

Feeding interactions between Atlantic salmon (*Salmo salar*) postsmolts and other planktivorous fish in the Northeast Atlantic

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Abstract: In recent decades, there has been a decline in the marine growth of Atlantic salmon (*Salmo salar*) over large parts of the distribution range. One hypothesis for this reduced growth is increased interspecific competition with other planktivorous pelagic fish in the ocean. Here, interactions between salmon postsmolts and other pelagic fish (mackerel (*Scomber scombrus*) and herring (*Clupea harengus*)) in the Northeast Atlantic were investigated. There was a low diet overlap between postsmolts and the two other planktivorous pelagic species. Both mackerel and herring were feeding predominantly on copepods and other small zooplankton, while salmon were feeding mostly on fish larvae. All three species feed on euphausiids and amphipods. Furthermore, postsmolts geographically overlapped with mackerel but had a low geographic overlap with herring. There was no correlation between the abundance or survival of salmon from key index rivers and the abundance of pelagic fish. This study did not find evidence to support the hypothesis that observed temporal changes in marine growth and survival of salmon can be explained by feeding interactions with pelagic fish.

Résumé : Au cours des dernières décennies, la croissance en mer des saumons atlantiques (*Salmo salar*) a connu une baisse dans de grandes parties de leur aire de répartition. L'augmentation de la concurrence d'autres espèces de poissons pélagiques planctonivores dans l'océan est une hypothèse qui pourrait expliquer ce phénomène. Les interactions des saumons au stade de post-saumoneau avec d'autres poissons pélagiques (maquereaux (*Scomber scombrus*) et harengs (*Clupea harengus*)) dans le nord-est de l'océan Atlantique ont été examinées. Le chevauchement observé des régimes alimentaires des post-saumoneaux et des deux autres espèces pélagiques planctonivores est faible. Les maquereaux et les harengs se nourrissent principalement de copépodes et d'autres petits organismes zooplanctoniques, alors que les saumons se nourrissent principalement de larves de poisson. Les trois espèces se nourrissent d'euphausiacés et d'amphipodes. En outre, s'il y a un chevauchement géographique des post-saumoneaux et des maquereaux, le chevauchement des post-saumoneaux et des harengs est faible. Il n'y a aucune corrélation entre l'abondance ou la survie des saumons issues de rivières-repères clés et l'abondance des poissons pélagiques. La présente étude ne relève aucune preuve appuyant l'hypothèse voulant que des interactions associées à l'alimentation avec des poissons pélagiques puissent expliquer les variations observées au fil du temps de la croissance et de la survie en mer des saumons. [Traduit par la Rédaction]

Introduction

The life cycle of Atlantic salmon (*Salmo salar*) involves a period with long migrations in the oceanic phase. Migration from nursery grounds in fresh waters to the ocean is seen as a strategy where different life stages utilize habitats that optimize fitness (Lucas and Baras 2001). Atlantic salmon typically spend between 1 and 3 years in the sea, but some individuals can stay more than 4 years before returning to their home rivers (Klemetsen et al. 2003). The timing of postsmolts leaving the river follows a south–north gradient, ranging from March–April in southern Europe to June–July in northern Europe (Otero et al. 2014). After entering the sea, postsmolts migrate rapidly out to the open ocean (Thorstad et al. 2004).

During the past few decades, wild Atlantic salmon populations have declined dramatically over much of the distribution range (ICES 2018a; Parrish et al. 1998). The reason for this decline is complex and not fully understood. However, reduced marine survival is assumed to explain parts of this decline (Potter and Crozier 2000). Interdecadal, interannual, and interseasonal variation in

marine survival of Atlantic salmon is in turn poorly understood. Mortality is estimated to be high during the first period in the sea when postsmolts are in estuaries and fjords (Thorstad 2012 and references therein), but there are few estimates of mortality for Atlantic salmon in the open ocean. Several populations have had temporal trends of reduced growth during the marine phase concurring with lower survival, a pattern that has occurred for decades (e.g., Friedland et al. 2000; Jonsson and Jonsson 2004; Todd et al. 2008; Jonsson et al. 2016). The reason for reduced growth and survival is not known, although several hypotheses has been proposed. One key hypothesis is reduced abundance of prey available for postsmolts due to reduced plankton production and bottom-up regulation driven by climate changes (Beaugrand and Reid 2012; Almodóvar et al. 2019). This is supported by correlations between warmer ocean temperatures and reduced individual growth (Jonsson et al. 2016; Todd et al. 2008). Parasites in the sea, for instance *Lepeophtheirus salmonis* and to a lesser extent *Caligus elongatus* (Jacobsen and Gaard 1997), can also impact

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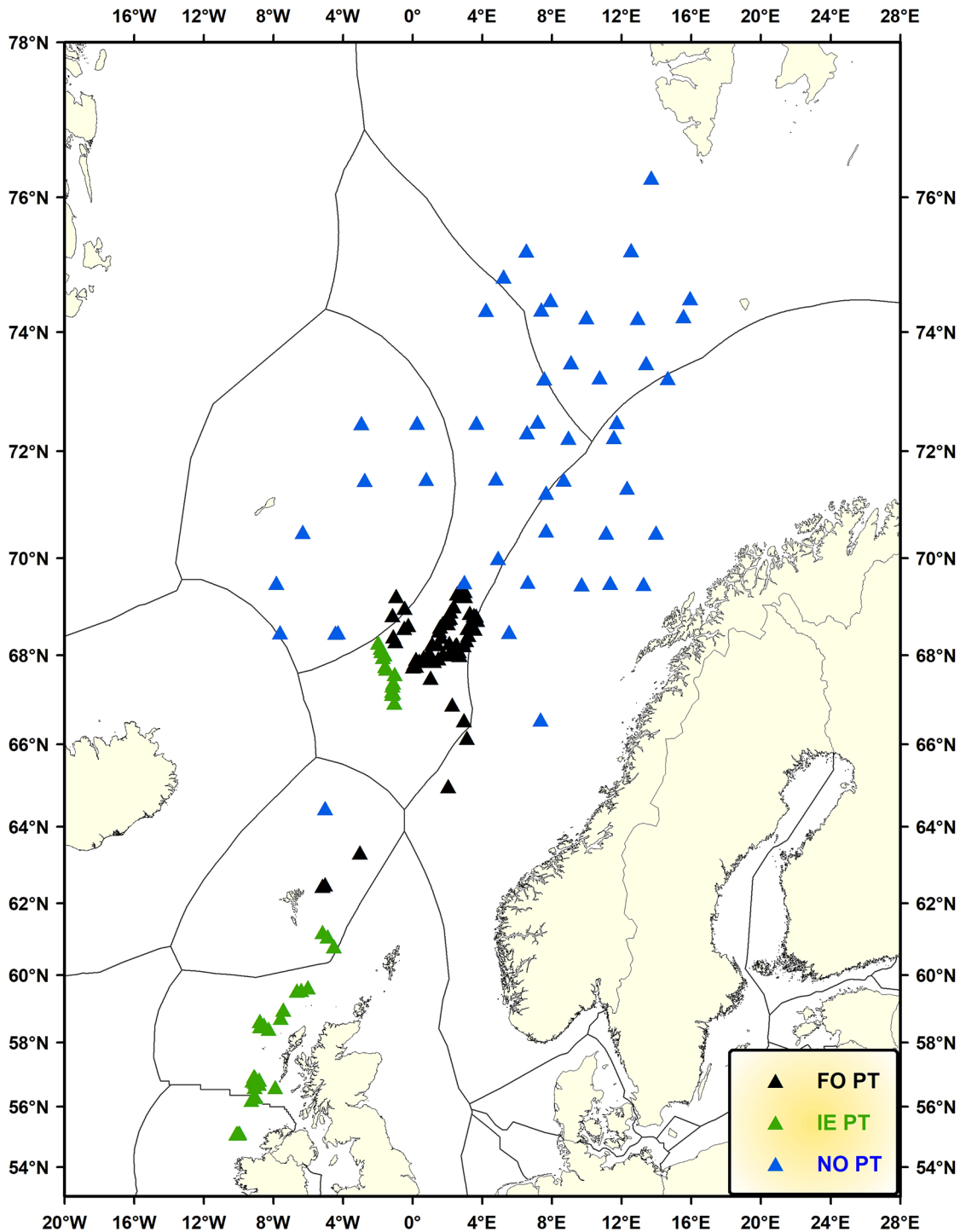
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Fig. 1. Overview of the survey area and the locations of pelagic trawl (PT) hauls for all surveys listed in Table 1. Figure produced in ArcGIS version 10.6. FO, Faroese survey; IE, Irish survey; NO, Norwegian survey.



marine growth and survival of salmon (Skilbrei et al. 2013). Increased production of farmed salmon with annual biomass exceeding 1.5 million tonnes in the Northeast Atlantic (ICES 2018a) has resulted in *Lepeophtheirus salmonis* being a major treat to Atlantic salmon (Forseth et al. 2017). Another hypothesis for the reduced salmon growth is increased interspecific competition with marine pelagic fish (Potter and Crozier 2000).

The migration routes in the sea for Atlantic salmon are not known in detail, but survey sampling and spatial models show

that postsmolts from the Northeast Atlantic migrate to a large extent into the eastern and central Norwegian Sea (Holm et al. 2000; Holst et al. 2000; Mork et al. 2012). Three other large pelagic fish stocks utilize the Norwegian Sea as feeding grounds during the spring and summer: blue whiting (*Micromesistius poutassou*), mackerel (*Scomber scombrus*), and Norwegian spring-spawning herring (NSSH, *Clupea harengus*) (Skjoldal et al. 2004; Utne et al. 2012). In 2018, the blue whiting, mackerel, and NSSH spawning stocks were estimated to be 5.4, 4.2, and 3.8 million tonnes,

Table 1. Overview of the periods, areas, number (N) of sampled salmon postsmolts, mackerel, and Norwegian spring-spawning herring (NSSH) and their respective mean weights (\pm standard deviation) for each survey.

