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Feeding Hotspots and Distribution of Fin and Humpback Whales in the Norwegian Sea From 2013 to 2018

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Fin whales (*Balaenoptera physalus*) and humpback whales (*Megaptera novaeangliae*) are commonly found in the Norwegian Sea during the summer months. Records from around 1995 to 2004 show that their distribution patterns were mainly associated with those of macro-zooplankton. More recent studies conducted from 2009 to 2012 demonstrate marked shifts, with fin whale distribution related to pelagic fish distribution, decreasing densities of humpbacks, and increased densities of toothed whales. During the same period, historically large abundances of pelagic planktivorous fish in the Norwegian Sea were reported. The goals of this study were to examine the summer distribution of fin and humpback whales from 2013 to 2018 and to assess the potential association between distribution and environmental impact factors. Results suggest a pronounced northerly shift in distribution for both species, a feeding hotspot for fin whales at the shelf area between Svalbard and Norway, and one near Bear Island for humpback whales. Fin whale distribution was associated with that of blue whiting (*Micromesistius poutassou*) and capelin (*Mallotus villosus*), whereas humpback whale distribution was associated with that of euphausiids (*Meganyctiphanes norvegica, Thysanoessa longicaudata*, and *Thysanoessa inermis*), capelin, and herring (*Clupea harengus*). However, a significant negative spatial correlation was found between whale occurrence and the widely expanding population of northeast Atlantic mackerel (*Scomber scombrus*). The results of this study suggest that the prey composition of fin and humpback whales in recent years contain a large proportion of fish. The apparent northerly shift in the distribution of these whale species is largely determined by the availability of prey, but it likely is also impacted by direct or indirect interspecific interactions, especially with killer whales (*Orcinus orca*). Such large-scale pronounced changes in distribution seem to confirm a high degree of plasticity in fin and humpback whale feeding in the Norwegian Sea.

Keywords: cetacean, distribution, feeding ecology, site fidelity, plasticity, pelagic fish, spatial overlap

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INTRODUCTION

How whales navigate during long-distance migration is still unknown, but theories include learning by experience and from conspecifics, and the use of the Earth's magnetic field, position of the sun, and bathymetric patterns (Dawbin, 1966; Stern, 2002; Horton et al., 2011; Garrigue et al., 2015). Little is known about the degree to which whales alter their migration routes or the plasticity of their habitat choice and distribution (Stern, 2002). However, the general perception is that baleen whales display strong site fidelity with little variation (Mackintosh, 1966; Katona and Beard, 1990; Clapham et al., 1993; Clapham, 2009).

Fin whales (*Balaenoptera physalus*) and humpback whales (*Megaptera novaeangliae*), which are both baleen whales, make annual feeding trips to high latitudes in summer and reside at tropical latitudes during the winter months, where calving typically occurs (Aguilar, 2009; Clapham, 2002, 2009; Nøttestad and Olsen, 2004; Horton et al., 2011). Traditional feeding grounds for humpbacks and fin whales in the Northeast Atlantic are located on the continental shelf areas near Iceland, Jan Mayen, Bear Island, coastal northern Norway, and Svalbard representing both the northern part of the Norwegian Sea and southwestern part of the Barents Sea ecosystems (Aguilar, 2009; Clapham, 2009; Víkingsson et al., 2009, 2015; Nøttestad et al., 2014c, 2015b; Moore et al., 2019). Unlike toothed whales, these species do not use echolocation to obtain information about their surroundings, communicate, or find food, although they may use smell to detect prey species at the surface (Tyack, 1986; Clapham, 2009). Fin and humpback whales feed on a variety of organisms depending on prey availability (Kawamura, 1980; Aguilar, 2009; Clapham, 2009), but they focus primarily on euphausiids (krill) and fish (Skern-Mauritzen et al., 2009; Moore et al., 2019). Their preferred prey in the Northeast Atlantic seems to be krill and small schooling fish species such as capelin (*Mallotus villosus*), herring (*Clupea harengus*), mackerel (*Scomber scombrus*), and blue whiting (*Micromesistius poutassou*) (Piatt and Methven, 1992; Nøttestad and Olsen, 2004; Skern-Mauritzen et al., 2009).

