APPLIED ECOLOGY

Ecological regime shift in the Northeast Atlantic Ocean revealed from the unprecedented reduction in marine growth of Atlantic salmon

Knut Wiik Vollset[1]*, Kurt Urdal[2], Kjell Utne[3], Eva B. Thorstad[4], Harald Sægrov[2], Astrid Raunsgard[4], Øystein Skagseth[3], Robert J. Lennox[1,4], Gunnel M. Østborg[4], Ola Ugedal[4], Arne J. Jensen[4], Geir H. Bolstad[4], Peder Fiske[4]

Ecological regime shifts are abrupt changes in the structure and function of ecosystems that persist over time, but evidence of contemporary regime shifts are rare. Historical scale data from 52,384 individual wild Atlantic salmon caught in 180 rivers from 1989 to 2017 reveal that growth of Atlantic salmon across the Northeast Atlantic Ocean abruptly decreased following the year 2004. At the same time, the proportion of early maturing Atlantic salmon decreased. These changes occurred after a marked decrease in the extent of Arctic water in the Norwegian Sea, a subsequent warming of spring water temperature before Atlantic salmon entering the sea, and an approximately 50% reduction of zooplankton across large geographic areas of the Northeast Atlantic Ocean. A sudden decrease in growth was also observed among Atlantic mackerel in the Norwegian Sea. Our results point toward an ecosystem-scale regime shift in the Northeast Atlantic Ocean.

INTRODUCTION

Marked changes are being observed in habitats worldwide that coincide with global climate change and other anthropogenic impacts (*1–3*). These changes can result in ecological regime shifts, in which abrupt changes to the structure and function of ecosystems persist across time in a new stable state (*4*). Some studies suggest that changes to temperature may trigger ecosystem shifts that then propagate across multiple trophic levels (*5*), but opponents argue that empirical ecological data seldom support hypotheses of abrupt changes (*6*). Our understanding of, and ability to predict, these regime shifts evidently remain insufficient, which limits our capability to mitigate social and economic consequences of environmental change.

Ecological regime shifts may elude detection because broad-scale and synchronous changes to key ecological metrics are logistically and methodologically challenging to measure, particularly in the open ocean. Migratory fish returning to freshwater after migrations to the open ocean offer a unique potential insight into conditions at sea. Atlantic salmon (*Salmo salar*) migrate from rivers around the North Atlantic Ocean and spend at least one year in the ocean, where they feed before returning to their natal rivers (*7*). Upon return, a proportion of the salmon is captured by anglers, who report size of each fish and often provide researchers with a scale sample (*8*). Experienced scale readers can reconstruct individual growth in length at different periods at sea by analyzing growth pattern in the scales (*9, 10*). By using these data in combination with information on capture site and biological information about the species, it is possible to reconstruct spatiotemporal patterns in marine growth and thereby infer detailed information on the marine conditions while the fish was at sea.

Norwegian rivers extend 14° of latitude (~58°N to 71°N) and yield about 20% of the total number of wild Atlantic salmon migrating

from the Atlantic Ocean each year. Atlantic salmon fishing is popular nationwide in Norway. Long-term biobanking of scales collected by anglers provides a unique opportunity to recover information about marine conditions at a large geographic scale, treating the Atlantic salmon as remote oceanographers that sample information on growth conditions in the distant marine waters across decades. Studies of growth have revealed that size at age of Atlantic salmon has been decreasing in large parts of the Northeast Atlantic along with reduced survival, particularly affecting southern populations (*8, 11, 12*). Several studies have suggested that changes in size and age at maturation (*12, 13*) of Atlantic salmon may be related to ocean warming and subsequent changes to marine ecosystem functioning (*14–19*). To investigate the spatiotemporal patterns of Atlantic salmon growth in the Northeast Atlantic Ocean, we compiled data on growth of individual fish during their first calendar year at sea, which corresponds to the life stage called post-smolt. Our data comprise growth estimates from more than 52,000 Atlantic salmon, from 180 rivers across Norway, during 1989–2016 (Fig. 1).

An abrupt, simultaneous, and persistent reduction in Atlantic salmon growth during the first year at sea occurred in and around 2005 for all southern Norwegian Atlantic salmon populations, indicating a large-scale shift in growth conditions for Atlantic salmon, which is a potential harbinger of changes at sea. We hypothesized that this apparent state shift in marine growth could be related to (i) temperature, (ii) prey availability, (iii) predation pressure, (iv) spillover effects from freshwater growth, or (v) human impacts. We extracted relevant biological and oceanographic data to evaluate these hypotheses, and in doing so, we investigated evidence for a large-scale regime shift in the Northeast Atlantic Ocean and synchronous ecosystem-scale changes to the marine habitat that Atlantic salmon and other fish rely on.

RESULTS

Synchrony in marine growth of Atlantic salmon

We sorted the individual fish growth data from 180 rivers covering the complete coastline of Norway into four geographic regions (northern,

[1]Norwegian Research Centre (NORCE), Laboratory for Freshwater Ecology and Inland Fisheries, 5008 Bergen, Norway. [2]Rådgivende Biologer AS, 5059 Bergen, Norway. [3]Institute of Marine Research, 5817 Bergen, Norway. [4]Norwegian Institute for Nature Research (NINA), 7485 Trondheim, Norway.
*Corresponding author. Email: knvo@norceresearch.no
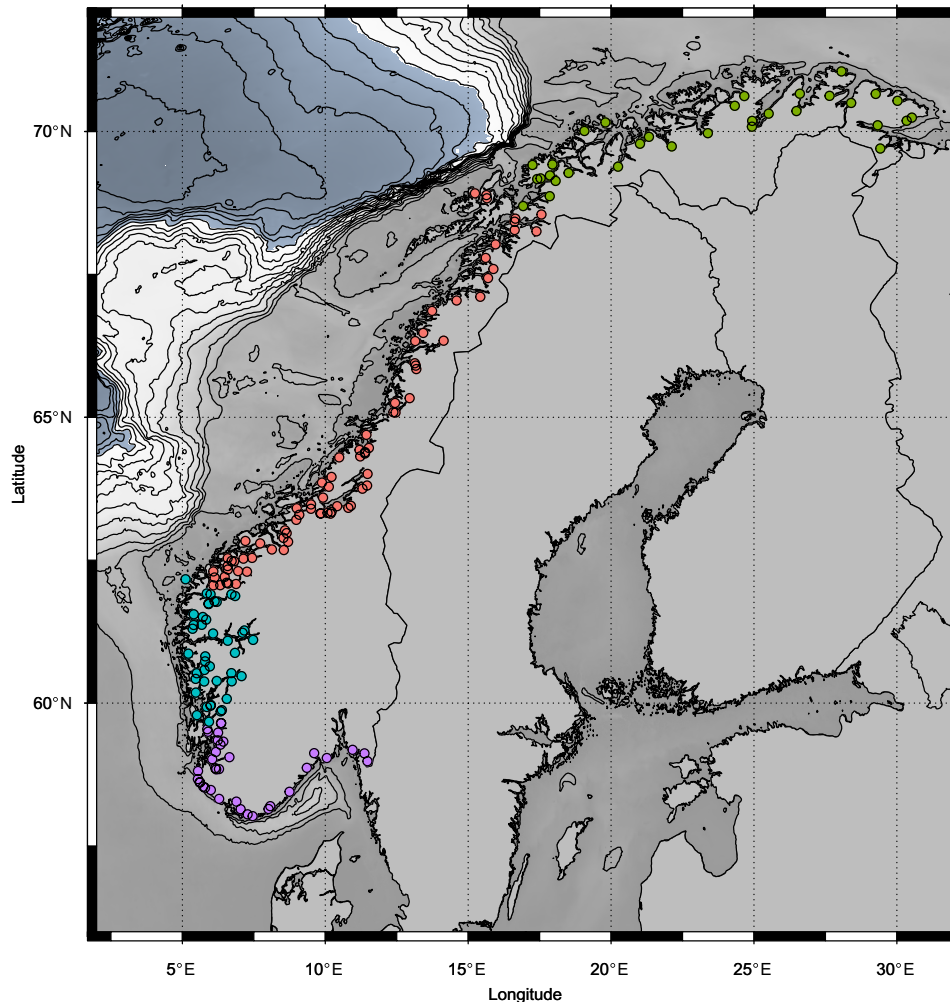
Fig. 1. Map of Norway showing locations where Atlantic salmon scales have been sampled. Color code indicates regional divisions into south-eastern (purple), south-western (cyan), middle (red), and north (green).

middle, south-western, and south-eastern) for spatial comparisons (Fig. 1). The among-year variation in growth during the first year at sea was lowest in the northern region and middle region and highest in the south, with a coefficient of variation (CV) ranging from about 5 to 8% (Table 1). The northern region differed from the three other regions in temporal pattern (Fig. 2), reflected in the low temporal synchrony in growth during the years 1989–2016 (Table 1). Growth was closely synchronized among salmon in the middle, south-western, and southern-eastern populations [correlation coefficient (r) > 0.8]. Growth of the south-eastern and south-western salmon was only marginally synchronized with the northern populations ($r \approx 0.1$) and was low between the middle and northern populations ($r \approx 0.3$).

