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Divergent trends in anadromous salmonid populations in Norwegian and Scottish rivers

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The Atlantic salmon (*Salmo salar*) is a charismatic anadromous fish of high conservation and economic value. Concerns have been expressed regarding the long-term viability of fisheries throughout the species's distributional range because of abundance variations that cannot currently be explained or predicted. Here, we analyse long-term catch data obtained over a wide geographical range and across a range of spatial subscales to understand more fully the factors that drive population abundance. We use rod catch data from 84 Norwegian rivers over 125 years (1876–2000) and 48 Scottish rivers over 51 years (1952–2002). The temporal correlation in catches is very long-term, with trends persisting over several decades. The spatial correlation is relatively short-range, indicating strong local-scale effects on catch. Furthermore, Scottish salmon populations exhibit recent negative trends in contrast to some more positive trends in Norway—especially in the north.

Keywords: Atlantic salmon; catches; time series; local effects; regional effects; sea surface temperature

1. INTRODUCTION

The Atlantic salmon (*Salmo salar*) spawns in fresh water in many countries bordering the northern North Atlantic Ocean basin. Salmon are anadromous fishes, migrating to sea as smolts (the life stage that leaves for sea) where they then grow fast before returning to spawn. Smolts originating in European rivers undertake long-distance feeding migrations across most of the longitudinal range of the northern Atlantic Ocean (Shearer 1992; Hansen & Jacobsen 2003). The species comprises a large number of discrete local breeding and rearing populations (Garcia de Leaniz *et al.* 2007). Spawning and rearing habitats are largely isolated at a range of scales, from among-continent, through among-rivers to within-river. This structuring means that the abundance of local population units has the potential to vary independently. Structuring also results in populations experiencing environmental conditions that often vary with the degree of spatial isolation and this provides the potential for adaptive genetic divergence (Garcia de Leaniz *et al.* 2007; Verspoor *et al.* 2007).

Atlantic salmon are of great economic and conservation importance and there is concern about recent declines in populations throughout the species's range (Friedland *et al.* 2003; Gallaugher & Wood 2004; ICES 2007). However, there has been little formal analysis of variations in patterns of population strength to establish the generality of the perceived declines. Such analysis, comparing trends in abundance over time across a range of geographical scales, is a potentially powerful approach to identify the importance of classes of candidate explanatory factors in determining the population strength. Correlations in abundance over time at local scales would indicate common responses to local factors, whereas correlations at large scales would suggest a common response of populations to more global factors.

Local factors include those that directly influence the production of smolts, and those influencing the mortality of fish during near-river migration in coastal areas, both as smolts and as returning adults. Further potential influences are weather and river flow, which affect the relationship between the rod catch and the actual population size of the returning fish. Such transient influences can be expected to be identified particularly by a correlation of residuals from any local time trends in catch.

Global factors that could be expected to have a common influence on populations across broad geographical scales are those occurring on the high seas where salmon from widely separated freshwater populations may share space, at least for some periods of time, during their main growth phase. Concerns about the effects of marine climate on the population strength have recently been underpinned by the identification of the possible detrimental effects of warming of ocean surface waters on marine performance of salmon (Todd *et al.* 2008). However, the likely influence of marine climate as a global factor depends on how the scale of any spatio-temporal differentiation of salmon populations