Survey	Period	Area	N			Weight (g)		
			Salmon	Mackerel	NSSH	Salmon	Mackerel	NSSH
1	11–13 May 2008	Northwest of Ireland	38	16	—	68 \pm 56	80 \pm 26	—
2	17–24 May 2008	Northwest of Ireland	130	18	—	55 \pm 17	60 \pm 7	—
3	2 July – 7 Aug. 2008	Northern Norwegian Sea	57	52	40	144 \pm 36	520 \pm 110	244 \pm 49
4	4–13 July 2008	Norwegian Sea	127	311	55	111 \pm 56	346 \pm 99	319 \pm 53
5	3–13 July 2009	Norwegian Sea	99	163	33	116 \pm 89	387 \pm 91	349 \pm 40
6	12 May 2009	Northwest of Ireland	7	—	—	70 \pm 22	—	—
7	16 July – 5 Aug. 2009	Norwegian Sea	9	25	—	124 \pm 32	345 \pm 71	—
8	16 July – 9 Aug. 2009	Northern Norwegian Sea	69	63	62	141 \pm 36	468 \pm 110	279 \pm 60
9	26–29 June 2009	Norwegian Sea	214	30	14	95 \pm 27	337 \pm 75	307 \pm 55

respectively (ICES 2018b, 2019b). The three stocks are important predators on zooplankton in the Norwegian Sea ecosystem (Skjoldal et al. 2004).

NSSH initiates feeding in the Norwegian Sea in March–April, while mackerel and blue whiting migrate into the Norwegian Sea in May–June. All three species inhabit the Norwegian Sea until returning to overwintering grounds in autumn or early winter. The diets of these species have been extensively studied and consist of a range of zooplankton species as well as fish larvae (Langøy et al. 2012; Óskarsson et al. 2016; Skaret et al. 2015; Bachiller et al. 2016). The diet of salmon in the sea varies with season and size (Jacobsen and Hansen 2001; Rikardsen and Dempson 2011). Post-smolts feed to a large extent on fish larvae and zooplankton (Rikardsen et al. 2004; Haugland et al. 2006; Hvidsten et al. 2009). Thus, postsmolts potentially compete with other pelagic fish for prey during summer.

There are now indications of less available prey for postsmolts and pelagic fish in the Northeast Atlantic compared with earlier decades, although all estimates in this regard have high uncertainty. For instance, the abundance of zooplankton in the Norwegian Sea has decreased since early 2000s (ICES 2019a). The abundance of some fish species, which are potential prey in coastal regions at the larval stage, are declining. Examples are sandeel (*Ammodytes marinus*) in the Northern North Sea and west of Ireland and the UK and sprat (*Sprattus sprattus*) in the North Sea (ICES 2018c).

Given the potential spatial and dietary overlap between post-smolts and pelagic fish in the Northeast Atlantic, we aim to investigate their interactions to evaluate whether this can explain the reduced growth and survival of salmon in the Northeast Atlantic. First, the diet overlap among postsmolts, mackerel, and NSSH while feeding northwest of Ireland and in the Norwegian Sea in spring and summer is estimated. Stomach content is analysed from fish sampled from nine pelagic surveys in 2008 and 2009. Second, the horizontal overlap between salmon and mackerel or NSSH is estimated with spatially explicit statistical modelling. The analyses are based on data from the same surveys. Third, time series of abundance of pelagic fish are correlated to abundance and survival of Northeast Atlantic salmon to examine whether abundance of pelagic fish is correlated with marine survival of salmon.

Materials and methods

Biological sampling for diet analyses

Fish samples from 161 pelagic trawl hauls were taken from nine different scientific surveys targeting salmon and other pelagic fish during spring and summer in 2008 and 2009. The surveys ranged from northwest of Ireland, to the central Norwegian Sea in June and July, and the northern Norwegian Sea in August (Fig. 1). The objective of these surveys was to sample postsmolts in the open ocean as part of the Salsea Merge project (<http://salmonatsea.com/the-salsea-merge-project/>), but mackerel and NSSH were

also caught in many of the trawl hauls due to their pelagic nature. The trawl's size selectivity of mackerel and NSSH is not known, but a range of individual sizes were caught, including large adult fish. The sampling did not follow standardized transects or equal distance spacing, but trawling was done over a large geographic area with more effort in areas with assumed high probability of postsmolt catch. More information about the surveys and biological sampling are presented in Table 1. Trawling was carried out at the surface at \sim 4 knots (1 knot = 1.852 km·h⁻¹) with either a dedicated salmon trawl or another similar pelagic trawl. Two large floats attached to each side and a float in the center kept the trawl at the surface during towing. Once the fish were on deck, they were individually weighed to the nearest gram, and the total length was measured with a 5 mm resolution. The stomachs were removed from the fish and frozen. Salmon larger than 1000 g were excluded from the analyses to ensure the dataset only included postsmolts (the largest postsmolt being 622 g). The stomach contents of 750 postsmolts, 678 mackerel and 204 herring (Table 1) were later analyzed in the laboratory. The stomach content was identified to species level when possible or to closest family if it was too digested for species identification.

The number of individual prey items within each prey group was counted for all sampled stomachs. The weight of all unique prey groups in each stomach was recorded for Norwegian and Irish samples, but not for the Faroese samples. To correct for this missing information from the Faroese samples, the weight of each prey group was estimated based on the median individual prey item weight multiplied by the number of prey items. The median weight of all prey items was calculated based on all identified prey in Irish or Norwegian samples. When all prey in the stomach could be identified, the calculated weight of the prey group was summarized and scaled to the measured total weight of the stomach content. If there were unidentified prey in the stomachs, the difference between the total stomach content weight and sum of estimated prey group weights was assigned to this group. There were no prey species in Faroese samples that were not identified in the samples from the two other countries. Prey species and groups from each stomach were oven-dried separately at 70 °C for more than 24 h, and the dry weight was recorded.

Diet analyses

Preliminary analyses revealed large spatial and temporal variation in the diet for all three species. The dataset was therefore split into four time periods due to the temporal and spatial coverage of the surveys. These periods were May, covering the areas northwest of Ireland, June covering the central Norwegian Sea, 1–15 July covering the southern and central Norwegian Sea, and 15 July – 10 August covering the central and northern Norwegian Sea. Data from samples collected in 2008 and 2009 were combined in the analyses.

Table 2. Time series of abundance or survival for salmon and pelagic fish.

Name	Year	Source	Description
Pelagic fish			
Mackerel SSB	1982–2017	ICES 2019b	Mackerel spawning stock biomass from the assessment
NSSH SSB	1982–2017	ICES 2018b	NSSH total stock biomass from the assessment
Blue whiting SSB	1982–2017	ICES 2018b	Blue whiting total stock biomass from the assessment
Total pelagic fish SSB	1982–2017	ICES 2018b	Total spawning stock biomass of mackerel, blue whiting and NSSH
IESSNS total	2007–2017	Olafsdottir et al. 2018	Survey index of mackerel in the Nordic seas
IESSNS Norwegian Sea	2007–2017	Olafsdottir et al. 2018	Survey index of mackerel in the Norwegian sea
Salmon			
NNEAC_1SW	1983–2017	ICES 2018a	PFA of 1 SW salmon returning to North European countries
SNEAC_1SW	1983–2017	ICES 2018a	PFA of 1 SW salmon returning to South European countries
NOR_1SW	1982–2015	Anonymous 2018	PFA of 1 SW salmon returning to the Norwegian coast
Imsa_1SW	1982–2016	ICES 2018a	Estimated marine survival for the river Imsa in Norway
Elidaar_1SW	1985–2016	ICES 2018a	Estimated marine survival for the river Elidaar in Iceland
Corrib_1SW	1982–2016	ICES 2018a	Estimated marine survival for the river Corrib in Ireland
Bush_1SW	1986–2016	ICES 2018a	Estimated marine survival for the river Corrib in N. Ireland
Dee_1SW	1993–2016	ICES 2018a	Estimated marine survival for the river Corrib in Scotland

Note: SSB, spawning stock biomass; NSSH, Norwegian spring-spawning herring; IESSNS, International Ecosystem Summer Survey in Nordic Seas; 1SW, one sea-winter; NNEAC, Northern Northeast Atlantic Commission; SNEAC, Southern Northeast Atlantic Commission.

For each period, the diet by weight was grouped into 12 different prey groups. Grouping was done based on preliminary analyses of the salmon diet. As a result of this, there are prey groups not relevant for NSSH or mackerel. Further, the group “Others” include prey organisms important for NSSH and mackerel, but not for postsmolts.

The diet overlaps between postsmolts and the two other species were calculated with Pianka’s index of niche overlap (Pianka 1974). This is a common index to evaluate whether two species have an overlapping diet (e.g., Langøy et al. 2012; Davis et al. 2015; Bachiller et al. 2018). The index is given by

$$(1) \quad O = \frac{\sum p_{ij}p_{ik}}{(\sum p_{ij}^2 \sum p_{ik}^2)^{0.5}}$$

where the overlap index between the two species (O) is in the range 0–1. p_{ij} and p_{ik} are the proportions of the i th prey group by weight in the diets of species j and k , respectively. If O is 0 there is no diet overlap between the two species, while a value of 1 means a complete overlap. Partly overlapping diets is not necessarily equal to niche overlap, as species using resources independently of each other may still utilize some of the same resources. To test whether the species use the same resources more than what is expected by chance, we compared the overlap index to a null expectation (RA3 algorithm, 1000 repetitions) using the R package EcoSimR (Gotelli et al. 2015).

