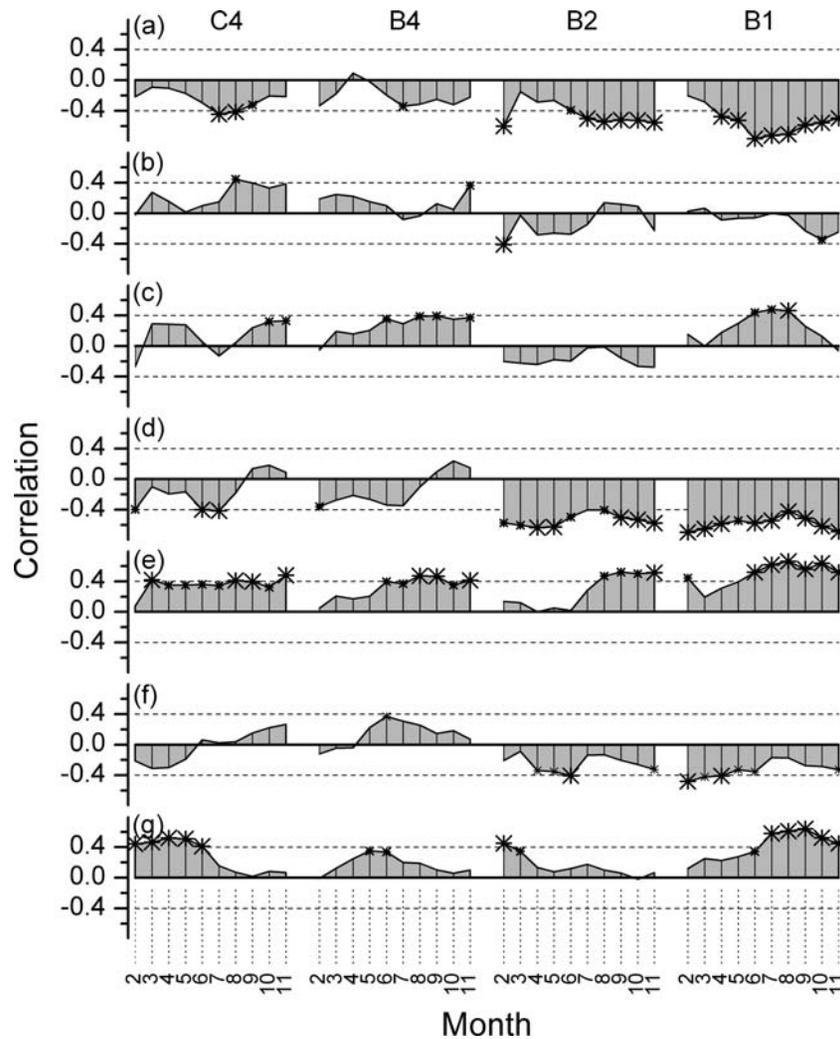
The first principal component of the return rates was negative and positively correlated with major plankton components of the CPR survey. PCI was negatively correlated with the first principal component of the return rates; these correlations were highly significant in areas B2 and B1 during summer and autumn (Figure 8a). Following a similar pattern, the correlations with the copepod *C. helgolandicus* were also negative and highly significant in the same areas over much of the year (Figure 8d), though the pattern was opposite for the copepod *C. finmarchicus* and total euphausiids, which were positively correlated, especially in area B1 during summer and autumn (Figure 8e and g, respectively). The remaining categories, total small copepods, total large copepods, and total amphipods, do not show any strong correlation patterns (Figure 8b, c, and f, respectively). To illustrate the magnitude of change in some foodweb components, consider the time-series of abundance of the copepod *C. finmarchicus*, which is not an important food item for post-smolts, but is a likely indicator of changes in food items (Figure 9). Euphausiids are a food item for post-smolts (Haugland *et al.*, 2006) and have declined by a similar fraction.

#### Retrospective patterns of post-smolt growth

The post-smolt growth of Atlantic salmon has declined over the past three decades compared with the period of robust growth in the 1970s that coincided with the period of good salmon recruitment in the Northeast Atlantic. The post-smolt growth increment increased during the 1960s into the 1970s for the Burrishoole 1SW stock, but began to decline by the end of the 1970s, and remained low through smolt year 1999 (Figure 10a). Qualitatively, we see the same pattern in the growth increments for the Girnock 2SW stock, and the North Esk 1SW and 2SW stocks, which span a similar number of years (Figure 10c and f, respectively). However, the Burrishoole and North Esk growth signatures were significantly correlated with the first principal component of the return rates, whereas the Girnock data were not (Table 4). The Girnock growth data show three distinct periods of post-smolt growth where the 95% confidence intervals generally do not overlap; these periods can be demarcated as smolt years 1964–1967, 1968–1976, and 1977–1983. Despite having the same general pattern of growth over time, low–high–low, there are a number of coordinates that influenced the relationship between Girnock growth and the first principal component of the return rates, in particular the high values in 1968/1969 and low values in 1973 and 1979. It is also worth repeating that the Girnock sampling rate was  $20 \text{ fish year}^{-1}$ , whereas the next lowest rate for a stock component was  $46 \text{ fish year}^{-1}$ . The Lagan stock post-smolt growth signatures were also sampled in a time frame similar to the first principal component of the return rates (Figure 10e). Despite lacking the well-defined time-series pattern seen in the Burrishoole and North Esk growth signatures, the Lagan data were significantly correlated with the first principal component of the return rates (Table 4). The data for the



**Figure 7.** Correlation between the first principal component of return rates of tagged salmon and smolt-year SST for the months May through December, panels (a) through (h), respectively. Light grey shading marks approximate regions with uncorrected correlations significant at  $p = 0.05$ , and dark grey represents approximate regions significant at  $p = 0.01$ . Asterisks mark discrete locations where autocorrelation-corrected correlations are significant at  $p^* = 0.05$  (\*) and  $p^* = 0.01$  (\*).