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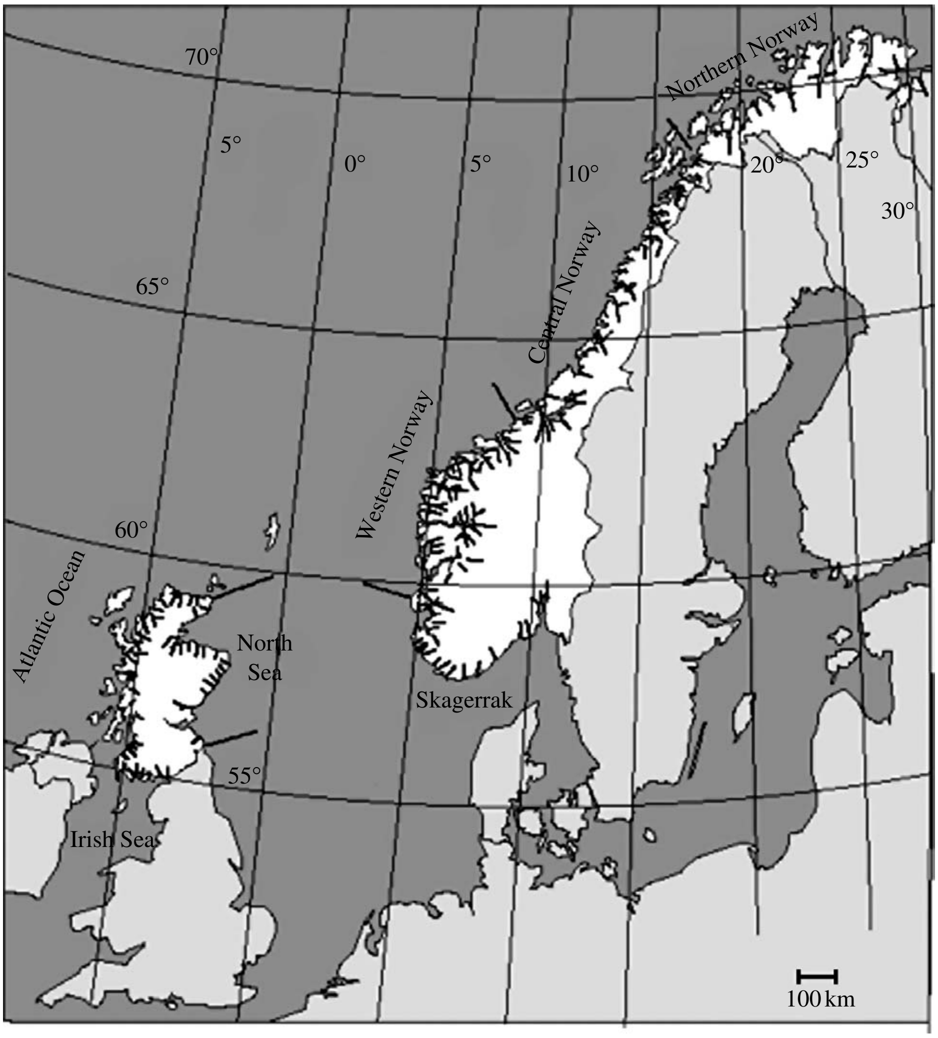

Figure 1. Study area. The sectors used in the analyses are indicated (Scotland: North Sea, Atlantic Ocean, Irish Sea; Norway: Skagerrak, Western Norway, Central Norway, Northern Norway). Detailed information about the salmon rivers is found in the table in the electronic supplementary material.

maps onto spatio-temporal variation in climate change. Based on tag recoveries, it has been suggested that salmon from both Norwegian and Scottish rivers feed in the same general ocean areas (Reddin & Friedland 1999; Hansen & Jacobsen 2003). However, it is also apparent that fish migrating to and from different rivers must pass through different ocean regions. Furthermore, salmon from Scottish rivers use different ocean regions, associated with whether or not they return predominantly early in the season after multiple years at sea (multiple sea winters, or MSW), or later in the year after a single sea winter (1SW; Shearer 1992). These among-population differences in marine habitat use may affect any influence of marine climate change on abundance.

In the present study, we have combined two of the most robust groups of time series available for European salmon populations, using long-term catch statistics from rod fisheries in both Norway and Scotland to examine trends over a broad range of latitudinal scales. The Norwegian time series are particularly long, covering more than 100 years, while the Scottish time series cover 51 years. The main aims of the analysis are to (i) examine the spatio-temporal dynamics of local catches of Atlantic salmon over a major part of the species's range of distribution in the eastern Atlantic and (ii) assess which class(es) of factor(s) is (are) likely to be responsible for the temporal changes in population size, using catch as a proxy for abundance.