The feeding ratio (FR) was calculated to quantify potential difference in feeding intensity for the three fish species. This is an estimate of the weight of the stomach content relative to the fish weight and is a snapshot of the stomach content at the time of sampling. FR was calculated by the following equation:

$$(2) \quad FR = \frac{100m_s}{m_f - m_s}$$

where m_f is the mass (g) of the fish and m_s is the mass (g) of the stomach content. A Mann–Whitney U test for nonparametric samples was used to test whether FR was significantly different between species.

Finally, as the three fish species can potentially feed on different sizes and (or) generations of prey, the most common prey organisms consumed by all three species were identified, and a Mann–Whitney U was applied to test whether the species preyed on the same size groups of prey.

Geographic overlap – statistical modelling

Data on salmon postsmolts, herring (NSSH), and mackerel geographic distribution from three surveys (Table 1 — surveys 7, 8, and 9) were used to assess the geographic overlap among the species. For these surveys, fish density estimates with fine geographic resolution for postsmolts, mackerel, and NSSH in the central and northern Norwegian Sea had been calculated. For mackerel, density estimates were calculated from trawl catches, where catch per unit effort (CPUE) was calculated by dividing the total weight of mackerel with distance trawled. Acoustic estimates of NSSH density were used to assess overlap between postsmolts and NSSH. The acoustic data was sampled with a 38 kHz split-beam echo sounder. The survey area was gridded into a 2° longitude × 1° latitude grid, and the area’s respective average nautical area scattering coefficient ($m^2 \cdot nmi^{-2}$; 1 nautical mile = 1.852 km) values were assigned to the trawl hauls within each grid cell.

Generalized additive models (GAMs; Wood 2006) were used with binomial error distribution to evaluate relationships between salmon presence–absence and spatial position, log-transformed herring acoustic backscatter, and log-transformed mackerel CPUE. Salmon presence–absence was used as the response variable instead of CPUE since the sampling design was not ideal for spatial modelling and because of the relatively low number of samples. Year was included as a random effect to account for differences between years that were not accounted for in the other variables, such as variations in sampling design. GAMs were fitted in the R library mgcv, using R version 3.5.3 (R Core Team 2019), and the approximate p values from the summary function and the shape of the smooth functions were used to evaluate spatial overlap among the species.

Time series analyses

To explore whether interactions between postsmolts and pelagic fish can explain some of the temporal trends for salmon abundance, time series of survival and abundance of salmon were correlated to pelagic fish abundance. Time series of abundance of pelagic fish were obtained from two different sources, International Council for the Exploration of the Sea (ICES) assessment estimates of spawning stock biomass (SSB) (ICES 2018b, 2019b) and International Ecosystem Summer Survey in Nordic Seas (IESSNS) biomass index (Olafsdottir et al. 2018). There has been an expansion, and possibly a shift, in the geographic distribution of mackerel in recent years (Nøttestad et al. 2016). The

Fig. 2. Histograms of the stomach content (by weight in percent) of salmon postsmolts and mackerel in May and map of the sampling location of postsmolts (blue rectangles) and mackerel (red circles). Figures and map produced in R (R Core Team 2019) with ggplot2 (Wickham 2016) and gmap (Kahle and Wickham 2013).

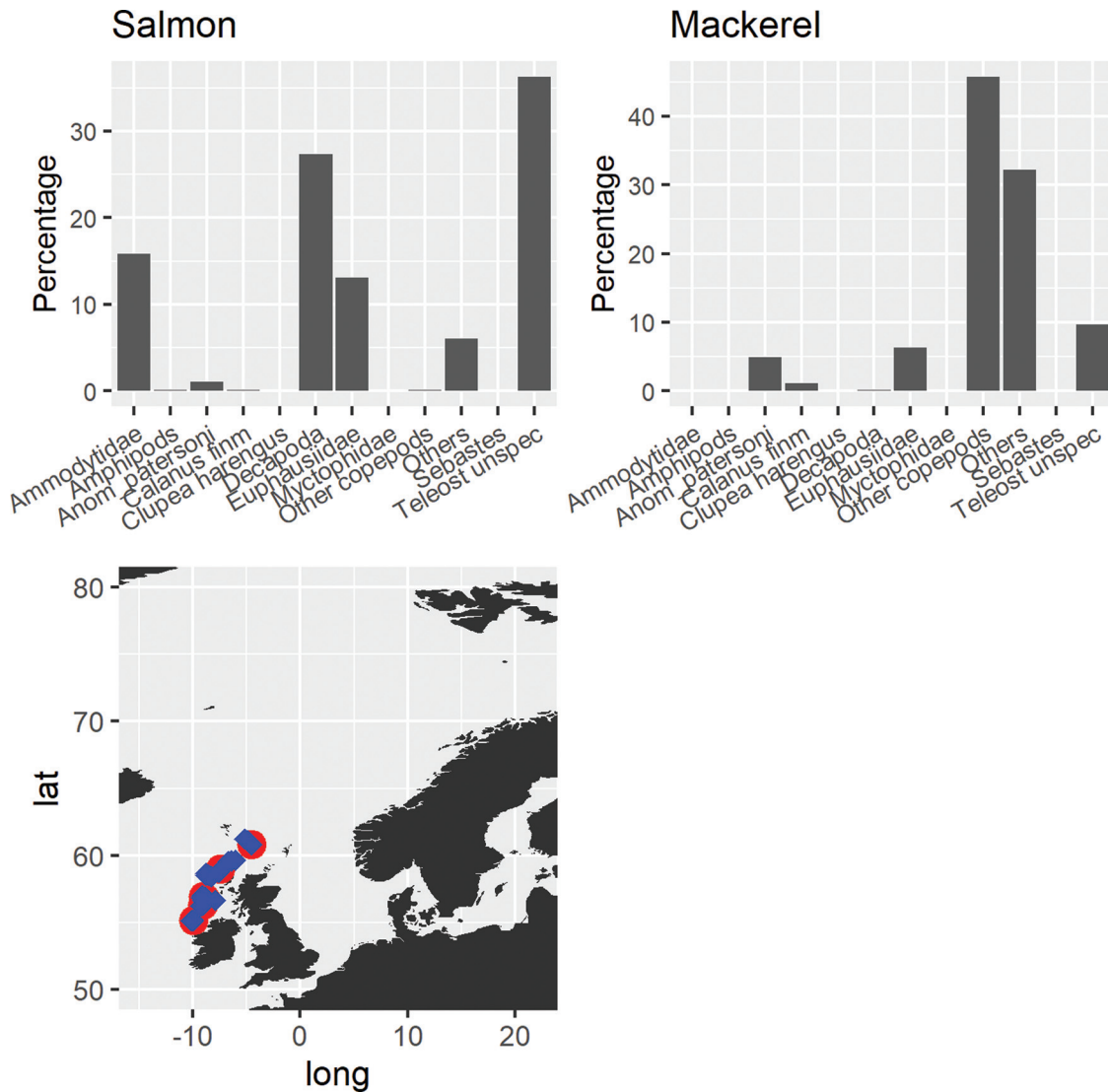


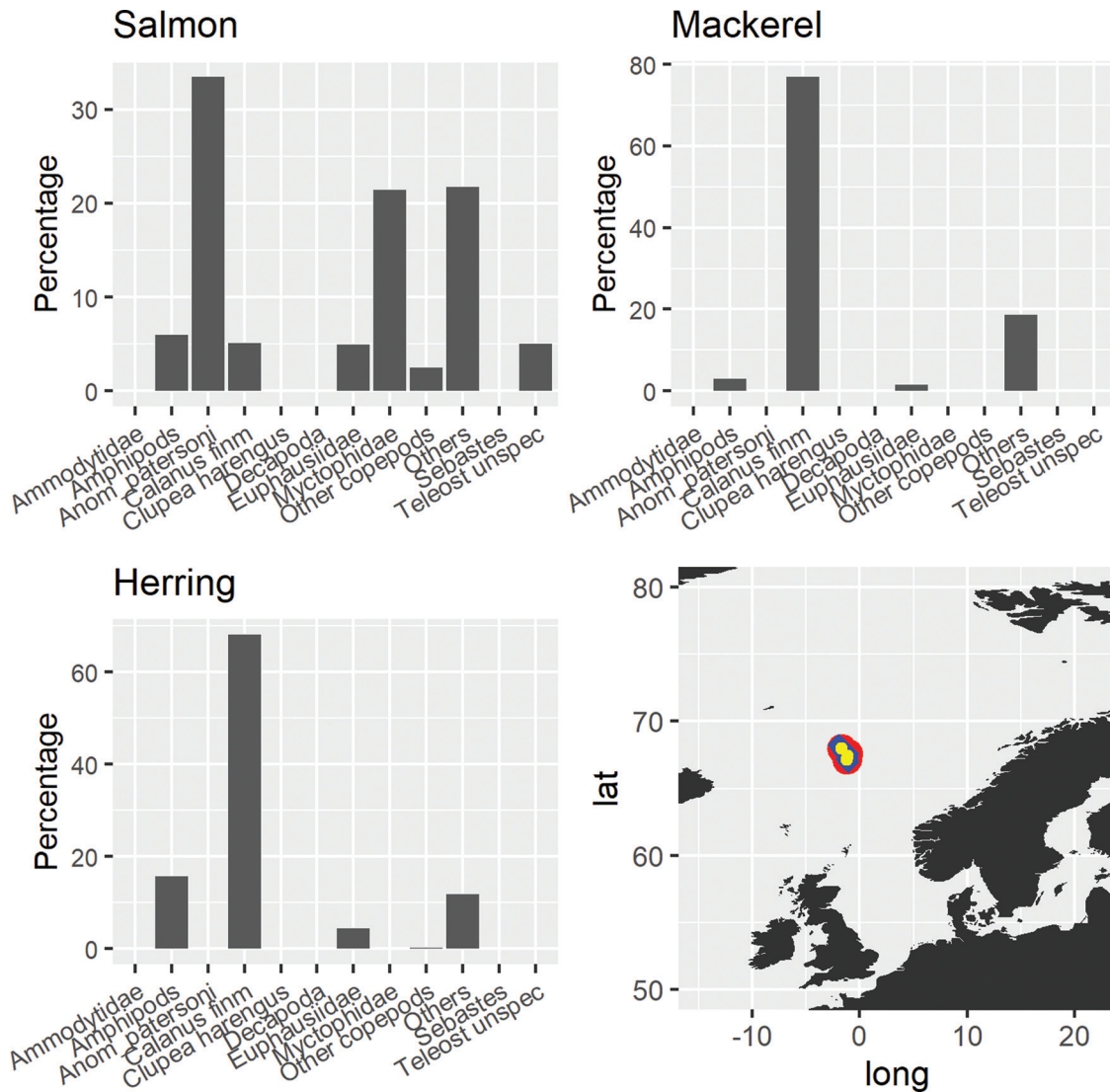
Table 3. Pianka's index of niche overlap of paired comparison between salmon postsmolts and the two species mackerel and NSSH.