## Changepoint analysis of growth and return of Atlantic salmon
Marine growth of Atlantic salmon

The growth of Atlantic salmon during the first year at sea decreased in 2005 in terms of early marine growth, relative growth (i.e., growth divided by size at seaward migration), and relative growth per day for the two southern regions and the middle region, whereas no such patterns occurred in the northern region (Fig. 2; see table S1

Table 1. Variation and between-region synchrony in relative growth of Atlantic salmon in the first summer and winter at sea. The CV is estimated as the SD of natural log of relative growth multiplied by 100. Additional parameter estimates for the model are given in table S3.

Region	Among-year CV	Correlation with region middle	Correlation with region south-western	Correlation with region south-eastern
North	4.9%	0.29	0.13	0.07
Middle	4.8%		0.87	0.81
South-western	6.5%			0.95
South-eastern	8.2%			

for description of terminology). In addition, although the absolute or relative growth appeared to be smaller in the northern region (Fig. 2, top and middle), the relative growth per day (Fig. 2, bottom) was higher in the north, indicating better conditions for growth after 2005 than for salmon from rivers in the south.
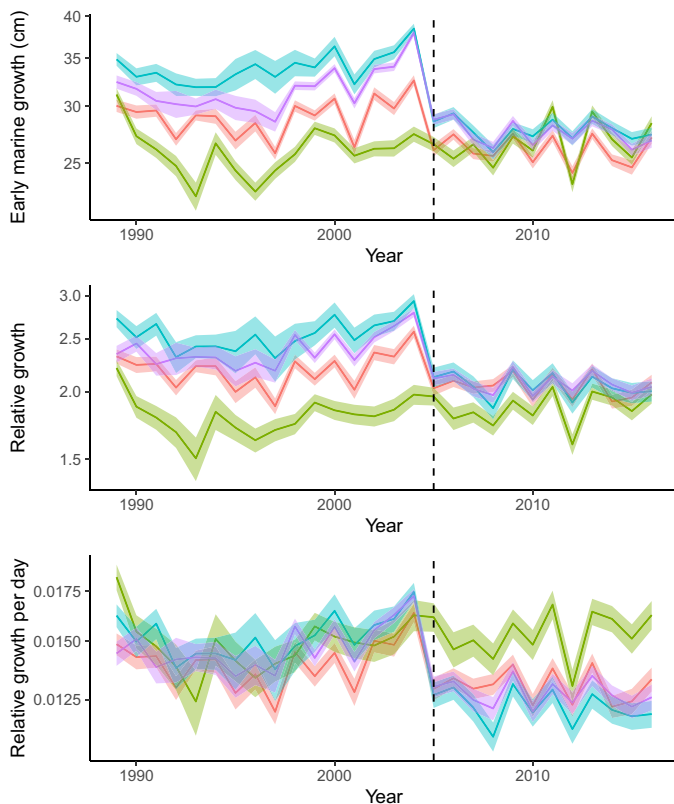
Fig. 2. Comparison of three growth measurements. Error envelopes are 95% confidence intervals from a model for each region, where year is a fixed effect and river (*N* = 180) is a random effect. Color code indicates regional divisions into south-eastern (purple), south-western (cyan), middle (red), and north (green). Relative growth is defined as early marine growth divided by the smolt size, while relative growth per day is relative growth divided by estimated days spent at sea until October 31.

The time series analysis indicated a clear shift in growth between 2004 and 2005 for Atlantic salmon from the two southern regions (fig. S1). The model with the lowest Bayesian information criterion (BIC) for the south-eastern region was a simple model with a piecewise constant mean and variance with a changepoint from 2004 to 2005 (fig. S1 and table S2). For the south-western region, a model with a piecewise linear trend over time performed best and identified not only a changepoint from 2004 to 2005 but also a smaller changepoint in 1998 (fig. S1 and table S2). The average estimated body length attained by the Atlantic salmon after the first winter at sea was reduced from 45.7 to 41.4 cm in the south-eastern region and from 47.9 to 41.2 cm in the south-western region. This corresponded to approximately 9 and 14% reduction in body length. Assuming isometry, this would correspond to a decrease in body mass of about 25 and 36%.

Despite a large decline from 2004 to 2005 in growth of Atlantic salmon from middle Norway, a model with a constant mean and variance performed equally well as all other models (fig. S1 and table S2). For the northern region, there was no observable changepoint according to the best fit model. Instead, a model with a positive linear trend over time with autocorrelated errors performed best and indicated a positive slope (fig. S1 and table S2).

The proportion of Atlantic salmon being larger than 3 kg in body mass when they returned to the rivers

The increase in proportion of Atlantic salmon being larger than 3 kg in body mass when they returned to the rivers, which are Atlantic salmon returning after more than 1 year at sea (Atlantic salmon smaller than 3-kg body mass have usually stayed only 1 year at sea; see fig. S2 for an evaluation of this assumption), indicates an overall trend of returning Atlantic salmon being larger and presumably older toward the end of the study period (Fig. 3A). For the two southernmost regions and the middle region, the best supported temporal trend model included a changepoint (fig. S3 and table S2). For the two southernmost regions, the changepoint in increased proportion of older fish was identified in 2005–2006 (fig. S3). For the middle region, a changepoint was identified in 2000–2001 (fig. S3). For the northern region, a model with a simple trend analysis was marginally better than a model with a simple changepoint in the mean (fig. S3). The average percentage of Atlantic salmon being larger than 3-kg body mass when they returned to the rivers before 2005 in the two southern regions was 35 and 48%. After 2005, this increased to 54 and 64%. The middle and northern region also experienced an increase in the proportion of Atlantic salmon being larger than 3 kg at return during this period, from 37 to 54% in the north and 40 to 53% in the middle region.

The increase in percentage of Atlantic salmon staying longer than 1 year at sea is also apparent on a larger geographic scale. According to the data reported by the International Council for the Exploration of the Sea (ICES) (*20*), there was a steep increase in the percentage of such older salmon from 2005 to 2007 in northern Europe (Fig. 3B). In southern Europe, the increase was more gradual and stabilized after 2011.

Body length of Atlantic salmon when leaving the rivers

The body length of Atlantic salmon when they leave the rivers and enter the sea, which is the life stage called smolt, decreased in the middle and the northern regions but increased in the south-western region (fig. S4). In the northern region, a model with a negative trend was supported, while in the south-western region, a model with positive trend was supported. There was no support for a trend in the south-eastern region. In the middle region, a more complex model with a trend and a changepoint was supported. At the start of the time series, the average size of smolts in the middle and northern region was 15.2 cm, while it was 13.5 cm in the southern regions. At the end of the time series, these values had converged, with an average of 14.4 and 14.0 cm, respectively.

