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Original Article

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Geographic distribution, abundance, diet, and body size of invasive pink salmon (*Oncorhynchus gorbuscha*) in the Norwegian and Barents Seas, and in Norwegian rivers

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We report for the first time the geographic distribution, abundance, diet, and body size of invasive pink salmon (*Oncorhynchus gorbuscha*) in the Norwegian and Barents Seas and Norwegian coast and rivers. We found that pink salmon have spread throughout the Norwegian Sea and along the Norwegian coast, and abundance increased by several orders of magnitude in 2017, with no signs that it has peaked. Marine pink salmon diet comprised mainly fish larvae, amphipods, and krill, but their relative importance varied with geographic distribution. North of 67.5°N, Amphipoda, herring, and saithe were more important, while south of 67.5°N, Euphausiidae and mesopelagic fish abounded. Pink salmon body size was larger in the northern rivers, and to the north of the Norwegian Sea and the Barents Sea, relative to the southern rivers and sea areas. Pink salmon were feeding in the ocean during the winter and spring, and in coastal areas immediately before return to the rivers, but not after they had entered the rivers. There was no geographical pattern in the seasonal timing of river ascent. The geographic pattern in abundance and diet of pink salmon, as reported here, offer a measure of the ecological effect of the invasion.

Keywords: diet, distribution, invasive species, northeast Atlantic, pink salmon.

Introduction

Invasive species can be a major threat to native biodiversity and ecosystem dynamics (Bax *et al.*, 2003; Simberloff *et al.*, 2013). Deliberate spreading of non-native species to new aquatic habitats is widespread and often motivated by economic gain or the wish to improve recreational fishing opportunities. Most introduced species are unable to establish persistent self-recruiting populations (Williamson, 1996); however, in some cases, introduced species can result in economic harm and widespread environmental effects (Pimentel *et al.*, 2005). Several species of salmonids have been spread by humans over large parts of the world, such as brown trout (*Salmo trutta*; MacCrimmon and Marshall, 1968), and multiple *Oncorhynchus* species (Crawford and Muir, 2008) including pink salmon (*O. gorbuscha*).

Pink salmon is an anadromous species native to river systems in the northern Pacific Ocean (Page and Burr, 1991). Pink salmon have a 2-year life cycle and die soon after spawning in rivers in the autumn. The eggs are incubated in the gravel and among rocks on the riverbed and normally hatch during the following winter or early spring. The fry emerge from the riverbed in March–May and leave the rivers soon afterwards. Then, they spend 1 year in the sea with rapid growth before returning to the river to spawn.

Pink salmon is a highly valued fish species, with ∼280000 tonnes caught in fisheries in Russia, Japan, Canada, and the United States in 2020 (NPAFC, 2021). The economic revenue from a commercial fishery targeting pink salmon raised interest in introducing the species to new geographic regions. In the 1950s, there were attempts to introduce pink salmon to tributaries in the eastern part of Canada, but the marine returns gradually declined, and the introduced fish died out (van Zyll de Jong *et al.*, 2004). In Russia, pink salmon were deliberately introduced to rivers draining into the White Sea and Barents Sea in the period 1955–1979 (Zubchenko *et al.*, 2010). These introductions were seen as largely unsuccessful, as self-sustaining populations were not achieved. In 1985, the stocking activity in northwestern Russia was re-initiated, but this time using eggs taken from a river further north on the Russian Pacific coast. This resulted in self-sustaining populations, and the stocking was stopped in 1999 (Zubchenko *et al.*, 2010). Pink salmon fry entering the White Sea resulted in adult pink salmon straying into Norwegian rivers and the Atlantic Ocean, with the first observations in Norwegian rivers in 1960 (Berg, 1977; Sandlund *et al.*, 2019). The number of pink salmon in Norwegian rivers remained low until a sudden increase in 2017, when >6000 individuals were caught or observed in Norwegian rivers (Sandlund *et al.*, 2019).

The marine phase of pink salmon's life cycle in the Atlantic Ocean is poorly understood. Individuals emigrating from rivers in northern Norway or northwestern Russia

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enter the Barents Sea or the White Sea. Recent observations of pink salmon around Greenland (Nielsen *et al*., 2020) and Ireland (Millane *et al*., 2019) showed that pink salmon can perform long distance migrations in the northeast Atlantic Ocean. Large parts of the northeast Atlantic Ocean are therefore potential feeding habitats. These productive areas are used as feeding grounds by several large fish stocks such as Norwegian spring-spawning herring (*Clupea harengus*), mackerel (*Scomber scombrus*), blue whiting (*Micromesistius poutassou)*, capelin (*Mallotus villosus*), and polar cod (*Boreogadus saida*; Utne *et al*., 2012; Hop and Gjøsæter, 2013). These ocean areas are also important feeding areas for Atlantic salmon (*Salmo salar*; Gilbey *et al*., 2021; Rikardsen *et al*., 2021). Pink salmon are known to impact the marine ecosystem through competition for prey with other fish and bird species in the North Pacific Ocean (Shiomoto *et al*., 1997; Ruggerone and Nielsen, 2004). Hence, it is important to understand the distribution of pink salmon in the Norwegian and Barents Seas and the potential ecological interactions, given the role of pink salmon as an invasive species. Furthermore, knowing the marine distribution of pink salmon can aid in understanding how factors in the marine phase regulate the geographic distribution and number of pink salmon entering the rivers, and can serve as a warning signal to invasion mitigation managers.

In this study, the first objective is to present pink salmon geographic distribution and abundance in the Norwegian and Barents Seas, Norwegian coast, and Norwegian rivers. The dataset includes pink salmon catches in scientific surveys and commercial fisheries at sea, in coastal bag- and bend-net fisheries for Atlantic salmon, by recreational fishers in rivers and coastal areas, by targeted removal of pink salmon in the rivers, and by monitoring surveys in the rivers. Second, we examine the temporal and spatial variation in abundance, body size, and stomach content of pink salmon sampled at sea and in rivers, as well as the timing of river entry after the ocean migration. These parameters are key for quantifying the impact of invasive species, as they provide information not only on the size of the invasion, but the ecological position of pink salmon in the marine environment and thus its potential interaction with other organisms (Kumschick *et al*., 2015).

Material and methods

Marine data

Data on the marine distribution of pink salmon mainly come from samples taken as bycatch in scientific surveys targeting other pelagic species. In addition, we considered pink salmon caught as bycatch in commercial fisheries targeting other pelagic species reported by the Norwegian reference fleet (Clegg and Williams, 2020), which is a random sample of fishing vessels that report detailed information about all bycatches. Pink salmon were caught in nine scientific surveys between 2013 and 2021 (Supplementary Table S1). Most of the catches were taken during the International Ecosystem Survey in Nordic Seas (IESNS), which covers the Norwegian Sea and represents a valuable time series of observations on the distribution of pelagic fishes since 1995. During the IESNS, trawling was done with medium-sized trawls on the surface and deeper in the water column, but the exact characteristics of the trawl varied among years and countries (Supplementary Table S1).

Data from the scientific survey trawl hauls ($N = 246$ individuals, Supplementary Table S1) were used to show temporal and geographic distribution of pink salmon catches, estimate the geographic area with the highest probability to catch pink salmon (capture probability, only using IESNS data), estimate the geographic variation in individual body length, and to explore diet during the marine phase. According to their body size, most individuals considered here were caught in the year they were expected to return to the rivers for spawning, and not as post-smolts during the first months after leaving the rivers. Twelve individuals were caught in the Barents Sea in December, which are the only post-smolts in our data, and thus were excluded from the body length analysis, but not from the diet analysis. The sporadic samples taken as bycatch in commercial fisheries from the reference fleet ($N = 17$) were included in the analyses of geographic distribution of pink salmon abundance, variation in body length, and diet, but not in the capture probability analysis.

Stomachs were retrieved for diet analyses from 134 pink salmon captured in the Norwegian and Barents Seas during 2015–2021, of which 95 were collected during the scientific surveys, 17 by the reference fleet, and 22 retrieved from illegal gillnets by the Norwegian Nature Inspectorate (SNO). Twelve of these were the post-smolts caught in December during scientific surveys, while the remaining were caught during May–June. The 22 individuals from the illegal gillnets were caught in fjords in northern Norway at three adjacent locations (~70°30′N 21°30′E) and were only considered in the diet analyses. The stomach content was visually identified to species level when possible, or to closest family if too digested for species identification. Prey taxonomic groups (see next paragraph) from each stomach were dried separately at 70°C for >24 h, and the dry weight was recorded. Due to assumed temporal and spatial differences in diet, the total diet composition in percentage of weight was aggregated into the following groups based on capture location: (1) southern Norwegian Sea (south of 67.5°N; $N = 35$) in early May, (2) the deep basin part of the northern Norwegian Sea (north of 67.5°N; $N = 18$) in late May, (3) the northern Norwegian continental shelf and into the Barents Sea in late May and early June (north of 67.5°N; $N = 47$), (4) northern Norwegian fjords in late June ($N = 22$), and (5) the western Barents Sea in December ($N = 12$).

