International Council for
the Exploration of the Sea   ICES CM 2009/E:14

Factors affecting year-to-year and within river variability of one-sea-winter Atlantic salmon in Norwegian rivers

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Abstract. Many Atlantic salmon, *Salmo salar*, populations are decreasing throughout its distributional range due to several factors acting in concert. A number of studies have documented the influence of freshwater and ocean conditions, climate variability and "man-made obstacles" including dams and aquaculture. However, most of the historical research has focused on single or few river analyses, and quantifying isolated effects rather than handling factors in conjunction. By using a multi-river mixed-effects model we estimated impacts of oceanic and riverine conditions, as well as human threats on both year-to-year and within river variability across 60 time series of recreational catch of one-sea-winter salmon (grilse) from Norwegian rivers over 29 years (1979−2007). Warm coastal temperatures at the time of smolt entrance into the sea and increased water discharge during upstream migration were associated with higher rod catches of grilse. When hydropower stations are present in the course of the river systems the strength of the relationship with runoff is reduced. Moreover, catches of grilse in the river increased significantly following the discontinuation of the harvesting of this life-stage at sea. However, a general decreasing temporal trend was still detected being stronger with the presence of salmon farms in the migration route of smolts in coastal/fjord areas. These results suggest that both ocean and freshwater conditions in conjunction with diverse human impacts contribute to shape interannual fluctuations and within river variability of wild Atlantic salmon.

INTRODUCTION

Wild Atlantic salmon (*Salmo salar*) populations have been decreasing throughout its geographic distribution raising a great concern due to its economic and conservation importance. A number of factors causing severe declines and even extirpations, primarily in the southern range, have been identified, though discerning individual mechanisms is complicated due to their likely action in concert (Parrish et al. 1998). Changes in stocks have been associated with a broad spectrum of environmental factors at most time scales (Jonsson and Jonsson 2004), and analyses of multiple populations reveal the importance of local-scale effects on catch (Vøllestad et al. 2009). Here, we focus on quantifying for the first time how one-sea-winter fish (grilse) varies in relation to oceanic and freshwater conditions, and human stressors at the population level using multiple time series of river catch (rod catches in most rivers, and additional fixed gear in few rivers.

The life history of Atlantic salmon in Norwegian rivers is complex. Spawning occurs in freshwater around October-January. Subsequent life stages of the species (i.e., eggs, alevins and fry) live in freshwater, with the latter juvenile phase (i.e., parr) staying for 1-6 years in the rivers before they transform into smolts and pursue oceanic feeding migrations. After 1-4 years at sea they attain sexual maturity, and return to freshwater in May-October to spawn with a high precision to their home natal areas (Webb et al. 2007). This diverse biology would potentially allow for the influence of numerous factors at different life stages including biotic effects, habitat characteristics, local riverine impacts, broad oceanic and weather influence so as several human impacts. As juveniles in freshwater, density-dependence and predator-prey interactions might play a fundamental role in shaping populations (e.g., Ward et al. 2008). Moreover, spatial habitat structure will affect population dynamics and carrying capacity (e.g., Finstad et

al. 2009), and environmental conditions experienced during the early development appear to influence growth rates of juveniles and age of seaward migration (Jonsson et al. 2005). Afterwards, when living in the marine environment it is believed that the largest component of natural mortality occurs during the first year at sea and climatic conditions will affect this phase in several ways (Jonsson and Jonsson 2004). Post-smolt survival has been often associated with sea surface temperature, which presumably modulates growth rates and control recruitment (Friedland et al. 2009). Marine predators might as well contribute to shape population variability when entrance to the sea as smolts (e.g., Hvidsten and Lund 1988) and/or to the returning run (e.g., Middlemas et al. 2006). Finally, upstream migration is affected by water flow and temperature, light conditions, pollution etc (see Thorstad et al. 2008a).