2. MATERIAL AND METHODS

(a) *Norwegian data*

Norwegian official statistics comprise river catch records for adult anadromous salmonids (Atlantic salmon; brown trout *Salmo trutta*; Arctic char *Salvelinus alpinus*) extending back to 1876. We analysed data from 84 Norwegian rivers with more than 100 years of data for the period 1876–2000 (see figure 1 and the table in the electronic supplementary material). The rivers are distributed along the coast from the border with Sweden in the southeast to the border with Russia in the northeast. The large spatial scale includes substantial variation in freshwater, coastal and ocean conditions.

From the start of the time series, fishermen were required to report total catches in each river to the local salmon management authorities (Hansen 1986). Prior to 1969, the records comprised the summed total catches (weight) of Atlantic salmon, anadromous brown trout and Arctic char. From 1969 onwards, catches were grouped according to species and from 1979 Atlantic salmon were differentiated into two weight categories (less than 3 kg and 3 kg or more). From 1992, the catch was further categorized into three weight categories (less than 3 kg, 3–7 kg and 7 kg or more).

The smallest group (less than 3 kg) corresponds to 1SW fish (grilse) and the larger groups to MSW fish.

The data were analysed at two temporal scales. First, the longest set of time series (starting in 1876) was used to analyse long-term trends. To do this, we used the sum of all weight categories of Atlantic salmon plus the catch of sea trout and Artic char in the years when the catch was differentiated (from 1969 onwards), and the total weight of all anadromous species prior to 1969. Among all rivers, anadromous brown trout comprised on average 29.5±24.2% (s.d.) of the total annual catch (weight) in the years when the catch records distinguished these species. Arctic char were generally infrequent and almost always comprised less than 5 per cent of the recorded catch (mean±s.d.: 0.5±2.0%). To test whether the inclusion of data with variable proportions of sea trout and Arctic char had a substantial effect on the analyses, we categorized the various river catches as containing more than 50, more than 70, more than 80 and more than 90 per cent Atlantic salmon (in the period 1969–2000) and compared the model outcomes. For the purposes of analysis, the rivers were grouped into four national sectors (Skagerrak, West Norway, Central Norway and North Norway; figure 1; L'Abée-Lund *et al.* 2006).

The incidence of escaped farmed Atlantic salmon in the river angling catch has been monitored annually since 1989 in several Norwegian rivers. Although considerable variation exists among rivers (0.3–23.1% between 1989 and 2000), the grand mean incidence of escaped salmon is relatively low (less than 10%) and no significant time trend is evident (Fiske *et al.* 2006). In general, the escaped farmed salmon enter Norwegian rivers late in the season and are not available to the sport fishery. Thus, the overall effect of escaped farmed salmon on catches, and therefore on estimates of abundance, is likely to be relatively small.

The record of Norwegian catches has undergone several improvements since 1876 and the quality of the data series has been improved over time, introducing a possible temporal bias. There was a change in reporting procedure in 1992, but that change was only to introduce more detail into the statistics, and does not influence our set of data. In general, all salmon fishing in Norway is during summer (June–August). The timing of the fishery varies between rivers and regions, but we have focused on total annual catch. There are no data on how effort has changed through time, but fishing methods have always been rod and line. Our main assumption, therefore, is that fishermen report their catches independently of fish size and species.