**Figure 8.** Correlation between the first principal component of return rates of tagged salmon and 3-month moving averages of log-transformed plankton component levels and abundance in SAHFOS standard areas B1, B2, B4, and C4. Numbers along abscissa represent the centre month of moving average. Panels (a) through (g) are for the levels and abundance of the PCI, total small copepods, total large copepods, *C. helgolandicus*, *C. finmarchicus*, total amphipods, and total euphausiids, respectively. Asterisks mark where autocorrelation-corrected correlations are significant at  $p^* = 0.05$  (\*) and  $p^* = 0.01$  (\*).

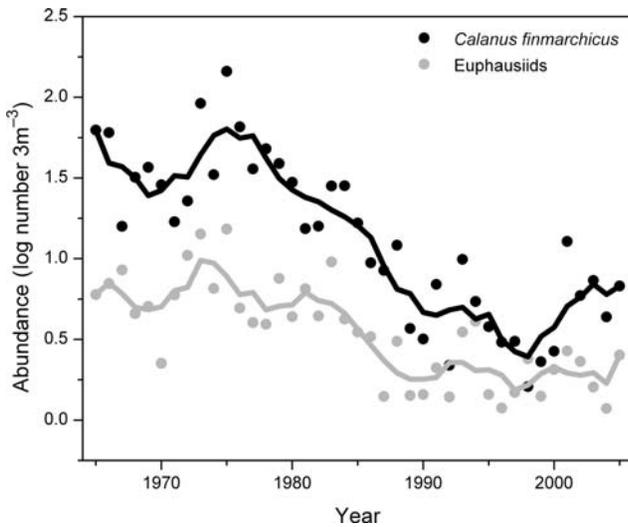
Drammen 1SW and 2SW stocks and 2SW fish captured in Greenland are both shorter time-series, but they both show declining trends (Figure 10b and d, respectively). The Drammen data were significantly correlated with the first principal component of the return rates, whereas the Greenland data were not (Table 4).

Analysis of circuli spacing partitioned into putative monthly increments suggests that growth during the fourth and fifth months of life at sea, which we estimate relate to August and September, is the most critical in determining patterns of post-smolt growth and survival. The correlation between the first principal component of the return rates and circuli spacings proportionally allocated to months for Burrishoole 1SW fish were highest and significant during the fourth and fifth months of life at sea (Figure 11a). Patterns were similar for the 1SW and 2SW Drammen fish and 2SW Greenland fish, with the highest correlations during the fourth and fifth months (Figure 11b, c, and e, respectively). The proportionally allocated growth increments for the Girnock and Lagan stocks were not significantly correlated

with the first principal component of the return rates (Figure 11d and f, respectively).

### Climate indices

Both NAO and AMO indices of climate change show dramatic shifts over the past four decades, but the forcing associated with the AMO appears to have had a greater effect on changes in salmon recruitment in the Northeast Atlantic. The NAO went from a predominantly negative to a positive phase from the 1970s into the 1990s, with some indication of a reversing sign in recent years (Figure 12a). The AMO also went from lower to higher values over the period, but the time-series pattern is different from the NAO pattern, showing a minimum in the 1970s and a continuing trend of increasing index values through the most recent decade (Figure 12b). The contrast in time-series pattern is reflected in the different degree of correlation with the first principal component of the return rates. The first principal component of the return rates is uncorrelated with the NAO (Figure 12c,