Besides, salmonids must face several obstacles and stressful factors during their life cycles. Human encroachments like hydropower development and stocking may alter migration patterns and abundance (L'Abée-Lund et al. 2006). Damming of the rivers alters the entire ecosystem affecting, for instance, parr growth (Jensen 2003) and migration of ascending adults (Thorstad et al. 2008a). Dam operations might indeed contribute to reduce the survivorship threatening salmonid populations (Hoekstra et al. 2007), though recent studies claim that mortality is not higher despite the presence of dams during a given period (Welch et al. 2008). Other human impacts include both coastal and oceanic fisheries with well-known structural changes on the spawning run of Norwegian populations after the ban of the drift net fishery in 1989 (Jensen et al. 1999). Furthermore, the exponential increase of aquaculture may contribute to the declines of wild fish. Negative impacts associated to farmed salmon have been known for years, for instance, disease transmission (e.g., Krkošek et al. 2007) and reduction of fitness in wild salmon due to interactions with escaped individuals (e.g., McGinnity et

al. 2003). Globally, populations that have a seaward migration close to salmon farms as smolts present reduced survival compared to non-exposed populations from the same region (Ford and Myers 2008).

The overall objective of this study is to quantify the oceanic, freshwater and human impacts on grilse rod catch throughout the Norwegian range of Atlantic salmon. By using a multi-river mixed-effects model we estimated the relative importance of the former factors on both year-to-year and within river variability across a unique dataset of 60 time series spanning from 1979 to 2007 of salmon caught in the rivers after a single sea winter.

MATERIAL AND METHODS

Catch data

The present study is based on the Norwegian official statistics of nominal catch of adult Atlantic salmon from Norwegian rivers situated over a wide geographical range (58º28'–71º03'N and 5º07'–30º32'E; Fig. 1) and spanning from 1979 to 2007. This large spatial and temporal framework encompasses considerable variation in freshwater, and ocean conditions. The legal fishing season is restricted to summer and early autumn, but differs somewhat among rivers. In Norway, systematic collection of data on the different salmonids fisheries began in 1876 resulting into a database with annual catch data for 558 rivers. Starting in 1979, Atlantic salmon was identified at the species level and differentiated into two weight categories (<3 kg and ≥3 kg). The smallest group (<3 kg) mainly corresponds to one-sea-winter (1SW) fish (grilse), and the larger group correspond to multi-sea-winter (MSW) fish (2SW, 3SW fish etc) (Jensen et al. 1999). We only used grilse catches in our analysis, and assumed that the reported values were based on a random sample of the total catch. The official catch statistics do not

distinguish between males and females, so sexes were treated together in the analyses. All analyses were based on the kilograms of grilse in the reported annual catch within each river. The rivers in the database varied considerably in size, as did the catches. In some rivers, catch was very low in some years, either because of small catches or because of problems with the reporting procedure. Therefore, we only considered rivers with complete reports for ≥15 seasons of data. A minimum catch of 20 individuals per year was required as well; otherwise the complete report for that river was not included in the analyses. This filtering prevented us from using very small rivers with few and incomplete data finally resulting in 60 rivers to be analyzed (Table 1). The quality of the data analyzed in this study has been discussed elsewhere (L'Abée-Lund et al. 2004; Vøllestad et al. 2009). Nevertheless, we are aware that recent studies show that the dynamics of fishermen are decisive in the referred "invisible collapse" of recreational freshwater fisheries (e.g., Post et al. 2008). However, even though the number of angling licenses in Norway seems to be declining (data not shown), no data were available on the behavior of anglers. We here assume that fishermen are equally prone to report fish independently of fish size. That is, the reported fish are a random sample of the fish captured in a river during a given year. Furthermore, we also assumed that recreational catches would reflect the true population abundance (Thorley et al. 2005), and that the age group studied (i.e., 1SW) would indicate the status and strength of the year class (Niemelä et al. 2005).

Environmental data

To test for ocean effects on interannual variability in grilse catch we computed temporal averages of sea surface temperature (SST) experienced by smolts during their time of entrance into the sea. We selected coastal grid cells (1º × 1º) from the Comprehensive

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Ocean–Atmosphere Data Set (COADS, http://icoads.noaa.gov/) whose centers were located nearby the ocean entry point of a given river (Table 1). SST was monthly averaged according to population-specific timing of smolt descent depending on latitude. That is, May for rivers south 63ºN; May–June for rivers between 63º–69ºN; and June–July for rivers north 69º.