Structural changes and dynamics in the Norwegian Sea's physical environment and biological species and biomass composition have been reported since the 2000s and onward (MacLeod et al., 2005; Loeng and Drinkwater, 2007; Laidre et al., 2010; Nøttestad et al., 2014c, 2015a; ICES (International Council for the Exploration of the Sea), 2016a, 2018a; NAMMCO, 2018; Frantzen et al., 2019). These changes include shifts in geographical nutrient levels, production, and distribution as well as a highly dynamic temperature regime in the Norwegian Sea between years (MacLeod et al., 2005; Learmonth et al., 2006; Simmonds and Isaac, 2007; Laidre et al., 2008; Simmonds and Eliott, 2009; Víkingsson et al., 2009, 2014, 2015; Nøttestad et al., 2014c, 2015a).

Surveys of the abundance and distribution of cetaceans in the Norwegian Sea and adjacent waters have been conducted regularly since 1987 (Øien, 1990; Nøttestad and Olsen, 2004; Pike et al., 2005; Víkingsson et al., 2009; Nøttestad et al., 2014c, 2015b; NAMMCO, 2018; Moore et al., 2019). Generally, whale sightings recorded in 2006 and 2007 (Nøttestad et al., 2014c) did not differ from those from the previous 10–15 years in terms of distribution and cetacean species composition (Skjoldal et al., 2004; Øien, 2009; Víkingsson et al., 2009). Distributions of both fin and humpback whales were associated with high densities of krill and amphipods (Nøttestad et al., 2014c). However, based on survey results from 2009 to 2012, Nøttestad et al. (2015b) reported that fin whales had switched to a more pronounced fish diet and that a very small number of humpback whales where observed in this area. During this same time period, historically large abundances of pelagic planktivorous fish such as Norwegian spring-spawning herring, northeast Atlantic mackerel, and blue whiting were reported in the Norwegian Sea (Utne et al., 2012; Berge et al., 2015; Nøttestad et al., 2016a; ICES (International Council for the Exploration of the Sea), 2018b). Consequently, more toothed whales were concentrated in this ecosystem during this period, including long-finned pilot whales (*Globicephala melas*) and killer whales (*Orcinus orca*). Because fin whales are large and swim fast, they do not have significant predators apart from the killer whale (Ford and Reeves, 2008; Aguilar, 2009). Predation by killer whales does not appear to be a significant factor for humpback whales (Clapham, 2000), except for young calves (Ford and Reeves, 2008). The presence of killer whales in the Norwegian Sea (Nøttestad et al., 2014b) may influence the spatial distribution of fin and humpback whales due to their avoidance of direct contact and potential predation risk posed by killer whales.

The goals of this study were to quantify and better understand the spatio-temporal distribution, overlap, and feeding ecology of fin and humpback whales within the dynamic and productive Norwegian Sea ecosystem. Sighting data for these two large baleen whale species were collected in July and August during six consecutive years from 2013 to 2018, and these data were compared to the corresponding available data for a wide spectrum of potential pelagic prey species and relevant physical parameters (temperature, bottom depth, and topography).

MATERIALS AND METHODS

Data Collection

Data were collected during the International Ecosystem Summer Surveys in the Nordic Seas (IESSNS) during six consecutive summer seasons from 2013 to 2018 (Nøttestad et al., 2013, 2014a,b,c, 2015a,b, 2016a,b, 2017; ICES (International Council for the Exploration of the Sea), 2018b; **Figure 1**). The data used herein were obtained from the Norwegian vessels surveying in the Norwegian Sea (**Figure 1**; ICES (International Council for the Exploration of the Sea), 2013, 2018b).