(b) *Scottish data*

The Scottish salmon catch statistics comprise data from 48 rivers over 51 years (1952–2002). In contrast to Norway, salmon return to Scottish rivers throughout the year and, although local regulations vary, rod fisheries are generally permitted between February and October. The rod catch data are compiled by month. Details on the data and how they are collected are given by Youngson *et al.* (2002). In larger rivers, exploitation rates vary with season and, therefore, among the different temporal components of the stock (Thorley *et al.* 2007). In addition, these stock components show different temporal trends in abundance (Youngson *et al.* 2002). Time of return is heritable, suggesting that the temporal stock components align with population structuring at the sub-catchment level (Stewart *et al.* 2002). However, in the present analysis, we use annual total catch values to permit a comparison between the Norwegian and Scottish time series. When analysing for long-term correlations in trends among pairs of the Scottish rivers we use the full time series, whereas when comparing overall catch trends with the Norwegian data we use only catches since 1969 (since for the Norwegian series it is only possible to differentiate Atlantic salmon from other salmonid catches from 1969 onwards).

Originally the catch statistics contained information only about caught and retained fishes. However, since 1994 a catch and release fishery has been introduced in many Scottish rivers. The numbers of salmon that are caught and released are reported separately, and we use the sum of retained and released salmon in the analysis.

The Scottish rivers were grouped into three sectors: eastern rivers draining to the North Sea (from the Tweed to the Wick); northern rivers draining to the Atlantic Ocean (from the Thurso to the Ormsary); and western rivers draining to the Irish Sea (from the Ayr to the Nith; figure 1). This segregation was on the assumption that conditions on ocean entry for returning adults may be important for understanding the catch dynamics.

(c) *Statistical analysis*

We use the log of the catch (+1, to avoid the problem of taking logs of zeros) in all the analyses that follow. We fit a trend to all rivers with more than 100 years data using the SPLUS procedure 'supsmu'. This is a scatter plot smoother that fits a running mean, with the number of points for the mean chosen by cross-validation. The time series can then be separated into a trend, and an almost (temporally) uncorrelated residual. To investigate the degree of correlation between individual rivers, we estimated the correlation between trends (and residuals) and geographical distance. An index of distance was estimated by numbering the rivers sequentially. In Scotland, the rivers were numbered from the Tweed on the east coast to the Nith on the west coast. In Norway, the rivers were numbered from southeast to north. In the absence of an objective means of measuring inter-river distance along the complex coastlines, and given the somewhat uniform geographical distribution of the rivers examined (figure 1), the distance between rivers was estimated as the difference between the index numbers.

In order to investigate spatial effects, the mean trends for the various geographical sectors were computed. For the long-term analysis of the Norwegian data, the means were based on trends from rivers with at least 100 years of data in order to reduce the number of missing values. Where values were missing, the trends were interpolated. To compare the Norwegian and Scottish data, a separate analysis was performed using only the data from 1969 onwards.

Sea surface temperatures averaged for the months April, May and June for the period 1950–1992 were assembled from the COADS (Comprehensive Ocean–Atmosphere Data Set) database (http://ingrid.ldgo.columbia.edu/SOURCES/.COADS/). The mean values are for the area 60–64° N, and for the longitudes 0–4° E and 0–4° W of Greenwich. Based on the smolt distribution data reported previously (Holm *et al.* 2003), these coordinates cover the main areas where post-smolts have been detected in the period following emigration from rivers. Temperature data were also considered with various time lags, to accommodate the fact that salmon from different rivers stay at sea for different lengths of time.