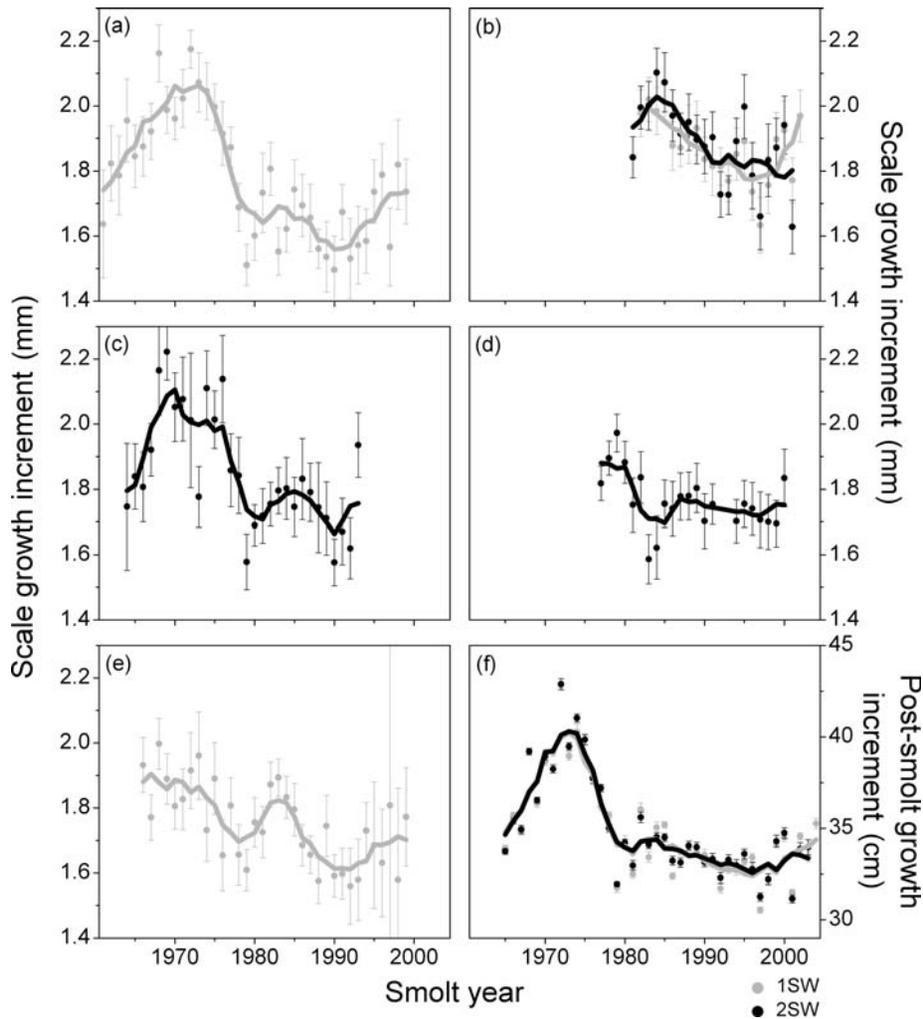


**Figure 9.** Mean abundance of *C. finmarchicus* and euphausiids in area B1 over the months July–October.

Table 5), whereas it is highly correlated with the AMO (Figure 12d). The NAO and AMO are uncorrelated with each other (Figure 12e).

**Discussion**

Our analysis here supports the hypothesis advanced in Friedland *et al.* (2000) that survival and recruitment of European salmon are mediated by growth during the post-smolt year. The central hypothesis is that faster growth during this period results in lower accumulated mortality on a cohort, and hence higher recruitment. We offer a number of significant extensions to the hypothesis and tests of corollary hypotheses with new and extended datasets. We extend the central hypothesis by showing a spatial and temporal match between increasing SST conditions and reduced growth and survival, so suggesting a direct link between temperature forcing and recruitment. Corollary to the original hypothesis of the role of post-smolt growth is the reinforcement of seasonal variation in growth and the specific role of summer growth. Finally, as has been reported, the Norwegian Sea foodweb has changed and represents a less



**Figure 10.** Post-smolt growth increment, as either scale growth increment or back-calculated growth, for index stocks by sea age of return and European origin fish captured at West Greenland vs. smolt year. Stocks and stock groups are as follows: (a) Burrishoole, 1SW; (b) Drammen, 1SW and 2SW; (c) Girnock, 2SW; (d) Greenland, 2SW; (e) Lagan, 1SW; and (f) North Esk, 1SW and 2SW. Lines are 5-year moving averages, and error bars are 95% confidence intervals.

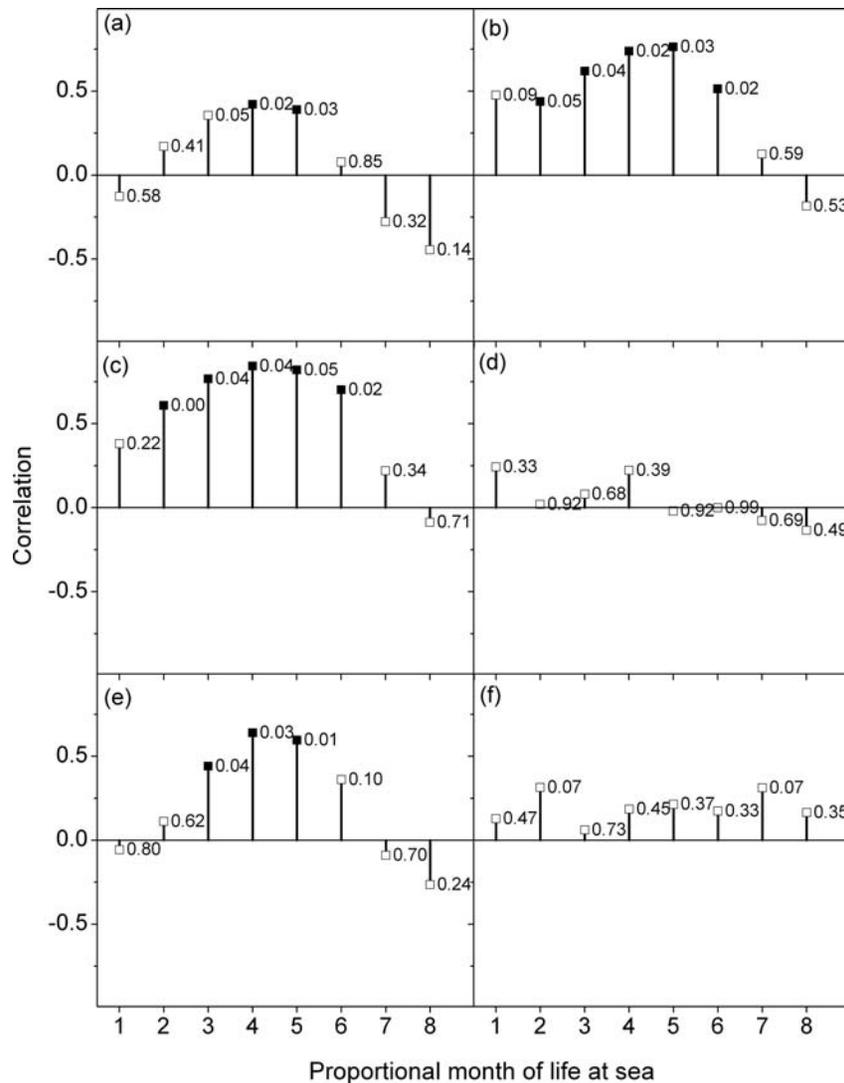
**Table 4.** Correlation between post-smolt growth increment by stock and sea age of return and first principal component of return rates of tagged salmon.