The content of all stomachs in each period was summarized to calculate the diet proportion by weight and categorized in up to 11 different prey groups for visualization purposes. For the samples from the Norwegian Sea, Norwegian continental shelf and Barents Sea in May–June, crustaceans were identified as (1) Copepoda, (2) Isopoda, (3) Amphipoda, including all amphipods except those of the genus *Themisto*, (4) *Themisto spp*., (5) Euphausiidae, or (6) Crustacea, including all crustaceans not included in the former groups or too digested to be identified to lower taxon. Teleosts were identified as (7) *C. harengus*, (8) mesopelagic fish (mainly lanternfishes from the genus *Benthosema* and other genus in the family Myctophidae, but also Mueller's pearlside, *Maurolicus muelleri*), or (9) Teleostei unspecified. In addition, prey could be identified as (10) Cephalopoda or (11) other invertebrates, which consisted of a range of different species of zooplankton and insects, each with a minor contribution to the total biomass of consumed prey. For the samples retrieved from illegal gillnets in a fjord in northern Norway ($N = 22$) and the 12 post-smolts caught in the Barents Sea in December, prey were identified as (1) Euphausiidae, (2) other invertebrates, (3) pricklebacks (*Stichaeidae spp*.), (4) saithe (*Pollachius virens*), or (5) Teleostei unspecified. To understand how the diet varied within the sampled geographic area, the diet proportion by weight was calculated for each geographic location and visualized as pie charts on a map, where diet was aggregated into the main prey groups: fish, amphipods, euphausiids, cephalopods, and other prey.

The feeding ratio (*FR*) is an estimate of the wet weight of the stomach content relative to the fish weight. It is a snapshot of the stomach content at the time of sampling. The *FR* was calculated by using the following equation:

$$FR = 100m_s / \left(m_f - m_s\right),$$

where m_f is the mass (g) of the fish and m_s is the mass (g) of the stomach content. The average *FR* for each sampling location was calculated.

Coastal fishery

Pink salmon were caught in two types of coastal fisheries in Norway. One fishery is a licensed salmonid coastal fishery using bag nets and bend nets inside fjords targeting Atlantic salmon on their return migration to the rivers. As this fishery exclusively targets salmonids, it is strictly regulated in terms of fishing periods and locations. Reporting the catch of pink salmon in this fishery has been mandatory since 2019 and catch data for pink salmon were not available prior to 2019. The number of pink salmon caught in this fishery was retrieved from Statistics Norway (www.ssb.no). The data were aggregated by county per year for the period 2019–2021. It should be noted that this fishery is not evenly distributed along the Norwegian coast; many areas in southern Norway are closed for this fishery, and the main activity is in the northern part of Norway. The fishing effort was equal in 2019 and 2020 (number of fishers and fishing period). In 2021, the fishing effort was reduced (fewer fishers and shorter season) or closed in many areas, particularly in and around the Tana fjord by the Barents Sea.

The second type of coastal fishery is the recreational fishery, from which we have reports of pink salmon caught by angling, gillnets, and trolling. This fishery is not strictly regulated, except various restrictions on the gillnet fishery (depth, mesh size, etc.). There was no reporting system in place before 2017. From 2017, some fishers have used a new reporting system to register their catches, but the reporting system has not been well known among the fishers, and fishers using it did not always report individual body length, weight, or total number of caught individuals. The total fishing effort for the Norwegian recreational coastal fishery is largely unknown (Vølstad *et al*., 2020), but here it is assumed to be constant from 2017 to 2021. Due to the opportunistic nature of the catch in the coastal fishery, and the lack of standardized reporting, the data from both coastal fisheries were used as supporting information to document the geographic distribution in the sea, but not in statistical analyses.

River observations

Data on river distribution of pink salmon come from four different sources: (1) catches reported by recreational anglers, (2) catches from targeted removal fishery of pink salmon, (3) after-season targeted removal of Atlantic salmon aquaculture escapees, where the number of pink salmon caught in the process is now also reported, and (4) observations during monitoring surveys by snorkelling or recordings of video cameras installed in numerous fishways, which were originally established for monitoring Atlantic salmon and brown trout spawners (Berntsen *et al*., 2018, 2020, 2022; Sandlund *et al*., 2019). It should be noted that reporting of pink salmon by anglers became mandatory only from 2019. However, the increased awareness of the pink salmon invasion among anglers resulted in increased reporting already in 2017. Thus, this data source is affected by the changes in reporting after 2017. River data (all four sources) were used to report the temporal and geographic distribution of pink salmon in Norwegian rivers and to estimate the geographic variation in body length and date of river ascent. In addition, 69 pink salmon sampled in eight rivers from 62 to 70°N between 1 August and 7 September were checked for stomach content following the same methods explained above for pink salmon caught at sea. Data from rivers and the IESNS were compared for (1) annual total catches to test temporal trends, and (2) body size to explore changes over time and between rivers and the sea.

Statistical analyses

All statistical analyses were performed in R statistical software (version 4.0.5; R core team, 2021).

Maps to visualize the temporal and geographic distribution of all pink salmon from marine, coastal, and river observations were produced with the R-package ggOceansMaps (version 1.2.6; Vihtakari, 2022). We also produced maps showing the geographic distribution of all trawl hauls during the IESNS survey, indicating whether pink salmon were present or absent for each odd year in the period 2013–2021.

To test for geographic trends in (1) body length when captured in the sea (using all marine data), (2) rivers (using all river data), (3) capture probability in the sea (using only IESNS data), and (4) time of river ascent (using river data), generalized additive mixed effect models (GAMMs) were used with a two-dimension thin-plate-regression-splines smoothing term for latitude and longitude (R package mgcv, version 1.8–38; Wood, 2011). The GAMMs with fish body length in sea and rivers, and timing of river ascent followed a Gaussian distribution, while the GAMM for capture probability in the sea followed a binomial distribution (presence/absence in each trawl haul with logit link).

To model pink salmon body length in the river phase, only the years 2017, 2019, and 2021 were considered, as these were the only years with several observations available per year and river. Due to the low number of years available, year was used as a fixed effect factor instead of a one-dimensional smoothing term, and pairwise comparisons between years were carried out with the R package emmeans (version 1.8.1-1; Lenth, 2022). For body size of pink salmon captured in the rivers, we repeated equivalent models only considering a subset of the data, only including fish caught during a 14-d period from the first individual was caught. This subset was used to ensure that the geographical differences were not due to differences among rivers in fishing effort during the season, because, e.g. targeted removal was concentrated in short periods and resulted in large catches in some rivers.

Preliminary analyses of capture probability considering all depths and whether trawl hauls occurred during the day or the night, indicated a significant effect of depth, but no effect of time of trawling (see Supplementary Material). Therefore, to

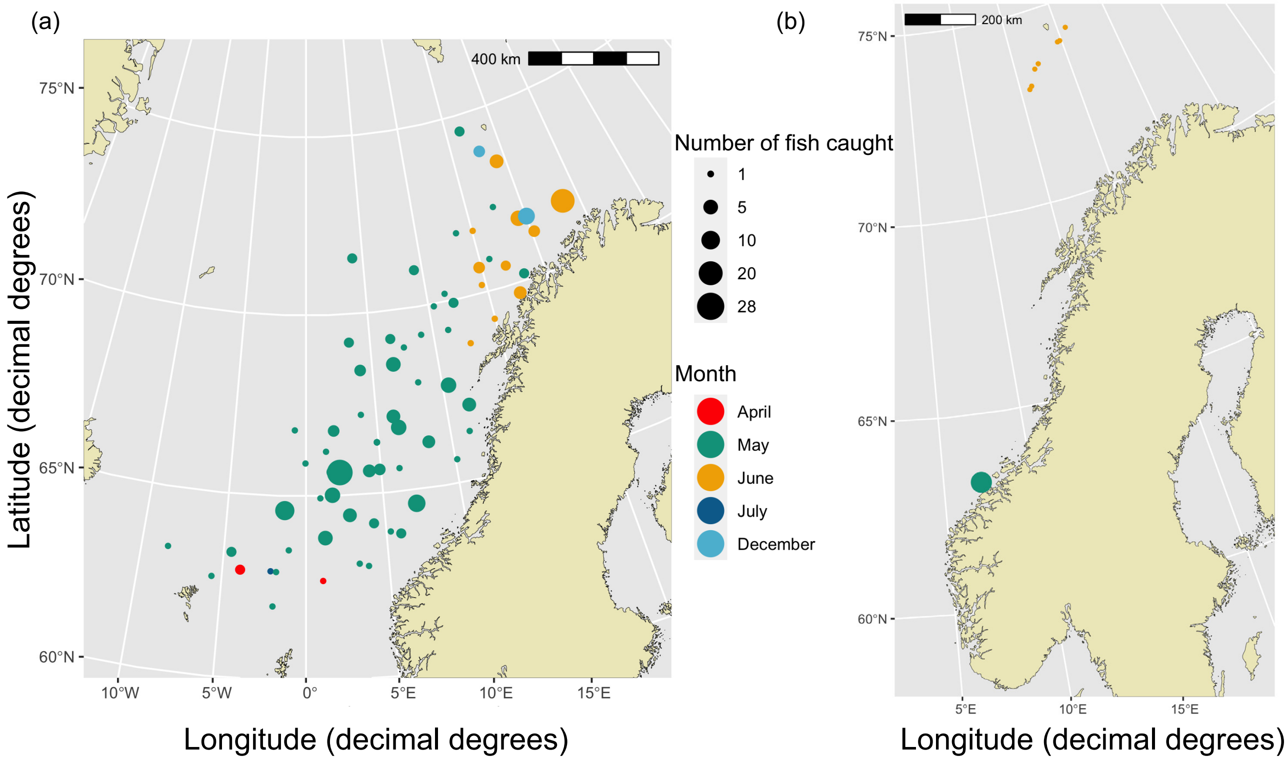

Figure 1. Geographical distribution of pink salmon catches reported from (a) nine scientific surveys (IESNS) between 2013 and 2021, and (b) sporadic samples from commercial fisheries from the Norwegian reference fleet in 2021. Dot size refers to the number of fish caught. Dot colour refers to the month the pink salmon were caught. Note that individuals caught in April–July are adults returning to the rivers for spawning, while those caught in December are probably post-smolts entering the sea in the spring the same year.