Marine data
Sea surface temperature when Atlantic salmon migrated to the sea

There was no indication of a changepoint in the temperature during seaward migration of Atlantic salmon smolts (in the spring) in the middle, south-western, and south-eastern regions (figs. S5 and S6). Instead, the temperature was similar for all these three regions and warmed linearly throughout the period. In the northern region, the temperature also increased over the whole study period but had a more marked increase after 2008, when a more complex model with a piecewise linear trend over time with autocorrelated errors was supported. In all these temperature data series, the temperature was approximately 8°C at the start of the time series and warmer than 9°C at the end of the time series.
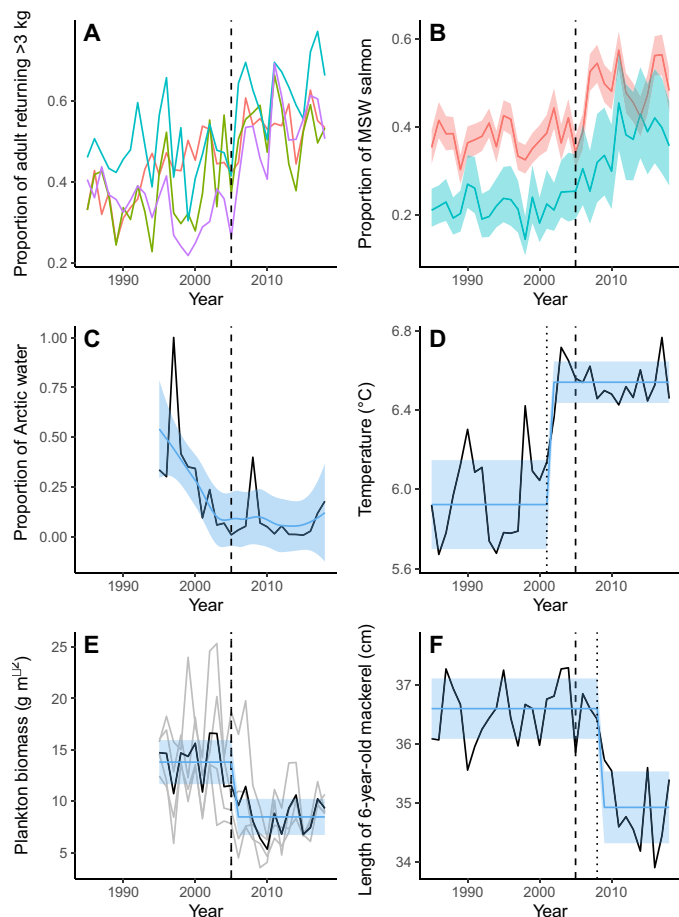
Fig. 3. Relevant biological and oceanographic data showing signals of ecological regime shifts associated to growth reduction of Atlantic salmon in 2005. (**A**) Proportion of Atlantic salmon returning to the Norwegian coast larger than 3 kg. Color code indicates regional divisions into south-eastern (purple), south-western (cyan), middle (red), and north (green). (**B**) Proportion of multi-sea-winter (MSW) salmon of the total number of salmon returning from the Atlantic Ocean at different years to Northern (in red) and Southern (in blue) Europe. Shaded areas show the 95% confidence interval. Northern Europe is Russia, Finland, Norway, Sweden, and Iceland (north and east region), while Southern Europe is Iceland (south and west region), United Kingdom (Scotland, Northern Ireland, England, and Wales), Ireland, and France. (**C**) Proportion of Arctic water in the Norwegian Sea in May. (**D**) Average sea surface temperature (SST) in the Norwegian Sea from January to May. (**E**) Zooplankton biomass defined as grams dry weight per square meter [extracted from ICES 2020 (*50*)], where gray lines are the four different survey areas and the black line is the average. (**F**) Length of 6-year-old mackerel. The dashed line is the identified changepoint in growth of Atlantic salmon in 2005, while the dotted line is the identified changepoint of the time series. Blue shaded areas indicate ±1 SD for the changepoint analysis and the 95% confidence intervals for the smooth function, while the blue line is the model predictions. Note that there was no identified changepoint in proportion of Arctic water, so a LOESS smoother is presented.

Proportion of Arctic water in the Norwegian Sea

The proportion of Arctic water in the Norwegian Sea, which is an index of influence of more productive Arctic water relative to less productive Atlantic water, decreased from 1996 to a nadir in 2005. The best supported model was a trend analysis with a changepoint in 2008 (table S3 and fig. S7). The trend suggests a decline until 2008, after which the proportion of Arctic water was low during the

remainder of the period when growth data were available (Fig. 3C). There seemed to be an increase at the end of the time series beginning in 2017.

Sea surface temperature in the Norwegian Sea and the Arctic front

The average sea surface temperature (SST) has warmed in the Norwegian Sea and at the Arctic front (Fig. 3D, figs. S8 and S9). The time series models of temperature in the Norwegian Sea before the Atlantic salmon outmigration supported a model with a piecewise constant mean and variance with a changepoint occurring in 2001–2002, whereas the other temperature time series, i.e., temperature in the Norwegian Sea from May to December and temperature in the Arctic front (fig. S8 displays region of temperature extraction), supported a model with a general positive trend and an autocorrelation structure (fig. S9 and table S3).

Zooplankton biomass

Zooplankton exhibited a clear shift from a higher to a lower abundance in all four marine regions (i.e., Norwegian basin, Lofoten basin, Arctic front, and east of Iceland; Fig. 3E and fig. S10) and declined to approximately half of the original abundance during the time series. All the time series on plankton supported a model including a clear changepoint. For the Norwegian basin, Lofoten basin, and Arctic front, a more complex model with a piecewise linear trend over time was better than a simpler model with a piecewise constant mean and variance (table S3). The changepoint occurred in 2002–2003 for the Norwegian basin, in 2001–2002 in the Lofoten basin, in 2003–2004 in the Arctic front, and in 2006–2007 east of Iceland (fig. S10).

Growth of marine fish

Length of 6-year-old Atlantic mackerel (*Scomber scombrus*) experienced a marked decrease during the time series (1985–2016), and the model with the strongest support was a model with a piecewise constant mean and variance with a changepoint from 2007 to 2008 (Fig. 3F and table S3). Length of 6-year-old herring (*Clupea harengus*) decreased over the time series and supported a model with a linear trend over time with autocorrelated errors (fig. S11 and table S3). For blue whiting (*Micromesistius poutassou*), the between-year variation was large, and the most complex model with a linear trend with two changepoints (1992 and 2010) had the lowest BIC (fig. S11 and table S3).

Prey fish

Landings of sand eel (*Gymnammodytes capensis*) and sprat (*Sprattus sprattus*), which are important prey for Atlantic salmon, decreased and even disappeared in surveys during the period before 2004. Because of zero inflation and uncertainty related to catch statistics, time series of sand eel and sprat were not analyzed (fig. S12). The recruitment index of Norwegian spring-spawning herring was variable from low to high and lacked strong recruitment since 2004. The large variance led to a poor fit to all time series models.

Correlation between growth of Atlantic salmon at sea and marine data

From the correlation analysis of growth and marine data (figs. S13 to S16), there were three important findings. (i) There was a strong positive correlation between growth of Atlantic salmon with average abundance of plankton ($r > 0.7$) and a negative correlation with SST in the Norwegian Sea ($r < -0.5$) in the two southernmost regions. These correlations were weaker in the middle region and largely absent in the northern region. (ii) There were only weak

correlations between growth of Atlantic salmon and index for Arctic water [except in the northernmost region ($r = 0.5$)] but a strong negative correlation between the index for Arctic water and average SST in the Norwegian sea ($r = -0.78$). (iii) There was a negative correlation between average SST in the Norwegian Sea and average plankton abundance ($r = -0.57$).

DISCUSSION

Unique data on body length growth during the first months at sea obtained from reading of scales from Atlantic salmon revealed an abrupt reduction in growth in the year 2005 for numerous populations migrating through the Norwegian Sea from southern and middle Norway. This reduced growth co-occurred with a decline in the number of Atlantic salmon that returned to the rivers during the subsequent year after having spent 1 year at sea (termed one-sea-winter Atlantic salmon or grilse). Our analysis revealed a coinciding oceanographic decrease in the extent of Arctic water in the Norwegian Sea. This decrease in Arctic water resulted in about 1° warming of temperature, which correlated with an almost 50% reduction in zooplankton abundance before out-migration of Atlantic salmon smolts from rivers to regions of the Norwegian Sea. A sudden reduction in body growth was also observed among Atlantic mackerel following this reduction in plankton. A reduced growth of Atlantic salmon around 2005 has also been observed in France and Scotland (8, 21), suggesting that the factors affecting southern Norwegian populations affected salmon populations across a large geographic area. We hypothesize that the oceanographic change in Arctic water caused a synchronous regime shift among trophic levels across a large area of the Northeastern Atlantic Ocean. This regime shift may be predicted by several competing mechanistic hypotheses, which we discuss in the context of potential top-down and bottom-up processes.