Period	Postsmolts–mackerel	Postsmolts–NSSH	N		
			Postsmolts	Mackerel	NSSH
May	0.22	—	175	39	—
June	0.22	0.22	214	30	14
Early July	0.55	0.64	226	474	88
Late July–Aug.	0.14	0.56	135	140	102

survey index from the IESSNS trawl survey is a biomass estimate treated as an index due to unknown catchability of the survey and its gear. The survey is conducted annually in July–August and covers the Norwegian Sea, the area around Iceland, and southeastern parts of Greenland waters. The IESSNS survey index is included, as the ICES stock estimate may not fully represent the changing abundance of mackerel within the Nordic seas (Olafsdottir et al. 2018). The IESSNS survey index for the

Norwegian Sea only, excluding the area around Iceland and Greenland, was also included, as the Norwegian Sea is a core feeding area for European postsmolts (Haugland et al. 2006). The data series for salmon included in the analyses are abundance and survival estimates for European salmon as provided by the ICES working group for North Atlantic Salmon (ICES 2018a) and estimated prefishery abundance (PFA) for Norway only (Anonymous 2018). Abundance estimates for Europe are PFA of 1 sea-winter

Fig. 3. Histograms of the stomach content (by weight in percent) of salmon postsmolts, mackerel, and Norwegian spring-spawning herring (NSSH) in June and map of the sampling location of postsmolts (blue rectangles), mackerel (red circles), and NSSH (yellow circles). Figures and map produced in R (R Core Team 2019) with ggplot2 (Wickham 2016) and ggmap (Kahle and Wickham 2013).



fish (ISW) for the Northern and Southern Northeast Atlantic Commission (NNEAC and SNEAC; ICES 2018a). NNEAC is a geographic domain including the Scandinavian countries, Russia, and the northern part of Iceland. SNEAC includes UK, Ireland, France, Spain, and southern part of Iceland. Time series of estimated marine survival for five index rivers (ICES 2018a) distributed across Europe are also included. For more information about these time series see Table 2.

The time series for pelagic fish were correlated (Pearson’s correlation) with the time series for salmon. Time series were checked for stationarity and autocorrelation, as autocorrelated time series with strong trends increase the risk of spurious correlations (Shumway and Stoffer 2000). First, the nonstationarity was corrected by fitting a linear model with year as predictor to the original dataset. A detrended dataset was then obtained by subtracting the original dataset with predicted values from the linear model. Autocorrelation in the datasets were corrected by fitting AR(1) or AR(2) models to the datasets using R package Arima (Hyndman et al. 2019).

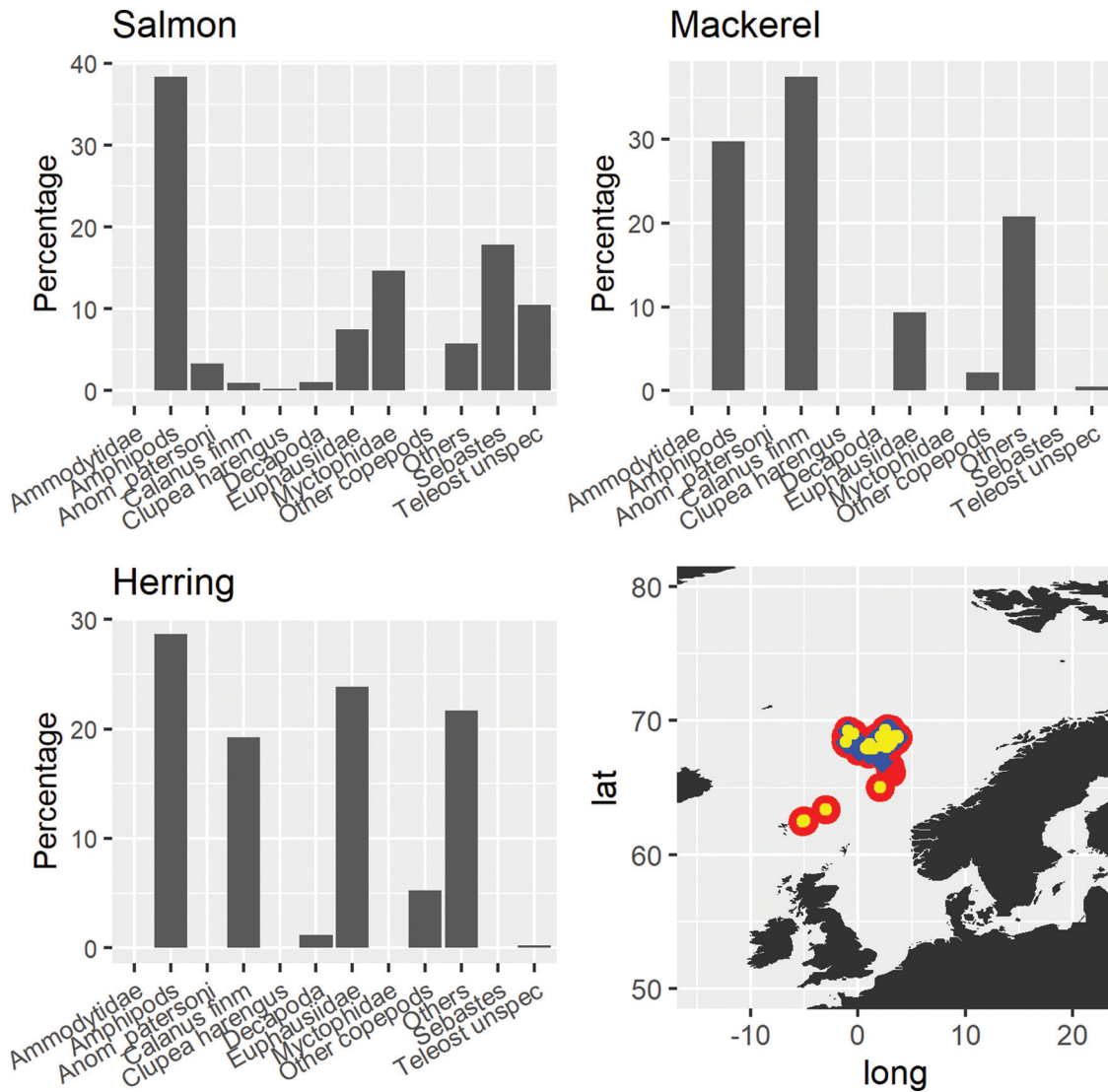
Results

Stomach content analyses and diet overlap

Stomachs from postsmolts and mackerel were sampled north-west of Ireland in May, but NSSH was not present in the area then (Fig. 2). The majority of mackerel sampled were juveniles weighing less than 100 g, which was similar to the weight of postsmolts sampled during this period (Table 1). Half of the diet by weight for postsmolts were fish larvae: 36% unidentified fish and 16% sand eel larvae. Other important prey were decapods (27%) and euphausiids (13%). The diet of mackerel consisted mainly of copepods and other zooplankton. Fish larvae made up nearly 10% of the mackerel diet, and euphausiids comprised around 6%. Pianka’s index for diet overlap between postsmolts and mackerel in this period and area was 0.22 and was not significant when compared with the null model ($p = 0.54$; Table 3).