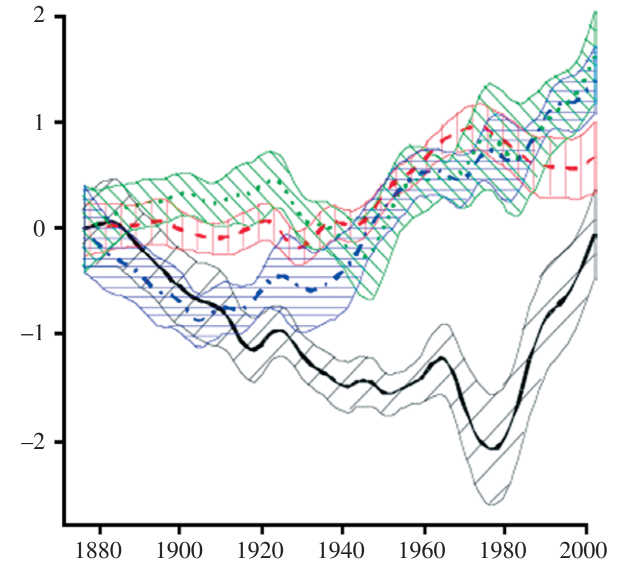

Figure 2. Long-term trends with 95% confidence envelopes for the Norwegian salmonid catch data—separated into four sectors (grey solid line, Skagerrak; red dashed line, Western; green dashed line, Central; blue dashed line, Northern). All scaled to start at zero and based on the mean ln-catch data (kg).

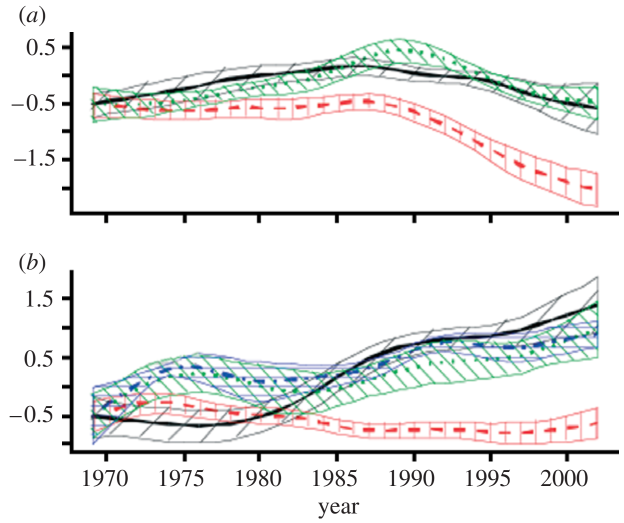

Figure 3. Short-term trends with 95% confidence envelopes for the (*a*) Scottish and (*b*) Norwegian Atlantic salmon catches—separated into four sectors in Norway (grey solid line, Skagerrak; red dashed line, Western; green dashed line, Central; blue dashed line, Northern) and three sectors in Scotland (grey solid line, North Sea; red dashed line, Atlantic; green dashed line, Irish Sea). Based on the mean ln-catch data (trends).

3. RESULTS

There was strong evidence for different long-term temporal trends in catch for the different Norwegian sectors (figure 2). In the Skagerrak sector, there has been a continuous decline in catch from 1880 until the late 1970s. Thereafter, catches increased markedly. For the other three sectors, there was a steady increase in catches after the late 1930s. After 1970, catches decreased in the Western region but continued to increase in the Northern and Central Norwegian rivers.

To compare the trends for catches in the Norwegian and Scottish rivers, we restricted the analysis to the period from 1969 onwards (figure 3). In Scotland, there are clear differences between the responses of the three sectors of rivers. Catches from rivers draining to the Irish and North Seas follow a similar overall trend with weak increase before and decrease after the mid-1980s. By contrast, catches in the Atlantic sector have declined dramatically since the early 1990s. The recent reduction in the catches observed in the Scottish rivers is not paralleled in any of the Norwegian sectors, where catches have been stable or only weakly declining (the Western Norway sector). Overall, there is therefore no correlation between the Scottish and Norwegian catch series.

The sea temperature data series spans the time interval between 1950 and 1992. The smoothed temperature trend (averaged over all three months and four stations) was significantly correlated with observed log(catch+1) within the Northern ($r=0.18$, $p=0.02$) and Central Norwegian sectors ($r=0.07$, $p=0.04$). There was no significant correlation in the cases of the Skagerrak and Western Norwegian sectors and none for any of the three Scottish sectors. When the temperature and catch data series were lagged by 5 years (the approximate generation time for salmon), the mean correlations increased to 0.36 and 0.29 ($p<0.001$) in the Northern and Central Norwegian rivers.