Temperature warmed during the sampling period. Ignoring possible bottom-up effects of food limitation on growth of Atlantic salmon, direct physiological limitations may be imposed by changing temperature regimes in the ocean, which affect growth rates and survival of Atlantic salmon. Atlantic salmon encounter a range of water temperatures in the marine environment; they make frequent dives past the thermocline to hundreds of meters and are, in general, found at water temperatures between 0° and 14°C (19, 22, 23). A possible explanation for the decreased growth of Atlantic salmon may therefore be the direct physiological effect of warming water temperatures and the effects on metabolism and exercise physiology. Warming temperatures worldwide have been implicated in changes in animal sizes, including a widespread decline in the size of Pacific salmon (24). Clark et al. (25) also suggested that warming will favor smaller-sized salmon because of a higher metabolic cost in response to activity in warmer water. The Northeast Atlantic is now warmer than it has been in millennia, but marine temperatures are unlikely to surpass temperatures that are considered to fall within the optimal window for Atlantic salmon (26). The average temperature warming in the North Atlantic during 1980–2020 is more likely to stimulate an increased and not decreased growth of Atlantic salmon, assuming that they are not food limited (27). We therefore argue that the change in temperature observed during the period is insufficient to explain an unprecedented collapse in growth and suggest that there are additional explanatory factors beyond physiological limitations imposed by temperature.

Data from the greater Northeastern Atlantic showed a clear decrease in the abundance of zooplankton just before the abrupt decrease in body growth of Atlantic salmon growth in 2005. These data suggest that the decline in growth of Atlantic salmon during the first months at sea is somehow linked to basin-scale shifts in plankton abundance and a regime shift in the North Atlantic that disfavors growth of Atlantic salmon during their first year at sea. Sudden changes in plankton composition have been reported earlier from the North Sea, which have also been correlated with Atlantic salmon abundance (15). Regime shifts in the plankton community may be a function of a top-down mechanism, for example, through predation from pelagic fish, such as mackerel. One possible mechanism is therefore that the decrease in zooplankton may be driven by the range expansion of mackerel. Contemporary decrease of mackerel growth in the Northeastern Atlantic has been studied in detail by Olafsdottir et al. (28). They suggested that the carrying capacity for planktivorous fishes was reached and that the observed decrease in growth of mackerel was a function of density-dependent competition among planktivores. At the same time, the feeding area of mackerel expanded northward by 50% during 2006–2013, leading to a larger geographic overlap with Atlantic salmon during their first months at sea (29). The simultaneous reduction in growth of Atlantic salmon and biomass of zooplankton, with a clear spatial expansion of mackerel, could indicate competition between mackerel and Atlantic salmon. Although mackerel and post-smolt salmon have some dietary overlap, they have sufficiently different feeding niches that they are not density co-dependent. Whereas mackerel mainly feed on copepods and other mesozooplankton (1 to 2 mm long), post-smolts of salmon feed on fish larvae, euphausiids, and Amphipoda (30). This suggests that direct competition between these species is unlikely and that the declining growth of the two species is a parallel response to a bottom-up process occurring across the Northeast Atlantic ecosystem rather than a result of competitive exclusion of Atlantic salmon by mackerel.

During their early marine life, the Atlantic salmon need energy-efficient prey, such as lipid-rich larvae of sand eel, herring, and sprat, to sustain their growth (31). Available data for these larval fish species follow the same general pattern as other indices, with lower abundances after 2005 than before that date. For sprat and sand eel, abundance seems to have decreased in the northern North Sea. In contrast, the recruitment of Norwegian spring-spawning herring has fluctuated markedly among years, but no high recruitment indices have been reported since 2004. A recent study in the Norwegian Sea supports the hypothesis that salmon post-smolt rely on fish larvae to maintain a high growth rate, showing that condition of Atlantic salmon post-smolt decreased with lower prevalence of fish larvae in their stomachs (32). A clear drop in condition factor was also observed in the 25-year time series occurring somewhere between 2003 and 2008 (32). The reasons for lack of recruitment of larval fish along the Norwegian coast are unknown, but top-down processes, such as predation (33), or bottom-up processes due to lack of suitable zooplankton during early life stages (34) have been proposed. A plausible explanation for the reduced growth in Atlantic salmon is therefore reduction in high-energy larval fish prey during the early marine life due to lack of recruitment following an ecological regime shift occurring in 2005. Toresen et al. (34) previously noted a reduction in zooplankton just before 2005 along the Norwegian coast during their herring surveys, supporting the hypothesis that a basin-scale regime shift occurred just before the Atlantic salmon growth collapse.

The simultaneous changes to temperature, zooplankton, and marine growth of Atlantic salmon and subsequent decrease in size of mackerel occurred after what seemingly was a sudden reduction in the transport of Arctic water into the Norwegian Sea. This observation may suggest that the simultaneous occurrences of shifts in physical and biological measurements are driven by a bottom-up process associated with abiotic environmental changes or at least that these changes were set in motion by a shift in distribution of Arctic water in the Norwegian Sea. The zooplankton density is higher in Arctic water than in Atlantic water, so conveyance of food may also have declined after 2005 (34). The reduced transport of Arctic water with high abundance of microzooplankton into the Norwegian Sea is therefore a plausible explanation for the shifts in growth and ecological regime.

Shifts in marine growth may also, in theory, have been the result of antecedent growth conditions in freshwater (35). Small body size differences at the time of first feeding in the marine environment may have consequences for the ability of Atlantic salmon post-smolts to use different prey. If the post-smolts are initially too small to use an abundant food source, which may be growing simultaneously, then Atlantic salmon may fail to keep pace with the size of prey and therefore grow poorly throughout the season. This is, in recruitment biology, termed "successful surf riding on size spectra," alluding to the need of individuals to have the right size to use the available prey (36). Consequently, a marked shift in marine growth may have been caused by a steady decline in size at age that, at some point, crosses a minimum size for prey exploitation in the marine environment. However, in our dataset, we show that Atlantic salmon entering seawater has become larger in the south and smaller in the north, which is the opposite trend of what we would expect if this was the underlying mechanism for the growth decline.

Among the largest anthropogenic impacts of wild Atlantic salmon in the North Atlantic are the effects of net-pen Atlantic salmon farming in coastal areas. Effects of Atlantic salmon farming include genetic introgression of farmed genes due to spawning of escaped farmed salmon and spillover effects of salmon lice (*Lepeophtheirus salmonis*) and other parasites and pathogens that disperse through the water column (37–39). In farm-intensive areas, mortality of wild Atlantic salmon due to salmon lice may be considerable, and for survivors, the marine growth may be affected (40). Introgression of escaped farmed salmon also affects marine survival (41, 42) and the size and life history of Atlantic salmon (43). However, there is key evidence that suggests that the observed decline in growth and decline in one-sea-winter fish that occurred in 2005 is not mainly driven by impacts of fish farms. (i) The steep decline in growth also occurred in the south-eastern region of Norway that was devoid of fish farms (although Atlantic salmon smolts migrating to sea have to migrate northward past regions of high fish farming activity). (ii) There is currently no evidence that there was a large shift in aquaculture production, number of escaped farmed salmon, or salmon lice infestation pressure numbers in 2005 across a large regional scale that could explain the patterns observed in Atlantic salmon growth. However, note that impacts of variable marine conditions are not disentangled from impacts of salmon lice. For example, the effects of salmon lice on marine growth of Atlantic salmon are much stronger during years of low marine survival compared to years with higher marine survival (40). In the face of apparent marked changes in the marine environment of Atlantic salmon, it seems even more important to reduce negative human impacts on Atlantic salmon populations in years with poor ocean conditions (19).

Atlantic salmon disappeared from large river ecosystems such as the Thames and the Rhine over a hundred years ago, eradicating runs of Atlantic salmon that were unmatched by most of the populations that we have today (44). Past declines have generally been related to overfishing, pollution, and destruction of freshwater habitats due to human activities (44). In contrast, the contemporary decline of Atlantic salmon in the Atlantic Ocean has occurred across multiple populations simultaneously, pointing to large-scale effects, such as climate change and shifts in marine conditions (45, 46).

