




Original Article

Poor feeding opportunities and reduced condition factor for salmon post-smolts in the Northeast Atlantic Ocean

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During the last few decades, many wild Atlantic salmon populations have declined dramatically. One possible contributing factor for the decline is reduced prey availability at sea. Here, we examine post-smolt diet and investigate if post-smolts show signs of selective feeding based on 2546 post-smolts sampled from west of Ireland to the northern Norwegian Sea over a 25-year period. We also test for changes over time in stomach fullness, diet, condition factor and body length. There was a clear reduction in condition factor for post-smolts sampled in the Norwegian Sea in the period 2003–2012. The post-smolt stomach fullness was also reduced in the same period. The reduction in condition factor is partly explained by reduced stomach fullness, including a reduction of highly energetic fish larvae and Amphipoda in the diet. Feeding on other prey, such as meso-zooplankton and insects, cannot substitute the high-quality fish larvae and Amphipoda in the post-smolt diet. This is the first study to document how salmon post-smolts feeding in the Norwegian Sea are affected by reduced feeding conditions. Possible causes for the observed changes in post-smolt feeding are ocean warming, decreased primary productivity, and reduced recruitment of important fish larvae.

Keywords: amphipoda, climate change, fish larvae, mackerel, Norwegian Sea

Introduction

Ecosystem change has accelerated in recent decades, in part due to anthropogenic impacts, many related to climate change and over-exploitation, and this can be a threat to species diversity and abundance (Sala *et al.* 2000, Thomas *et al.* 2004). Adapting to changing environmental conditions is an integral part of the evolutionary history of most marine species (Crozier and Hutchings 2014). However, the unprecedented rates of change expected due to present climate change compromise the potential for adaptive adjustment, increase maladaptation, and are likely to reduce the abundance of

many species and increase species extinctions (Sala *et al.* 2000). Understanding the nature and extent of impacts of ecosystem change on species can help to identify the potential for mitigative actions and counter potential threats.

During the past few decades, many wild Atlantic salmon populations have declined dramatically (Parrish *et al.* 1998; ICES 2019). In the same period, salmon from many populations, especially from southern and central Europe, have shown reduced individual growth during the marine phase concurring with a lower survival at sea (e.g. Friedland *et al.* 2000; Jonsson and Jonsson 2004; Todd *et al.* 2008; Jonsson *et al.* 2016). One possible explanation for the

trends is reduced prey availability in the sea. Several studies have shown that the reduced number of Atlantic salmon returning from the sea to natal rivers is correlated to large-scale changes in the marine environment, such as increased water temperature or decreased abundance of phytoplankton or herbivorous zooplankton (Beaugrand and Reid 2012; Todd *et al.* 2012; Jonsson *et al.* 2016; Almodóvar *et al.* 2019; Olmos *et al.* 2020). Although there is strong evidence for an effect of water temperature or plankton abundance on salmon growth and survival, the direct mechanisms are not fully understood.

A major challenge for understanding marine growth and survival of salmon is the lack of samples from the high seas where salmon spend most of their adult lives, since most studies addressing these issues rely on aggregated indices from adult returns to rivers or coastal fisheries. In general, the limited number of salmon sampled at sea restricts our understanding of processes with temporal or spatial variability in the important marine habitat that directly affect salmon. There is limited knowledge on which prey items are preferred by post-smolts in the Northeast Atlantic to ensure rapid growth, and on the interannual variation and trends in abundance of these prey species. Furthermore, many populations in the Northeast Atlantic have experienced reduced individual body size of fish returning to the rivers (e.g. Friedland *et al.* 2000; Todd *et al.* 2008), but spatial and temporal variability in individual growth and energy allocation during the ocean phase are largely unknown. This means that it is unclear whether the reduced growth is due to changes in coastal waters during the spring, in the Norwegian Sea during the summer, at the winter-feeding areas, or a combination.

In the first period after leaving the river, salmon smolts feed mainly on terrestrial insects and marine invertebrates, but start to include fish larvae in the diet when migrating through fjords or along coastal areas (Sturlaugsson and Thorisson 1995; Rikardsen *et al.* 2004; Hvidsten *et al.* 2009). Post-smolts migrating in coastal areas tend to specialize on few key items and ignore other available prey species (Andreassen *et al.* 2001). They migrate rapidly into the open ocean (Thorstad *et al.* 2004). The migration routes of salmon at sea are not known in detail, but post-smolts in the Northeast Atlantic migrate to a large extent into the eastern and central Norwegian Sea during their first summer at sea (Holm *et al.* 2000; Mork *et al.* 2012). Here, the post-smolts feed on a combination of invertebrates and fish larvae (Haugland *et al.* 2006). As the fish grow bigger the diet turns increasingly piscivorous (Jacobsen and Hansen 2001; Salminen *et al.* 2001; Rikardsen and Dempson 2011). Encountering sufficient prey of correct size and quality is of crucial importance for post-smolts, as sufficient prey will enable them to grow out of the size window for many predators to increase their chance of survival (Thorstad *et al.* 2012). There is spatial and temporal variation in marine feeding conditions (e.g. Dixon *et al.* 2017; Dixon *et al.* 2019). Analyses of interannual changes in prey availability indicate a positive correlation between abundance of fish larvae and the proportion of fish larvae in the diet for salmon both in the Baltic and the Norwegian Sea (Salminen *et al.* 2001; Haugland *et al.* 2006). The availability of fish larvae seems to be important for post-smolt growth (Rikardsen and Dempson 2011), but most data to support this conclusion come from diet investigations in the fjord phase of post-smolt migration.

Here we used previously published post-smolt stomach content data (Haugland *et al.* 2006; Utne *et al.* 2021), as well as new data to explore if changes in diet and stomach fullness at the marine feeding grounds can explain variation in post-smolt body length and condition factor over time. The analyses are based on post-smolts

sampled with pelagic trawls in the Northeast Atlantic during spring and summer from 1995 to 2019. This dataset comprises an extensive number of stomach ($n = 2546$) from post-smolts sampled over three decades in their main feeding areas during the summer. The first objective of this study is to describe the general post-smolt diet and investigate whether post-smolt show signs of selective feeding. The second objective is to test for changes in stomach fullness, diet, condition factor and body length for post-smolts sampled over a 25-year period in the Northeast Atlantic.

Material and methods

Post-smolt sampling

The dataset available for analysis includes salmon post-smolts sampled during 40 different scientific surveys in the Northeast Atlantic (Figure 1, Supplementary data S1). This includes seven surveys northwest of Ireland and the UK and 33 surveys in the Norwegian Sea. All analyses were carried out by splitting the data geographically into the Norwegian Sea and north and west of Ireland (hereby referred to as “off Ireland”). The Norwegian Sea is here defined as north of 60°N and west of 17°E and all sampling took place between June 15th and August 19th. No western or northern boundary was defined as the northernmost fish were caught at 76° 16' N and the westernmost at 07° 50' W, which is within the Norwegian Sea. The area off Ireland is defined as south of 63°N and east of 0°E and sampling took place between May 11th and June 15th. The aim of the surveys varied from dedicated sampling of salmon, mapping salmon geographic distribution, and ecosystem surveys targeting other pelagic species, but during which post-smolts were caught as bycatch. All post-smolts were sampled using either a dedicated salmon trawl or another similar trawl towed at the surface with a speed of 3–5 knots (5.6–9.3 km h⁻¹). A total of two large floats attached to each side and a float in the center kept the trawl at the surface during towing. Details about the trawl hauls and biological sampling in the years 1995–2009 are given by Holm *et al.* (2000), Haugland *et al.* (2006), and Utne *et al.* (2021). From 2012 and onwards, post-smolts were sampled during the International Ecosystem Summer Survey in the Nordic Seas (IESSNS), where a standardized pelagic swept area trawl method was used aiming to provide an annual abundance index and the geographical distribution of mackerel (*Scomber scombrus*; Nøttestad *et al.* 2016). The IESSNS trawl hauls were at the surface at predetermined locations, normally with 45–70 nmi (83 340–129 640 m) distance between trawl hauls. These surveys cover the entire Norwegian Sea. The trawls are designed to catch pelagic fish such as salmon, herring, blue whiting, and mackerel. The three latter species are normally less than 1 kg. The trawls have meshes of several meters by the opening and these are gradually reduced towards the codend, which is normally 20 or 32 mm. Thus, the sampling should cover the full size-range of post-smolts, including the largest post-molt. Salmon larger than 35 cm before August and larger than 40 cm in August (Jacobsen *et al.* 2001) were excluded from further analyses to ensure that the dataset only included post-smolts. For the analyses, we assume that post-smolts of different body sizes had similar catchability by the trawl, although there is not enough data available to confirm this claim.