Index	Sea age	<i>r</i>	<i>n</i>	<i>p</i>	<i>N</i> *	<i>p</i> *
Burrishoole	1SW	0.530	35	<b>0.001</b>	20	<b>0.016</b>
Drammen	1SW	0.653	21	<b>0.001</b>	11	<b>0.029</b>
Drammen	2SW	0.557	21	<b>0.009</b>	17	<b>0.020</b>
Girnock Burn	2SW	0.344	29	0.067	13	0.249
Greenland	2SW	0.265	22	0.234	10	0.460
Lagan	1SW	0.545	34	<b>0.001</b>	34	<b>0.001</b>
North Esk	1SW	0.650	40	<b>0.000</b>	25	<b>0.000</b>
North Esk	2SW	0.661	39	<b>0.000</b>	24	<b>0.000</b>

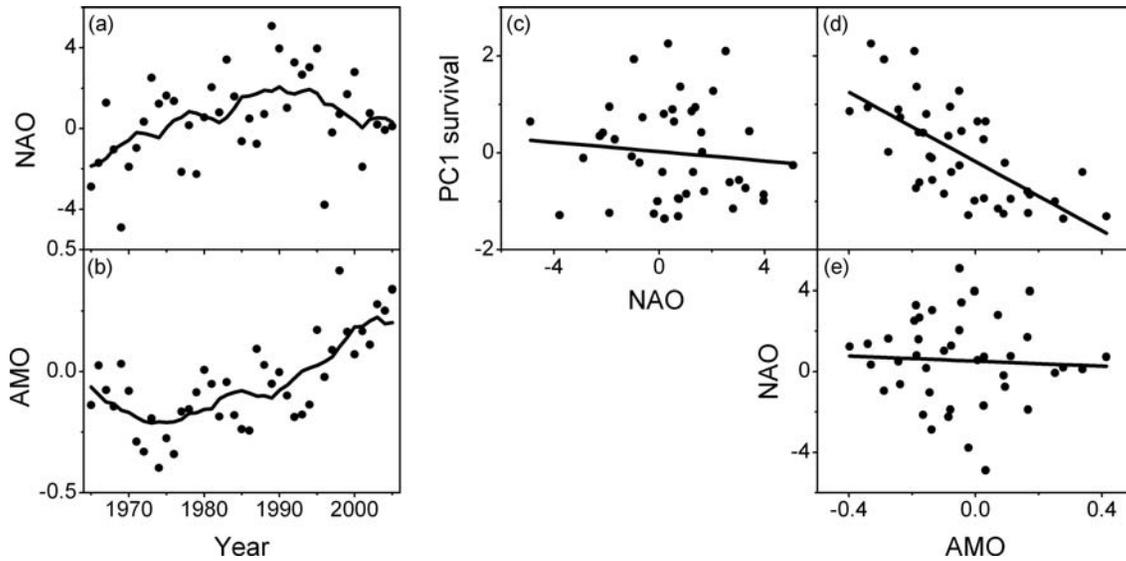
*n*, observed sample size; *p*, probability value of correlation; *N*\*, effective sample size after correction for autocorrelation; *p*\*, probability of correlation after correction for autocorrelation. Significance at *p* = 0.05 emboldened.

productive environment for Atlantic salmon post-smolts. We assert that our replicate tests elevate our confidence in accepting the growth-survival hypothesis of recruitment control, but we recognize that survival of salmon is not one-dimensional and that other factors affect the stock complex and individual stocks within the complex. Regional stocks are likely disproportionately affected by stressors in fresh water (Fivelstad *et al.*, 2004) and predation by marine mammals (Butler *et al.*, 2006; Middlemas *et al.*, 2006), among other factors. We also feel we have an incomplete test of the role of smolt size on recruitment.

Our data on the effect of smolt size on recruitment is limited to two stocks, with one stock suggesting that smolt size plays no role and the other suggesting that it may either control recruitment or contribute to the pattern of post-smolt growth realized later in the post-smolt year. The first interpretation that smolt size is a factor controlling recruitment is supported by examples of where size at



**Figure 11.** Correlation between the first principal component of return rates of tagged salmon and the proportionally allocated monthly growth increment for (a) Burrishoole, 1SW; (b) Drammen, 1SW; (c) Drammen, 2SW; (d) Girnock, 2SW; (e) Greenland, 2SW; and (f) Lagan, 1SW. Coordinates are labelled with autocorrelation-corrected *p*-levels of the correlation coefficients; correlations significant at *p*\* = 0.05 are marked with filled symbols.



**Figure 12.** Time series plots of (a) the NAO and (b) the AMO climate indices, and scatterplots of (c) the first principal component of return rates of tagged salmon and the NAO, (d) first principal component of return rates of tagged salmon and the AMO, and (e) the NAO and AMO climate indices.