estimate capture probability from the IESNS, all hauls catching pink salmon and all other hauls with a maximum depth of the headline at 50 m or less were considered (i.e. both day and night hauls). The depth threshold was set to 50 m based on the preliminary analyses showing that only four pink salmon were caught at greater depth in a total of 760 trawl hauls. Of the pink salmon caught at shallower depths than 50 m, the probability of capture during the day and night did not differ (Supplementary Table S2). Capture probability (presence/absence) instead of number of fish caught, was tested for temporal and geographic distributions due to a high proportion of zero catches in the data set (only IESNS data, because effort and methods were standardized among years in this data set). Catch per unit of effort was calculated by dividing the number of fish caught per trawl haul by the towing distance in nautical miles.

The date of first capture of pink salmon in each river and year was used as a proxy for the start of river ascent (Sandlund *et al.*, 2019). This date was calculated as a consecutive day number starting from the first of June as reference. For river data, we included river identity as a random effect. We also tested for temporal trends in all variables, but year of capture was treated differently for marine and river data. For marine data, year was included as a random effect due to the high correlation between year and spatial position to avoid multicollinearity issues.

A Spearman correlation coefficient was calculated to test for similarities in temporal trends between the total number of fish caught per year in rivers (excluding catches reported by anglers) and in the IESNS during 2013–2021. We performed such correlation twice, considering catches in even and odd years, and only considering catches in odd years. Mean body length per month (April–September) was compared between pink salmon caught in rivers and at sea including all years when data on length were collected (1993–2021 in rivers and 2013–2021 at sea). A linear mixed effect model (LMM) with Gaussian distribution for body length was performed with phase (river vs. sea) as a fixed effect and year as a random effect. R packages ggplot2 (version 3.3.5; Wickham, 2016) and wesanderson (version 0.3.6; Ram and Wickham, 2018) were used for additional plots.

Results

Temporal and geographic distribution of pink salmon catches

Data from the marine scientific surveys showed that pink salmon distribution covers the whole latitudinal range of the Norwegian Sea on the eastern side towards the Norwegian coast (Figure 1a). The first pink salmon were caught as bycatch during the marine scientific surveys in 2013, despite annual surveys in this area since 1995. The geographic distribution of sampled pink salmon is partly a function of survey coverage (Supplementary Figure S1), which does not extend south of the Norwegian Sea (62°N) in the spring. The southernmost individuals were caught in late-April or early May, while individuals further north in the Norwegian Sea were caught throughout May, and individuals in the Barents Sea were caught in June (Supplementary Figure S1). One individual was caught in the Norwegian Sea in July 2021, and 12 individuals were caught in the western part of the Barents Sea

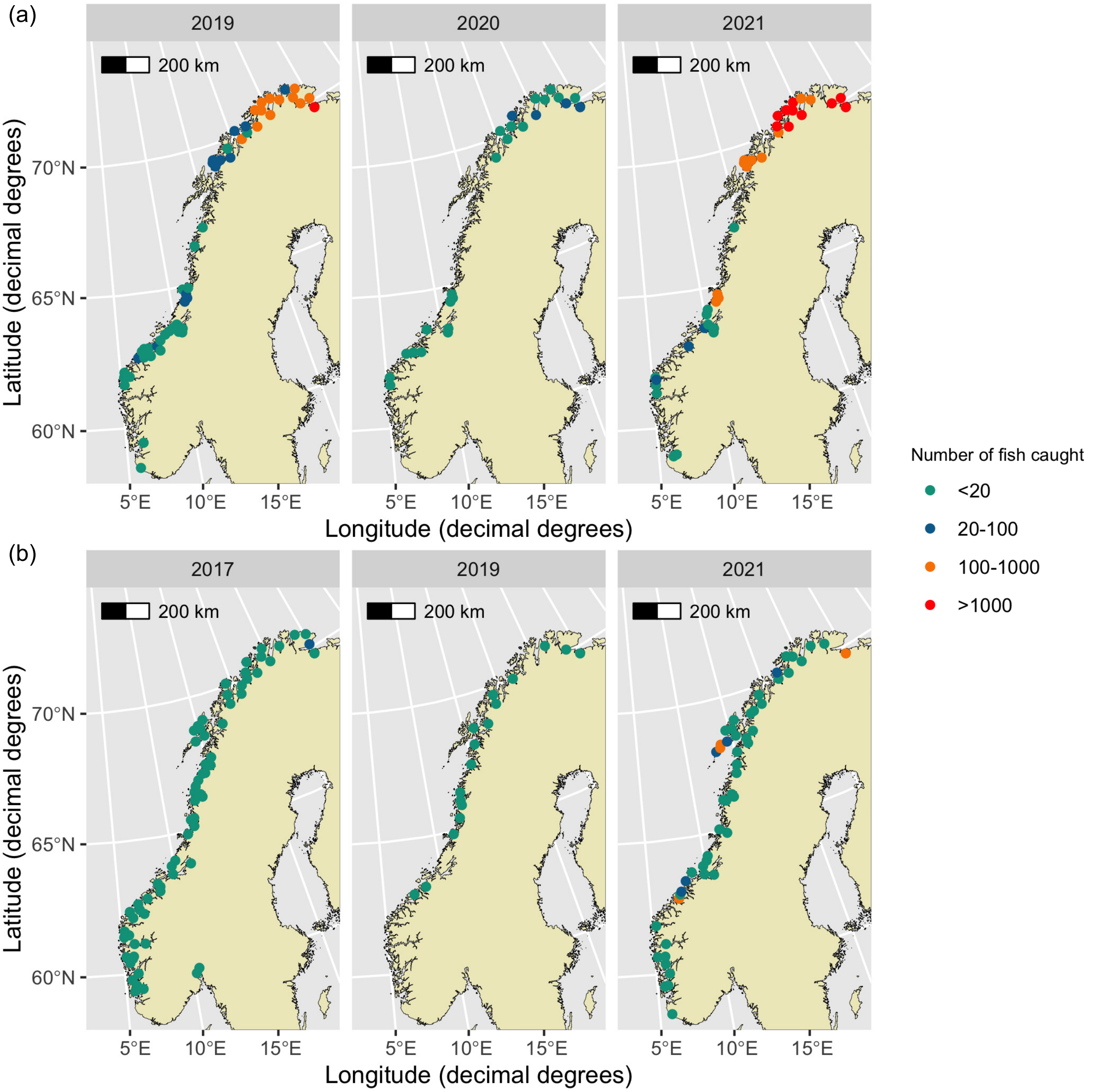

Figure 2. Geographical and temporal distribution of pink salmon coastal catches reported from licensed salmonid (top panels) and recreational (bottom panels) fishers. Dot colour refers to the number of fish caught grouped in four categories.

in December 2018. Pink salmon were caught as bycatch close to the coast off Kristiansund in May 2021 ($N = 10$), and south of Bear Island in the western part of the Barents Sea in June 2021 ($N = 7$) by commercial fishers targeting saithe and haddock, respectively (Figure 1b).

In the coastal fisheries, pink salmon were also caught in the North Sea (Figure 2), which is south of the scientific survey coverage (Figure 1a). The total annual catches in the licensed salmon fishery (mainly bag nets), were higher in 2021 than earlier years despite stricter regulations and a reduced fishing effort (5929 pink salmon caught in 2019, 214 in 2020, and 38933 in 2021, Figure 2a). The reported catches of pink salmon in the coastal recreational fishery were 259 pink salmon in 2017, 0 in 2018, 28 in 2019, 0 in 2020, and 1254 in 2021 (71% caught by angling, 28% by gill nets, 1% by unspecified gear, Figure 2b). Hence, catches in both licensed and recreational coastal fisheries showed that pink salmon were present all along the Norwegian coast, more abundant on odd years, and catches were largest in 2021.