To test for freshwater effects we estimated the daily variation in total runoff for each river catchment (Table 1). Water flow affects early life stages of this species (e.g., Jensen and Johnsen 1999), and is also important for the ascending adult salmon during the upstream migration (see review by Thorstad et al. 2008a). Disentangling the effect of water flow during specific periods in the life cycle is difficult due to strong collinearity in water flow among various seasons (runoff during upstream migration is related with runoff during spawning [October–January], $r^2 = 0.8$; and with water flow during early life [May–August], $r^2 = 0.9$). Moreover, the length of the parr period and thus smolt age varies between 1-6 years depending on the rivers. Thus identifying appropriate time lags is rather complex as information on smolt age is not available for each river considered in this study. Therefore, daily discharge (m^3/s) for each river catchments was estimated for the summer upstream migration months (June–August) coincident with the Norwegian recreational fishery season. We used a spatially distributed version of the Hydrologiska Byråns Vattenbalansavdelning (HBV) model developed by the water balance section of the Swedish Meteorological and Hydrological Institute (Bergström 1995, http://www.smhi.se/foretag/m/hbv_demo/html/welcome.html). The model performs water balance calculations for 1-km^2-grid cell elements that are characterized by their altitude and land use. Each grid cell may be divided into two land-use zones with differing vegetation: a lake zone and a glacier zone. The algorithms used in the model

are described in Sælthun (1996). The model was run with daily time steps, and data inputs were precipitation and air temperature. Daily runoff data for the individual grid cells were subsequently aggregated to monthly discharge for the respective catchments. The model was calibrated with available information about climate and hydrological processes from gauged catchments in different parts of Norway, and parameter values were transferred to other catchments based on a classification of landscape characteristics (Beldring et al. 2003).

Human impacts

Atlantic salmon has been exploited in the open sea since a long time with increasing intensity and using different kind of nets. In Norwegian home waters several restrictions and management measures have been introduced, though, seldom, the effects of the management changes have been evaluated by follow-up studies (but see Jensen et al. 1999). To examine the relationship of the (coastal) sea fishery with the river catches we compiled the proportion of grilse caught at sea in each year and landed in each Norwegian county from the Norwegian official catch statistics (Table 1).

To determine the potential impact of salmon farming on the smolts migrating past net pens on their way to the feeding areas in the open ocean, we compiled data on the presence of aquaculture operations (licences) in each Norwegian municipality from http://www.fiskeridir.no/fiskeridir/akvakultur/registre (Fig. 1). This resulted in 29 out of 60 rivers draining in areas with at least the presence of one license established during the study period. The data is used as presence/absence data, and we took into account the fact that farming was established at different times across municipalities (Table 1).

Finally, to estimate how the presence of hydroelectric dams might impact on the upstream migration and/or abundance (as reflected in catch) we gathered data from

on the presence of hydropower stations in each river. In total, 28 out of 60 rivers contained at least one hydroelectric scheme along the salmon-producing part of the river (Table 1).

Statistical analyses

Data were analyzed using a restricted maximum likelihood linear mixed-effects model (random grouping factor $n = 60$ rivers, $n = 1707$ observations) following methods described in Pinheiro and Bates (2000). A preliminary analysis consisted in fitting separate linear models per river to choose parameters to account for between-river variation. Displaying confidence intervals on intercept and slopes suggested that a random effect could be needed to account for river-to-river variability in the intercept, and time and runoff slopes. Model selection analysis did support including random effects on the intercept and time (Year) slope. Therefore, according to these preliminary results we fitted a model of the form:

$$C_{it} = (\beta_0 + a_i) + \beta_1 F_{it-1} + \beta_2 HP_{it} + \beta_3 R_{it} + \beta_4 SST_{it-1} + \beta_5 SF_{it} + (\beta_6 + b_i)Y_{it} + \\ \beta_7 F_{it-1} \times Y_{it} + \beta_8 HP_{it} \times Y_{it} + \beta_9 HP_{it} \times R_{it} + \beta_{10} HP_{it} \times F_{it-1} + \varepsilon_{it}$$

(1)

where C is the ln-transformed catch of grilse for each river i at a time t. βs are the fixed effects with covariates as follows: F is farming (dichotomous variable) one-year lagged assuming that aquaculture effects are important during smolt migration, HP is hydropower (dichotomous variable), R is ln-transformed runoff (continuous variable), SST is sea surface temperature (continuous variable) one-year lagged to accommodate the oceanic effects over smolts during time of entrance into the sea, SF is the sea fishery (continuous variable), and Y is year (continuous variable). For meaningful interpretation of the interaction terms, subtracting the mean centered R and Y. a and b are the random river (i) effects assumed to be independent for different rivers and to follow a normal distribution with mean zero and variances σ_a^2 and σ_b^2, respectively. Different error