The long-term temporal trend in catch between pairs of rivers was significantly correlated with distance for both the Norwegian and Scottish rivers (figure 4). The mean correlation coefficient for adjacent Norwegian rivers was 0.45 (s.e. 0.04), reaching 0 for the more distant pairs of rivers. Reanalysis using rivers with more than 50, more than 70, more than 80 and more than 90 per cent of Atlantic salmon in the catch generated the same picture and a very consistent trend (fig. 1 in the electronic supplementary material). For Scottish rivers, the mean correlation was 0.31 (s.e. 0.06), being the highest both at low coastal distances (as for Norwegian rivers) and for high coastal distance (fig. 2 in the electronic supplementary material). The geography of Scotland made it necessary to do a separate analysis—the main point being that rivers regarded as far away in this analysis are actually rather close together 'as the crow flies', but on the east and west coasts of the country. We therefore analysed for spatial correlations for each sector separately. This analysis gave a somewhat different impression (figure 4). In the Irish Sea sector, there was a decreasing correlation with distance, whereas in the North Sea and Atlantic sectors there were overall low correlations between catches in pairs of rivers. For the residual series, the mean correlation coefficient for the adjacent Norwegian and Scottish rivers was 0.19 (0.01) and 0.22 (0.03), respectively. In both the Norwegian and Scottish rivers, the spatial correlations between trend series are considerably greater than between residual series. Thus, the spatial correlation is largely due to long-term rather than short-term fluctuations, although there is clearly some short-term correlation as well.

Other factors than spatial correlation may produce these trends. Trends were therefore determined for the first half of the Norwegian time series, and the rivers divided into clusters according to the correlation in their trends, after removing the correlation assumed owing to the spatial effect. When this was repeated using the latter part of the time series, there was no association between

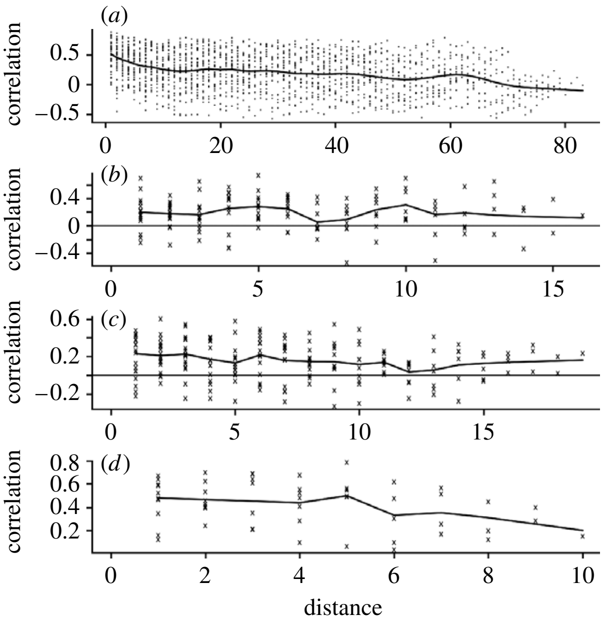

Figure 4. Pairwise correlations between trends in Atlantic salmon catch time series and geographical distance for the set of rivers: (*a*) Norwegian, (*b*) Scottish—North Sea, (*c*) Scottish—Atlantic and (*d*) Scottish—Irish Sea. For (*b*) the North Sea and (*c*) the Atlantic sector, the zero line is included to aid interpretation.

the clusters formed using the first part of the data and those formed from the second part. Thus, apart from any correlation due to their being close to one another, rivers that were highly correlated at one period were no more or less likely to be highly correlated in another. The time series were not long enough to perform this analysis on the Scottish data.