Data on pink salmon in the rivers from 1976 also showed that pink salmon were widely distributed from north to south in Norway (Figure 3), appearing for the first time in the southernmost part of the country (south of 60°N) in 1997, but with annual occurrence in the south only from 2015. Since 2015, the annual catch of pink salmon in the rivers has increased every odd year (Table 1). The largest increase in percentage occurred from 2015 to 2017, but the annual river catches continued to increase every odd-numbered year after that. Catches were higher in odd years than in even years for all data sets (Figures 2 and 3, and Supplementary Figure S1).

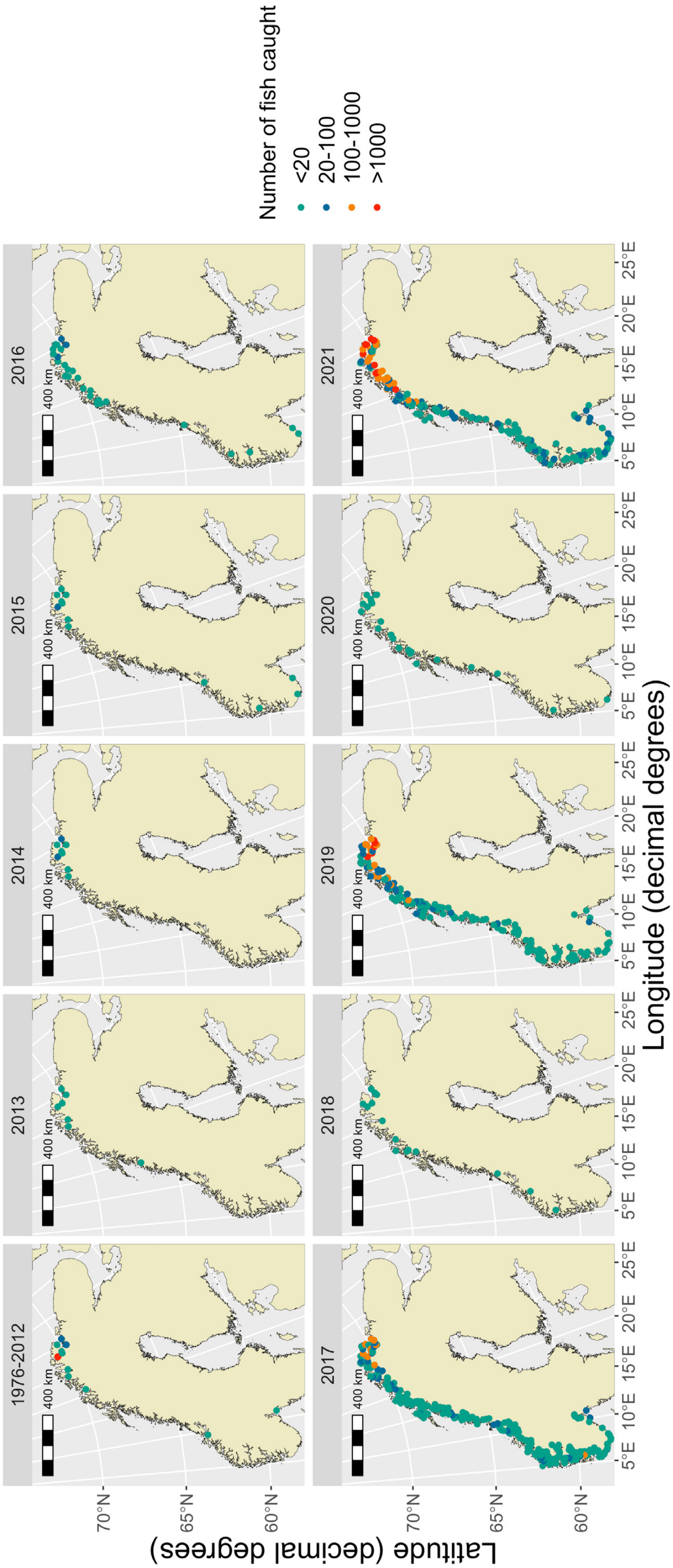

Figure 3. Geographical and temporal distribution of pink salmon from river observations since 1976, including angling, targeted removal fishing, and drift counting by snorkelling. Dot colour refers to the number of fish caught grouped in four categories. Note that years from 1976 to 2012 are pooled and dot size refers to the sum of pink salmon caught in this period.

Table 1. Total annual river catches of pink salmon in Norway, and maximum annual number of pink salmon caught in a single river.

Year	Total catch	Maximum catch in a river
2015	88	48
2016	236	98
2017	11 483	1 958
2018	41	10
2019	15 721	1 646
2020	41	7
2021	112 485	20 153

Table 2. Annual average ($\bar{x}$) scientific survey catch of pink salmon given as individuals per nautical mile (ind./nmi) and standard deviation for odd years.

Year	$\bar{x}$ ind./nmi	SD ind./nmi
2013	0.21	0.91
2015	0.03	0.16
2017	0.26	0.52
2019	0.29	0.76
2021	0.69	1.31

Marine observations: probability of capture, body size, and diet

Probability of capture was affected by the geographic position of the trawl haul, after controlling for annual sampling differences (GAMM; year: estimated df = 0.94, maximum df = 1, $c^2 = 13.46$, $p = 0.0002$). Capturing pink salmon was more likely in the eastern part of the Norwegian Sea and around 65°N (GAMM; longitude and latitude: estimated df = 4.2, maximum df = 6, $c^2 = 11.73$, $p = 0.05$) than in other areas of the Norwegian and Barents Seas. A second model only considering odd years showed that there was a higher probability of capture near the Norwegian coast around 65°N, while north of 70°N the probability of capture was higher further away from the coast (GAMM; longitude and latitude: estimated df = 4.5, maximum df = 6, $c^2 = 14.36$, $p = 0.029$; Figure 4), still controlling for the annual differences in sampling (GAMM; year: estimated df = 0.98, maximum df = 1, $c^2 = 20.7$, $p < 0.001$). In odd years, the average annual catch per unit of effort ranged from 0.03 to 0.69 individuals/nautical mile in 2015 and 2021, respectively (Table 2), while in even years, the catch was much lower (0–0.02 individuals/nautical mile). There was large variation in the number of pink salmon caught per trawl haul (see standard deviations in Table 2). In 61% of the trawl hauls that caught pink salmon in odd years, more than one individual was captured.

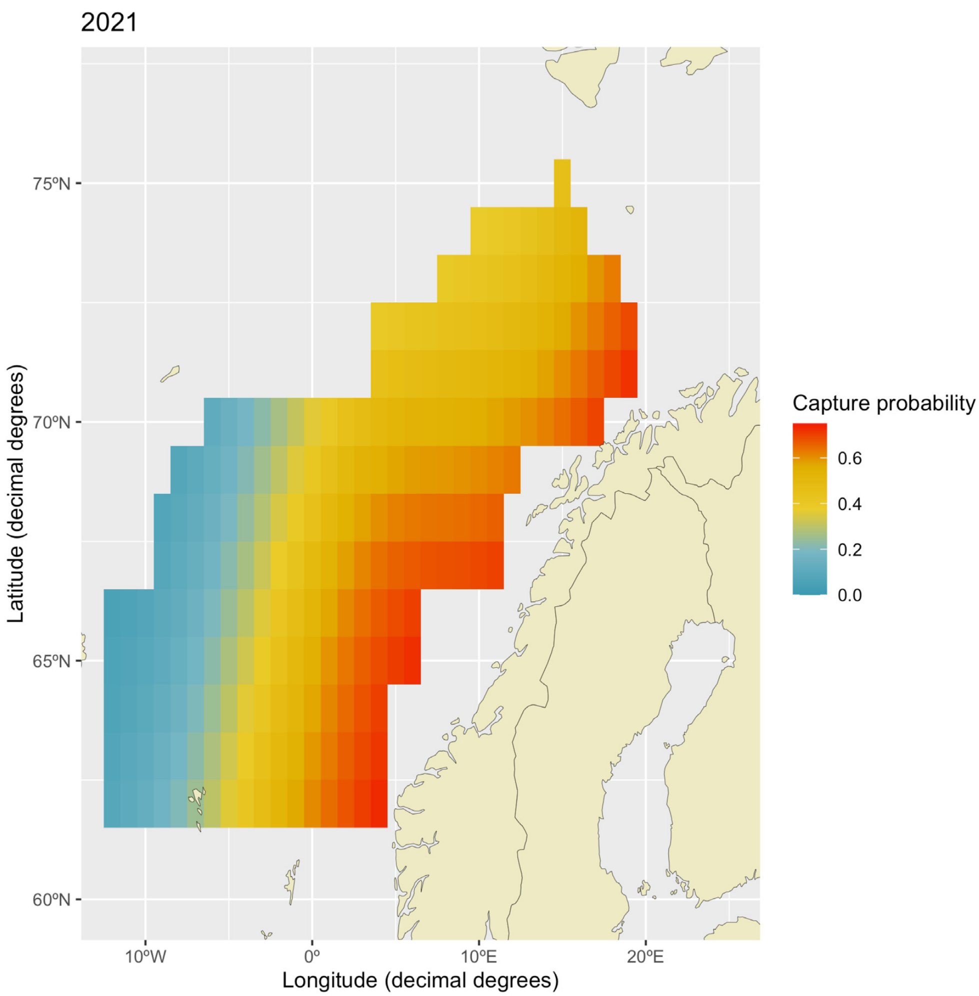

Figure 4. Geographical distribution of the capture probability of pink salmon in the Norwegian Sea in 2021, where warmer colours show higher probability of capture relative to colder colours. Annual patterns can be found in Supplementary Figure S3.