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structures were used to model serial correlation. Bayesian Information Criterion (BIC) indicated that an autoregressive and moving average process of order 1 provided the better fit of the data, i.e.:

$$\varepsilon_{it} = \phi\varepsilon_{it-1} + \theta\eta_{it-1} + \eta_{it} \tag{2}$$

finally, heteroscedasticity was handled by modeling the variance of ε_{it} as an exponential function of R:

$$Var(\varepsilon_{it}) = \sigma^2 \exp(2\delta R_{it}) \tag{3}$$

For some rivers, the data clearly indicated that the reporting of the various weight-groups was biased in the years 1979–1982 due to the change in reporting procedure that probably was not effectively implemented in all rivers (L'Abée-Lund et al. 2004). To reduce any effects of biased weight categorization, and to err on the conservative side, we rerun our statistical model excluding years 1979–1982 from the doubtful rivers. Results did not change.

Within the studied rivers, two suffered liming processes (i.e., acidification that reduces water quality criteria for the sensitive smolt stage) and other four were infested by the parasitic monogenean *Gyrodactylus salaris*. Moreover, during the studied years a stocking program has been implemented in one river and fish ladders were built in four more rivers. Although these facts could have some impacts, for instance, the parasitic infestation has led to rapid and dramatic declines in some Atlantic salmon populations (Johnsen and Jensen 1986); we considered them as negligible. Indeed, excluding these rivers from the analysis did not alter our conclusions.

All analyses were performed on R 2.6.2 software (R Development Core Team 2008) and using the "nlme" library (Pinheiro and Bates 2000).

RESULTS

Table 2 shows the estimated parameters and hypothesis tests of the optimal model. Coastal temperature at the time of smolt entrance into the sea was positively related with the following year's catches of grilse in the river. In addition, water discharge during upstream migration was positively associated with higher catches in the river. The strength of the latter relationship was weaker when hydropower stations were present in the river. Catches of grilse in the river increased significantly when harvesting of this life-stage at sea was discontinued. On top of these effects, a general decreasing temporal trend in catches was detected. This decreasing trend was stronger with the presence of salmon farms in the corresponding draining areas (Table 2 and Fig. 2a). Furthermore, it is worth noting that, on the one hand, catch in rivers with presence of farms relative to rivers without aquaculture production is higher during most of the study period, but the difference diminishes with time (β_1 in equation 2). The catch is even lower when dams are present ($\beta_1 + \beta_{10}$) (Fig. 2b). On the other hand, at low values of runoff catches are higher in those rivers with presence of dams relative to rivers without hydropower stations (β_2). However, at high values of runoff the difference reverses and the decrease in catch strengthens with the presence of farming industry ($\beta_2 + \beta_{10}$) (Fig. 2c).

We found strong support for modeling the within group serial correlation with an autoregressive and moving average process of order 1 (Table 2). The positive and negative coefficients of the *AR* and *MA* components indicate strong positive autocorrelation at lag 1. Figure 3 shows the observed versus the fitted values for the model depicted in Table 2. Within group residuals are normally distributed and do not show any apparent variability. Random effects are, as well, normally distributed and independent.

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DISCUSSION

Our study demonstrates that oceanic and freshwater conditions at different time scales appear to be important for shaping the year-to-year variation among grilse populations caught in Norwegian rivers. Furthermore, the presence of aquaculture operations strengthens the decreasing trend of the populations compared to rivers non-exposed to farming. In addition, the presence of hydropower stations in the course of the rivers interacts with the water flow and weak the relationship of the catches with runoff. However, it must be bear in mind that these results only identify significant effects of environmental factors and human impacts from the smolt to the adult stage.