Sampling in late June was conducted within a small geographic area in the central Norwegian Sea (66°N–67°N, 1°W–2°W). The postsmolts captured here had an average weight close to 100 g, while the mackerel and NSSH were on average more than 300 g

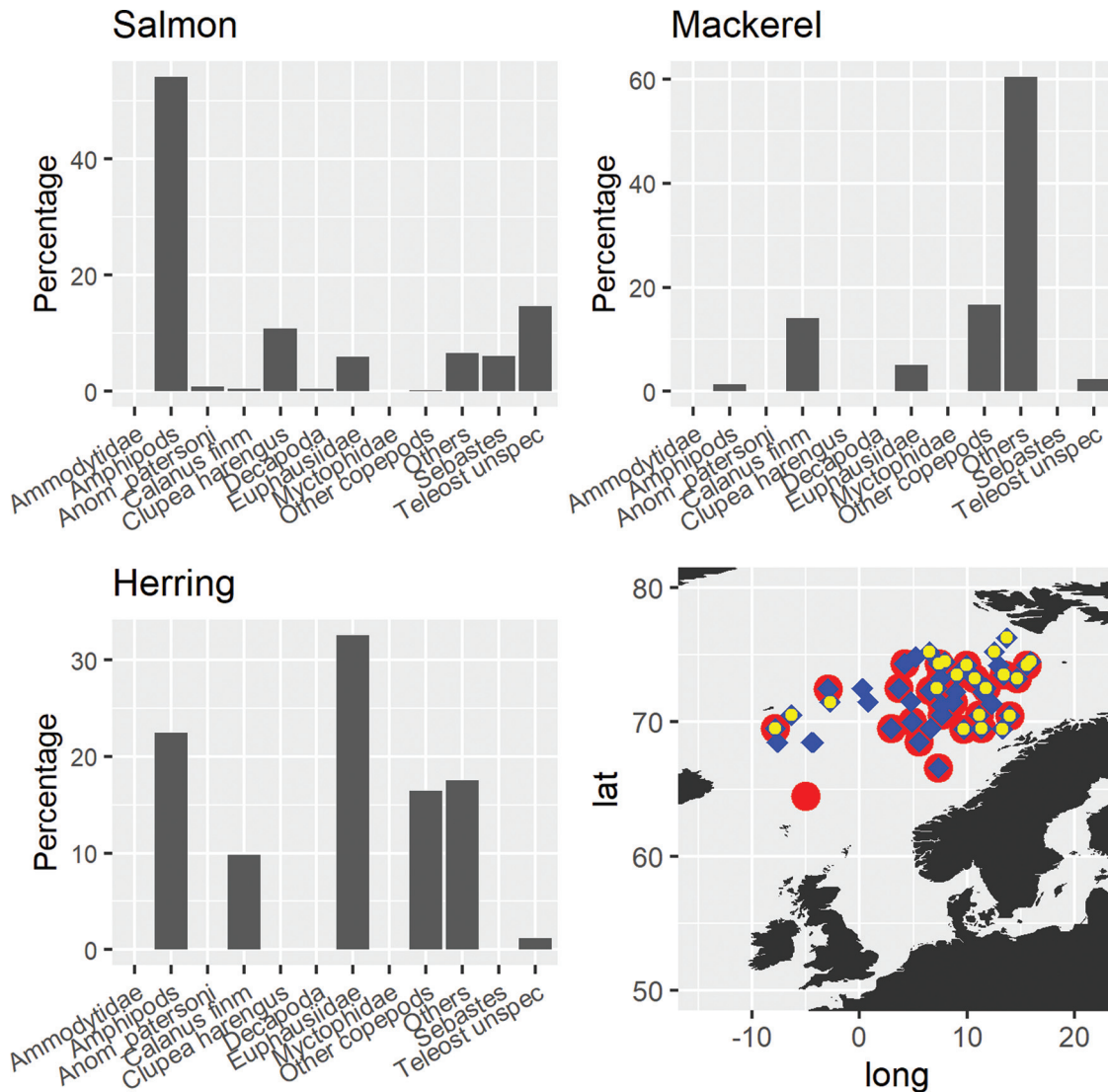
Fig. 4. Histograms of the stomach content (by weight in percent) of salmon postsmolts, mackerel, and NSSH in the first half of July and map of the sampling location of postsmolts (blue rectangles), mackerel (red circles), and NSSH (yellow circles). Figures and map produced in R (R Core Team 2019) with ggplot2 (Wickham 2016) and ggmap (Kahle and Wickham 2013).



(Table 1). All three fish species preyed upon copepods (Fig. 3). The proportion of *Calanus finmarchicus* by weight in the diet of mackerel and NSSH was 77% and 68%, respectively. This prey item was not a major component of the postsmolt diet, as it only made up 5% of the total stomach content. The dominating prey item in postsmolt stomachs was the copepod *Anomalocera patersoni*, which comprised 33% of the diet by weight. Further, Myctophidae larvae comprised 22% and undetermined fish 5% of the diet. These prey groups were not found in any of the mackerel or NSSH stomachs in this period. All three species also preyed upon amphipods and euphausiids, but these did not constitute a major part of the diet for any of the three species. These two prey groups comprised 25% of NSSH diet, 4% of the mackerel diet, and 11% of the postsmolt diet. Pianka's index for the overlap in diet between postsmolts and mackerel in the same period was 0.22 (Table 3), which is identical to the overlap between postsmolts and NSSH in this period, as well as the diet overlap between postsmolts and mackerel in May. The diet overlap was not significant between postsmolts and mackerel ($p = 0.31$) nor between postsmolts and NSSH ($p = 0.39$).

Sampling in early July covered southern and central parts of the Norwegian Sea. The postsmolts had an average weight of more than 100 g, while mackerel and NSSH weighed on average more than 300 g (Table 1). The proportion of copepods in the diet had decreased for all three species compared with the samples from late June, but *Calanus finmarchicus* still made up 19%, 37%, and 1% of the diet for NSSH, mackerel, and postsmolts, respectively (Fig. 4). Amphipods were an important part of the diet for all three species, comprising 38% of the diet of postsmolts and 29%–30% for NSSH and mackerel. Euphausiids were also preyed upon by all three species, but they were more important for NSSH than the two other species. In addition, postsmolts preyed on Myctophidae, *Sebastes* spp., and unidentified fish larvae. These prey items were only found to a minor extent in mackerel or NSSH stomachs. The diet overlaps between postsmolts and the two other species in July was higher than what was observed in May and June. Pianka's overlap index was 0.55 and 0.64 for postsmolts–mackerel and postsmolts–NSSH (Table 3), respectively. Although the diet overlap was higher than during the earlier periods, it was still not significant compared with the null

Fig. 5. Histograms of the stomach content (by weight in percent) from salmon postsmolts, mackerel, and NSSH in July–August and map of the sampling location of postsmolts (blue rectangles), mackerel (red circles), and NSSH (yellow circles). Figures and map produced in R (R Core Team 2019) with ggplot2 (Wickham 2016) and ggmap (Kahle and Wickham 2013).



models ($p = 0.11$ and $p = 0.16$ for mackerel and NSSH, respectively), which assume random feeding on available prey. Two postsmolts had pieces of plastic in their stomachs.

Sampling in late July and early August covered large parts of the Norwegian Sea. The postsmolt mean weight increased to between 100 and 150 g. The NSSH were adults with a mean weight of more than 300 g, but with smaller adolescent herring in the northeastern region (entrance of the Barents Sea). Mackerel were the same size as in early July, with a mean weight of more than 300 g. Amphipods were still the dominating prey in the post-smolt stomachs, comprising 54% of the stomach content by weight. NSSH stomachs contained 22% amphipods, but these only constituted 1% of the stomach content of mackerel (Fig. 5). Fish larvae remained an important part of the diet for postsmolts and was composed of 11% herring larvae, 15% unidentified fish larvae, and 6% *Sebastes* spp. larvae. Euphausiids were a dominant component of the diet for NSSH (32%), while the prey group “others” were dominating for mackerel (60%). Both of these groups were present in the postsmolt stomachs, but only as 6% and 7% of the diet by weight. Piankas diet overlap index was 0.56

between postsmolts and NSSH in late July and early August, while it was 0.14 between postsmolts and mackerel (Table 3). The diet overlap between postsmolts and NSSH was still not significant compared with the null model ($p = 0.13$) nor between post-smolts and mackerel ($p = 0.52$).

The lack of prey group weights for the Faroes samples made it necessary to estimate these weights based on the total stomach weight and prey group weights from Norwegian or Irish samples. The Faroese samples are approximately 1/4 of the total postsmolt dataset. The diet composition from the Faroese samples are similar to the Irish and Norwegian samples from the Norwegian Sea. However, for postsmolts the proportion of *Sebastes* and Myctophidae larvae is 5%–10% higher, while the proportion of herring larvae and *Anomalocera patersoni* is 5%–10% lower in the Faroese samples compared with the Irish and Norwegian data from the Norwegian Sea. For mackerel and NSSH, there are only small difference in the diet with the exception being that amphipods comprised nearly 30% of the diet in the Faroese mackerel stomachs compared with only 1% in the remaining mackerel stomachs sampled in the Norwegian Sea. Since the Faroese samples are

Table 4. The number of individual fish with *Themisto* spp. and euphausiids in sampled stomachs and the minimum, mean, median, and maximum dry weight of the individual prey items.

		Postsmolts	Herring	Mackerel
<i>Themisto</i>	Number	142	39	34
	Min. (mg)	0.01	0.025	0.03
	Median (mg)	0.42	0.44	0.18
	Mean (mg)	1.10	0.57	2.30
	Max. (mg)	23.76	1.91	57
Euphausiids	Number	75	38	24
	Min. (mg)	0.01	0.02	0.02
	Median (mg)	0.67	0.25	0.11
	Mean (mg)	7.96	3.27	0.87
	Max. (mg)	250.00	83.30	11.03

taken in other parts of the Norwegian Sea, some deviation from the Norwegian and Irish samples is to be expected.

Comparison of prey weight for postsmolts and mackerel–NSSH

Postsmolt, NSSH, and mackerel all feed on euphausiids and amphipods. The analyses on targeted prey size were done for each prey group separately. As nearly 98% of the consumed amphipods were *Themisto* spp., the analyses for amphipods only include this genus.