**Table 5.** Correlation between climate indices and first principal component of return rates of tagged salmon.

Index 1	Index 2	<i>r</i>	<i>n</i>	<i>p</i>	<i>N</i> *	<i>p</i> *
NAO	PC1 survival	-0.104	41	0.520	41	0.520
AMO	PC1 survival	-0.674	41	<b>0.001</b>	28	<b>0.001</b>
AMO	NAO	0.054	41	0.740	41	0.740

*n*, observed sample size; *p*, probability value of correlation; *N*\*, effective sample size after correction for autocorrelation; *p*\*, probability of correlation after correction for autocorrelation. Significance at *p* = 0.05 emboldened.

ocean entry appears to have conferred some level of survival advantage for salmon (Kallio-Nyberg *et al.*, 2004; Jutila *et al.*, 2006), but there are also examples where these relationships have not continued over time (Ward, 2000) or have specifically shown that for some populations, trends in declining survival are associated with increasing smolt size (Kallio-Nyberg *et al.*, 2006). Some of the data supporting the size at ocean entry are conditioned on the exaggerated size contrast from hatchery products. Moreover, for this factor to be a source of recruitment control for the stock complex, it must be found in all the component stocks. It is not found in the North Esk stock so, considering the number of measurements made on that stock, the test must be considered conclusive. The second effect that smolt size confers some growth advantage during the post-smolt period is less controversial. There are data that show that fresh-water growth can be related or unrelated to the growth that follows in the marine environment (Einum *et al.*, 2002; Friedland *et al.*, 2006). The size at ocean entry for the Figgjo stock correlated with subsequent post-smolt growth, so it appears that for some stocks, it is the combined effect of fresh-water and post-smolt growth that controls recruitment. These data underscore the desirability of collecting additional data on size of smolts at ocean entry.

The forcing effect of temperature appears to be a direct effect of temperature on growth and an indirect effect of temperature, because it relates to change in thermal regime in the Northeast

Atlantic. Previous analyses of thermal habitat (Friedland *et al.*, 1993, 1998, 2000) clearly showed some level of climate variation co-varying with salmon recruitment in Europe. However, these analyses failed to characterize the region of the Norwegian Sea shown to be the post-smolt nursery (Holm *et al.*, 2000). The data contributed to interpretations of the role of SST that are at variance with the current analysis, suggesting that the decline in growth is related to a decline in temperature (Jonsson and Jonsson, 2004). The regime of recent increasing temperatures focused in the Norwegian Sea and to which we relate the recent decline in salmon is not uniform throughout the region, as evidenced by the way the SST correlations with survival rate breaks down to the north and south of the post-smolt nursery. An increase of SST above optimal growth levels to temperatures that may be inhibiting growth appears to be affecting Atlantic salmon and salmon species elsewhere (Wells *et al.*, 2007).

Although we identified a critical period of post-smolt growth and survival, we do not believe that our data suggest that a critical size mechanism is controlling recruitment. Beamish and Mahnken (2001) suggested that recruitment in Pacific salmon was related to growth and the attainment of critical size to survive stressful segments of the first year at sea. The concept was applied to coho salmon (*Oncorhynchus kisutch*) in the Strait of Georgia (Beamish *et al.*, 2004) and is based mainly on data that compare the growth of fish caught during the post-smolt year with fish believed to be from the same cohort but caught after the post-smolt year. We cannot replicate their test because we do not have post-smolt scale collections over the study period. However, if Atlantic salmon need to attain a minimum size to survive their first winter, we would expect to see uniformity of post-smolt growth response across years, not the highly contrasted growth response seen in our data. We believe that our data support a mortality model where post-smolts with longer juvenile stage duration will suffer higher rates of predation because of an extended period in a stage experiencing greater mortality, a concept that has been applied to larval (Houde, 1997) and juvenile fish (Sogard, 1997). The alternative response seen in some species, of increased

growth resulting in a decline in fitness to avoid predation, does not appear to be consistent with our data (Lankford *et al.*, 2001).

The trophic shifts in the Norwegian Sea show some level of complementary change with respect to food items directly utilized by salmon vs. those affecting other species upon which salmon may prey. Beaugrand and Reid (2003) examined changes among a set of variables similar to those analysed here, but they chose to use catch data to condition the response of salmon. Our findings are similar to theirs, but we conditioned our correlates on abundance and return rates, which we believe should support both sets of findings. The conspecifics *C. helgolandicus* and *C. finmarchicus* are the dominant zooplankton species in the Northeast Atlantic and spatially separated by their associated SST (Planque and Batten, 2000). The complementary correlations between salmon survival and the abundance of these taxa is a reflection of the shift in the plankton community in the southern part of the post-smolt nursery. Whereas *C. finmarchicus* has declined in abundance, *C. helgolandicus* has increased, although the densities of *C. helgolandicus* have never attained the same levels as those of *C. finmarchicus* previously. The resulting trophic cascade has caused a shift in the production of gadoid species (Beaugrand *et al.*, 2003), as has been seen elsewhere (Frank *et al.*, 2005), and an increase in phytoplankton standing crop, which we suspect has resulted in an increase in the benthic flux and a loss of energy from the ecosystem. Salmon have obviously not been a beneficiary of the change in energy flow in the Norwegian Sea ecosystem, so until we can determine which changes in the trophic structure are impacting salmon, we can only speculate on them based on short-duration studies of post-smolt feeding and where components of the diet may have changed and resulted in the decline of post-smolt growth (Haugland *et al.*, 2006).