Data from marine surveys showed that pink salmon body length (mm) increased towards the north in the Norwegian Sea and Barents Sea, with individuals being on average around 50 mm longer in northern than southern areas. This effect of geographic position was significant after controlling for annual differences in sampling effort (GAMM; longitude and latitude: estimated df = 10.9, maximum df = 14.6, $F = 6.82$, $p < 0.001$; Figure 5), although those annual differences were not significant (GAMM; year: estimated df ∼ 0, maximum df = 1, $F = 0$, $p = 0.38$). There is a correlation between geographic position and sampling date (Figure 1a), with fish sampled further north being sampled later in May and June, relative to late April and early May in the south. The geographic pattern in body length (Figure 5) may therefore be a result of length growth during the spring, as geographic position and date cannot be disentangled in the available dataset (Supplementary Figure S1).

There was geographic variation in *FR* and diet (Figure 6 and 7). Data on the 100 individual pink salmon caught at sea in May and June showed that in the southern Norwegian Sea (south of 67.5°N), a large portion of the diet consisted of Euphausiidae (28%) and fish (58%). Most of the fish could not be identified to species due to the degree of digestion, but lanternfishes from family Myctophidae and *M. muelleri* were found in stomachs in the western area and herring in stomachs from pink salmon close to the Norwegian coast (Figure 6a). Further north in the Norwegian Sea (north of 67.5°N), in the deep basin, the amphipod *Themisto sp*. constituted a large proportion of the diet (43%), together with various other zooplankton (23%) and Cephalopoda (16%; Figure 6b). North of 67.5°N, but along the Norwegian continental shelf and into the Barents Sea, the pink salmon diet was dominated by small fish—reaching to 58% when combining 0-group (i.e. young-of-year) herring (most abundant, 15%), mesopelagic, and unspecified fish (Figure 6c). Only 8 of 100 stomachs were empty. For the 22 individuals sampled in late June along the Norwegian coast from illegal gillnets, none had empty stomachs, and the diet by weight was 92% fish and 8% Euphausiidae, where the fish diet was composed of 29% prickleback, 37% saithe, and 34% unidentified Teleostei (Figure 6d). For the 12 post-smolts sampled in December south of the Bear Island in the western Barents Sea, the diet was by weight dominated by Euphausiidae (∼66%) and fish (29%) from the Teleosti unspecified group, and only one stomach was empty (Figure 6e).

The *FR* of individual pink salmon sampled during scientific surveys in May and June was on average 0.59 (range 0–3.35), while for the 22 fish caught in late June in coastal waters along northern Norway, the average was 0.98 (range 0.04–2.87). The *FR* for post-smolts caught in the western Barents Sea in December could only be calculated for three individuals and the average was 0.89 (range 0.01–1.72). These data indicated that pink salmon, due to its ability to feed on different prey organisms, can maintain a relatively high *FR* over a large geographic area (Figure 7) and at different times of the year.

River observations: body size, date of river ascent, and diet

The body length of pink salmon caught in rivers increased from south to north (GAMM, estimated df = 2.0, maximum df = 2.0, $F = 11.47$, $p < 0.001$; Figure 8a). Body length differed among years, being shorter in 2019 (465 ± 3.17 mm; $\bar{x}$ ± se) than in 2021 (514 ± 2.69 mm; $\bar{x}$ ± se) and 2017 (500 ± 3.44 mm; $\bar{x}$ ± se; Table 3). Pink salmon were also heavier in northern than in southern rivers (GAMM, estimated df = 2.79, maximum df = 3.04, $F = 32.02$, $p < 0.001$; Figure 8b). Pink salmon caught in 2021 (1523 ± 23.0 g; $\bar{x}$ ± se) and 2017 (1490 ± 24.8 g; $\bar{x}$ ± se) were heavier than pink salmon caught in 2019 (1394 ± 24.3 g; $\bar{x}$ ± se; Table 3). Geographical differences in body weight were maintained even when we subset our data to fish caught during the 14 d from the first pink salmon was caught in the river (GAMM, estimated df = 2.0, maximum df = 2.0, $F = 28.17$, $p < 0.001$). Thus, the geographical weight differences found within this early period of river ascent indicated differences in pink salmon body weight at river entry when returning from the sea. The geographical differences in body length in this subset of data were no longer present (GAMM, estimated df = 3.1, maximum df = 3.7, $F = 1.20$, $p = 0.363$), which could be due to the smaller sample size, or just lack of difference in length.

Pink salmon ascended rivers at approximately the same time throughout whole Norway, as including longitude and latitude did not improve the model fit (difference in deviance = −691.82, df = −1.5, $F = 2.64$, $p = 0.09$; see also Supplementary Table S5). Date of river ascent differed among years (GAMM, estimated df = 2.0, maximum df = 2.0, $F = 363.29$, $p < 0.001$). In 2013, the average river ascent occurred on day 48 (18 July), and from then it was delayed each year until 2018, when it peaked on day 66 (5 August). After 2018, river ascent was observed to be earlier each year, reaching day 58 (28 July) in 2021 (Supplementary Figure S3). When pink salmon entered the rivers, they had stopped feeding. All 69 pink salmon captured in rivers that were checked for stomach content had empty stomachs.

Comparison of marine and river observations

Marine and river annual catches followed the same trend over time when considering catches in both even and odd years (Spearman correlation, $rho = 0.84$, $p = 0.005$; Supplementary Figure S5). However, there was no significant correlation between marine and river annual trend in catches in odd years only (Spearman correlation, $rho = 0.87$, $p = 0.054$). The first correlation probably only reflected the difference in abundance of odd- and even-year populations. Pink salmon caught in the sea were on average 73 ± 3.8 mm ($\bar{x}$ ± se) shorter than of those caught in the rivers, combining all length data from all months (LMM, $t = -19.39$, $p < 0.001$; Figure 9). Pink salmon caught in the sea were on average 30 ± 5.3 mm ($\bar{x}$ ± se) longer each month, as sampling proceeded from April to June (LMM, $t = 5.68$, $p < 0.001$), while pink salmon caught in rivers were on average 5 ± 0.9 mm ($\bar{x}$ ± se) shorter each month, as sampling proceeded from June to September (LMM, $t = -6.18$, $p < 0.001$; Figure 9).

Discussion

We report for the first time on the geographic distribution, abundance, and diet of pink salmon in the Norwegian and Barents Seas, Norwegian coast and rivers. We show that introduced pink salmon is widely distributed throughout the Norwegian Sea and along the Norwegian coast, and that numbers increased by several orders of magnitude from 2015 to 2017, and thereafter increased further with no indication that