Handling of post-smolt samples

Once the fish were on deck, they were weighted to the nearest gram and the total length was measured with a 5 mm resolution. Fulton's

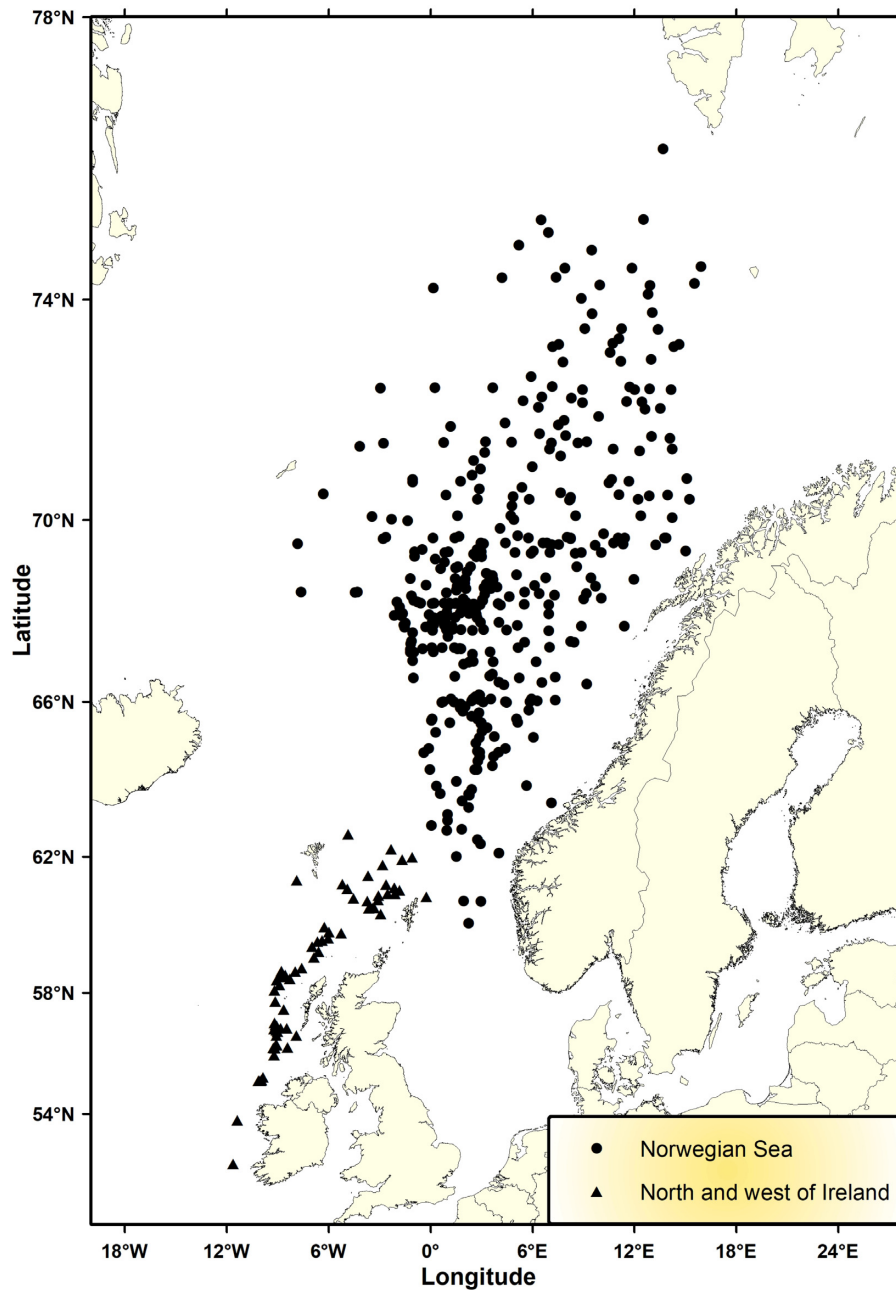


Figure 1. The geographic distribution of the total sample of post-smolts analysed from this study ($n = 2393$). Each symbol represents a location where post-smolts were sampled, but the number of individuals within each location vary from one to tens of post-smolts.

condition factor (CF) was calculated for all sampled fish, following equation 1:

$$CF = 100 (w/l^3), \tag{1}$$

where w is the body weight (excluding the weight of the stomach content) in grams and l is the length in cm. Fulton’s condition factor is not a suitable index for fish with allometric growth. Initial analyses of the length–weight relationship were performed to ensure that the assumption of isometric growth holds true for the post-smolts presented in this manuscript (see Supplementary Figures S1 and S2).

The stomachs were removed from the sampled fish on deck and frozen. Stomachs were sampled from all 2546 post-smolts collected over 19 years presented in this work. The stomach content was identified to species level when possible, or to closest family if too digested for species identification. The weight of all unique prey groups in each stomach was recorded for all samples, except for the stomachs from two surveys in the Norwegian Sea in 2008 and 2009. For these samples, the weight of the different prey groups was estimated from total stomach content weight and the median weight of prey from other samples (see Utne *et al.* 2021 for more information). Prey species and groups from each stomach were dried separately at 70°C for more than 24 h, and the dry weight was recorded.

The feeding ratio (FR) is an estimate of the wet weight of the stomach content relative to the fish weight (without stomach content). It is a snapshot of the stomach content at the time of sampling. The feeding ratio was calculated following equation 2:

$$FR = 100 m_s / (m_f - m_s), \quad (2)$$

where m_f is the mass (g) of the post-smolt and m_s is the mass (g) of the stomach content. In addition prey-group specific FR values were calculated, where FR_{fish} , FR_{amf} , FR_{eup} , and FR_{oth} are equivalent to FR where m_s is the mass of only fish, Amphipoda, Euphausiidae, and other prey (Copepoda, insects and various types of mesozooplankton), respectively. FR_{zoo} is the sum of FR_{amf} , FR_{eup} , and FR_{oth} .

For both data sets, i.e. from the Norwegian Sea and off Ireland, stomach samples from all years was combined to calculate the diet composition split into the main prey species or groups. A two-step clustering approach was applied to calculate the average diet for all years combined. The calculations follow the approach described in Buckel *et al.* (1999) but is extended to also include average stomach content weight (\bar{w}) for each trawl station. The mean proportional contribution of a prey type by weight (w_k) was calculated by

$$w_k = \frac{\sum_{i=1}^n \bar{w}_i m_i q_{ik}}{\sum \bar{w}_i m_i}, \quad (3)$$

where m is the number of sampled post-smolts and \bar{w} is the average weight of the stomach content of the sampled fish at trawl haul i . q_{ik} was calculated by

$$q_{ik} = \frac{w_{ik}}{w_i}, \quad (4)$$

where w is the total weight of the stomach content and w_k is the weight of prey type k in the sample. The following prey groups were included in the main analyses; Ammodytidae, Amphipoda., *Anomalocera patersoni*, *Clupea harengus*, Copepoda, Euphausiidae, Gadidae, *Sebastes spp.*, Teleostei unspecified, "other fish", and "other invertebrates." The consumed fish were either larvae or 0-group. The group "other invertebrates" consist of a range of different species of zooplankton and insects, each with a minor contribution to the total biomass of consumed prey. The post-smolt stomach content from 1995 to 2003 and 2008 to 2009 has previously been published per year or month (Haugland *et al.* 2006; Utne *et al.* 2021), and is here combined with stomach samples from the years 2012–2019 to give an overview of the post-smolt diet by smoothing out interannual variation to give an understanding of the general diet before examining for changes over years.

Statistical analyses

Differences in diet associated with feeding ratio

The diet of post-smolts with the 25% highest feeding ratio was compared to the diet of post-smolt in the group with the 25% lowest FR, for both regions. The threshold at 25% is somewhat arbitrary, but preliminary analyses revealed that the results were not sensitive to threshold level, as a threshold of 50% resulted in the same significant relationships. The species identified in the diet were aggregated into five main prey groups: Amphipoda, Euphausiidae, Copepoda, fish larvae, and "others." Differences in the proportion of post-smolts consuming the five different prey groups were tested with Chi-square tests. In addition, the post-smolts were split into two groups based on whether fish larvae were present or not in the stomachs. The objective was to test if stomach fullness was associ-

ated with feeding on fish larvae, and further, if feeding on fish larvae was associated with reduced feeding on zooplankton. Generalized Linear models (GLMs) were applied to test for difference in feeding ratio between the two groups.

$$FR_x = \alpha + \beta * fish_i + \varepsilon. \quad (5)$$

The response variable FR_x was either FR and FR_{zoo} , α is the model intercept, β is a linear coefficient, $fish$ is either 0 or 1 depending on whether fish larvae were present in the stomach for post-smolts number i and ε is a normal distributed random term. The model was run separately with data from the Norwegian Sea and off Ireland. As the distributions of FR-values were highly skewed, a gamma distribution with "log-link" was applied for the response variables.