The vessels followed predetermined transect lines at a nominal speed of 10 knots, and each sampling station was spaced approximately 60 nautical miles apart (**Table 1**). Cetacean sightings were made with the naked eye and binoculars between stations and when possible documented with photographs and video. The visual observations were made from the vessel bridge or bridge roof top (9–11 m above sea level) by designated whale observers during all light hours. All cetaceans observed were registered with time, position, number, and species or the nearest taxonomic group possible. Station work included collection of meso- and macro-zooplankton and nekton. To collect meso- and to some extent macro-zooplankton, a 180 μm meshed WPII net with an mouth opening of 0.25 m^2 was hauled vertically from 200 m, or 5 m above the bottom at shallower stations, at 0.5 m/s. The size ranges of meso- and macro-zooplankton sampled with the WPII net ranged between 1 to approximately 45 mm. The net was rinsed with seawater on deck before the codend was emptied. Half of the samples were size fractioned, dried (24 h

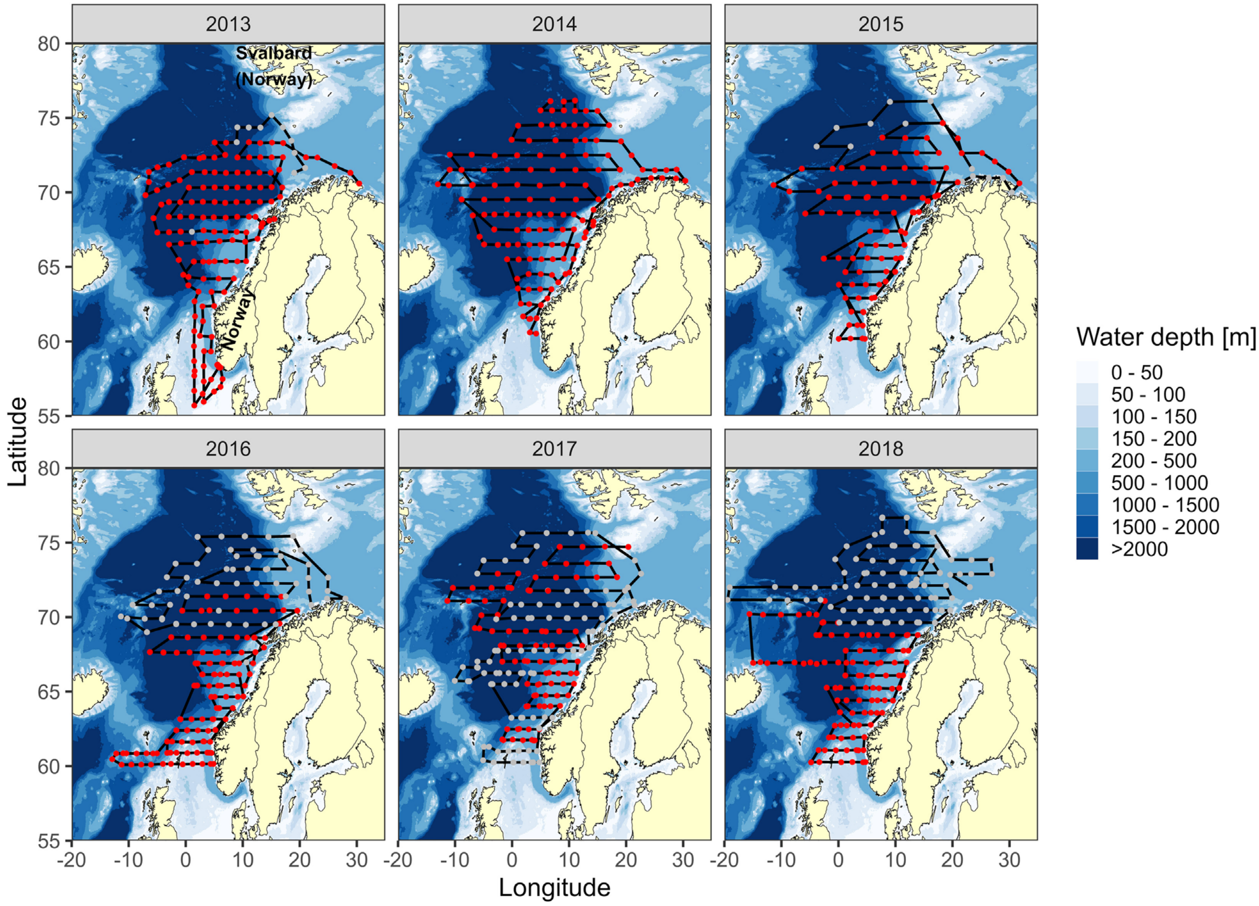

FIGURE 1 | Survey area in the Norwegian Sea during the IESSNS from 2013 to 2018. Each year was covered by two Norwegian vessels. Lines illustrate cruise tracks, and data points along the lines represent stations for biological (trawl and zooplankton) and oceanographic (CTD casts) data sampling. Gray data points represent stations where zooplankton and CTD casts could not be included for further statistical analyses in this study.

at 70°C), frozen, and weighed, and values were converted to biomass following the procedures described in the Working Group on International Pelagic Surveys (ICES (International Council for the Exploration of the Sea), 2014). The other half of the zooplankton samples were fixated in 4% formaldehyde and borax buffered seawater for taxonomic species determination on shore. Nekton and macro-zooplankton were sampled using a Multpelt 832 trawl (mesh size 22 mm in codend). The trawling depth of the sampling trawl was 0–35 m. Trawl gear methods for rigging and operations followed the manual for International Pelagic Surveys (ICES (International Council for the Exploration of the Sea), 2013, 2014). Trawl catches were sorted to the nearest taxonomic level, counted, and weighed.