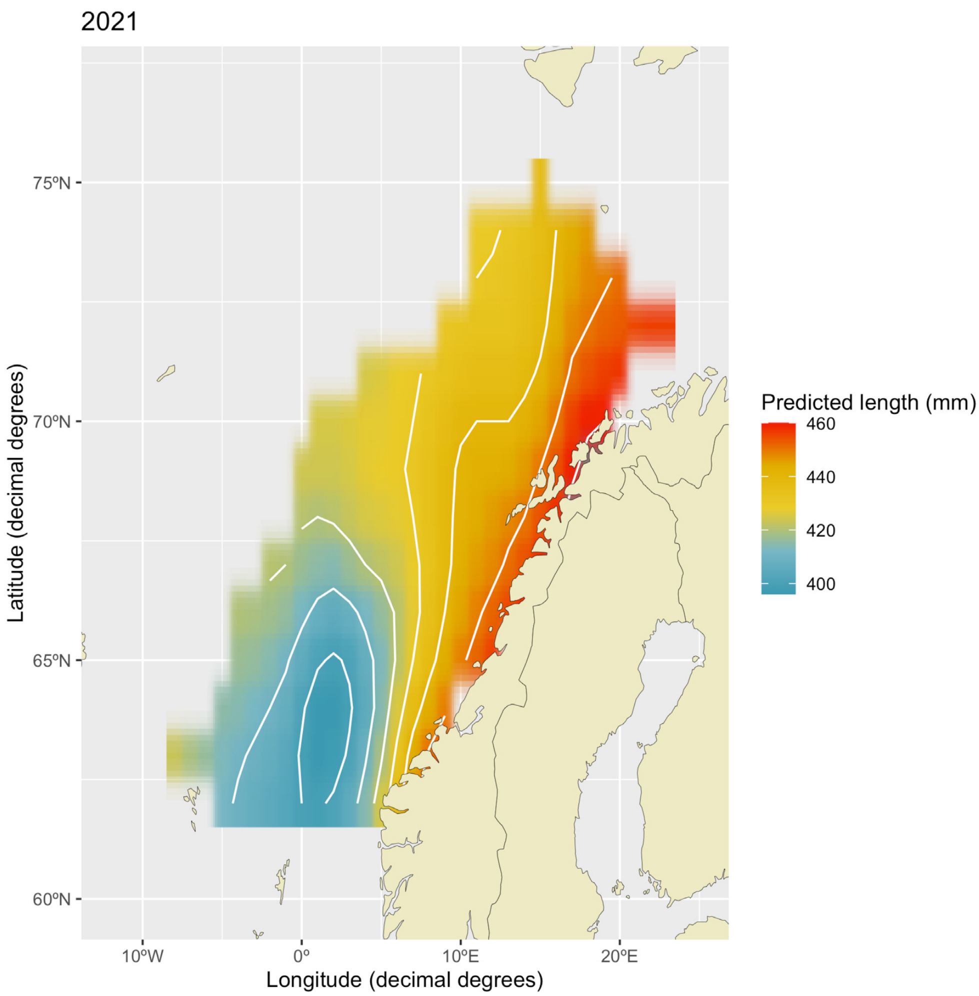

Figure 5. Geographical distribution of pink salmon body length (mm) from the marine catches in the Norwegian Sea in 2021 only (2013–2019 have equal patterns). Warmer colours show higher probability of capture relative to colder colours. Twelve individuals caught in December were excluded from the analysis.

the number of pink salmon has peaked yet. The marine diet of introduced pink salmon in the north Atlantic Ocean and Barents Sea area was mainly constituted of amphipods, small fish, and Euphausiidae. Finally, we present the geographical pattern with increased body size of adult pink salmon from southern to northern rivers, and a lack of geographical pattern considering the seasonal timing of river ascent prior to spawning.

The first observation of pink salmon in Norwegian rivers was made in 1960, and the numbers remained low and concentrated in the most northern rivers of the country (Berg, 1977; Sandlund *et al.*, 2019). However, since 2015, the distribution of pink salmon in rivers spanned the latitudinal range of the country. Our records confirm the 2-year life cycle of pink salmon, and that the population in odd years seems to have established more successfully than the even-year population in Norway, as previously reported by others (Gordeeva and Salmenkova, 2011; Sandlund *et al.*, 2019; Paulsen *et al.*, 2022). However, an even-year population has been established albeit at much lower abundance. It should be noted that the actual numbers of pink salmon caught, and the abundance in the rivers, are higher than reported in this study, due to limitations in the catch statistics and monitoring. Pink salmon mitigation programs require information about potential number of individuals entering the rivers each year (VKM *et al.*, 2020). Catches from the IESNS in spring could be used as early a warning signal of abundance in rivers in summer. However, according to the present data, IESNS catches could forecast the known 2-year abundance fluctuation of pink salmon, but not accurately predict river abundance in odd years and, hence, give a precise alert of the scale of the invasion to river managers and scientists.

Data in this study indicate a likely marine migration route for pink salmon in the Norwegian and Barents Seas, although it must be considered that the marine survey catches were strongly affected by spatial and temporal patterns in survey coverage. The probability of pink salmon capture in the Norwegian Sea was highest in odd years on the eastern side towards the Norwegian coast and up towards the entrance to the Barents Sea. Pink salmon were caught around Faroe Islands in April and early May, gradually moving northwards in the Norwegian Sea in May, and finally into the Barents Sea in June. This indicates that pink salmon might migrate northwards in the Norwegian Sea during the spring, many of them relatively close to the Norwegians coast, before entering the Barents Sea and rivers in northern Norway. The relatively high number of marine samples from the scientific surveys indicate that these individuals originate from and return to rivers in

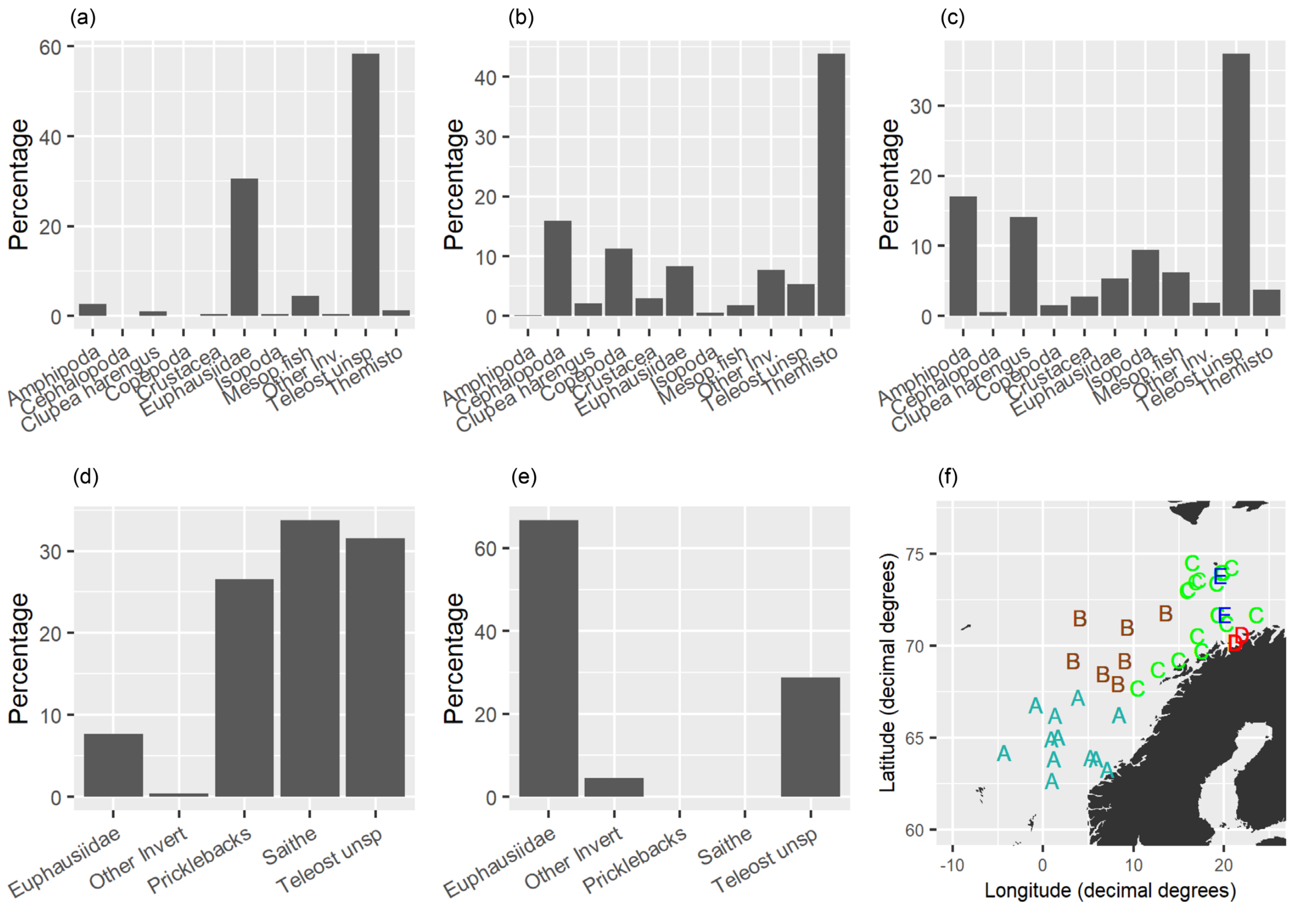

Figure 6. Histogram of total pink salmon stomach content in proportions (by weight) for all samples from scientific surveys in May and June within (a) the southern Norwegian Sea, (b) the northern Norwegian Sea, and (c) the northern Norwegian shelf and the Barents Sea. (d) shows stomach content of pink salmon caught by gillnets in coastal waters in northern Norway in late June by the reference fleet, while (e) shows stomach content of pink salmon caught in scientific surveys in the Barents Sea in December. (f) shows map of the sampling locations for the data presented in panels a–e.

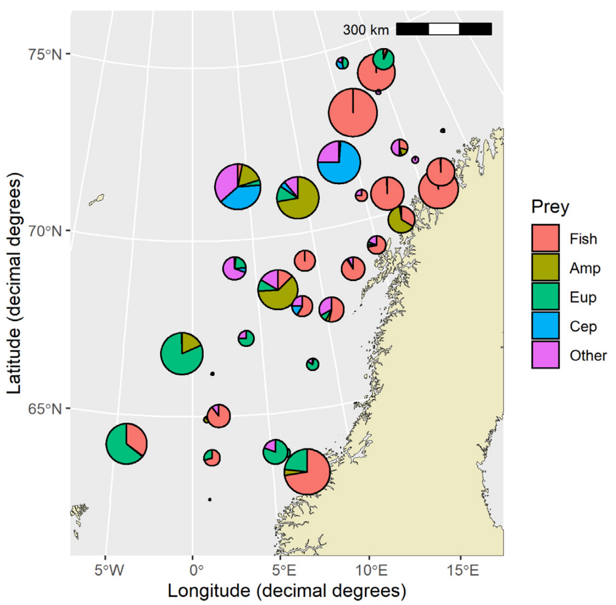

Figure 7. Average pink salmon diet for each marine sampling location in May and June, where the stomach content is aggregated into the groups fish, Amp—Amphipoda, Eup—Euphausiidae, Cep—Cephalopoda, and other—all other prey. Size of the pies refers to average *FR* per sampling location (range 0–1.99) for the individuals caught at the sampling location.

northern Norway or Russia, as these are the only rivers with hundreds or thousands of returning pink salmon in the previous years.