Temporal trends in post-smolts body length, condition factor, and diet

The annual average body length, condition factor, and feeding ratio with corresponding standard deviations were calculated to illustrate large-scale temporal trends in these parameters. The temporal development in diet composition, broken down by proportion of fish larvae, Amphipoda, Euphausiidae, and other prey, were also illustrated.

Generalized additive models (GAM) were used to investigate the multivariate relationship between post-smolts feeding and individual size (Hastie and Tibshirani, 1990). The main objective of using these models was to examine if there were temporal changes in post-smolts size and feeding ratio, and whether any feeding indices (FR , FR_{fish} , FR_{amf} , FR_{eup} , and FR_{other}) are associated with post-smolt condition factor or body length. Feeding ratio and the other indices are correlated and cannot be included in a model simultaneously. There was a strong correlation ($r_p = 0.79$, $p < 0.001$) between latitude and day of sampling for data from the Norwegian Sea, caused by post-smolts migrating northwards during the summer (Haugland *et al.*, 2006). The models could therefore not include both variables simultaneously, and only latitude was used. This accounted for both temporal and geographical potential sampling bias. From 2012 and onwards, all samples were collected in July and early August. To minimize errors due to uneven sampling design, samples in June (before 2012) in the Norwegian Sea were removed from the dataset before running the GAM. The following model was run for condition factor:

$$CF_i = \alpha + \beta * FR_{xi} + s(lat_i, lon_i) + s_s(year_i) + \varepsilon_i, \quad (6)$$

where α is the intercept term, FR_x is one of the FR indices (FR , FR_{fish} , FR_{amf} , FR_{oth} , and FR_{eup}) with linear coefficient β for fish number i , ε is a normal distributed error term, s_1 is a two-dimension smoothing term used for latitude and longitude and s_2 is a one-dimensional smoothing term used for year. An identical model approach was run for body length for the data from the Norwegian Sea. Similar models for condition factor and body length as for the Norwegian Sea were applied for data sampled off Ireland. Year was added as a random effect for the region off Ireland as interannual variation in survey design and few years of sampling made the data unsuited for disentangling temporal and spatial effects in this region. In the model for the Norwegian Sea, the number of knots in the model was restricted to five for the one-dimensional smoothing term to avoid overfitting of the smoother. A 12 cm post-smolt off Ireland with $FR > 8$ was identified as an outlier and removed from

the dataset as this datapoint had too much leverage on the model fit.

For the feeding indices, the following model was run to estimate temporal changes while taking into account geographic variation (and its correlated temporal variation):

$$FR_x = a + s(lat_i, lon_i) + s_s(year_i) + \varepsilon_i, \quad (7)$$

where FR_x is either FR , FR_{fish} , or FR_{zoo} , and the remaining terms are as given by equation (4). The feeding indices are zero-inflated and overdispersed and a two-step hurdle model was therefore applied in the model for these indices. A hurdle model was applied instead of other alternative zero-inflated models because there can be different mechanisms regulating which prey items are preyed upon and the quantity consumed (Zuur and Ieno 2016). The model consists of a binomial model for the probability of presence of prey in the stomach and a gamma model for the conditional part. For the binomial model a logit-link was applied, while for the gamma model a log-link was applied as the distribution of FR -values is skewed with occasional high values. The number of one-dimensional knots was restricted to five.

GAMs were fitted in the R library “mgcv” (Wood 2011), and the approximate p -values from the summary-function and the shape of the smooth functions were used to evaluate the effect of the covariates. The data were inspected for outliers, normality, collinearity, and independence prior to modelling. The parsimony principle was used to select the best model from all possible combinations of explanatory variables by selecting the model with the lowest Akaike Information Criterion (AIC) (Burnham and Anderson, 2002). All statistical analyses were carried out using R software (version 3.6.3; R Core Team, 2020). All figures and maps were produced with the package ggplot2 (Wickham 2016). All model assumptions were assessed for homoscedasticity and normally distributed errors visually using Q–Q plots and residual variation vs. fitted values and leverage. Spatial autocorrelation can cause an underestimation of confidence intervals and was therefore visually evaluated by plotting the model residuals on a map. If there were indications of spatial patterns in the residuals, a wild bootstrapping was performed on the model. This involves randomly switching sign of all scaled model residuals. The new residuals are added to the model predictions to fit a new GAM. The operation was repeated 1000 times to estimate mean and confidence intervals for each covariate response. For a further explanation of the bootstrap approach, see Fall *et al.* (2018) and references therein.

Results

Key prey species for post-smolts

Stomachs were sampled from post-smolts caught in the Norwegian Sea from late June to mid-August in 1995–2003, 2008, 2009, 2012–2016, 2018, and 2019 ($n = 2081$; Figure 2a). The post-smolts had an average size varying from 15.2 to 36.0 cm and 95 to 333 g (Supplementary data S1). The diet consisted of 57.3% fish larvae by weight. A large proportion of these fish larvae were not identified to species level, but *Clupea harengus*, *Gadidae*, *Sebastes spp.*, and *Ammodytidae* larvae were part of the diet (Figure 2b). Amphipoda and Euphausiidae were also important and made up 37.0% of the diet by weight. The remaining 5.7% of the diet by weight consisted of Copepoda and other zooplankton species. Terrestrial insects were also occasionally consumed by post-smolts in the Norwegian Sea.

Stomachs were sampled from post-smolts caught off Ireland in May and June in 1995, 1996, 1997, 2004, 2008, and 2009 ($n = 463$; Figure 2c). The post-smolts had an average weight of 54–85 g and were 17.3–21.1 cm long (Supplementary data S1). Fish larvae made up total 60.6% of the diet by weight. The most common fish larvae were *Ammodytidae* and *Gadidae*, constituting 24.7% and 13.4% of the diet, respectively (Figure 2d). *Clupea harengus* and *Sebastes spp.* larvae were also consumed by post-smolts in this region. Zooplankton made up the remaining part of the diet, with the largest groups being “other invertebrates” with 17.0% and *Anomalo-cera patersoni* with 11.6%. “Other invertebrates” constituted a wide range of different species, all of lower importance for the post-smolt diet in this region.

Diet associated with feeding ratio and high and low condition factor

In the Norwegian Sea, post-smolts with high feeding ratio (25% highest percentile) consumed more fish larvae and Amphipoda, and less Copepoda and “others” relative to post-smolt with low feeding ratio (25% lowest) (Figure 3a and b; Table 1). The consumption of Euphausiidae was similar in both groups.

Post-smolts consuming fish larvae had an average feeding ratio of 1.01 ± 0.96 and 43% of these post-smolts had not consumed other prey than fish larvae. For post-smolts feeding on fish larvae the average FR_{zoo} was 0.20 ± 0.46 (0.36 ± 0.56 when excluding 0-values). Post-smolts not consuming fish larvae had an average FR_{zoo} of 0.59 ± 0.48 . Post-smolts that had consumed fish larvae had a higher FR (glm, $t = -9.805$, $p < 0.001$) but lower FR_{zoo} (glm, $t = 6.283$, $p < 0.001$) than those that had been consuming only zooplankton and other invertebrates.

Post-smolts off Ireland with the 25% highest feeding ratio had consumed more fish larvae and Euphausiidae and less “other prey” compared to post-smolts with the 25% lowest feeding ratio (Figure 3c and d; Table 1). Post-smolts consuming fish larvae had an average feeding ratio of 0.75 ± 0.89 , while the average FR_{zoo} was 0.07 ± 0.16 (0.11 ± 0.18 when excluding 0-values). Post-smolts that had not consumed fish larvae had an average FR_{zoo} of 0.13 ± 0.27 (Figure 3 e–h). Post-smolts that had consumed fish larvae had a higher FR than those that only had consumed zooplankton (glm, $t = -10.96$, $p < 0.001$), but there was not a significant difference when fish larvae were excluded from the stomach content (glm, $t = 0.457$, $p = 0.65$).