The dry weight of the consumed *Themisto* spp. individuals ranged from 0.01 to 57 mg, but the majority of the individuals consumed by all three fish species were less than 1 mg (Table 4). The average weight of *Themisto* spp. from postsmolts and NSSH stomachs were not significantly different (Mann–Whitney test, $p = 0.75$), while there were larger *Themisto* spp. in postsmolt stomachs than in mackerel stomachs (Mann–Whitney test, $p < 0.001$).

The dry weight of the consumed euphausiids ranged from 0.01 to 250 mg (Table 4), but the majority consumed by all three fish species was less than 5 mg. There were larger euphausiids in postsmolts than in NSSH and mackerel stomachs (Mann–Whitney test, $p = 0.001$ and $p < 0.001$, respectively).

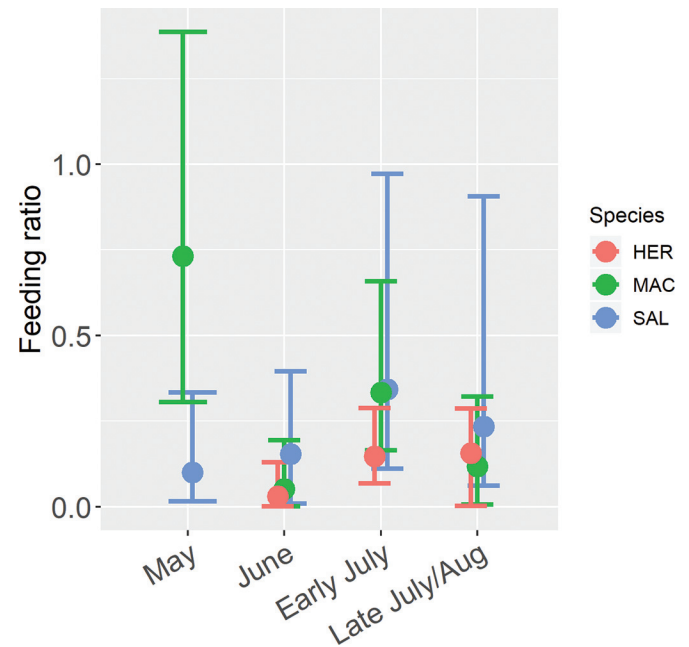
Feeding ratio (FR)

The FR is a measurement of the weight of the stomach content relative to the weight of the fish. The FR was highly variable for all three species (Fig. 6). In May, the median FR for postsmolts was 0.1 northwest of Ireland. In the same region, the median FR for mackerel was 0.73, which was significantly higher (Mann–Whitney test, $p < 0.001$) compared with postsmolts. In late June, the median FR for postsmolts was 0.15, which was significantly higher than for NSSH and mackerel (Mann–Whitney test, $p = 0.04$ and $p = 0.01$, respectively), which had median values of 0.03 and 0.05, respectively. In early July, postsmolts had a median FR of 0.34, which was significantly higher (Mann–Whitney test, $p < 0.001$) than that of NSSH (0.15) and at the same level as for mackerel (0.33; Mann–Whitney test, $p = 0.7$). In late July and early August, postsmolts had a median FR of 0.23, which was significantly higher than the 0.16 for NSSH and 0.12 for mackerel (Mann–Whitney test, $p < 0.001$).

Spatial overlap

The GAM for salmon probability of occurrence was based on 170 trawl hauls (56 from 2008 and 114 from 2009). The model explained 38.6% of the deviance in the probability of catching salmon in a trawl haul. Salmon were more likely to occur in the northern part of the survey area, while occurrence south of 67°N was very low during July and early August when the surveys were conducted. Sampling year and herring density were nonsignificant in the model ($p > 0.05$), but there was a clear increase in the

Fig. 6. Median feeding ratio (circles) with 25% and 75% quantiles (error bars) for salmon, mackerel and Norwegian spring-spawning herring. Herring were not present in the area sampled in May. Figure produced in R (R Core Team 2019) with ggplot2 (Wickham 2016).



probability of occurrence with the log of mackerel CPUE ($p < 0.001$; Fig. 7). Note that the mackerel effect appears linear due to the log-transformation of the mackerel covariate, but if plotted on raw scale, the main effect would occur at low mackerel densities as the fitted smooth function decelerates at higher values.

Time series analyses

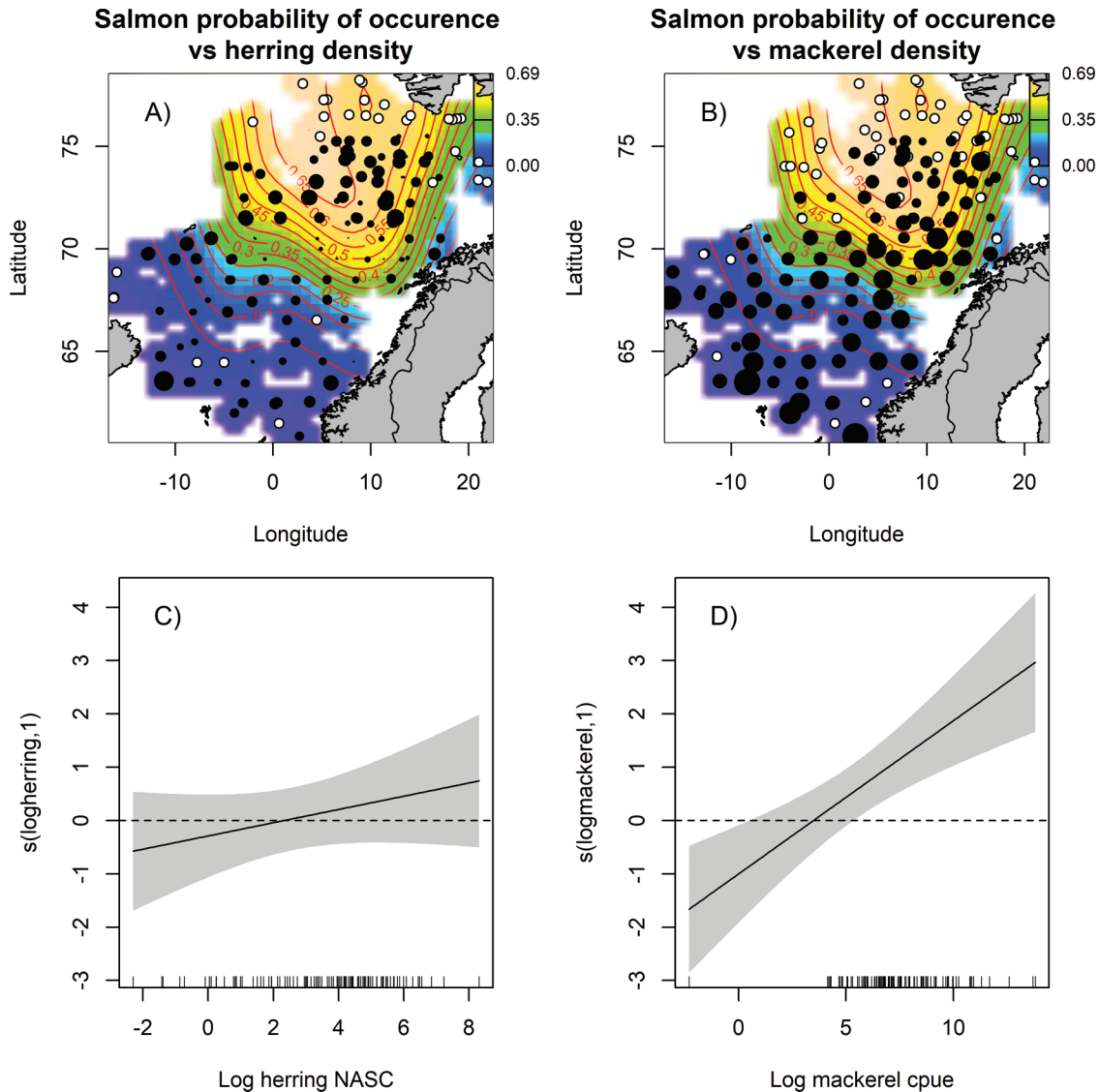
The 1SW PFA for both NNEAC and SNEAC, as well as Norway only, have declined since the 1980s to present. Estimated marine survival for the five index rivers shows interannual variation but a general declining trend, except for Elidaar (Iceland) where survival also is variable but without a temporal trend. The abundance of mackerel decreased during the late 1980s and throughout the 1990s to a low level in the early 2000s before it increased again around 2007. Both NSSH and blue whiting stocks were low in the 1980s but started to increase in the 1990s. Blue whiting abundance peaked in 2003, while NSSH abundance peaked in 2008. The combined SSB for mackerel, NSSH, and blue whiting increased since 1982 until 2004 and has remained fairly stable since then (Fig. 8).

A total of six pelagic fish time series were correlated against eight salmon time series (Table 5). There was no significant correlation between most of the time series. There is a positive correlation between mackerel SSB and estimated salmon PFA for Norway, blue whiting SSB and salmon PFA in NNEAC, estimated marine survival for salmon from Elidaar and NSSH SSB, and between the IESSNS index and estimated marine survival for salmon from the river Corrib. There is a significant negative relationship between salmon PFA in NNEAC and NSSH SSB.