4. DISCUSSION

This analysis of long-term trends in river catches of Atlantic salmon from Norway and Scotland has demonstrated high levels of homogeneity at small geographical scales, but strong heterogeneity at larger scales. For both countries, we found significant correlation between adjacent rivers, this correlation generally decreasing with geographical distance. However, when analysing the three sectors in Scotland separately, we found such a significant trend only for the Irish Sea sector (with the same trend present but not significant) for the Atlantic and North Sea sectors). This pattern suggests that the observed between-river correlations are due in part to the effect of environmental factors that are shared between adjacent freshwater catchments, rather than just coastal effects.

River catches from anglers are indirect but robust indices of salmon abundance (L'Abée-Lund *et al.* 2006). Importantly, they record only those fishes that escape coastal fisheries to enter the rivers. Due consideration must be given to the variation in interceptory coastal fisheries if rod catches are to be used to infer variations in other components of marine mortality and freshwater production of smolts. However, catches are particularly valuable in relating directly to the fraction of the population that is available to spawn, which indicates the resilience of the population.

A striking finding of this study is the radical difference in patterns of long-term trends in rod catches between Scotland and much of Norway. Catches have declined in each of the Scottish sectors from the late 1980s and early 1990s onwards, and have been particularly precipitous in the Atlantic sector. These declines cannot be accounted for by changes in coastal netting in Scotland, since such netting effort has decreased progressively over this period (Youngson *et al.* 2002). This reduction in coastal netting will have increased the proportion of the returning stock available to be captured by rods and therefore the trends in decline of fishes arriving at the coasts will be even greater than those indicated by the rod catch data.

By contrast, catches have increased since the early 1990s in Northern Norway, Central Norway and Skagerrak but declined slightly in the Western region of Norway. The longer-term trends indicate dramatic declines in catches in rivers draining to the Skagerrak sector until the 1980s, with a substantial increase afterwards. This pattern can probably be attributed to the effects of acidification of fresh waters in this region (Hesthagen & Hansen 1991), with a peak in SO_2 deposition occurring in the 1970s. Acidification had profound effects on the productivity of susceptible rivers and has caused the extinction of several large salmon populations. Recently, large reductions in the emissions of SO_2, in combination with significant liming activity, have resulted in improvements in water quality in many rivers in this region (Skjelkvåle *et al.* 2003). This habitat improvement has led to increased recruitment in populations that survived the period and the re-establishment of salmon in rivers where the original populations had become extinct (Kroglund *et al.* 2001; Sandøy & Langåker 2001).

In the Northern region of Norway, catches have increased progressively since the 1940s, a pattern that is not matched in the other sectors. In Northern Norway, human impacts on the rivers have been minor. In principle, the observed increasing trend in catches could be due to increased fishing effort, increased reporting, decreased salmon mortality or increased freshwater productivity. There is very little information available on how fishing effort has varied over time in any river or sector. Niemelä (2004) analysed variation in the numbers of recreational fishermen fishing in the River Teno (Norwegian Tana) in Finland during 1960–2004. There was a tendency that the number of recreational fishermen increased between 1960 and 1970, and that it has been stable afterwards. This suggests that the number of recreational fishermen cannot explain the increase in river catch since 1970. Furthermore, we have no indication that there has been an increase in reporting rates, and catches have continued to increase after 1992, when changes were made in legislation to enforce accurate reporting.

In both Central and Western Norway, there has been a strong increase in human activity since the 1940s. Hydropower development has resulted in habitat loss, and fish transfer and salmon farming have been implicated in the increased prevalence of the potentially harmful ectoparasites, *Gyrodactylus salaris* and *Lepeophtheirus salmonis*, with losses of fitness due to interbreeding of escaped farmed fishes with wild ones (McGinnity *et al.* 2003, 2004). Most of these impacts appeared after the late 1980s and, because of their strong local dimension, their effects will not be uniformly evident among rivers. The adverse effects of *L. salmonis* are most pronounced where complex seaward migrations are required along the fjordic coastlines typical of the Western Norwegian sector (see Thorstad *et al.* 2004; Økland *et al.* 2006; Hedger *et al.* 2008).