Temporal trends in post-smolts’ body length, condition factor, and diet

For post-smolts sampled in the Norwegian Sea, there was a temporal trend in the condition factor during the 25-year period (Figure 4a). The average condition factor in 1995 and 1996 was 1.03–1.07 increasing to 1.11–1.22 from 1997 to 2003. Then after some years with no sampling, the samples in 2008–2009 and 2013–2019 indicate a drop in the condition factor to the range 0.82–0.89 for the last seven years in the period. In 2012, the average condition factor was 1.03, but the low number of samples that year ($n = 14$) makes this measure sensitive to different factors, for instance spatial effects. A similar drop was not apparent for post-smolts body length (Figure 4b). The average body length of the post-smolts was within the range 21.5–26.5 cm for all years, except for in 1997. In this year, the samples were dominated by 30 post-smolts sampled in a single

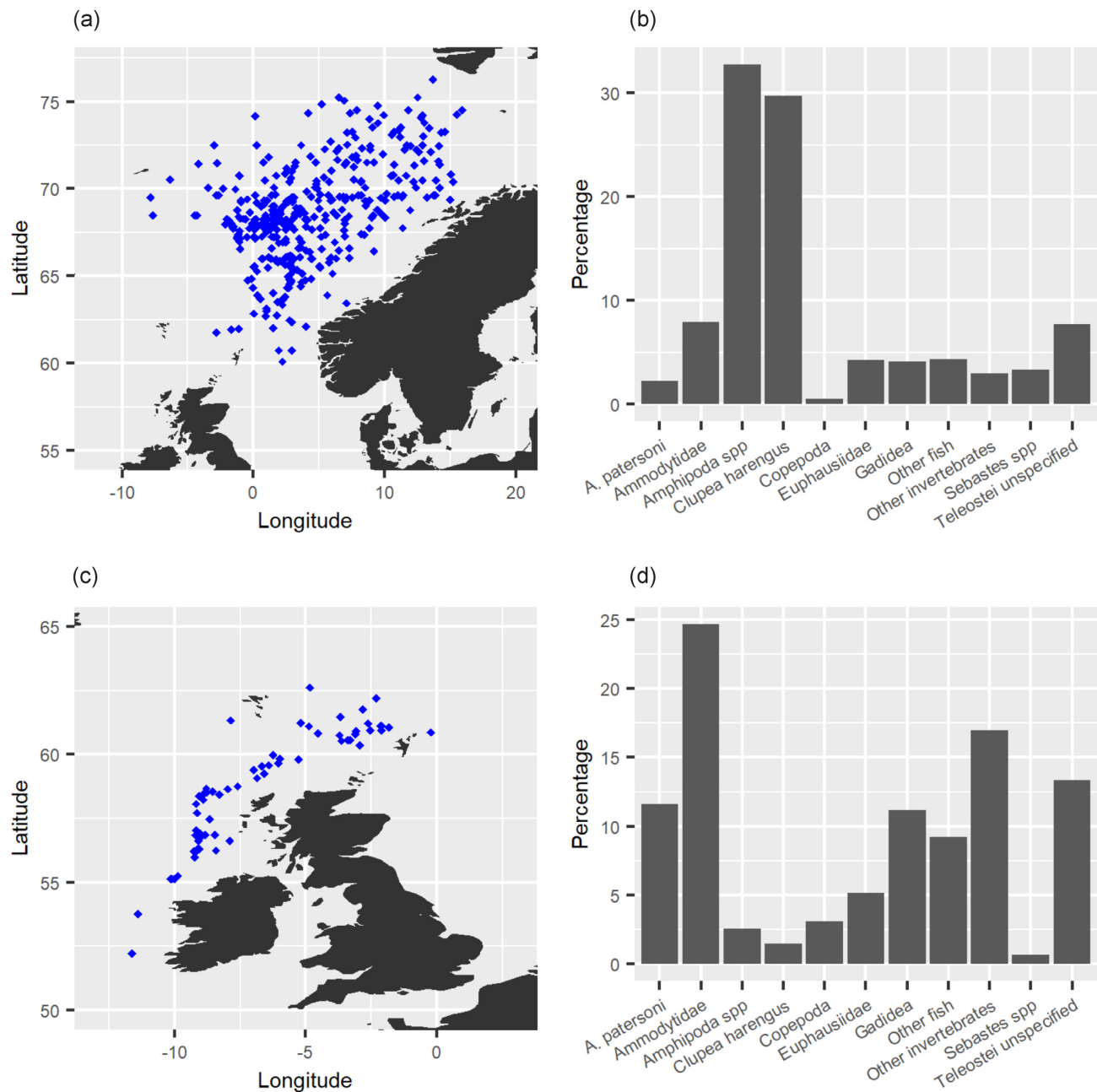


Figure 2. Map of sampling locations (blue circles) and histograms of stomach content by weight for post-smolts sampled in the Norwegian Sea (panel a and b) and off Ireland (panel c and d). Each circle represents at least one sampled post-smolt stomach at that location. See Supplementary Table S1 for more information about sampling periods.

trawl haul on 16th June. There was large variation in the average feeding ratio among years, with values varying from 0.25 to 1.35 (Figure 4c). The highest feeding ratio was recorded in 1997, 1998, and 2002, with annual average values of 1.28, 1.35, and 1.17 respectively. The lowest feeding ratios were observed in 2012, 2014, 2015, and 2016, with annual average values of 0.25–0.29. The relative proportion of fish larvae, Amphipoda, Euphausiidae, and “others” in the diet also varied among years. For fish larvae, the percentage varied from more than 90% in 1997, 1998, and 2002 to values around 30% and 20% in 2009 and 2019 (Figure 4d).

For post-smolts sampled off Ireland, the average condition factor was in the range 0.87–1.15, while the average body length was in

the range 16.7–21.1 cm (Figure 5a and b). The feeding ratio was between 0.52 and 0.83 during the first four years, before it dropped to 0.33 and 0.03 in 2008 and 2009 (Figure 5c), respectively. Most of the stomach content consisted of fish larvae in all years. The lowest proportion of fish larvae in the diet was observed in 2008, with 60% fish larvae (Figure 5d).

The results from the GAM for body length with geographic position (longitude and latitude) as covariate explained 39.3% of the variation in body length for post-smolts sampled in the Norwegian Sea (Table 2). There was no trend in body length over time as including year did not improve the model fit. Further, there was also no association between body length and any of the feeding indices.