It has been shown that the number of adults surviving in the ocean are related with the number of descending smolts from which these adults were produced suggesting that density-dependence appears to be important for freshwater juvenile survival, whereas density-independent factors seem to be important for the ocean survival of the fish (Jonsson et al. 1998). Several investigations have reported the effects of marine conditions on the survival of Atlantic salmon. Post-smolt survivorship appears to be related with sea surface temperature on both sides of the Atlantic in a way that warmer distribution of SST in spring defines a specific suitable thermal habitat linked to increased survival (Friedland et al. 1998). In turn, increased survival appears to be strongly growth mediated (Friedland et al. 2000, Peyronnet et al. 2007). These positive effects of temperature seem to be especially important during the earlier part of ocean living when energetic demands and physiological stress are higher. In fact post-smolt growth in summer may be responsible for survival at sea and subsequent determining the returning run (McCarthy et al. 2008). Besides, negative relationships with SST during the latter part of the ocean residence are also evident showing a decrease in growth related with warmer temperature (Todd et al. 2008) and suggesting a prey-

mediated mechanism concurrent with the decline in recruitment (Friedland et al. 2009). Our results show a strong positive relationship between grilse caught in the rivers and the mean SST at the time of smolts descending to the sea (i.e., one year before). Furthermore, this correlation is consistent throughout the latitudinal range examined and agrees with recent results across several Norwegian rivers (e.g., Hvidsten et al. 2009, Niemelä et al. 2004). This finding agrees with the hypothesized benefit that descending salmon should experience from the precise encounter with the 'optimal' thermal habitat around 8°-10°C (note that 75% of our SST values range from 7.46 to 8.53°C), which would favor higher growth rates. In turn, it has been proposed an indirect link between SST and suitable food items during initial marine feeding enhancing survival of post-smolts (Hvidsten et al. 2009). Associations between ocean temperature and survival rates of different salmonids have been described in other areas even showing opposite latitudinal effects with suggested underlying mechanisms related with the abundance of predator and prey likely associated with variations in coastal SST (e.g., Mueter et al. 2002). Therefore, initial weeks at sea will be crucial for shaping survival. However, the contribution of (a) specific mechanism(s) during early sea migration and its connection(s) with the effects in the latter months of ocean living remains to be understood.

Upstream migration patterns in Atlantic salmon are complex and likely controlled by several factors. River flow has been highly reported as an important variable that stimulates and governs the spawning migration though frequently constraint by several barriers (Thorstad et al. 2008a). Indeed, regulated rivers can induce even more complex responses on the migratory behavior of the adult fishes according to the outlet flow from a hydropower station (Thorstad et al. 2003). Our results show that increased water runoff during upstream migratory months is strongly related with the grilse caught in

the rivers. Although, the strength of this relationship weakens by ~74% when a hydropower station is present. Several studies have examined the effect of water discharge showing, for instance, positive associations between flow and swimming activity (Erkinaro et al. 1999), and a body-sized dependence on runoff according to the size of the stream (Jonsson et al. 2007). Upstream ascending is physiologically demanding, and, to some extent, river migrations success is related with water temperature. In this sense, there appears to be a narrow window with a critical upper temperature threshold that leads to increased mortality due to the collapse of the aerobic scope at least in certain species (Farrell et al. 2008). Indeed, warmer water temperatures are generally associated with lower water discharges. Upstream migration is vulnerable to the presence of several man-made obstacles on the fish's way to the spawning grounds. In fact, damming has been claimed as one of the severe threats preventing recovery of endangered salmon populations, however, their impacts seem to be river-specific for both Atlantic (L'Abée-Lund et al. 2006) and Pacific species (Levin and Tolimieri 2001, Welch et al. 2008). In this sense, we did not find an overall steeper time drop in catches for those dammed rivers (i.e., β_8 in equation 2, Table 2) as has been shown for single river analyses (e.g., Ugedal et al. 2008). We have identified that there is a general effect of runoff favoring the abundance, but the flow regime loses importance in presence of a hydropower station in the course of the rivers. This interaction is complex and can be regime specific. When runoff is low, catches are higher in those rivers with presence of dams relative to rivers without hydropower stations, however, at high values of runoff the difference reverses. This could suggest that there exists more complexity not captured by our model, maybe related with habitat characteristics (L'Abée-Lund et al. 2004), and pointing to the importance of site-specific responses to the same environmental variables as has been shown elsewhere

(Crozier and Zabel 2006, Hodgson et al. 2006).