Discussion

The present study addresses potential interactions between salmon postsmolts and other pelagic fish species, which has been hypothesized to affect postsmolts negatively (Potter and Crozier 2000). Here we present a large dataset with good spatial and temporal coverage that provides new insights into the level of

Fig. 7. Results from generalized additive models (GAMs), showing (A–B) the partial effect of spatial position on salmon probability of occurrence, ranging from blue (low) to yellow (high) probability. Black circles are proportional to (A) the log of herring density and (B) the log of mackerel density (circle size is not comparable between plots). Circles filled with white show stations without reports of catch of herring or mackerel. Panels C and D show GAM smooth functions of the partial effects of herring and mackerel density, respectively, on salmon probability of occurrence. The y axis represents deviation from mean predicted value for changing values of the covariate (x axis) on the scale of the linear predictor (i.e., on the logit link scale used here, a value of 2 on the y axis corresponds to a 76% increase in salmon probability of occurrence compared with the mean). Figures and map produced in R (R Core Team 2019) with ggplot2 (Wickham 2016) applying R packages mapdata version 2.3.0. and itsadug (van Rij et al. 2017).



interactions between salmon and other pelagic fish in the sea. Our analyses did not reveal evidence for strong interactions between postsmolts and pelagic fish when estimating the diet and spatial overlap or by correlating time series of salmon abundance and survival with pelagic fish abundance. Each of the three processes (diet, spatial distribution, temporal abundance–survival) are discussed separately before a broader overview is presented.

Stomach content and feeding ratio (FR)

The diet during summer feeding in the Northeast Atlantic has previously been described for postsmolts, mackerel, NSSH, and blue whiting (e.g., Rikardsen et al. 2004; Prokopchuk and Sentyabov 2006; Haugland et al. 2006; Hvidsten et al. 2009; Langøy et al. 2012; Bachiller et al. 2016). However, there are few studies addressing the diet of postsmolts after the initial estuary and fjord entry. The

novelty of this study lies in its analysis of diet of postsmolts and other pelagic fish sampled during the same surveys, where most of the samples come from trawl hauls catching at least two of the named species. The data presented from this study supports earlier findings for each of the species. Mackerel and NSSH mainly feed on various zooplankton species, with *Calanus finmarchicus* as an important part of the diet (Prokopchuk and Sentyabov 2006; Langøy et al. 2012; Bachiller et al. 2016). For postsmolts, the diet is mainly composed of fish larvae and amphipods (Rikardsen et al. 2004; Haugland et al. 2006). The relative abundance of the different prey organisms in the Northeast Atlantic is not known in detail, but *C. finmarchicus* constitutes a large part of the planktonic biomass in the Norwegian Sea during spring and summer (Melle et al. 2004). It is therefore likely that postsmolts selectively feed on fish larvae and a few zooplankton species, while mackerel and NSSH are more opportunistic

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Fig. 8. Temporal development of time series for salmon and pelagic fish used in correlation analyses. Figure produced in R (R Core Team 2019). 1SW, one sea-winter; NNEAC, Northern Northeast Atlantic Commission; SNEAC, Southern Northeast Atlantic Commission; PFA, prefishery abundance; SSB, spawning stock biomass; NSSH, Norwegian spring-spawning herring; IESSNS, International Ecosystem Summer Survey in Nordic Seas.

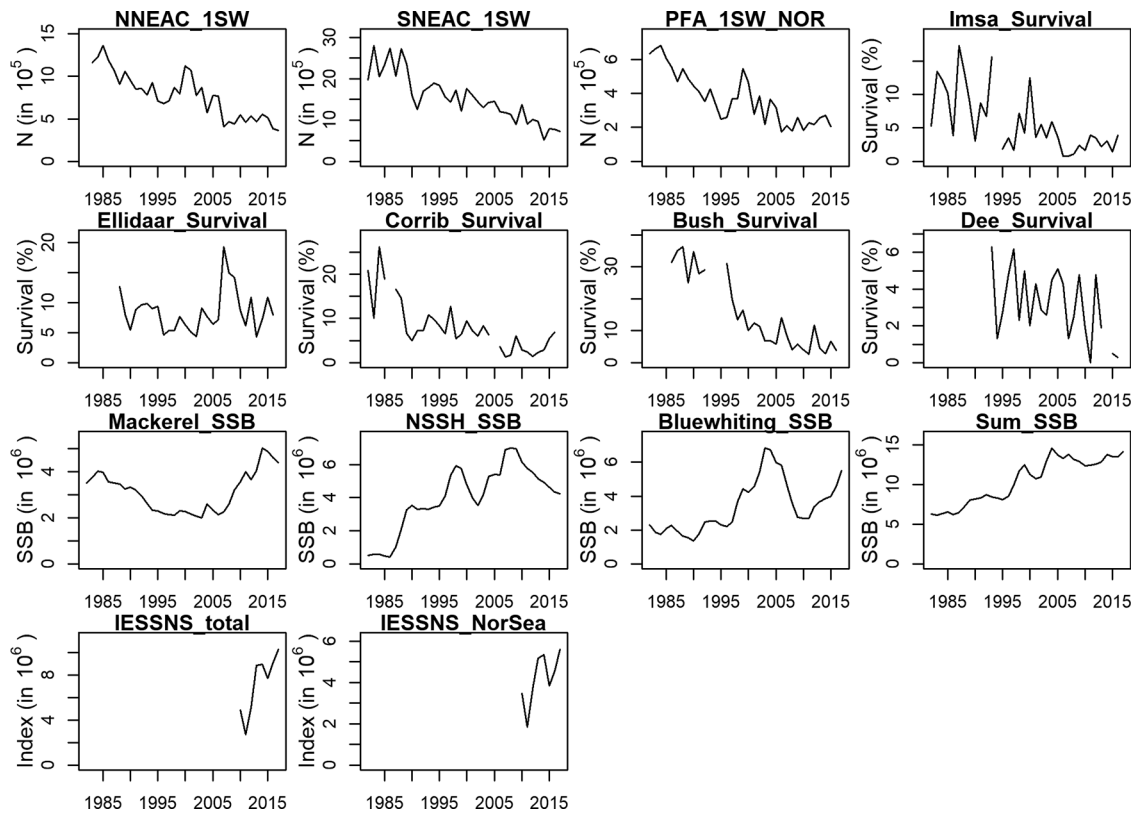


Table 5. Pearson's correlations between time series of one sea-winter (1SW) salmon and pelagic fish.

Salmon	Pelagic fish					
	Mackerel SSB	NSSH SSB	BW SSB	Pelagic SSB	IESSNS Total	IESSNS NS
NNEAC 1SW	-0.117	-0.473**	0.365*	-0.172	0.523	0.608
SNEAC 1SW	-0.182	-0.041	-0.103	-0.211	-0.164	-0.128
NOR_1SW	0.454**	-0.080	-0.255	0.035	0.549	0.525
Imsa	0.078	-0.104	-0.192	-0.166	0.576	0.512
Elidaar	0.010	0.432*	-0.203	0.194	-0.535	-0.550
Corrib	0.135	-0.181	0.104	-0.045	0.752*	0.549
Bush	-0.121	-0.030	-0.164	-0.315	0.498	0.450
Dee	-0.009	0.058	0.046	0.098	0.150	0.387

Note: BW, blue whiting; IESSNS NS, IESSNS survey for Norwegian Sea only; see Table 2 for other definitions. Significance levels are indicated as follows: *, $p < 5\%$; **, $p < 1\%$.

in the prey search (Langøy et al. 2012). Selective prey search for postsmolts has previously been shown (Jacobsen and Hansen 2000; Salminen et al. 2001; Renkawitz and Sheehan 2011). Even in June in the Norwegian Sea, where *C. finmarchicus* most likely were abundant given the high proportion of this prey in NSSH and mackerel stomachs and the high abundance of *C. finmarchicus* generally observed in the Norwegian Sea at this time period (Bagoien et al. 2012), postsmolts barely consumed *C. finmarchicus*. Overall the diet overlap is low and never significant between postsmolts and the other two species. Many of the prey organisms are consumed by all three species, but in varying proportions. The exception being amphipods, which composed a large part of the diet for all three species in July. Although mackerel feed on smaller amphipods than postsmolts, they both feed on juvenile amphipods, and the minor difference in amphipod size may be due to

small-scale geographic variation in size distribution or the filter feeding capability of mackerel (Macy et al. 1998). The results indicate that all three fish species mainly feed on juvenile *Themisto* (Noyon et al. 2011). The large proportion of amphipods in the diet in early July for all three species gives the highest diet overlap between postsmolts and mackerel and NSSH in this period. Euphausiids are another prey item consumed by all three species. However, it is not the dominant prey item for postsmolts in any of the sampled time periods. There are observations of unidentified fish larvae in the mackerel stomachs in July but not in June. We hypothesize that this is herring larvae, as herring is only identified from postsmolt stomachs sampled in July and the fact that mackerel have previously been reported to prey on herring larvae (Skaret et al. 2015). Mackerel in Icelandic waters feed on larvae of sandeel and mesopelagic fish (Óskarsson et al. 2016). Hence,

mackerel and postsmolts prey on larvae of the same fish species. One sea-winter salmon and older salmon can prey on mackerel and herring in the Norwegian Sea (Jacobsen and Hansen 2001). The stomach samples presented here did not find evidence for mackerel predation on salmon postsmolts. Further, mackerel predation on salmon has not been mentioned in any previous publications presenting the diet of mackerel in the Northeast Atlantic (Langøy et al. 2012; Óskarsson et al. 2016; Skaret et al. 2015; Bachiller et al. 2016). The FR is not a measurement of whether the fish consume enough energy for growth and metabolism, but differences in FR between species can be an indication of interspecific competition. The FR is generally higher for postsmolts than for NSSH. However, NSSH start their feeding season before postsmolts and are more dependent on feeding in the spring (Varpe and Fiksen 2010). A lower FR during the summer for NSSH than for postsmolts is as expected, as salmon feed intensively throughout the summer (Haugland et al. 2006). Mackerel had a much higher feeding ratio than postsmolts in May, but this was south of the Norwegian Sea. Later in the summer, in the Norwegian Sea, postsmolts had a similar or higher FR as mackerel. Salmon have a faster somatic growth in the sea than mackerel. Thus, it is reasonable to assume that salmon need a higher daily energy intake than mackerel to achieve normal somatic growth. However, this can also be achieved by feeding on higher-energy prey or by lower energy utilization, for instance associated with metabolism.