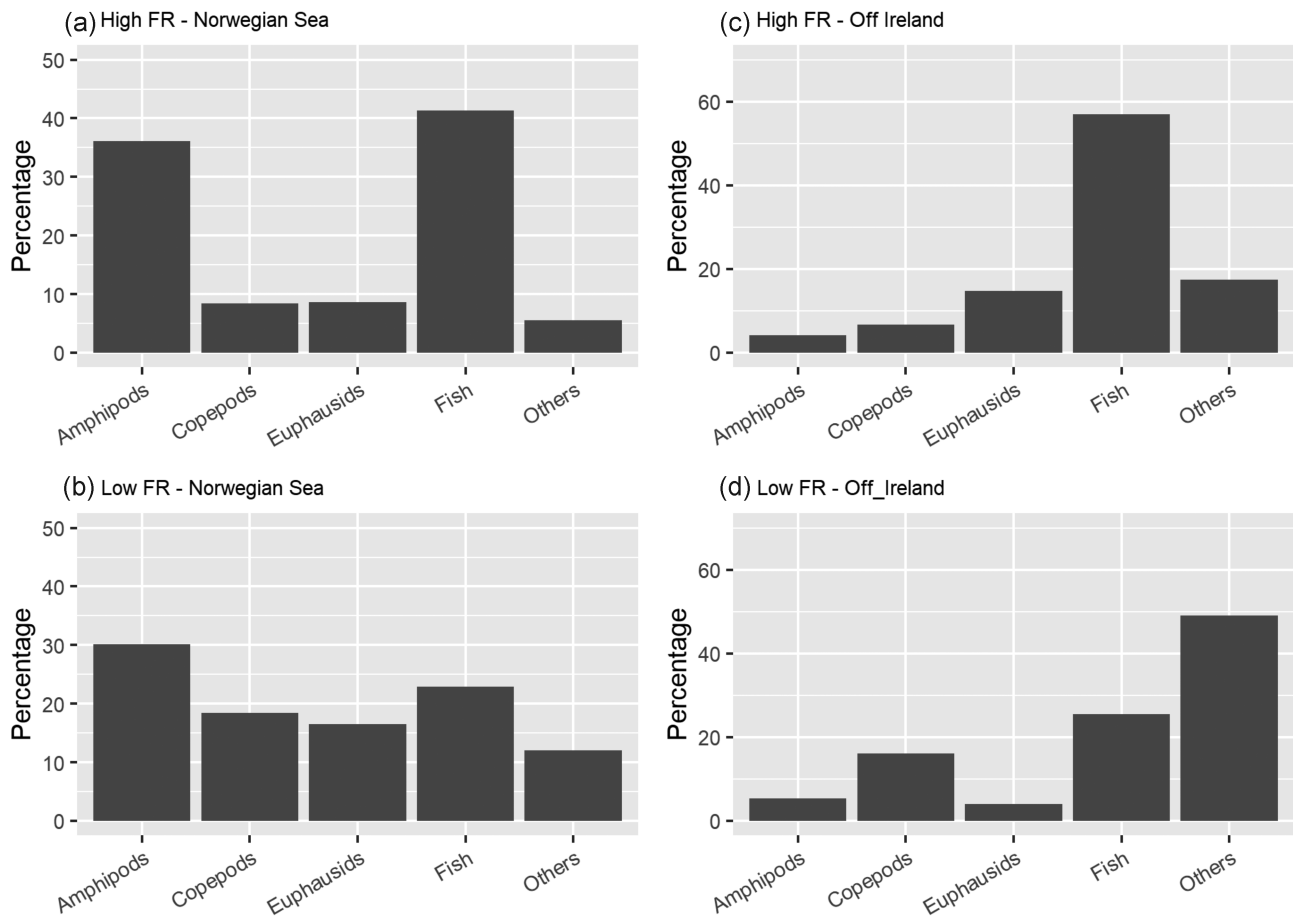


Figure 3. Diet composition (by weight) for post-smolts belonging to the group with the (a) 25% highest feeding ratio in the Norwegian Sea (b) 25% lowest feeding ratio in the Norwegian Sea, (c) 25% highest feeding ratio off Ireland, and (d) 25% lowest feeding ratio off Ireland.

Table 1. Summary statistics of chi-squared test of the proportion of individuals with different prey groups present in the stomach for post-smolts sampled in the Norwegian Sea and off Ireland. Text in front of test results (e.g. High FR>) indicates which group had a higher proportion of the given prey in the stomach content. The notation high FR is used for the group of post-smolts with 25% highest feeding ratio, and low FR for the group with 25% lowest feeding ratio. No text in front of the statistical test means there is no significant difference between the two groups.

	Norwegian Sea (d.f = 1, n = 946)	Ireland (d.f.=1, n = 208)
Fish	High FR>, $\chi^2 = 255.7, p < 0.001$	High FR>, $\chi^2 = 98.2, p < 0.001$
Amphipoda	High FR>, $\chi^2 = 9.0, p = 0.003$	$\chi^2 = 0.6, p < =0.44i>$
Euphausiidea	$\chi^2 = 0.9, p < =0.34i>$	High FR>, $\chi^2 = 18.2, p < 0.001$
Copepoda	Low FR>, $\chi^2 = 51.5, p < 0.001$	$\chi^2 = 3.1, p < =0.07i>$
Other	Low FR>, $\chi^2 = 4.9, p = 0.027$	Low FR>, $\chi^2 = 5.7, p = 0.017$

The best model for condition factor explained 63.7% of the variation for post-smolts in the Norwegian Sea (Table 2). Both geographic position (latitude and longitude) and year (Figure 6a) contributed to explain the observed variation for condition factor. In addition, the model fit for condition factor improved when including one of the feeding ratio indices FR, FR_{fish}, and FR_{amf} as covariate. The model explaining most of the observed variation in condition factor had both FR_{fish} and FR_{amf} included as covariates, although this model only gave a marginally better fit than the model including FR ($\Delta AIC < 1$). When FR was split into FR_{fish}, FR_{amf}, FR_{eup}, and FR_{oth}, only FR_{fish} and FR_{amf} had a significant effect, which was a positive linear association with the condition factor (Figure 6c and d).

In other words, post-smolt condition factor increased with higher stomach fullness in general. Feeding on fish larvae and Amphipoda was positively correlated to condition factor while feeding on Euphausiids and various other zooplankton and insects was not significantly associated with higher condition factor.

The generalized additive model for body length with geographic position (longitude and latitude) and year (as random effect) as covariates explained 33.5% of the variation for post-smolts off Ireland (Table 2). Including any of the feeding indices did not improve the model fit for body length.

The best model for condition factor explained 36.8% of the variation for post-smolts off Ireland (Table 2). Inclusion of either FR,

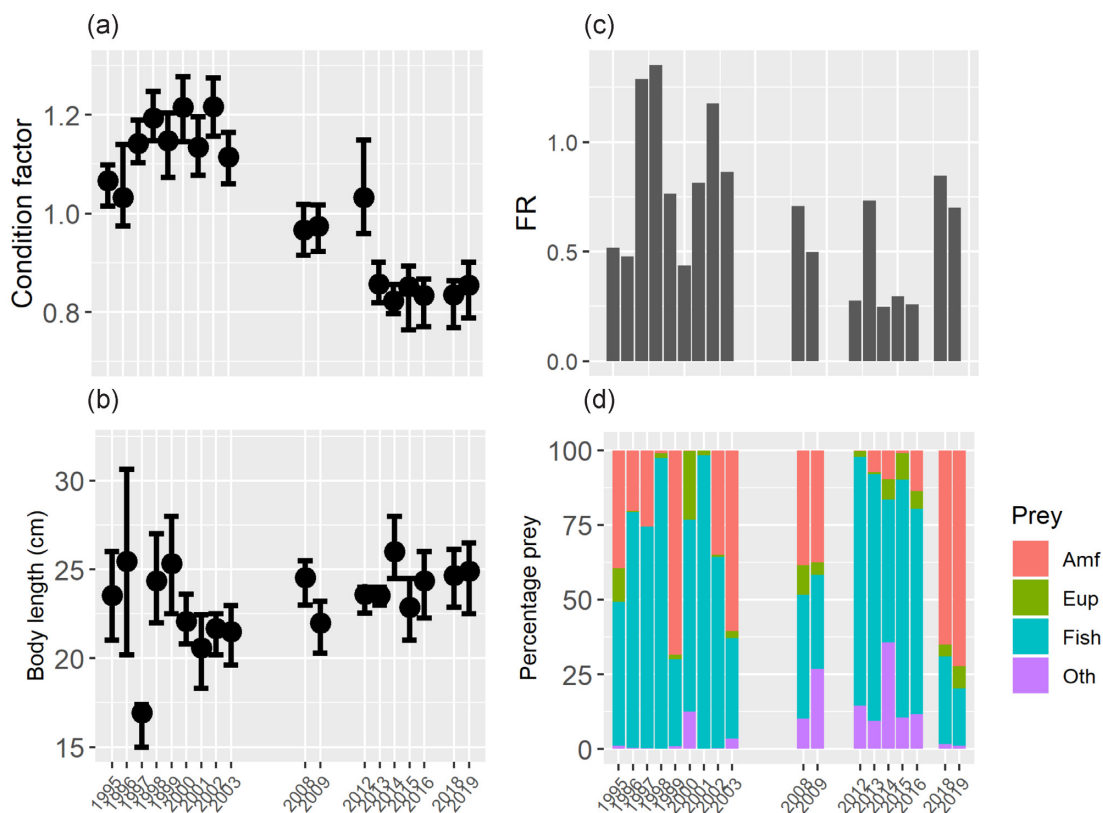


Figure 4. Temporal development for post-smolts sampled in the Norwegian Sea in late June, July and early August. (a) Condition factor, (b) body length (cm), (c) feeding ratio, and (d) annual average weight of prey groups in %.

FR_{amf} , FR_{eup} , or FR_{fish} as covariates improved the model fit while FR_{oth} did not have a significant effect. The best model fit was obtained by including FR_{fish} and FR_{amf} with positive relationships between condition factor and both feeding indices (Figure 6d and e). Hence, the condition factor for post-smolts sampled off Ireland is correlated with consumption of fish larvae and Amphipoda, although the latter was only consumed in small quantities and had a minor effect on the model fit. In addition, geographic position and year (as a random variable) were significant covariates in the model.

The results from the hurdle model showed there were temporal trends in post-smolts diet in the period 1995–2019. The gamma-model shows that feeding ratios increased in the period 1995 to 2001–2003 for post-smolts collected in the Norwegian Sea (Figure 7a). Thereafter, feeding ratios decreased until 2012 and remained low the following four years before increasing again in 2018 and 2019. Both FR_{fish} and FR_{zoo} showed an increasing pattern until 2001–2003, and thereafter decreased, but while FR_{fish} remained low after 2012, FR_{zoo} increased rapidly in 2018 and 2019 (Figure 7b and c). Plotting the model residuals for FR_{fish} revealed patterns of spatial autocorrelation. The mean effect and confidence intervals estimated with the wild bootstrapping approach were similar to those estimated by the original model and did therefore not alter the main results and conclusions.