Salmon farming in Norway experienced an exponential expansion over the past 40 years reaching ~750 000 tons and 863 licenses in 2008 (Fig. 1a). Our results show an overall decreasing trend (~1.4% yr^{-1}) during the study period that is steeper if aquaculture operations are present in the draining area. In other words, half of the catches could be lost in ~15 years compared to ~50 years. We cannot distinguish any concrete negative agent regarding our data. However, numerous studies have reported direct and indirect effects of farmed salmon on wild populations (see review by Thorstad et al. 2008b), and global analyses have shown that migrating smolts that pass by net pens dramatically reduce their survival rates (Ford and Myers 2008) presumably associated with parasitic (lice) infestations (Bjørn et al. 2009, Costello 2009), which could be even enhanced due to wild fish movements connecting farming areas (Uglem et al. 2009). Furthermore, it is sufficiently documented the negative impacts on genetics due to inter-breeding (Thorstad et al. 2008b). Our results also show that catches in rivers with presence of farms relative to rivers without aquaculture production was higher during most of the study period, though the difference narrowed in time. This result could suggest, to some extent, that salmon numbers are higher in rivers draining in aquaculture zones due to the escapees. Indeed, the average proportion of escaped salmon in the catches has decreased since the final 80s and is overall low (<10%) (Fig. 1b, Fiske et al. 2006).

Our model shows that catches of grilse in the rivers increased significantly with the drop of harvesting this life-stage at sea. It has been reported that sea fishery can influence catches in the rivers, for instance, after the ban of the drift net fishery in 1989 there has been described structural changes on the spawning run of Norwegian populations (Jensen et al. 1999). Consequently, coastal waters exploitation reduced its

intensity.

First order autoregressive and moving average parameters were highly significant indicating strong positive autocorrelation at lag one. In mid- to late summer the growth trajectories in a sibling salmon population diverge conforming two groups of potential emigrants and resident individuals that will remain in freshwater for at least one more year before metamorphosing into the migratory smolt stage. This life-history flexibility seems to be genetically fixed but environmentally driven developing a bimodal distribution of the juvenile salmon population (Thorpe et al. 1992). Therefore, we suggest that finding a strong positive autocorrelation at lag one is consistent with the alternative smolting strategies adopted by individual salmons within the same population.

We can conclude that year-to-year variability of grilse in Norwegian rivers is influenced by both oceanic and freshwater factors, and these overall relationships are within river consistent. A decreasing trend is apparent, though less pronounced in northern rivers, and the presence of salmon farms in the draining areas increases this reduction in catches. In addition, rivers with hydropower stations tend to affect the relationship with water flow. Therefore, management actions need to take into account the complexity described here and be focused on reducing the impact of human encroachments if wild salmon populations are to be conserved.

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TABLE 1. Summary of the variables used in the large-scale analysis ($n = 60$ one-sea-winter Atlantic salmon time series).

Variable	Mean	Range	Brief description
Catch (C, in kg)	1776	25–45 020	Nominal catch (mainly rod) of one-sea-winter fish (1SW).
Temperature (SST, in ºC)	8.09	5.83–13.00	Coastal sea surface temperature expected to influence smolts.
Runoff (R, in m^3/s)	99.16	0.69–1618	Water flow expected to affect upstream migration.
Coastal fishery (SF, in kg)	0.57	0.02–0.98	Proportion of 1SW catch in the open ocean potentially influencing river catch.
Time (Y, in yr)	1993	1979–2007	Time trend of catches.
Farming (F)	29*	na	Presence/absence of net pens potentially influencing smolts.
Damming (HP)	28**	na	Presence/absence of hydroelectric stations potentially influencing upstream migration.

na: not applicable.
*Number of rivers out of 60 draining in areas with at least the presence of one farming license established during the study period.
**Number of rivers out of 60 that contained at least one hydroelectric scheme along the salmon-producing part of the river.

TABLE 2. Parameter estimates and statistical significance from the optimal mixed-effects model with River as random grouping factor (60 levels). Abbreviations are described in Table 1. Note that when categorical variables are involved the baseline case for comparison is the absence of farms and hydropower stations.