The importance of fish biomass and other ecosystem components

Although the diet overlap is low, mackerel and (or) NSSH can potentially affect the prey availability for salmon due to their larger biomass. The biomass of prey consumed by the pelagic fish quickly exceeds the biomass consumed by salmon when there is an overlapping diet. The mackerel stomachs sampled in the Norwegian Sea consisted of 0%–2% fish larvae, while it was almost 10% in the mackerel stomachs sampled northwest of Ireland. These were lower than the proportion of fish larvae in postsmolt stomachs. However, there are many more mackerel compared with postsmolts feeding in the Northeast Atlantic. If ~50% of the mackerel stock feed in the Norwegian Sea (Olafsdottir et al. 2018), there are now more than 2 million tonnes of mackerel in the postsmolt feeding areas. Further, assuming the postsmolts are 120 g, 3 500 000 adult fish return annually to their home rivers, a survival rate of 5%, and they all feed in the Norwegian Sea, there are <10 000 tonnes of postsmolts. The abundance of mackerel, NSSH, and blue whiting are orders of magnitude larger than that of postsmolts (ICES 2018b), and so is the total consumption. NSSH, mackerel, and blue whiting are estimated to consume 100–150 million tonnes of prey annually (Bachiller et al. 2018), but this also includes feeding outside of the Norwegian Sea ecosystem. Hence, even with a low diet overlap, interactions with pelagic fish may potentially affect the feeding conditions for postsmolts. However, according to Skjoldal et al. (2004), the pelagic fish are not assumed to be the most important predators on zooplankton in the Norwegian Sea ecosystem. Amphipods are estimated to consume nearly 200 million tonnes of prey annually, mainly smaller zooplankton (Skjoldal et al. 2004). Mesopelagic fish and the squid *Gonatus* are also important predators, with estimated annual consumption of 110 and 45 million tonnes wet weight prey, respectively (Skjoldal et al. 2004). Changes in biomass or spatial distribution of the key invertebrate predators in the Norwegian Sea ecosystem can most likely affect marine feeding conditions for both salmon and other pelagic fish.

Spatial overlap

The spatial overlap between postsmolts and NSSH is low. The probability of observing postsmolts did not increase with NSSH density. Hence, postsmolts and NSSH do not tend to aggregate in the same geographic areas. Further, the vertical overlap is most

likely low since NSSH are normally located deeper than postsmolts (Huse et al. 2012; Holm et al. 2000). Postsmolts were found in the northern part of the Norwegian Sea, while adult NSSH were found farther southwest during the summer (ICES 2009). There was, however, a geographic overlap between postsmolts and juvenile NSSH in part of the distribution area of the postsmolts. Although the spatial modelling did not indicate that postsmolts and NSSH aggregated in the same geographic areas in 2008 and 2009, the geographic overlap between NSSH and postsmolts could have been greater in earlier periods, as the NSSH stock was found farther east and north in the Norwegian Sea in July–August during the 1990s and early 2000s (Utne et al. 2012). Mackerel, on the other hand, tend to aggregate in the same areas as postsmolts. The analyses presented here using data from 2008 and 2009 showed that mackerel are not found as far north as postsmolts, and there are large areas in the central and southern Norwegian Sea where mackerel are abundant but postsmolts were absent (Fig. 7b). However, a northward expansion of the mackerel stock after 2008–2009 (Nøttestad et al. 2016) has most likely resulted in a higher geographic overlap between postsmolts and mackerel in the past decade. Both species are located close to the surface during the summer (Nøttestad et al. 2016; Holm et al. 2000). However, the differences in diet during late June could indicate a small difference in feeding depth, as postsmolt feed on *A. patersoni*, a copepod living close to the surface, whereas mackerel fed mainly on *C. finmarchicus*, which are found in shallow depths but not directly at the surface.

Correlation analyses

Interactions with the NSSH stock have previously been suggested as a potential explanatory variable for changes in salmon abundance (Haugland et al. 2006), and the time series analysis presented here shows a negative correlation between NSSH abundance and PFA for NNEAC, which could potentially be due to feeding interactions. However, the result must be treated with caution, as data from 2000 and 2007 greatly affected the result, and the correlation is not significant when these years are excluded. These years are not classified as outliers and are therefore not excluded from the final calculations. The limited spatial and dietary overlap between postsmolts and NSSH reduce the probability of strong population regulating mechanisms between the two species. Postsmolts have a higher spatial overlap with mackerel, and interactions between these two species should therefore be expected to be higher than between postsmolts and NSSH. The time series for salmon PFA and survival were correlated against both stock estimates and survey indices of mackerel abundance, without revealing any significant negative correlation for any of the time series. The positive correlations between mackerel SSB and salmon PFA in Norway and between the IESSNS index and marine survival for salmon from the river Corrib in Ireland cannot be explained by feeding interactions. Perhaps bottom-up processes are affecting both postsmolts and mackerel, but this link is beyond the scope of this study. Overall, the lack of correlation between the time series of abundance of pelagic fish and salmon indicates that feeding interactions between Atlantic salmon postsmolts and other pelagic species in the Norwegian Sea are not the main drivers for the observed reduction in salmon PFA and marine survival.

Sources of uncertainty

There are several sources of uncertainty within the datasets used and also within the analyses. The digestion rate for fish larvae is faster than that for copepods (Hallfredsson et al. 2007). The proportion of fish larvae in the diet may therefore have been underestimated for all three fish species in this study. Sampling of fish was only done with surface hauls, and both diet and stomach fullness can change with vertical distribution of the fish. This is especially the case for NSSH, which also feed at several

hundred metres depth (Nøttestad et al. 2007). Further, the lack of prey group weights for the Faroes samples made it necessary to estimate these weights based on the total stomach weight and prey group weights from Norwegian or Irish samples. The comparison of stomach samples from the Norwegian Sea from different nations showed that the lack of prey weights from Faroese samples did not have a large effect on the presented results. Testing the resource overlap against a null model using weights can have limitations, as the models do not test for independence or spatial and temporal sources of variation. Further, testing by prey weight can give a biased estimate of selectivity due to size differences between prey (Araújo et al. 2011). We included these analyses in the study, as the size difference between fish larvae and zooplankton were relatively small, as stomachs of several species were sampled from the same trawl hauls, and trawl hauls were normally taken over a larger geographic area.

Concluding remarks

It is generally difficult to make firm conclusions concerning large-scale marine processes with high temporal and spatial variability. The mechanisms affecting spatial distribution and marine survival for postsmolts or for mackerel and NSSH are still not understood. However, potential feeding interactions resulting in reduced growth and survival of postsmolts could be revealed by indices such as diet overlap, spatiotemporal overlap, and negatively correlated abundance series. Postsmolts prey on larvae of herring and blue whiting (Haugland et al. 2006; Rikardsen and Dempson 2011), while 1SW and older salmon feed partly on both juvenile and adult pelagic fish (Jacobsen and Hansen 2001). In the Pacific Ocean, large jack mackerel (*Trachurus symmetricus*) have been observed to consume salmon smolts (Emmett and Krutzikowsky 2008). Mackerel predation on salmon postsmolts in the Northeast Atlantic can potentially happen as mackerel partly feed on small fish opportunistically (Iversen 2004). However, some species of Pacific salmon have smaller smolt than Atlantic salmon, making the smolt vulnerable to smaller predators such as jack mackerel. No salmon postsmolts were observed in the 678 mackerel stomachs presented here, nor have other publications of mackerel diet in the Northeast Atlantic reported such findings (Langøy et al. 2012; Óskarsson et al. 2016; Skaret et al. 2015; Bachiller et al. 2016). Postsmolts and mackerel or herring can compete directly for prey in areas or periods with limited prey or indirectly through trophic regulation ultimately affecting prey species. Fish larvae and carnivorous zooplankton often feed on *C. finmarchicus*, which is the most important prey for mackerel and NSSH. Pelagic fish may therefore potentially affect postsmolt feeding through competitive foraging. The species may also negatively affect each other due to aggregation in areas, causing a high fish density, in turn attracting predators that otherwise would migrate elsewhere. However, all the mentioned interactions should lead to a negative correlation between the abundance of pelagic fish and postsmolt if the interactions were strong. In our study, the diet overlap between postsmolts and NSSH or mackerel is low, and postsmolts have a low geographic overlap with NSSH. However, postsmolts overlap geographically with mackerel. Further, there is a weak to no correlation between the abundance or survival of salmon from key index rivers and the abundance of pelagic fish. In conclusion, it has not been shown in this study that the observed temporal changes in marine growth and survival of salmon is a result of feeding interactions with pelagic fish. It should, however, be emphasized that biological interactions occurring over large geographic areas and with large spatial and temporal variation can seldom be fully understood from biological sampling alone. Even though there seems to be limited interactions between postsmolts and pelagic fish in the Northeast Atlantic in general, there may still be local feeding interactions with pelagic fish negatively affecting postsmolts from certain regions in some years.

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