In the binomial models for FR_{fish} and FR_{zoo} , geographic position (longitude and latitude) and year explained part of the variation in the probability of finding fish larvae or zooplankton in the post-smolts stomachs. The probability of finding zooplankton in

the stomach was lower when the probability of finding fish larvae in the stomach was high (Figure 7d).

Discussion

There was a reduction in condition factor for post-smolts in the Northeast Atlantic in the period 2003–2012. This pattern was clear for fish sampled in the Norwegian Sea, while it was not that obvious for the fish sampled off Ireland, probably due to limited data. The condition factor remained low the following years (2013–2019). The reduction is partly explained by lower post-smolt stomach fullness and reduced feeding on fish larvae and Amphipoda. This is the first study of post-smolts sampled at the marine feeding grounds in the Northeast Atlantic that documents a decadal trend in condition factor and how this is linked to feeding. The combination of low condition factor and low stomach fullness in the later part of the investigated period strongly indicates limited prey available for post-smolts during their first months at sea. There was a positive correlation between stomach fullness and post-smolt condition factor for fish sampled in the Norwegian Sea and off Ireland. It is unknown if the observed drop in condition factor, as seen in the Norwegian Sea, is also evident further south due to the lack of samples off Ireland in recent years. The tendency of reduced condition factor also west and north of Ireland in 2008 and 2009 (the last years with data in this region) suggests that the reduced feeding conditions also occurred in this area. A declining condition factor has also been shown for Scottish 1-seawinter salmon caught in or close to their natal rivers (Todd *et al.* 2008; Bacon *et al.* 2009). Although the observed decline

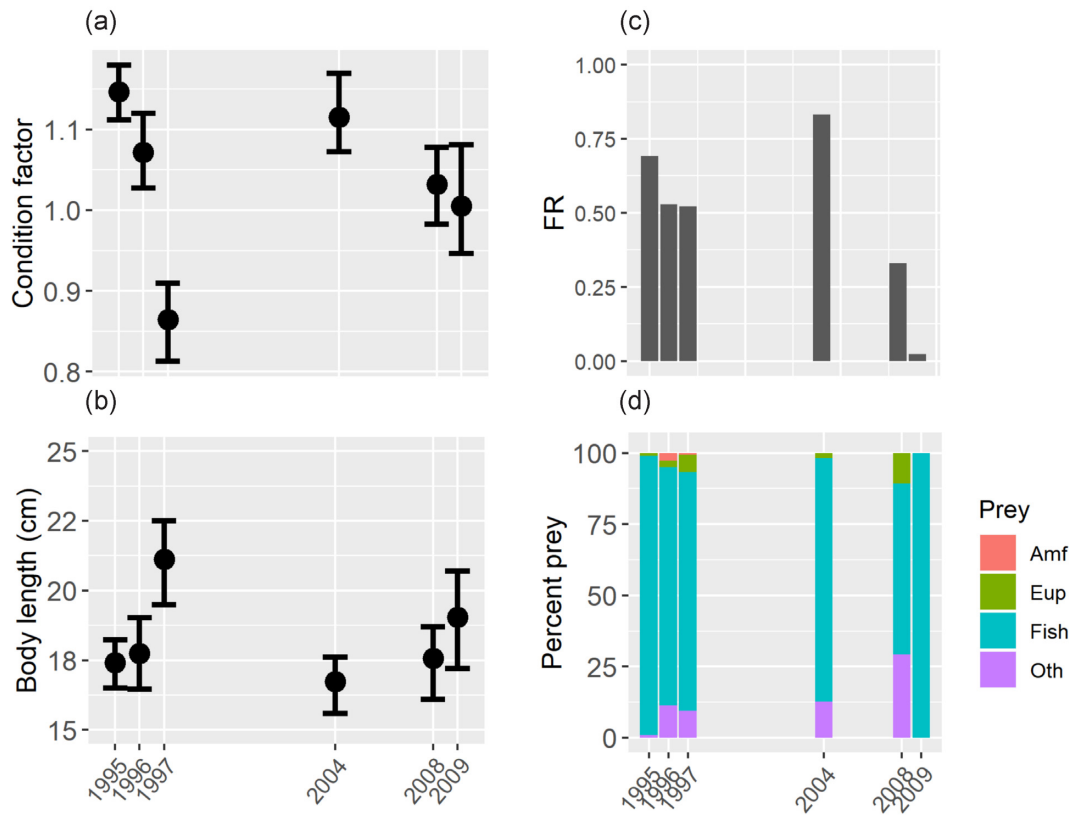


Figure 5. Temporal development for post-smolts sampled off Ireland in mid-May to mid-June. (a) Condition factor, (b) body length (cm), (c) FR, and (d) Annual average weight of prey groups in %.

Table 2. Comparison of model fit on the effect of different indices of feeding ratio (FR) on post-smolt body length and condition factor. All models include geographic position and year (fixed effect for the Norwegian Sea data and random effect for data sampled northwest of Ireland). The best model according to the parsimony principle and its parameters are displayed in bold. AIC—Akaike information criterion, GCV—minimized generalized cross-validation score, UBRE—Unbiasd risk estimator, amp—Amphipoda, eup—Euphausiids, and Δ AIC is the difference in AIC score compared to the best model. The table only includes tested models with significant terms.

Model	Δ AIC	Dev, Expl. (%)	GCV/UBRE score	AIC
Northwest of Ireland—Body length (BL)				
$BL \sim \alpha + s(lat,lon) + s(year) + \epsilon$	0	33.5	4.4717	1994.56
Northwest of Ireland—Condition factor (CF)				
$CF \sim \alpha + s(lat,lon) + s(year) + \epsilon$	20.20	33.5	0.0086	-881.90
$CF \sim \alpha + s(lat,lon) + \beta * FR + s(year) + \epsilon$	9.97	35.2	0.0084	-892.13
$CF \sim \alpha + s(lat,lon) + \beta * FR_{fish} + s(year) + \epsilon$	5.40	35.8	0.0083	-896.69
$CF \sim \alpha + s(lat,lon) + \beta * FR_{amf} + s(year) + \epsilon$	16.73	34.2	0.0085	-885.37
$CF \sim \alpha + s(lat,lon) + \beta * FR_{eup} + s(year) + \epsilon$	17.75	34.1	0.0086	-884.34
$CF \sim \alpha + s(lat,lon) + \beta_1 * FR_{fish} + \beta_2 * FR_{amf} + s(year) + \epsilon$	0.00	36.8	0.0082	-902.10
Norwegian Sea—Body length				
$BL \sim \alpha + s(lat,lon) + \epsilon$	0	39.3	6.7179	4355.13
Norwegian Sea—Condition factor				
$CF \sim \alpha + s(lat,lon) + s(g_year) + \epsilon$	13.83	62.9	0.0090	-1722.59
$CF \sim \alpha + s(lat,lon) + \beta * FR + s(year) + \epsilon$	0.23	63.6	0.0088	-1736.18
$CF \sim \alpha + s(lat,lon) + \beta * FR_{fish} + s(year) + \epsilon$	2.22	63.5	0.0088	-1734.19
$CF \sim \alpha + s(lat,lon) + \beta * FR_{amf} + s(year) + \epsilon$	12.73	63.1	0.0089	-1723.68
$CF \sim \alpha + s(lat,lon) + \beta_1 * FR_{fish} + \beta_2 * FR_{amf} + s(year) + \epsilon$	0.00	63.7	0.0088	-1736.41

in condition factor was associated with reduced stomach content in the Norwegian Sea, post-smolts could potentially also have experienced reduced feeding opportunities in coastal waters, which may have contributed to the low condition factors observed. There are

similar trends in marine growth and mortality for salmon originating from distant rivers (Jensen *et al.* 2011; Olmos *et al.* 2019). This indicates that the conditions in open ocean feeding grounds have changed, as individuals originating from different European regions