Occurrences of large-scale shifts in marine conditions that propagate through marine ecosystems are often difficult to observe because of lack of observation on biologically relevant scales. Atlantic salmon scales are unique in this sense because the spatially explicit observations of the fish returning to their home rivers allow us to understand detailed temporal patterns and spatial patterns in marine growth. This illustrates how local versus basin-scale changes affect the marine growth of Atlantic salmon and helps to test for impacts of human activity in rivers and coastal areas versus large-scale ecosystem effects in the sea. Using a large dataset of Atlantic salmon growth based on fish scale analyses, we have revealed an unprecedented shift in growth occurring after 2004, which should have large implications for conservation, management, and genetic evolution of Atlantic salmon, as well as for other marine species in the North Atlantic. In contrast to the belief that marine growth is steadily decreasing, the data rather indicate a sudden and marked drop in growth of Atlantic salmon after migrating out of the southern and middle rivers of Norway in 2005, after which growth never fully recovered. Here, we have described how the observed decline in growth happened simultaneously to shifts in several biological and physical measurements, corroborating the hypothesis of a basin-scale change in ecosystem functioning in the Northeast Atlantic driven by the reduced transport of Arctic water with high abundance of microzooplankton into the Norwegian Sea.

MATERIALS AND METHODS
Scale analyses
Scale samples of adult Atlantic salmon were compiled from 180 rivers, which comprise almost half of all Atlantic salmon rivers in Norway, during 1989–2016. The scales were collected by anglers when sport fishing in the various rivers. The back-calculation of fish length was based on the linear relationship between fish length and the diameter of the fish scale from the center of the scale to the edge (9). We focused on the average growth across four large geographic regions: south-eastern, south-western, middle, and north Norway (Fig. 1). In total, 52,371 Atlantic salmon were sampled by fishers. For each individual fish, the following data were used: length at capture (in cm), back-calculated freshwater growth (in cm), back-calculated early marine growth (in cm), and smolt year, which is the year that they migrated from the rivers as juveniles to the sea. Freshwater growth was defined as the distance from the center of the scale to the end of the freshwater zone in the scale. Early marine growth, also termed post-smolt growth, was measured as the distance between the end of the freshwater zone and the end of the first winter at sea.

Proportion of multi-sea-winter adult returns of Atlantic salmon

The proportion of multi-sea-winter (MSW) returns were estimated from the number of adult Atlantic salmon returning to the rivers after the marine migration extracted from the official numbers reported to ICES. These are data estimated using the "run reconstruction method" (*47*), which, in most countries, are informed by recreational and artisanal fishing catches (corrected for unreported catches) and an exploitation rate. Some countries also inform their estimates by count data and catch-and-release fisheries. Detailed descriptions of the method and population size estimates are provided in (*20, 47*). For the Norwegian data, the threshold of what is considered an MSW fish is body mass ≥3 kg.

Marine data
Sea surface temperature

Weekly measurements of SSTs were extracted from the National Oceanic and Atmospheric Administration (www.ncdc.noaa.gov) from the period 1989 to 2018. SSTs were extracted in three ways: First, average SSTs were extracted from four polygons describing the areas occupied by early marine life of Atlantic salmon from the four regions of Norway during the early sea migration in the summer. Because the timing of migration from rivers to the sea varies among the latitudinal gradients in the four regions (*48*), temperature averages per year were extracted from May for the south-eastern region, June for the south-western region, July for the middle region, and August for the northern region. Second, average SSTs from the adult feeding grounds were extracted by drawing a polygon, encompassing what is believed to be the approximate feeding ground of Norwegian Atlantic salmon. Third, temperatures from the Norwegian Sea were extracted where a large number of Atlantic salmon post-smolts of southern Atlantic salmon populations have been observed (*49*). We extracted two indices from the last two polygons: (i) average temperature from January to May as an index of temporal changes in the ecosystem before the smolt out-migration and (ii) average temperatures from May to October, which could indicate direct effects of temperature on growth of Atlantic salmon during their early marine migration. Maps of temperature extraction are shown in figs. S5 and S8.

Proportion Artic water in the Norwegian Sea

The Norwegian Sea can either be dominated by water from the North Atlantic, which is warm and saline or cold and fresh, or by water from the East Icelandic current, which is cold and saline (defined by $S = 34.6$ to 34.9 and $T < 4°C$). The relative proportion of Arctic water into the Norwegian Sea in spring can be used as an index of influence of Arctic water relative to Atlantic water in the Norwegian Sea (range from 0 to 1). Arctic water has been associated with higher abundances of the zooplankton *Calanus hyperboreus*, which is known to be an important food source for many pelagic fish species. The annual index was extracted from (*50*).

Plankton abundances

Biomass of zooplankton in May has been estimated annually since 1995 for the Norwegian Sea. The sampling stations are evenly distributed between 14°W and 20°E in areas covering Atlantic water, Arctic water, and the Arctic frontal zone. The sampling was done with a WP2 plankton net, which is a plankton net with an opening of 1 m² hauled vertically from depth of 200 m to the surface. The majority of the sampled zooplankton with this gear is mesozooplankton because individuals larger than 2 mm can escape (*51*). The sampled

area was divided into four subregions to examine regional differences: (i) southern Norwegian Sea including the Norwegian Sea basin, (ii) Northern Norwegian Sea including the Lofoten basin, (iii) Jan Mayen Arctic front, and (iv) east of Iceland. More information about the zooplankton sampling is given in ICES (*50*). Mesozooplankton (<2 mm) are not important prey for Atlantic salmon early marine life but are an important constituent of the marine ecosystem and an important bottom-up biological forcing in the marine ecosystem. Macroplankton are likely more important prey than mesozooplankton (*30*), but samples are not readily available.

Body growth of marine fish

To evaluate whether similar patterns in marine growth have occurred for similarly sized marine fish that potentially compete with Atlantic salmon, average body length for 6-year-old Norwegian spring-spawning herring, mackerel, and blue whiting in the Norwegian Sea were retrieved from (*50*). These are fish that are the dominating pelagic species in the Norwegian Sea, which is a region with an average sea depth of 1800 m. They were sampled during the winter when their feeding was reduced to a minimum and growth had ceased. Demersal fish species in the Norwegian Sea were not investigated, because they are of low abundance, not regularly monitored, and do not normally interact with Atlantic salmon. More information about the time series and individual body growth of these pelagic fish species is given in (*50*).

Prey fish data

Early life stages of marine fish are important prey for Atlantic salmon in their early marine life, particularly herring, sprat (*S. sprattus*), and sand eel (*Ammodytes* sp.*) (*31, 52*). Data on temporal development of sand eel and sprat biomass are scarce, so commercial landings of these species were retrieved and used as a proxy for annual abundance. Data on annual commercial landings of sand eel for ICES management area 5r (the northern North Sea) for the years 1985–2018 were retrieved from (*53*). Annual commercial landings of sprat along the western coast of Norway for the years 1985–2011 were provided by the Norwegian Fishermen's Sales Organization for Pelagic Fish. The exact age distribution for sprat and sand eel in commercial catches varied with year and location and was only reported for the larger fisheries (e.g., sand eel in southern North Sea). Catch at age was not reported for sand eel for the northern North Sea and for sprat along the Norwegian coast. However, sprat and sand eel targeted by commercial fisheries are typically 1 to 3 years old. In addition, a small proportion of the catches consists of individuals older than 3 years. On the basis of this general knowledge, we assume that sprat and sand eel in commercial catches were, on average, 2 years old.

Estimated historic recruitment of Norwegian spring-spawning herring was retrieved from the analytic stock assessment (*54*). The model back-calculates historic year-class strength based on commercial catch-at-age data [virtual population analysis (VPA) model] adjusted according to fishery-independent (e.g., surveys) indices. Since recruitment age in the assessment was 2 years old, year minus two was applied for the annual recruitment estimates to represent larval abundance. Herring spawn along the Norwegian coast. Hatching larvae are passively transported northward during spring and early summer as they grow, making them available as prey to Atlantic salmon during their early marine life if they overlap in space and time (*30*).

Data analysis
Growth analysis

Growth estimates from scales may be affected by the size of the fish when they leave the rivers and enter the sea. To correct for this error, a

relative growth estimate can be used where the early marine growth is divided by the freshwater growth of the individual, which we refer to as relative growth. In addition, the timing of out-migration will vary by up to 2 months from north to south in Norway, meaning that the time to grow before winter is shorter for northern populations. Putative monthly growth estimates indicate that growth is limited from November, and we therefore calculate growth from day of out-migration to 31 October. Day of out-migration was calculated according to (55) using a model that explains out-migration date based on latitude, longitude, air temperature during winter, and river discharge. The estimated growth is called relative growth per day. All three growth estimates are presented and discussed; however, for the rest of the analysis, relative growth was used and termed early marine growth.