TABLE 1 | Survey effort during IESSNS by Norwegian vessels in July and August, 2013–2018.

Year	Survey period (d/m)	Vessel	Length of cruise track (nautical miles)
2013	6/7-29/7	Libas	4213
2013	6/7-29/7	Eros	3454
2014	2/7-28/7	Brennholm	4283
2014	2/7-28/7	Vendla	3462
2015	3/7-28/7	Brennholm	4395
2015	1/7-28/7	Eros	4511
2016	1/7-30/7	Vendla	3813
2016	1/7-30/7	M. Ytterstad	3731
2017	5/7-4/8	Vendla	5735
2017	5/7-4/8	Kings Bay	4969
2018	4/7-5/8	Vendla	5275
2018	4/7-5/8	Kings Bay	5205

A SEABIRD (Sea-Bird Scientific, Bellevue, WA, United States) Conductivity Temperature Depth (CTD) sensor or SAIV (SAIV A/S, Environmental Sensors and Systems, Bergen, Norway) CTD sensor was hauled vertically from 0 to 500 m depth at each station. Bottom depth was extracted from the National Oceanic and Atmospheric Administration using the function getNOAA.bathy (NOAA)[1] from the marmap package (Pante and Simon-Bouhet, 2013). The area between Norway and Svalbard is characterized by a shallow shelf region dividing the Norwegian Sea from the

[1] https://www.noaa.gov/

Barents Sea, with depths varying from 100 to 400 m in the east and dropping down to depths of >1000 m further west into the deep Norwegian Sea ecosystem (**Figure 1**).

Data Analysis

Data were analyzed and figures and maps were created using R, version 3.6.3 (R Development Core Team)[2]. Separate maps showing sightings and kernel areas of fin whales, humpback whales, and killer whales were created by using the R libraries maps and mapdata (Becker and Wilks, 1993; Brownrigg, 2018) and ggplot2 (Wickham, 2016). Kernel areas were determined by two-dimensional kernel density estimation (kde2d). Each kde2d was performed by pooling observations for all years and using the stat_density_2d function from the ggplot2 package, which utilizes the kde2d function from the MASS library (Venables and Ripley, 2002). It is important to note that kde2d does not distinguish between land and water, so it smoothes the kernel areas across land points.