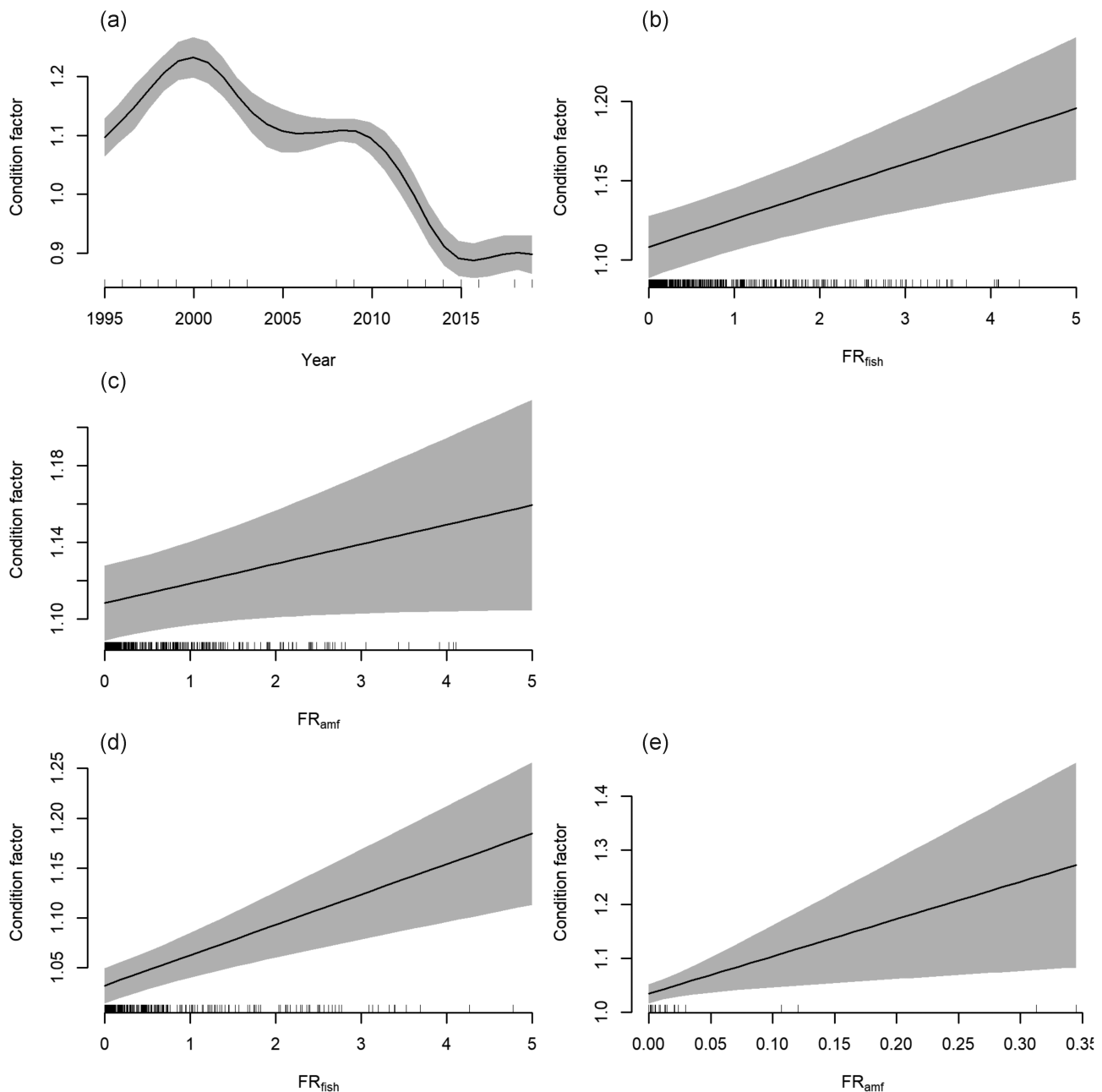


Figure 6. Partial plots of covariates in post-smolt condition factor models. (a) temporal trend in condition factor for individuals sampled in the Norwegian Sea during 1995–2019, (b) condition factor as a function of FR_{fish} in the Norwegian Sea (c) condition factor as a function of FR_{amf} in the Norwegian Sea, (d) condition factor as a function of FR_{fish} off Ireland, and (e) condition factor as a function of FR_{amf} off Ireland.

often utilize the same feeding grounds in the Norwegian Sea (e.g. Jacobsen *et al.* 2001; Jensen *et al.* 2012). Reduced availability of prey due to bottom-up processes at common feeding grounds is hypothesized to be an important driver for the observed changes (Olmos *et al.* 2020; Beaugrand and Reid 2012; Almodovar *et al.* 2019). However, the direct mechanisms have not been fully understood. Previous studies have linked salmon growth and survival to primary production and herbivorous zooplankton (Peyronnet *et al.* 2008; Friedland *et al.* 2009), but phytoplankton and meso-zooplankton (1–2 mm) are not important prey for post-smolt, although important for energy flow in the ecosystems (Haugland *et al.* 2006; Utne *et al.* 2021). The results presented here are the first to document

that the reduction in condition factor occur or is already occurring during the first summer in the ocean. This is directly linked to consumption of important prey for salmon post-smolt, and therefore improves our understanding of how changing conditions in a restricted spatiotemporal region affects salmon growth.

Post-smolts feeding on fish larvae in the Northeast Atlantic had significantly less of the group “other prey” in the stomachs compared to post-smolts not feeding on fish larvae. In addition, the binomial model for presence of fish larvae and zooplankton in post-smolt stomachs showed a pattern with lower probability for post-smolts to consume zooplankton if they consumed fish larvae, and vice versa. We interpret this as evidence for selective prey search

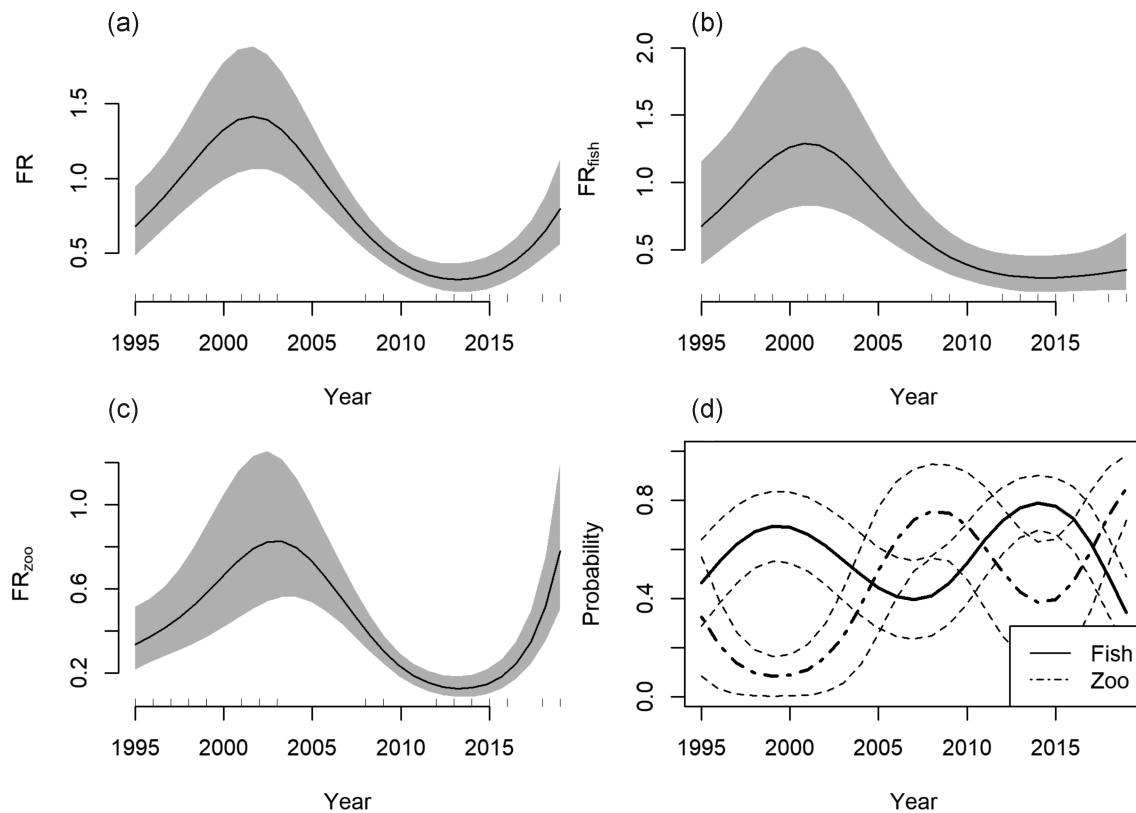


Figure 7. Partial plots of annual trends from the gamma-model for (a) FR, (b) FR_{fish}, (c) FR_{zoo}, and (d) the probability for having fish and zooplankton in the stomachs for post-smolts in the Norwegian Sea estimated with the binomial model. Note that the figure presents predicted values for a fixed position in the central Norwegian Sea (65°N 8°E). The gray shaded area (panel a-c) and the dotted lines (in panel d) show the 95% confidence interval for smoothers.

by post-smolts, where the focus on zooplankton is reduced when actively targeting fish larvae. However, we cannot state how spatial differences in availability of fish larvae and zooplankton affected the results. Furthermore, post-smolts with full stomachs had a diet dominated of fish larvae and Amphipoda while close to empty stomachs were dominated of Copepoda and the group “others.” This shows that targeting fish larvae can potentially be more beneficial. A diet dominated by fish is not necessarily more energy rich than a diet dominated by meso-zooplankton (see Smith *et al.* 2009 and references therein). However, fish larvae are more easily digested than zooplankton which have a hard exoskeleton (Hallfredsson *et al.* 2007), enabling a higher maximum daily energy intake when feeding on fish larvae. In addition, post-smolt feeding success may depend more on prey with optimal size rather than prey abundance in general (Jacobson *et al.* 2018). The available fish larvae are larger than zooplankton and gives therefore more energy per prey consumed. The results presented here support selective prey search as earlier suggested by Jacobsen and Hansen (2001), Renkawitz and Sheehan (2011), and Utne *et al.* (2021).