Statistical analysis of synchrony in Atlantic salmon early marine growth

To understand whether Atlantic salmon growth in different rivers and regions of Norway was controlled by similar mechanisms, we first evaluated synchrony in growth. We estimated the CV and the correlation among regions in the natural logarithm of early marine growth ($\mathbf{g}$) using the mixed effect model

$$\mathbf{g} = \mathbf{Xb} + \mathbf{Z}_1\mathbf{u}_1 + \mathbf{Z}_2\mathbf{u}_2 + \mathbf{e}$$

where $\mathbf{X}$ is the fixed effects design matrix, $\mathbf{Z}_1$ and $\mathbf{Z}_2$ are random effect design matrices, $\mathbf{b}$ includes the intercept and the fixed effect contrast to each region, $\mathbf{u}_1$ is the random effect of river, $\mathbf{u}_2$ is the random effect of smolt year within region, and $\mathbf{e}$ is the residual vector. Both the random effect of river and the residuals were assumed to be independent and normally distributed, while the random effect of smolt year within rivers was assumed to be multivariate normally distributed according to $\mathbf{u}_2 \sim N(\mathbf{0}, \mathbf{U} \otimes \mathbf{I})$, where $\mathbf{0}$ is a column vector of zeros, $\mathbf{U}$ is the among regions variance matrix (with four dimensions), $\otimes$ is the Kronecker product, and $\mathbf{I}$ is the identity matrix with dimensions equal to number of smolt years. From the variance matrix $\mathbf{U}$, we can calculate the among region correlations. The model was fitted in R using the package lme4 (56).

Changepoint analysis

We applied the envcpt() function from the EnvCpt package (57) in R, which applies an automatic model selection between a variety of trend, changepoint, and autocorrelation models (i.e., time series analysis). For simplicity, we removed the second-order autocorrelation structure models (AR2) because they have similar fits to the data as AR1. The eight models fitted to each time series (y_t) were as follows:

1) A constant mean and variance (model abbreviation: Mean)

$$y_t = \mu + e_t$$

where the subscript t denotes year (1989–2016); μ is the mean; and e_t is the error term, which is assumed to be normally distributed and independent and identically distributed (I.I.D.) with a mean of zero and variance σ^2.

2) A piecewise constant mean and variance (model abbreviation: Mean cpt)

$$y_t = \begin{cases} \mu_1 + e_t, & t \leq \mathbf{c}_1 \\ \mu_2 + e_t, & \mathbf{c}_1 < t \leq \mathbf{c}_2 \\ \vdots \\ \mu_m +, & \mathbf{c}_{m-1} < t \leq n \end{cases}$$

where $\mathbf{c}$ is a vector of years at which the changepoints occur, with respective means (μ) in the various segments between the different changepoints.

3) A constant mean with autocorrelated errors [model abbreviation: Mean + AR(1)]

$$y_t = \mu + \varphi\, y_{t-1} + e_t$$

where φ is the autocorrelation parameter.

4) A piecewise constant mean with autocorrelated errors [model abbreviation: Mean cpt + AR(1)]

$$y_t = \begin{cases} \mu_1 + \varphi_1 y_{t-t} + e_t, & t \leq \mathbf{c}_1 \\ \mu_2 + \varphi_2 y_{t-1} + e_t, & \mathbf{c}_1 < t \leq \mathbf{c}_2 \\ \vdots \\ \mu_m + \varphi_m y_{t-1} + e_t, & \mathbf{c}_{m-1} < t \leq n \end{cases}$$

5) A linear trend over time (model abbreviation: Trend)

$$y_t = \lambda + \beta t + e_t$$

where λ is the intercept and β is the slope of the trend.

6) A piecewise linear trend over time (model abbreviation: Trend cpt)

$$y_t = \begin{cases} \lambda_1 + \beta_1 t + e_t, & t \leq \mathbf{c}_1 \\ \lambda_2 + \beta_2 t + e_t, & \mathbf{c}_1 < t \leq \mathbf{c}_2 \\ \vdots \\ \lambda_m + \beta_m t + e_t, & \mathbf{c}_{m-1} < t \leq n \end{cases}$$

7) A linear trend over time with autocorrelated errors [model abbreviation: Trend + AR(1)]

$$y_t = \lambda + \beta t + \varphi\, y_{t-1} + e_t$$

8) A piecewise linear trend over time with autocorrelated errors [model abbreviation: Trend cpt + AR(1)]

$$y_t = \begin{cases} \lambda_1 + \beta_1 t + \varphi_1 y_{t-t} + e_t, & t \leq \mathbf{c}_1 \\ \lambda_2 + \beta_2 t + \varphi_2 y_{t-t} + e_t, & \mathbf{c}_1 < t \leq \mathbf{c}_2 \\ \vdots \\ \lambda_m + \beta_m t + \varphi_m y_{t-1} + e_t, & \mathbf{c}_{m-1} < t \leq n \end{cases}$$

The EnvCpt packages fit the model according to maximum likelihood estimation. Changepoints are located using the pruned exact linear time algorithm described in (52).

An alternative modeling approach using a generalized additive model (GAM) was also explored. Spatial patterns were taken into account in the GAM by a smoother with an interaction between latitude and longitude. River was defined as a random effect, and year was included as smoother for each region separately. The GAM modeling confirmed the changepoint analysis, and we do not present these results.

The BIC was used to select the time series model with the highest support. Models with ΔBIC < 2 were viewed as having equal support. In such cases, the simplest model was selected over a more complex model. For illustration purposes, data supporting models with a trend (e.g., models 3, 5, and 7) were plotted using the loess smooth function in ggplot (58), while time series supporting a model

with a changepoint (models 2, 4, 6, and 8) were illustrated with a stepwise plot with a vertical dotted line, indicating where the changepoint in the dataset occurs.

We first applied the changepoint analysis to the early marine growth of Atlantic salmon. Because the dataset was not complete for all river/year combinations, we used the estimated early marine growth from the linear mixed model in the synchrony analysis for each region as input. The same method was used for smolt size extracted from the scales. From data of number of Atlantic salmon returning to the river, we calculated the proportion of Atlantic salmon registered as >3 kg for each region, with the rationale that salmon larger than 3 kg has spent another year at sea, reflecting a life history response to reduced growth conditions (see fig. S2 for an evaluation of this assumption). Second, we applied the changepoint analysis for each of the time series of marine data. Last, we calculated the (Pearson) correlation coefficients between early marine growth of Atlantic salmon and all explanatory variables, where the estimates per year of relative growth from the different regions were taken from the linear mixed model used in the synchrony analysis.