In addition to changes in survival and recruitment, Atlantic salmon stocks have shown changes in other biological features that are likely related to changes in the ocean environment. Quinn *et al.* (2006) report changes in body size and return timing of salmon in Irish rivers, and identified exploitation patterns and ocean productivity as likely factors producing these population shifts. L'Abée-Lund *et al.* (2004) attributed changes in the pattern of maturation schedules for salmon stocks in Norway to changes in ocean migrations, which would likely be affected by the same set of oceanographic changes we here attribute to influencing salmon recruitment. Boylan and Adams (2006) related changes in the NAO to changes in population trends in the River Foyle in Ireland. As some of the characteristics appear to be matching trends in the NAO, it is important to remember that different aspects of the life history of salmon may be responding to changes in SST reflected by the AMO index differently from the way they respond to the atmospheric forcing reflected better in the NAO signal.

The combined set of factors acting on salmon in the Northeast Atlantic has thwarted conservation measures designed to recover the stocks (Boisclair, 2004), so underscoring the need to understand the position of the species within its ecosystem. Salmon have experienced an ensemble shift in climate conditions, foodweb composition, and likely predator groupings similar to the regime shifts described for Pacific salmon (*Oncorhynchus* spp.) and co-varying conditions in the Gulf of Alaska (Mueter *et al.*, 2007). The question we now face is whether there is reason to believe we will return to former stock conditions associated with the oscillatory states of climate forcing or whether climate change will result in a shift in resource distribution and

productivity? In an analysis of the potential effect of climate change on species viability, Schwartz *et al.* (2006) found that extinction vulnerability increases with decreasing distribution size. Atlantic salmon oceanic distribution is broad, but as a diadromous fish, its distribution is biphasic between the ocean and fresh water. Salmon fresh-water distribution is also broad, but salmon are locally adapted and in some contexts, an individual river stock needs to be viewed and managed as a species (Taylor, 1991). Predictions of climate change over the next century suggest that temperature increases over land will exceed those expected over the surface of the oceans (Boer *et al.*, 2000), with much of Europe experiencing temperature increases of  $\sim 9^{\circ}\text{C}$ , and most of the regions associated with salmon-rearing experiencing change of  $\sim 4^{\circ}\text{C}$  (Rowell, 2005). In this context, we may look to changes in the marine environment as the forcing factor controlling stock complex productivity, but the changing state of conditions in fresh water may be the more important factor controlling species distribution and viability.

### Acknowledgements

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### References

- Beamish, R. J., and Mahnken, C. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. *Progress in Oceanography*, 49: 423–437.
- Beamish, R. J., Mahnken, C., and Neville, C. M. 2004. Evidence that reduced early marine growth is associated with lower marine survival of coho salmon. *Transactions of the American Fisheries Society*, 133: 26–33.
- Beaugrand, G., Brander, K. M., Lindley, J. A., Souissi, S., and Reid, P. C. 2003. Plankton effect on cod recruitment in the North Sea. *Nature*, 426: 661–664.
- Beaugrand, G., and Ibanez, F. 2004. Monitoring marine plankton ecosystems. 2. Long-term changes in North Sea calanoid copepods in relation to hydro-climatic variability. *Marine Ecology Progress Series*, 284: 35–47.
- Beaugrand, G., and Reid, P. C. 2003. Long-term changes in phytoplankton, zooplankton and salmon linked to climate. *Global Change Biology*, 9: 801–817.
- Beaugrand, G., Reid, P. C., Ibanez, F., Lindley, J. A., and Edwards, M. 2002. Reorganization of North Atlantic marine copepod biodiversity and climate. *Science*, 296: 1692–1694.
- Bilton, H. T. 1975. Factors influencing the formation of scale characters. *International North Pacific Fisheries Commission Bulletin*, 32: 102–108.
- Boer, G. B., Flato, G., and Ramsden, D. 2000. A transient climate change simulation with greenhouse gas and aerosol forcing: projected climate to the twenty-first century. *Climate Dynamics*, 16: 427–450.
- Boisclair, D. 2004. The status of Atlantic salmon (*Salmo salar*) populations and habitat. *Canadian Journal of Fisheries and Aquatic Sciences*, 61: 2267–2270.
- Booker, D. J., Wells, N. C., and Smith, I. P. 2008. Modelling the trajectories of migrating Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, 65: 352–361.
- Boylan, P., and Adams, C. E. 2006. The influence of broad scale climatic phenomena on long term trends in Atlantic salmon