It is possible that pink salmon have a marine migration pattern like Atlantic salmon, with some individuals staying in the eastern part of the Barents Sea, while others migrate westward and into the northern part of the Norwegian Sea (Gilbey *et al.*, 2021; Rikardsen *et al.*, 2021). Pink salmon migrating into the northern Norwegian Sea could follow the ocean circulation pattern and be transported southwards with arctic water, in accordance with the merry-go-round hypothesis (Dadswell *et al.*, 2010). This could explain why some individuals stray into areas such as western Greenland (Nielsen *et al.*, 2020), Ireland, and Scotland (Millane *et al.*, 2019), while many individuals end up in the southern Norwegian Sea. The migration patterns in the Barents Sea are, however, mainly unknown, and so is the proportion of pink salmon that stay there during the entire marine phase, or that remain within the White Sea.

It is peculiar that no pink salmon post-smolts have been identified from the Barents Sea ecosystem survey targeting pelagic fish and 0-group fish (i.e. young-of-year) during the autumn annually since the 1980s [Protozorkevich and van der Meeren (eds.), 2020]. This might suggest that the post-smolts are located deeper in the water column during the autumn, enabling them to avoid the pelagic trawls at or close to the surface. Alternatively, post-smolts might remain in the White

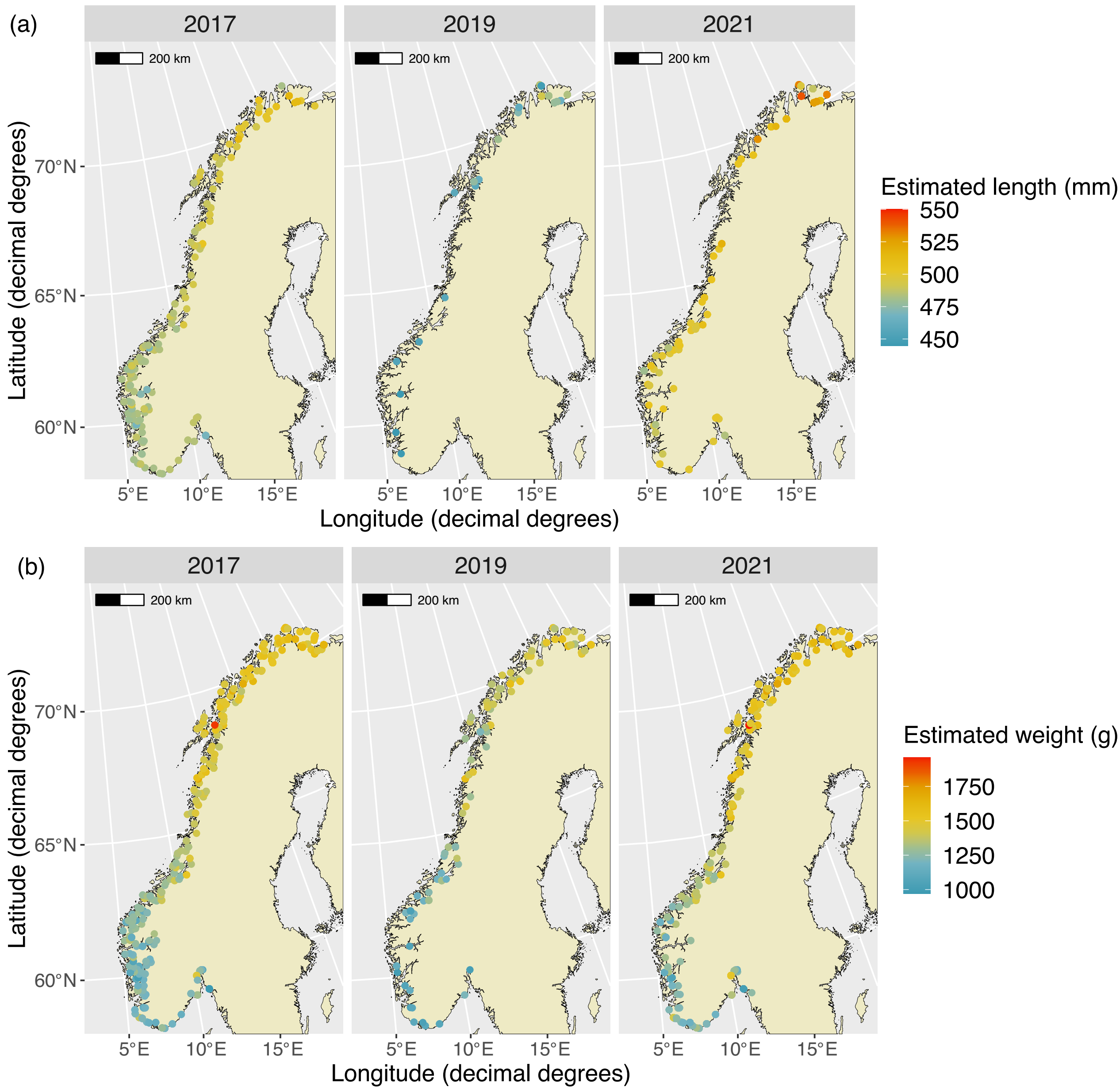

Figure 8. Geographical and temporal variation in (a) body length and (b) body weight of pink salmon in the river catches. Circles refer to rivers where pink salmon were caught, and colours refer to predicted body length in millimetres and weight in grams.

Table 3. Estimated differences in body length (mm) and weight (g) during the river phase between years.

Pairwise comparison	Estimated difference	SE	df	*t*-ratio	*p*
2017–2019	34 mm	3.7	4 669	9.34	<0.0001
2017–2021	−14 mm	3.6	4 669	−4.51	<0.0001
2019–2021	−49 mm	2.6	4 669	−18.57	<0.0001
2017–2019	96 g	16.0	11 531	6.004	<0.0001
2017–2021	−33 g	13.9	11 531	−2.397	0.042
2019–2021	−129 g	12.0	11 531	−10.807	<0.0001

SE refers to standard error and df to degrees of freedom. Sample size for length was $N = 653$, 994, and 3066, respectively, for 2017, 2019, and 2021. Sample size for weight was $N = 1889$, 2943, and 6796, respectively, for 2017, 2019, and 2021.

Sea and close to the Norwegian coast longer and only migrate into the Barents Sea later in the year. The large variation in the average number of pink salmon caught per trawl haul, and the fact that more than one individual was caught in 61% of the trawl hauls that caught pink salmon, may indicate that pink salmon aggregate or school when at sea. This agrees with observations from the Pacific Ocean, where pink salmon tend to aggregate in small shoals in the open ocean, although more loosely organized than in coastal waters (Groot and Margolis, 1991).

Most pink salmon were caught in surface waters (upper 50 m), but they were not more likely caught during night time, as is also the case in the Pacific Ocean (Radchenko *et al.*, 2018). Our data might also indicate that large individuals start the spawning migration and enter the rivers before smaller ones, as in June, river fish were larger than fish caught at sea.