SUPPLEMENTARY MATERIALS

REFERENCES AND NOTES

1. K. Brander, Impacts of climate change on fisheries. *J. Mar. Syst.* **79**, 389–402 (2010).
2. J. B. C. Jackson, M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, J. Erlandson, J. A. Estes, T. P. Hughes, S. Kidwell, C. B. Lange, H. S. Lenihan, J. M. Pandolfi, C. H. Peterson, R. S. Steneck, M. J. Tegner, R. R. Warner, Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**, 629–637 (2001).
3. D. Pauly, V. Christensen, J. Dalsgaard, R. Froese, F. Torres Jr., Fishing down marine food webs. *Science* **279**, 860–863 (1998).
4. R. Biggs, S. R. Carpenter, W. A. Brock, Turning back from the brink: Detecting an impending regime shift in time to avert it. *Proc. Natl. Acad. Sci. U.S.A.* **106**, 826–831 (2009).
5. G. Beaugrand, M. Edwards, K. Brander, C. Luczak, F. Ibanez, Causes and projections of abrupt climate-driven ecosystem shifts in the North Atlantic. *Ecol. Lett.* **11**, 1157–1168 (2008).
6. H. Hillebrand, I. Donohue, W. S. Harpole, D. Hodapp, M. Kucera, A. M. Lewandowska, J. Merder, J. M. Montoya, J. A. Freund, Thresholds for ecological responses to global change do not emerge from empirical data. *Nat. Ecol. Evol.* **4**, 1502–1509 (2020).
7. Ø. Aas, A. Klemetsen, S. Einum, J. Skurdal, *Atlantic Salmon Ecology* (John Wiley & Sons, 2010).
8. C. D. Todd, N. N. Hanson, L. Boehme, C. W. Revie, A. R. Marques, Variation in the post-smolt growth pattern of wild one sea-winter salmon (*Salmo salar* L.), and its linkage to surface warming in the eastern North Atlantic Ocean. *J. Fish Biol.* **98**, 6–16 (2020).
9. N. N. Hanson, G. W. Smith, S. J. Middlemas, C. D. Todd, Precision and accuracy of Dahl-Lea back-calculated smolt lengths from adult scales of Atlantic salmon *Salmo salar*. *J. Fish Biol.* **94**, 183–186 (2019).
10. T. Heidarsson, T. Antonsson, S. S. Snorrason, The relationship between body and scale growth proportions and validation of two back-calculation methods using individually tagged and recaptured wild Atlantic salmon. *Trans. Am. Fish. Soc.* **135**, 1156–1164 (2006).
11. A. J. Jensen, P. Fiske, L. P. Hansen, B. O. Johnsen, K. A. Mork, T. F. Næsje, Synchrony in marine growth among Atlantic salmon (*Salmo salar*) populations. *Can. J. Fish. Aquat. Sci.* **68**, 444–457 (2011).
12. B. Jonsson, N. Jonsson, J. Albretsen, Environmental change influences the life history of salmon *Salmo salar* in the North Atlantic Ocean. *J. Fish Biol.* **88**, 618–637 (2016).
13. J. Otero, A. J. Jensen, J. H. L'abée-Lund, N. C. Stenseth, G. O. Storvik, L. A. Vøllestad, Contemporary ocean warming and freshwater conditions are related to later sea age at maturity in Atlantic salmon spawning in Norwegian rivers. *Ecol. Evol.* **2**, 2192–2203 (2012).
14. C. D. Todd, K. D. Friedland, J. C. MacLean, N. Hazon, A. J. Jensen, in *Atlantic Salmon Ecology*, Getting into hot water? Atlantic salmon responses to climate change in freshwater and marine environments, O. Aas, S. Einum, A. Klemetsen, J. Skurdal, Eds. (Wiley-Blackwell, 2010), pp. 409–443.
15. G. Beaugrand, P. C. Reid, Relationships between North Atlantic salmon, plankton, and hydroclimatic change in the Northeast Atlantic. *ICES J. Mar. Sci.* **69**, 1549–1562 (2012).
16. G. Beaugrand, E. Goberville, C. Luczak, R. R. Kirby, Marine biological shifts and climate. *Proc. Biol. Sci.* **281**, 20133350–20133350 (2014).
17. K. Friedland, Marine survival of North American and European Atlantic salmon: Effects of growth and environment. *ICES J. Mar. Sci.* **50**, 481–492 (1993).
18. C. D. Todd, B. D. M. Whyte, J. C. MacLean, C. W. Revie, M. E. Lonergan, N. N. Hanson, A simple method of dating marine growth circuli on scales of wild one sea-winter and two sea-winter Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* **71**, 645–655 (2014).
19. E. B. Thorstad, D. Bliss, C. Breau, K. Damon-Randall, L. E. Sundt-Hansen, E. M. Hatfield, G. Horsburgh, H. Hansen, N. Ó. Maoiléidigh, T. Sheehan, Atlantic salmon in a rapidly changing environment—Facing the challenges of reduced marine survival and climate change. *Aquat. Conserv.* **31**, 2654–2665 (2021).
20. ICES, Working Group on North Atlantic Salmon (WGNAS). *ICES Scientific Reports* **3**, 29 (2021); https://doi.org/10.17895/ices.pub.7923.
21. C. Tréhin, E. Rivot, L. Lamireau, L. Meslier, A.-L. Besnard, S. D. Gregory, M. Nevoux, Growth during the first summer at sea modulates sex-specific maturation schedule in Atlantic salmon. *Can. J. Fish. Aquat. Sci.* **78**, 659–669 (2021).
22. J. F. Strøm, E. B. Thorstad, A. H. Rikardsen, Thermal habitat of adult Atlantic salmon *Salmo salar* in a warming ocean. *J. Fish Biol.* **96**, 327–336 (2019).
23. G. L. Lacroix, Population-specific ranges of oceanic migration for adult Atlantic salmon (*Salmo salar*) documented using pop-up satellite archival tags. *Can. J. Fish. Aquat. Sci.* **70**, 1011–1030 (2013).
24. K. B. Oke, C. J. Cunningham, P. A. H. Westley, M. L. Baskett, S. M. Carlson, J. Clark, A. P. Hendry, V. A. Karatayev, N. W. Kendall, J. Kibele, H. K. Kindsvater, K. M. Kobayashi, B. Lewis, S. Munch, J. D. Reynolds, G. K. Vick, E. P. Palkovacs, Recent declines in salmon body size impact ecosystems and fisheries. *Nat. Commun.* **11**, 4155–4155 (2020).
25. T. D. Clark, M. R. Donaldson, S. Pieperhoff, S. M. Drenner, A. Lotto, S. J. Cooke, S. G. Hinch, D. A. Patterson, A. P. Farrell, Physiological benefits of being small in a changing world: Responses of Coho salmon (*Oncorhynchus kisutch*) to an acute thermal challenge and a simulated capture event. *PLOS ONE* **7**, e39079 (2012).
26. J. M. Elliott, J. A. Elliott, Temperature requirements of Atlantic salmon Salmo salar, brown trout *Salmo trutta* and Arctic charr *Salvelinus alpinus*: Predicting the effects of climate change. *J. Fish Biol.* **77**, 1793–1817 (2010).
27. S. O. Handeland, A. K. Imsland, S. O. Stefansson, The effect of temperature and fish size on growth, feed intake, food conversion efficiency and stomach evacuation rate of Atlantic salmon post-smolts. *Aquaculture* **283**, 36–42 (2008).
28. A. H. Olafsdottir, A. Slotte, J. A. Jacobsen, G. J. Oskarsson, K. R. Utne, L. Nøttestad, Changes in weight-at-length and size-at-age of mature Northeast Atlantic mackerel (*Scomber scombrus*) from 1984 to 2013: Effects of mackerel stock size and herring (*Clupea harengus*) stock size. *ICES J. Mar. Sci.* **73**, 1255–1265 (2015).
29. L. Nøttestad, K. R. Utne, G. J. Óskarsson, S. Þ. Jónsson, J. A. Jacobsen, Ø. Tangen, V. Anthonypillai, S. Aanes, J. H. Vølstad, M. Bernasconi, H. Debes, L. Smith, S. Sveinbjörnsson, J. C. Holst, T. Jansen, A. Slotte, Quantifying changes in abundance, biomass, and spatial distribution of Northeast Atlantic mackerel (*Scomber scombrus*) in the Nordic seas from 2007 to 2014. *ICES J. Mar. Sci.* **73**, 359–373 (2015).
30. K. R. Utne, K. Thomas, J. A. Jacobsen, J. Fall, N. Ó. Maoiléidigh, C. T. Broms, W. Melle, Feeding interactions between Atlantic salmon (*Salmo salar*) postsmolts and other planktivorous fish in the Northeast Atlantic. *Can. J. Fish. Aquat. Sci.* **78**, 255–268 (2021).
31. M. Haugland, J. C. Holst, M. Holm, L. P. Hansen, Feeding of Atlantic salmon (*Salmo salar* L.) post-smolts in the Northeast Atlantic. *ICES J. Mar. Sci.* **63**, 1488–1500 (2006).
32. K. R. Utne, B. D. Pauli, M. Haugland, J. A. Jacobsen, N. Maoileidigh, W. Melle, C. T. Broms, L. Nøttestad, M. Holm, K. Thomas, Poor feeding opportunities and reduced condition factor for salmon post-smolts in the Northeast Atlantic Ocean. *ICES J. Mar. Sci.* **78**, 2844–2857 (2021).
33. Å. Husebø, E. K. Stenevik, A. Slotte, E. Fossum, A. Salthaug, F. Vikebø, S. Aanes, A. Folkvord, Effects of hatching time on year-class strength in Norwegian spring-spawning herring (*Clupea harengus*). *ICES J. Mar. Sci.* **66**, 1710–1717 (2009).
34. R. Toresen, H. R. Skjoldal, F. Vikebø, M. B. Martinussen, Sudden change in long-term ocean climate fluctuations corresponds with ecosystem alterations and reduced recruitment in Norwegian spring-spawning herring (*Clupea harengus*, Clupeidae). *Fish Fish.* **20**, 686–696 (2019).
35. I. C. Russell, M. W. Aprahamian, J. Barry, I. C. Davidson, P. Fiske, A. T. Ibbotson, R. J. Kennedy, J. C. Maclean, A. Moore, J. Otero, T. Potter, C. D. Todd, The influence of the freshwater environment and the biological characteristics of Atlantic salmon smolts on their subsequent marine survival. *ICES J. Mar. Sci.* **69**, 1563–1573 (2012).
36. J. Pope, J. G. Shepherd, J. Webb, Successful surf-riding on size spectra: The secret of survival in the sea. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **343**, 41–49 (1994).
37. K. W. Vollset, R. I. Krontveit, P. A. Jansen, B. Finstad, B. T. Barlaup, O. T. Skilbrei, M. Krkošek, P. Romunstad, A. Aunsmo, A. J. Jensen, I. Dohoo, Impacts of parasites on marine survival of Atlantic salmon: A meta-analysis. *Fish Fish.* **17**, 714–730 (2016).
38. T. Forseth, B. T. Barlaup, B. Finstad, P. Fiske, H. Gjøsæter, M. Falkegård, A. Hindar, T. A. Mo, A. H. Rikardsen, E. B. Thorstad, L. A. Vøllestad, V. Wennevik, The major threats to Atlantic salmon in Norway. *ICES J. Mar. Sci.* **74**, 1496–1513 (2017).