- population size: an example from the River Foyle, Ireland. *Journal of Fish Biology*, 68: 276–283.
- Brett, J. R. 1979. Environmental factors and growth. *In* *Fish Physiology*. 8. Bioenergetics and Growth, pp. 599–675. Ed. by W. S. Hoar, D. J. Randall, and J. R. Brett. Academic Press, New York.
- Butler, J. R. A., Middlemas, S. J., Graham, I. M., Thompson, P. M., and Armstrong, J. D. 2006. Modelling the impacts of removing seal predation from Atlantic salmon, *Salmo salar*, rivers in Scotland: a tool for targeting conflict resolution. *Fisheries Management and Ecology*, 13: 285–291.
- Carlin, B. 1955. Tagging of salmon smolts in the River Lagan. Report of the Institute of Freshwater Research, Drottningholm, 36: 57–74.
- Casey, K. S., and Cornillon, P. 2001. Global and regional sea surface temperature trends. *Journal of Climate*, 14: 3801–3818.
- Einum, S., Thorstad, E. B., and Næsje, T. F. 2002. Growth rate correlations across life-stages in female Atlantic salmon. *Journal of Fish Biology*, 60: 780–784.
- Enfield, D. B., Mestas-Nunez, A. M., and Trimble, P. J. 2001. The Atlantic multidecadal oscillation and its relationship to rainfall and river flows in the continental US. *Geophysical Research Letters*, 28: 2077–2080.
- Fivelstad, S., Olsen, A. B., Stefansson, S., Handeland, S., Waagbø, R., Kroglund, F., and Colt, J. 2004. Lack of long-term sublethal effects of reduced freshwater pH alone on Atlantic salmon (*Salmo salar*) smolts subsequently transferred to seawater. *Canadian Journal of Fisheries and Aquatic Sciences*, 61: 511–518.
- Frank, K. T., Petrie, B., Choi, J. S., and Leggett, W. C. 2005. Trophic cascades in a formerly cod-dominated ecosystem. *Science*, 308: 1621–1623.
- 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.
- Friedland, K. D., Clarke, L. M., Dutil, J.-D., and Salminen, M. 2006. The relationship between smolt and post-smolt growth for Atlantic salmon (*Salmo salar*) in the Gulf of St Lawrence. *Fishery Bulletin US*, 104: 149–155.
- Friedland, K. D., Hansen, L. P., and Dunkley, D. A. 1998. Marine temperatures experienced by post-smolts and the survival of Atlantic salmon, *Salmo salar* L., in the North Sea area. *Fisheries Oceanography*, 7: 22–34.
- Friedland, K. D., Hansen, L. P., Dunkley, D. A., and MacLean, J. C. 2000. Linkage between ocean climate, post-smolt growth, and survival of Atlantic salmon (*Salmo salar* L.) in the North Sea area. *ICES Journal of Marine Science*, 57: 419–429.
- Friedland, K. D., Reddin, D. G., and Kocik, J. F. 1993. Marine survival of North American and European Atlantic salmon: effects of growth and environment. *ICES Journal of Marine Science*, 50: 481–492.
- Garrett, C., and Petrie, B. 1981. Dynamical aspects of the flow through the Strait of Belle Isle. *Journal of Physical Oceanography*, 11: 376–393.
- Haugland, M., Holst, J. C., Holm, M., and Hansen, L. P. 2006. Feeding of Atlantic salmon (*Salmo salar* L.) post-smolts in the Northeast Atlantic. *ICES Journal of Marine Science*, 63: 1488–1500.
- Hays, G. C. 1994. Mesh selection and filtration efficiency of the Continuous Plankton Recorder. *Journal of Plankton Research*, 16: 403–412.
- Holm, M., Holst, J. C., and Hansen, L. P. 2000. Spatial and temporal distribution of post-smolts of Atlantic salmon (*Salmo salar* L.) in the Norwegian Sea and adjacent areas. *ICES Journal of Marine Science*, 57: 955–964.
- Houde, E. D. 1997. Patterns and trends in larval-stage growth and mortality of teleost fish. *Journal of Fish Biology*, 51: 52–83.
- Hurrell, J. W., Kushnir, Y., and Visbeck, M. 2001. The North Atlantic oscillation. *Science*, 291: 603–605.
- ICES. 2001. Report of the Working Group on North Atlantic Salmon. ICES Document CM 2001/ACFM: 15.
- ICES. 2007. Report of the Working Group on North Atlantic Salmon. ICES Document CM 2007/ACFM: 13.
- Jonsson, B., and Jonsson, N. 2004. Factors affecting marine production of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, 61: 2369–2383.
- Jutla, E., Jokikokko, E., and Julkunen, M. 2006. Long-term changes in the smolt size and age of Atlantic salmon, *Salmo salar* L., in a northern Baltic river related to parr density, growth opportunity and post-smolt survival. *Ecology of Freshwater Fish*, 15: 321–330.
- Kallio-Nyberg, I., Jutla, E., Jokikokko, E., and Saloniemi, I. 2006. Survival of reared Atlantic salmon and sea trout in relation to marine conditions of smolt year in the Baltic Sea. *Fisheries Research*, 80: 295–304.
- Kallio-Nyberg, I., Jutla, E., Saloniemi, I., and Jokikokko, E. 2004. Association between environmental factors, smolt size and the survival of wild and reared Atlantic salmon from the Simojoki river in the Baltic Sea. *Journal of Fish Biology*, 65: 122–134.
- Klein Tank, A. M. G., Wijngaard, J. B., Können, G. P., Böhm, R., Demarée, G., Gocheva, A., Mileta, M., et al. 2002. Daily dataset of 20th-century surface air temperature and precipitation series for the European climate assessment. *International Journal of Climatology*, 22: 1441–1453.
- Lankford, T. E., Billerbeck, J. M., and Conover, D. O. 2001. Evolution of intrinsic growth and energy acquisition rates. 2. Trade-offs with vulnerability to predation in *Menidia menidia*. *Evolution*, 55: 1873–1881.
- L'Abée-Lund, J. H., Vøllestad, L. A., and Beldring, S. 2004. Spatial and temporal variation in the grilse proportion of Atlantic salmon in Norwegian rivers. *Transactions of the American Fisheries Society*, 133: 743–761.
- McCarthy, J. L., Friedland, K. D., and Hansen, L. P. 2008. Monthly indices of the post-smolt growth of Atlantic salmon from the Drammen River, Norway. *Journal of Fish Biology*, 72: 1572–1588.
- Middlemas, S. J., Barton, T. R., Armstrong, J. D., and Thompson, P. M. 2006. Functional and aggregative responses of harbour seal predation to changes in salmonid abundance. *Proceedings of the Royal Society B*, 273: 193–198.
- Moss, J. H., Beauchamp, D. A., Cross, A. D., Myers, K. W., Farley, E. V., Murphy, J. M., and Helle, J. H. 2005. Evidence for size-selective mortality after the first summer of ocean growth by pink salmon. *Transactions of the American Fisheries Society*, 134: 1313–1322.
- Mueter, F. J., Boldt, J. L., Megrey, B. A., and Peterman, R. M. 2007. Recruitment and survival of Northeast Pacific Ocean fish stocks: temporal trends, covariation, and regime shifts. *Canadian Journal of Fisheries and Aquatic Sciences*, 64: 911–927.
- Perry, A. L., Low, P. J., Ellis, J. R., and Reynolds, J. D. 2005. Climate change and distribution shifts in marine fishes. *Science*, 308: 1912–1915.
- Peyronnet, A., Friedland, K. D., Ó Maoileidigh, N., Manning, M., and Poole, W. R. 2007. Links between patterns of marine growth and survival of Atlantic salmon *Salmo salar*, L. *Journal of Fish Biology*, 71: 684–700.
- Planque, B., and Batten, S. D. 2000. *Calanus finmarchicus* in the North Atlantic: the year of *Calanus* in the context of interdecadal change. *ICES Journal of Marine Science*, 57: 1528–1535.
- Potter, E. C. E., Crozier, W. W., Schön, P.-J., Nicholson, M. D., Maxwell, D. L., Prévost, E., Erkinaro, J. et al. 2004. Estimating and forecasting pre-fishery abundance of Atlantic salmon in the Northeast Atlantic for the management of mixed-stock fisheries. *ICES Journal of Marine Science*, 61: 1359–1369.
- Pyper, B. J., and Peterman, R. M. 1998. Comparison of methods to account for autocorrelation in correlation analyses of fish data. *Canadian Journal of Fisheries and Aquatic Sciences*, 55: 2127–2140.