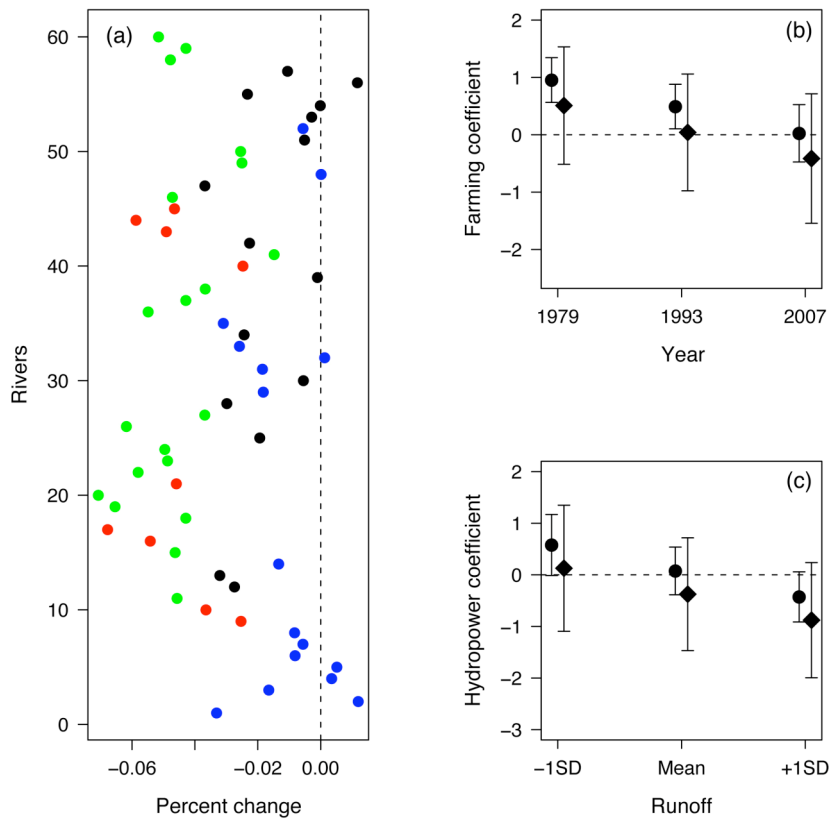| Fixed effects	Estimate	95% CI	t-value	P-value
Intercept	6.763	6.270; 7.256	26.889	<0.0001
F	0.493	0.105; 0.881	2.489	0.0129
HP	0.076	−0.386; 0.538	0.323	0.7467
R	0.411	0.288; 0.534	6.545	<0.0001
SST	0.091	0.054; 0.128	4.844	<0.0001
SF	−1.713	−2.043; −1.384	−10.199	<0.0001
Y	−0.014	−0.031; 0.003	−1.643	<0.1006
$F \times Y$	−0.033	−0.052; −0.015	−3.490	0.0005
$HP \times Y$	0.004	−0.015; 0.023	0.428	0.6687
$HP \times R$	−0.305	−0.476; −0.134	−3.493	0.0005
$F \times HP$	−0.451	−1.082; 0.179	−1.404	0.1606
Random effects				
Intercept	0.882	0.712; 1.092	na	na
Y	0.023	0.013; 0.039	na	na
Corr. structure				
ϕ_1	0.716	0.578; 0.814	na	na
θ_1	−0.297	−0.412; −0.173	na	na
Var. func.	−0.035	−0.057; −0.014	na	na
Residual SD	0.737	0.680; 0.800	na	na

na: not applicable.

FIG. 1. Map of the study area showing the distribution of salmon farming along the Norwegian coast. The size of the dots indicates the number of licenses in each municipality. The insets show (a) the cumulative time trends in farming licenses (broken line) according to the year of starting activities and the total farmed salmon production (dotted line) in Norway; and (b) the time trends of the estimated catches in freshwater (broken line) and in the sea (dotted line) of Atlantic salmon of aquaculture origin.