39. S. Karlsson, O. H. Diserud, P. Fiske, K. Hindar, Widespread genetic introgression of escaped farmed Atlantic salmon in wild salmon populations. *ICES J. Mar. Sci.* **73**, 2488–2498 (2016).

40. K. W. Vollset, B. T. Barlaup, K. D. Friedland, Context-dependent impact of an ectoparasite on early marine growth in Atlantic salmon. *Aquaculture* **507**, 266–274 (2019).

41. I. A. Fleming, K. Hindar, I. B. Mjølnerød, B. Jonsson, T. Balstad, A. Lamberg, Lifetime success and interactions of farm salmon invading a native population. *Proc. Biol. Sci.* **267**, 1517–1523 (2000).

42. Ø. Skaala, F. Besnier, R. Borgstrøm, B. Barlaup, A. G. Sørvik, E. Normann, B. I. Østebø, M. M. Hansen, K. A. Glover, An extensive common-garden study with domesticated and wild Atlantic salmon in the wild reveals impact on smolt production and shifts in fitness traits. *Evol. Appl.* **12**, 1001–1016 (2019).

43. G. H. Bolstad, K. Hindar, G. Robertsen, B. Jonsson, H. Sægrov, O. H. Diserud, P. Fiske, A. J. Jensen, K. Urdal, T. F. Næsje, B. T. Barlaup, B. Florø-Larsen, B. Lo, E. Niemelä, S. Karlsson, Gene flow from domesticated escapes alters the life history of wild Atlantic salmon. *Nat. Ecol. Evol.* **1**, 0124 (2017).

44. H. J. R. Lenders, T. P. M. Chamuleau, A. J. Hendriks, R. C. G. M. Lauwerier, R. S. E. W. Leuven, W. C. E. P. Verberk, Historical rise of waterpower initiated the collapse of salmon stocks. *Sci. Rep.* **6**, 29269–29269 (2016).

45. K. D. Friedland, B. V. Shank, C. D. Todd, P. McGinnity, J. A. Nye, Differential response of continental stock complexes of Atlantic salmon (*Salmo salar*) to the Atlantic multidecadal oscillation. *J. Mar. Syst.* **133**, 77–87 (2014).

46. M. Olmos, M. R. Payne, M. Nevoux, E. Prévost, G. Chaput, H. Du Pontavice, J. Guitton, T. Sheehan, K. Mills, E. Rivot, Spatial synchrony in the response of a long range migratory species (*Salmo salar*) to climate change in the North Atlantic Ocean. *Glob. Chang. Biol.* **26**, 1319–1337 (2020).

47. E. C. E. Potter, W. W. Crozier, P.-J. Schön, M. D. Nicholson, D. L. Maxwell, E. Prévost, J. Erkinaro, G. Gudbergsson, L. Karlsson, L. P. Hansen, J. C. MacLean, N. Ó. Maoiléidigh, S. Prusov, Estimating and forecasting pre-fishery abundance of Atlantic salmon (*Salmo salar* L.) in the Northeast Atlantic for the management of mixed-stock fisheries. *ICES J. Mar. Sci.* **61**, 1359–1369 (2004).

48. J. Otero, J. H. L'Abée-Lund, T. Castro-Santos, K. Leonardsson, G. O. Storvik, B. Jonsson, B. Dempson, I. C. Russell, A. J. Jensen, J.-L. Baglinière, M. Dionne, J. D. Armstrong, A. Romakkaniemi, B. H. Letcher, J. F. Kocik, J. Erkinaro, R. Poole, G. Rogan, H. Lundqvist, J. C. MacLean, E. Jokikokko, J. V. Arnekleiv, R. J. Kennedy, E. Niemelä, P. Caballero, P. A. Music, T. Antonsson, S. Gudjonsson, A. E. Veselov, A. Lamberg, S. Groom, B. H. Taylor, M. Taberner, M. Dillane, F. Arnason, G. Horton, N. A. Hvidsten, I. R. Jonsson, N. Jonsson, S. McKelvey, T. F. Naesje, Ø. Skaala, G. W. Smith, H. Saegrov, N. C. Stenseth, L. A. Vøllestad, Basin-scale phenology and effects of climate variability on global timing of initial seaward migration of Atlantic salmon (*Salmo salar*). *Glob. Chang. Biol.* **20**, 61–75 (2013).

49. K. A. Mork, J. Gilbey, L. P. Hansen, A. J. Jensen, J. A. Jacobsen, M. Holm, J. C. Holst, N. Ó. Maoiléidigh, F. Vikebø, P. McGinnity, W. Melle, K. Thomas, E. Verspoor, V. Wennevik, Modelling the migration of post-smolt Atlantic salmon (*Salmo salar*) in the Northeast Atlantic. *ICES J. Mar. Sci.* **69**, 1616–1624 (2012).

50. ICES, Working Group on the Integrated Assessments of the Norwegian Sea (WGINOR; outputs from 2019 meeting). *ICES Scientific Reports* **2**, 29 (2020); http://doi.org/10.17895/ices.pub.5996. 46 pp.

51. W. Melle, B. Ellertsen, H. R. Skjoldal, Zooplankton: The link to higher trophic levels, in *The Norwegian Sea Ecosystem*, H. R. Skjoldal, Ed. (Tapir Academic Press, 2004), pp. 137–202.

52. A. H. Rikardsen, M. Haugland, P. A. Bjørn, B. Finstad, R. Knudsen, J. B. Dempson, J. C. Holst, N. A. Hvidsten, M. Holm, Geographical differences in marine feeding of Atlantic salmon post-smolts in Norwegian fjords. *J. Fish Biol.* **64**, 1655–1679 (2004).

53. ICES, Report of the Herring Assessment Working Group for the Area South of 62°N (HAWG). 29-31 January 2018 and 12-20 March 2018. ICES HQ, Copenhagen, Denmark. ICES CM 2018/ACOM:07 (ICES,2018); 960 pp.

54. ICES, Report of the Working Group on Widely Distributed Stocks (WGWIDE), 28 August-3 September 2018, Torshavn, Faroe Islands. ICES CM 2018/ACOM:23 (2018); 488 pp.

55. K. W. Vollset, R. J. Lennox, A. Lamberg, Ø. Skaala, A. D. Sandvik, H. Sægrov, E. Kvingedal, T. Kristensen, A. J. Jensen, T. Haraldstad, B. T. Barlaup, O. Ugedal, Predicting the nationwide outmigration timing of Atlantic salmon (*Salmo salar*) smolts along 12 degrees of latitude in Norway. *Divers. Distrib.* **27**, 1383–1392 (2021).

56. D. Bates, M. Mächler, B. Bolker, S. Walker, Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48 (2015).

57. R. Killick, C. Beaulieu, S. Taylor, H. Hullait, EnvCpt: Detection of Structural Changes in Climate and Environment Time Series, R package version 0.1. 1 (2016).

58. H. Wickham, W. Chang, M. H. Wickham, Package "ggplot2." Create Elegant Data Visualisations Using the Grammar of Graphics Version, 2 (1), pp. 1–189 (2016).