- Quinn, T. P., McGinnity, P., and Cross, T. F. 2006. Long-term declines in body size and shifts in run timing of Atlantic salmon in Ireland. *Journal of Fish Biology*, 68: 1713–1730.
- Reddin, D. G., and Friedland, K. D. 1999. A history of identification to continent of origin of Atlantic salmon (*Salmo salar* L.) at west Greenland, 1969–1997. *Fisheries Research*, 43: 221–235.
- Reddin, D. G., and Short, P. B. 1991. Postsmolt Atlantic salmon (*Salmo salar*) in the Labrador Sea. *Canadian Journal of Fisheries and Aquatic Sciences*, 48: 2–6.
- Richardson, A. J., and Schoeman, D. S. 2004. Climate impact on plankton ecosystems in the Northeast Atlantic. *Science*, 305: 1609–1612.
- Rowell, D. P. 2005. A scenario of European climate change for the late twenty-first century: seasonal means and interannual variability. *Climate Dynamics*, 25: 837–849.
- Ruggerone, G. T., Farley, E., Nielsen, J., and Hagen, P. 2005. Seasonal marine growth of Bristol Bay sockeye salmon (*Oncorhynchus nerka*) in relation to competition with Asian pink salmon (*Oncorhynchus gorbuscha*) and the 1977 ocean regime shift. *Fishery Bulletin US*, 103: 355–370.
- Ruggerone, G. T., Nielsen, J. L., and Bumgarner, J. 2007. Linkages between Alaskan sockeye salmon abundance, growth at sea, and climate, 1955–2002. *Deep Sea Research II*, 54: 2776–2793.
- Schwartz, M. W., Iverson, L. R., Prasad, A. M., Matthews, S. N., and O'Connor, R. J. 2006. Predicting extinctions as a result of climate change. *Ecology*, 87: 1611–1615.
- Shearer, W. M. 1990. The Atlantic salmon (*Salmo salar* L.) of the North Esk with particular reference to the relationship between both river and sea age and time of return to home waters. *Fisheries Research*, 10: 93–123.
- Smith, T. M., and Reynolds, R. W. 2003. Extended reconstruction of global sea surface temperatures based on COADS data (1854–1997). *Journal of Climate*, 16: 1495–1510.
- Smith, T. M., and Reynolds, R. W. 2004. Improved extended reconstruction of SST (1854–1997). *Journal of Climate*, 17: 2466–2477.
- Sogard, S. M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bulletin of Marine Science*, 60: 1129–1157.
- Taylor, E. B. 1991. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. *Aquaculture*, 98: 185–207.
- Todd, C. D., Hughes, S. L., Marshall, C. T., MacLean, J. C., Lonergan, M. E., and Biuw, E. M. 2008. Detrimental effects of recent ocean surface warming on growth condition of Atlantic salmon. *Global Change Biology*, 14: 1–13.
- Ward, B. R. 2000. Declivity in steelhead (*Oncorhynchus mykiss*) recruitment at the Keogh River over the past decade. *Canadian Journal of Fisheries and Aquatic Sciences*, 57: 298–306.
- Warner, A. J., and Hays, G. C. 1994. Sampling by the Continuous Plankton Recorder survey. *Progress in Oceanography*, 34: 237–256.
- Wells, B. K., Grimes, C. B., and Waldvogel, J. B. 2007. Quantifying the effects of wind, upwelling, curl, sea surface temperature and sea level height on growth and maturation of a California chinook salmon (*Oncorhynchus tshawytscha*) population. *Fisheries Oceanography*, 16: 363–382.

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