FIG. 2. (a) Estimated percent change per year in abundance of grilse associated with the presence of farms and hydropower stations based on the mixed-effects model. Black dots indicate rivers without farms and hydropower stations ($\beta_6 + b_i$); green dots show rivers with farms but no presence of hydropower stations ($\beta_6 + b_i + \beta_7$); blue dots indicate rivers without farms but presence of hydropower stations ($\beta_6 + b_i + \beta_8$); and red dots show rivers with presence of both encroachments ($\beta_6 + b_i + \beta_7 + \beta_8$). (b) Farming coefficients without (β_1; dots) and with the presence of hydropower stations ($\beta_1 + \beta_{10}$; diamonds) obtained from models with different year centering (subtracting the min, mean and max). (c) Hydropower coefficients without (β_2; dots) and with the presence of farms ($\beta_2 + \beta_{10}$; diamonds) obtained from models with different runoff centering (subtracting the mean and ± 1SD). The bars represent 95% confidence intervals.
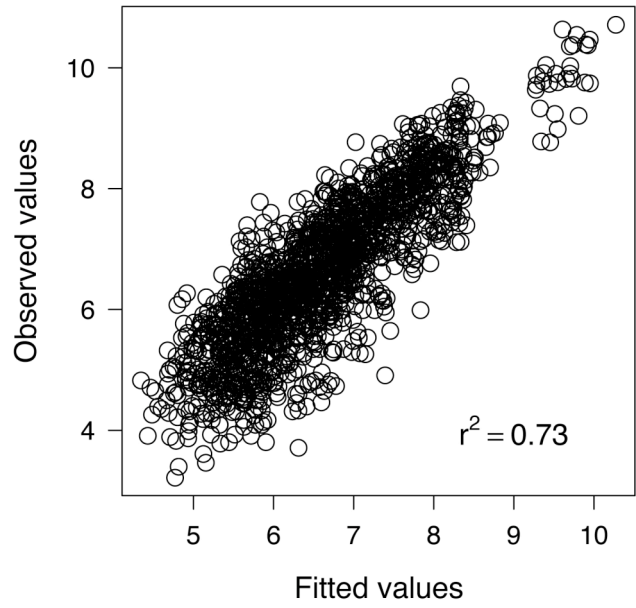
FIG. 3. Observed versus fitted values plot for model depicted in Table 1.
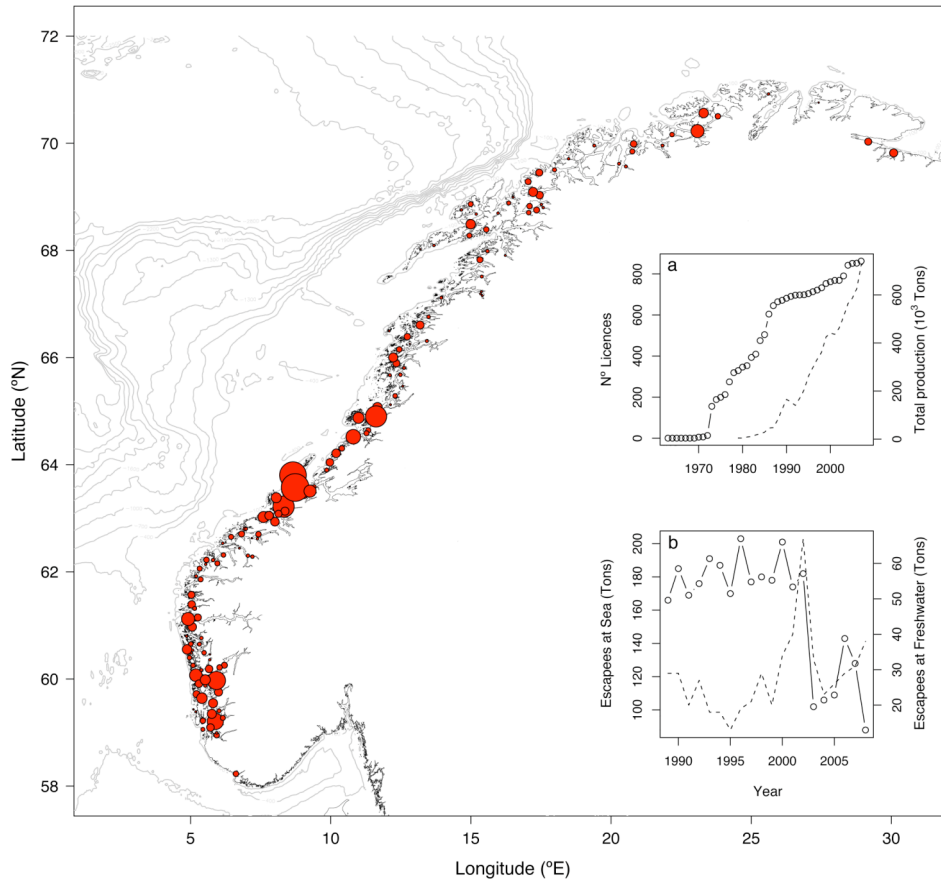
Otero et al. FIG. 1

Otero et al. FIG. 2

Otero et al. FIG. 3