Considering the patterns across the Scottish and Norwegian data, and accounting for the effects of freshwater habitat recovery in the Skagerrak region, overall, there is a trend of increasing catches in the north and decreasing catches in the south. Independent direct estimates of marine mortality using trapping sites at the rivers North Esk in Scotland (Friedland *et al.* 2000) and Imsa in Southern Norway (Jonsson & Jonsson 2004) mirror the picture from rod catches of an increase in marine mortality since the 1980s across the southern end of the Scotland–Norway transect.

Although the Scottish and Norwegian salmon populations are often assumed to use common ocean areas for feeding and growth (Holm *et al.* 2003), the few available data indicate that salmon from Northern Norwegian rivers have a more northerly distribution during the first year at sea than those from Southern Norway (Hansen & Jacobsen 2003; Rikardsen *et al.* 2008). Furthermore, salmon from more southern latitudes, moving to their northern feeding areas, have to migrate through ocean regions that are not used by fishes from northern rivers. It is therefore quite possible that the variations in distribution and associated survival of salmon at sea may explain the differences in the long-term trends at the largest spatial scales examined in the present study. A similar mechanism may explain the variations in abundance trends of fishes returning at different times of year within the Scottish rivers (Youngson *et al.* 2002). A positive correlation between catch and an index of summer sea surface temperature was detected in time series for Northern Norway, but it cannot plausibly be regarded as potentially explanatory since mean temperature values fluctuated widely over the period of comparison.

Within the Scottish populations, MSW salmon returning early in the year (February–May) have declined particularly acutely since *ca* 1990 (Youngson *et al.* 2003). Such fishes are not represented in the Norwegian fisheries. Their demise in Scotland may explain some of the difference between the Norwegian and Scottish trends. However, the Atlantic sector fisheries are based primarily on summer MSW salmon and grilse, and the declines of early-running fishes noted elsewhere cannot account for the extreme declines evident in this sector. As for the western sector of Norway, the Atlantic sector rivers drain into an area with a high density of marine salmon farms; the Scottish aquaculture industry is concentrated in the Atlantic sector and essentially absent from the North Sea and Irish Sea sectors. Not only is abundance decreasing strongly in the Atlantic sector but there are also only low average levels of correlation between pairs of rivers within the sector and no evidence for a relationship with distance. Although other explanations are possible, some of the differences between the Atlantic sector and the other Scottish sectors might be due to local effects of intensive salmon aquaculture on affected rivers. Equally, it is also notable that the Norwegian sector having the highest density of salmon farms has experienced a reduction in salmon abundance not seen in the other Norwegian sectors. Any effects associated with the presence of aquaculture might occur through direct interactions or indirectly through diseases or outbreeding but, if so, the effects appear not to extend beyond the regional level.

The complexities evident in the data suggest a multiplicity of effects, highlighting the challenges for managing the resource (Potter *et al.* 2003; Youngson *et al.* 2003; Crozier *et al.* 2004). However, rather than indicating any underlying global influence acting on all of the geographical regions, the analysis suggests a trend of healthy populations in the north and decline in the south. Northern Norwegian populations of salmon are those most adjacent to cool oceanic regions that are likely to be highly productive of food (Gross *et al.* 1988). Fishes from southern populations must undergo much more extensive migrations through wider areas of the ocean to reach productive northern feeding areas, when they may be vulnerable to human exploitation, predation, energy deficit and other mortality agents. Ocean warming following from predicted climate change may have detrimental effects on the more southern populations (see Todd *et al.* 2008), less so on the northern populations—especially in Northern Norway. In conclusion, we find both large-scale regional differences and fine-scale similarities in long-term catch trends for salmon across the Norwegian and Scottish fisheries, indicating the presence of effects at both local and regional scales, but not globally.

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