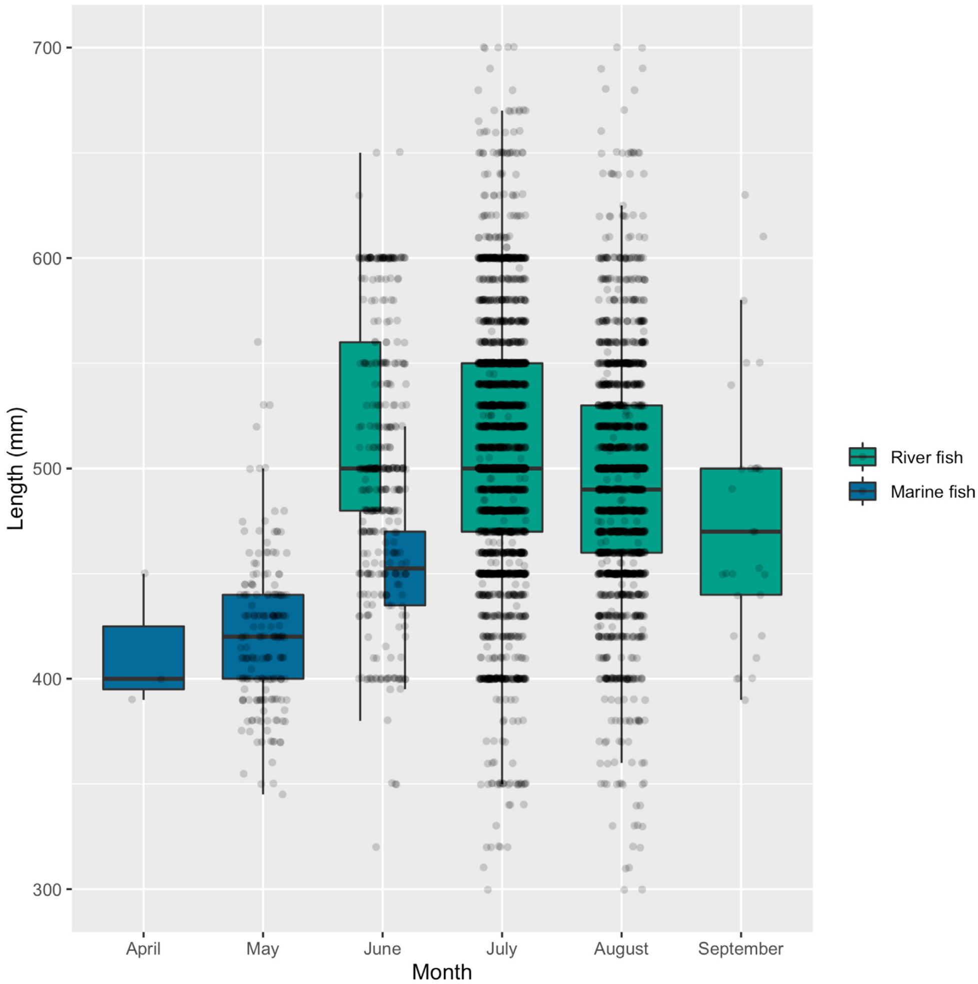

Figure 9. Mean body length (mm) of pink salmon caught in the sea (blue) and rivers (green) from April to September. Thick horizontal bars refer to the median, lower, and upper hinges of the boxes correspond to the first and third quartiles, while lower and upper whisker extends from the hinge to the smallest and largest value no further than 1.5 ∗ IQR from the hinge. Circles represent the actual observations. Please note that outliers are not marked differently; however, values beyond the end of the whiskers are outliers.

Moreover, the average body length of pink salmon in the rivers decrease from June to September. Similar migration patterns are observed in the Russian Pacific region, where large individuals, particularly males, start the migration to the rivers earlier (Radchenko *et al*., 2018).

The dominance of Euphausiids, fish, and amphipods in the diet of pink salmon in the Norwegian Sea is very similar to previously reported stomach content of Atlantic salmon sampled in the same area during the summer and early winter (Jacobsen and Hansen, 2001; Utne *et al*., 2022) and of pink salmon in the Pacific Ocean (Radchenko *et al*., 2018). The relative abundance of the important prey groups in the pink salmon diet varied geographically. For instance, the species of fish depended on whether the pink salmon was caught on the shelf along the Norwegian coast and into the Barents Sea (herring, saithe, pricklebacks) or south in the Norwegian Sea (Mueller's pearlside and lanternfishes). The returning Atlantic salmon in the study of Aykanat *et al*. (2020) had a more piscivorous diet (mainly herring and other small fish) than pink salmon in the same region, but this might be due to size differences, with returning Atlantic salmon in their study generally being larger than the pink salmon in this study. However, in general terms, pink salmon in the Norwegian and Barents Seas had a higher proportion of fish in their diet than pink salmon in the Pacific Ocean (Qin and Kaeriyama, 2016), probably reflecting differences in prey abundance between the two oceans.

The marine pink salmon stomach content seems to reflect the abundance of prey in the different areas in this study. This, together with the fact that the average *FR* was 0.59, indicates that pink salmon feed on what is available rather than showing a preference for specific prey. Radchenko *et al*. (2018) concluded pink salmon has low prey selectivity in the Pacific and thus a high variation in diet among seasons and regions. The prey species found in pink salmon might present patchiness and geographic variation, and other species than those reported here might be important in other areas. As expected, returning pink salmon in the rivers were not feeding in the river, as indicated by their empty stomachs.

In the North Pacific Ocean, pink salmon are known to impact the marine ecosystem through competition for prey with other fish and birds (Shiomoto *et al*., 1997; Ruggerone and Nielsen, 2004). In the Norwegian and Barents Seas, pink salmon, based on the diet found here, can potentially compete with other abundant pelagic fish species such as herring, capelin, polar cod, blue whiting, and Atlantic salmon. In numbers, these other species, except Atlantic salmon, are at present several orders of magnitude more numerous (ICES, 2021a, b) than pink salmon returning to Norwegian and Barents Seas rivers. Pink salmon in the Atlantic Ocean are therefore not expected to have a large-scale effect on the ecosystem, due to their relatively low numbers in the sea until now. However, pink salmon may still have local effects from grazing on fish larvae and other prey in estuaries, fjords, and other coastal areas, particularly given that pink salmon abundance has constantly increased since 2015. Pink salmon have a diet that most likely overlaps with other coastal pelagic species such as saithe (*Pollachius virens*; Nedreaas, 1985), sea trout (*Salmo trutta*), and Artic charr (*Salvelinus alpinus*; Rikardsen *et al*., 2007), which feed on small fish and various zooplankton species, and are present in estuaries and coastal regions throughout the year. Pink salmon feeding in Norwegian coastal waters can potentially impact both prey abundance and the competitors for prey, and future research on this issue is encouraged.

For pink salmon caught in the marine surveys, body length was larger in the northeast of the Norwegian Sea and into the Barents Sea than further south. However, this geographical difference in body length could not be disentangled from the temporal differences in our data from the scientific survey. Thus, the increase in length might be due to growth from April to June, in the last months before they enter the rivers. A similar growth pattern is found between north and south on the western Pacific Ocean (Radchenko *et al*., 2018). Little is known about pink salmon growth rate in the Atlantic Ocean, but a recent study on growth rate based on scales analyses concluded that post-smolt pink salmon experienced a decline in growth during the first weeks of their marine phase in late spring–early summer, followed by an increased growth during the late summer and early autumn, which declined again during the winter (Paulsen *et al*., 2022). However, Paulsen *et al*. (2022) only considered pink salmon during the first summer at sea and their data set cannot be directly compared with our data. Our post-smolt samples from December suggest that pink salmon can maintain a high feeding level during the winter, and lower water temperatures linked with lower metabolic and digestion rates might be the explanation for a slow growth during the winter, as also suggested for pink salmon in the Pacific Ocean (Radchenko *et al*., 2018).

Pink salmon were longer and heavier in the northern than southern rivers in Norway, following a similar geographic pattern for body length as observed in the Norwegian Sea. This geographical difference in size was maintained for weight even when considering only individuals caught by angling within the first 2 weeks of river entry, thus, showing that pink salmon were larger in the north than in the south, when they returned from the ocean and entered the rivers early in the season. The reason for this latitudinal difference is unknown but may indicate that the geographic areas used during the marine migration, and hence feeding conditions, differed between fish entering southern and northern rivers. If pink salmon entering northern rivers had a greater tendency to migrate to northern ocean areas in the Barents Sea and the northeast Atlantic Ocean, the results may reflect better feeding conditions for pink salmon in these areas than further south in the Norwegian Sea. A difference in marine growth between northern and southern populations has also been shown for Atlantic salmon (Vollset *et al*., 2022) and pink salmon in the Pacific (Radchenko *et al*., 2018). Despite the geographical difference in body size, we did not find any geographical difference in date of river ascent, confirming earlier studies (Sandlund *et al*., 2019). The first pink salmon were caught in rivers around mid-end July throughout Norway in all study years. We cannot identify where in the river each pink salmon was caught, as we only have reports of pink salmon being caught or observed on a river basis. Therefore, the exact date of river ascent has associated uncertainty.

The present study documents for the first time the abundance and distribution of pink salmon in the Norwegian Sea, which increased by several orders of magnitude in 2017 and showed no signs of decreasing. We also present for the first-time pink salmon diet in the sea in the Norwegian and Barents Seas. Both abundance and diet are key parameters for quantifying the impact of pink salmon as an invasive species in the Norwegian Sea and rivers, as they provide a measure of the size of the invasion and point to which other species in the ecosystem are affected by the invasion.

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Supplementary Data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Conflict of interest

The authors declare no conflicts of interest.

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Author contributions

B.D.P., K.R.U., H.H.B., and E.B.T.: conceptualization; H.H.B., E.H., S.M., and K.R.U.: data acquisition; B.D.P. and K.R.U.: formal analysis; B.D.P. and K.R.U.: writing—original draft; and B.D.P., H.H.B., K.R.U., E.B.T., E.H., S.M., V.W., and K.R.U.: writing—review and editing:.

Data availability

Data on marine catches and stomach content is available at the Norwegian marine data centre (10.21335/NMDC-2092844686). The rest of the data were derived from sources already in the public domain: data of river catches were obtained from Statistics Norway (ssb.no), online river catch reports (lakseboersen.no), and from Berntsen *et al*., 2018, 2020, 2022. Data of coastal marine catches were derived from the Norwegian Environmental Agency (recreational fishery, upon request) and Statistics Norway (salmonid fishery).

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