Feeding on Amphipoda was associated with increased condition factor for post-smolts, both off Ireland and in the Norwegian Sea. This is an important prey for post-smolts and one-sea-winter salmon feeding in the Norwegian Sea during the summer, autumn, and winter (Jacobsen and Hansen 2001; Haugland *et al.* 2006). There are two abundant species of Amphipoda in the Norwegian Sea, *Themisto libellula* and *T. abyssorum*. Both species were present in the sampled post-smolt stomachs but *T. abyssorum* was

most common (not presented in the results). This is a species inhabiting Atlantic water masses, is of smaller size and found in less dense aggregation, and often deeper, than *T. libellula*, which is primarily found in Arctic water masses (Melle *et al.* 2004). Given the positive association between post-smolt condition factor and Amphipoda during the summer, we hypothesize that the importance of Amphipoda for post-smolt feeding and growth increases during the autumn as post-smolt migrate out of the central Norwegian Sea. The diet and spatial distribution of post-smolts during the autumn and winter are largely unknown but tagged Norwegian kelt show a preference for feeding in Arctic water masses or along the arctic front in the northwestern Norwegian Sea (Strøm *et al.* 2018). We therefore hypothesize that post-smolts to a large degree leave the central Norwegian Sea in the autumn and migrate westward towards Greenland and into Arctic water masses. This is a region where *T. libellula* is abundant (Melle *et al.* 2004) and small pelagic fish are mainly absent. Hence, given the importance of Amphipoda on post-smolt feeding in the Norwegian Sea, and the abundance of large *T. libellula* when entering Arctic water, it is likely that Amphipoda increases in importance after the first summer feeding period.

The stomach fullness was reduced in the period 2003–2012, as shown in the present study, but the mechanisms behind the changes are to a large degree unknown. To understand changes in marine mortality for salmon, much effort has been put into linking marine water temperature and indices of salmon survival. There is compelling evidence for the correlation between the two, as salmon re-

turn rates to river have decreased simultaneously with increasing water temperatures (e.g. Todd *et al.* 2008; Almodovar *et al.* 2019). However, the observed changes in marine mortality for salmon are not always directly linked to ocean warming (Soto *et al.* 2018). To understand how ocean warming affects salmon, it is necessary to understand how ocean circulation and primary production are affected by climate change. There have been large changes in water transport and circulation patterns in the Northeast-Atlantic since the 1990-ies. The strength of both the subpolar-gyre and the East-Icelandic current was reduced in the early 2000s, and this has reduced the inflow of nutrients and plankton west and north of Ireland and into the Norwegian Sea (Hatun *et al.* 2017, Kristiansen *et al.* 2019). This is not expected to affect post-smolt directly, but its impact on the Norwegian Sea ecosystem can have a negative effect on important prey for post-smolt. One possibility is that water circulation in the Norwegian Sea partly regulates survival of fish larvae in the region and may also affect the transport of zooplankton and thus prey availability for post-smolts. Changing water circulation and reduced primary productivity have been linked to reduced fish recruitment in the North Sea and along the Norwegian coast (Clausen *et al.* 2018; Toresen *et al.* 2019). Furthermore, prey availability for salmon post-smolts might have decreased in some regions due to commercial fishing, as recruitment overfishing can affect the abundance of fish larvae. Larvae of Ammodytidae in the North Sea and Scorpaenidae in the Norwegian Sea are preyed upon by post-smolts (Haugland *et al.* 2006), and the consumed Scorpaenidae can be either *Sebastes norvegicus* or *S. mentella*. The abundance of Ammodytidae in the northern North Sea and *S. norvegicus* in the Norwegian Sea was reduced in the beginning of the 21st century (ICES 2020a, b) partly due to a large commercial fishery prior to the stock reductions. Increased predation pressure on plankton and fish larvae by other predators in the Northeast Atlantic might also have affected prey availability for post-smolts. The geographic range of Northeast Atlantic mackerel (*Scomber scombrus*) feeding migrations has increased since 2007 (Nøttestad *et al.* 2016) and mackerel prey upon fish larvae when available, including larvae of herring (Skaret *et al.* 2015), sandeel and mesopelagic fish (Oskarsson *et al.* 2016). Although this does not seem to be the main driver for reduced salmon marine survival observed since the 1980s (Utne *et al.* 2021), competition with mackerel may have impacted salmon post-smolts more in recent years due to a northward expansion of mackerel feeding grounds (Nøttestad *et al.* 2016) and therefore an increased geographic overlap between post-smolts and mackerel during the summer.

There was no significant reduction in body length with time for fish sampled in the Norwegian Sea. This contrasts with the findings of Jensen *et al.* (2012), who found a drop in scale growth (which is correlated to body length) between 2002/2003 and 2008/2009. The drop in condition factor and not in body-length indicates that post-smolts maintain growth in length in their first months at sea even when energy reserves are low, perhaps to grow out of the size window where they are most vulnerable to predation. A similar result was found by Stefansson *et al.* (2012) who studied smolt migration from the river, through the fjord, coastal areas, and the open ocean. Their results indicated that the post-smolts prioritize somatic growth throughout their early marine migration, and that surplus energy is stored.

Some of the surveys in the 1990s and early 2000s were designed to sample as many post-smolt as possible to identify migration routes which were virtually unknown, leading to extensive trawling in likely post-smolt migratory pathways thereby limiting the

geographic area covered by the surveys. Salmon originating from many European countries mix in the same marine regions (Jacobsen *et al.* 2001; Jensen *et al.* 2012), and small spatial or temporal differences in sampling can affect from where the sampled salmon originate. Hence, trends in body length can be sensitive to sampling bias due to non-directed or altered survey design. For this reason we acknowledge that even though the results do not indicate a change in body length in the period 1995–2019, a minor decreasing trend may be masked by the large variation in body length for post-smolts originating from different areas combined with potential survey sampling biases.

This study has revealed how changes in condition factor are related to reduced consumption of prey at the feeding grounds. Linking information on diet, feeding, and prey availability with genetic identification of salmon can potentially help us to understand the mechanisms resulting in different survival and growth for salmon originating from various European regions. The temporal changes in post-smolt condition factor, diet, and stomach fullness have only been observed since the mid 1990ies, with the drop after 2003 for fish sampled in the Norwegian Sea. The presented results can therefore not explain declining growth and adult return rates in earlier decades (Parrish *et al.* 1998). In a marine environment where multiple factors impact salmon growth and survival, reduced prey availability in the open ocean during the first spring and summer is a stressor which would have a negative effect on salmon. Linking the observed changes in condition factor and post-smolt diet with regional return rates can potentially be an important step towards understanding how changing marine conditions affect salmon survival. Salmon managers cannot easily take action to compensate for reduced availability of marine prey, especially if the ecosystem control is due to bottom-up effects (see discussion in Frederiksen *et al.* 2006). In such cases, climate driven changes in plankton communities may ultimately affect the growth, reproduction or mortality of top-predators such as salmon. However, understanding how varying prey abundance affects salmon in the sea can guide managers to take necessary compensating measurements such as reduced coastal and river exploitation, especially in periods with poor feeding conditions in the sea.

Data availability statement

The data underlying this article are available at NMDC, at <https://doi.org/10.21335/NMDC-484551947> and <https://doi.org/10.21335/NMDC-1006080862>.

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Supplementary data

Supplementary material is available at the ICES/JMS online version of the manuscript.

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