The kernel areas allowed us to evaluate whether abiotic or biotic measures differed between the areas where the whales normally occur compared to the other areas of the survey. Therefore, we divided sampling stations into two groups: those inside and outside the kernel areas. We then compared these two areas with respect to samples and measures, such as temperature and prey species abundance. Each variable was tested using a linear mixed-effects model (lme) or generalized linear mixed-effects model (glmm); lme was used when CTD data was the response variable and glmm was used when catch data or bottom depth was the response variable. In both type of models, year was set as a random effect factor to account for the clustering of observations within years.

To obtain an overview of where prey was found compared to the kernel areas of the whales, we created maps in which kernel areas of the whales were combined with catch data of potential prey. We only created these maps for fish prey, as data for small prey (e.g., krill) were incomplete and did not cover the whole survey area.

To explore whether fin and humpback whales avoid areas where mackerel normally is most abundant, we used the kde2d of each whale species and counted the number of times high catches of mackerel (defined as $\geq$ the median value of 500 kg) was found inside the kernel areas (success) compared to outside (failure) in a binomial test. Prior to analysis, we set the probability of this event to occur (success) to $p = 0.2$. This probability was conservative because the kernel density area of each whale species was much larger than 20% of the area covered by high catches of mackerel. We used the same method to test the spatial overlap between killer whales and mackerel and between killer whales and fin or humpback whales. For the latter two tests, success was defined as a killer whale sighting within the kernel area of fin or humpback whales independent of group size of killer whales in the sighting.

We tried to analyze our data using maximum entropy analysis to determine species niches and distribution. However, our data were not suitable for this method because the samples of small prey and environmental variables were incomplete. The model did not perform well and did not recognize the areas with highest density of whales, and therefore we do not report these results.

[2]http://www.r-project.org

RESULTS

A total of 608 cetacean observations, including 2565 individuals, were made in the Norwegian Sea during the IESSNS between 2013 and 2018. Thirteen different species were observed during the six summer seasons. Fin, humpback, killer, minke (*Balaenoptera acutorostrata*), and sperm (*Physeter macrocephalus*) whales as well as white-beaked dolphins (*Lagenorhynchus albirostris*) were observed every year. Other species were only observed in certain years: harbor porpoise (*Phocoena phocoena*) in 2013; bottlenose whale (*Hyperoodon ampullatus*) and sei whale (*Balaenoptera borealis*) in 2014; pilot whale in 2014 and 2016; white-sided dolphin (*Lagenorhynchus acutus*) from 2016 to 2018; and blue whale (*Balaenoptera musculus*) in 2018. In addition, 163 individuals were not identified to species, and they were distributed all over the Norwegian Sea.

Fin and humpback whales were among the most common species sighted; of the 608 observations, 133 (21.9%) were fin whales and 72 (11.8%) were humpback whales. Most observations were made between 70°N and 77°N and within 0°E to 30°E, which was the largest continuous kernel area for both whale species (**Figure 2**). Seventy-one individual (11.7% of the total) killer whales were sighted, and these observations were distributed between 75°N and 60°N and 10°W 20°E.

For both fin and humpback whales, the comparison between inside and outside the kernel areas showed a statistically significant difference for all four fish prey (mackerel, herring, capelin, and blue whiting) tested (**Figure 3** and **Tables 2**, **3**). However, with respect to biological significance, the clearest difference between inside and outside the kernel areas was for mackerel, with significantly fewer mackerel inside than outside for both of the baleen whale species.

The maps showing catch of the four main prey fish in the survey area compared to feeding hotspots of fin and humpback whales, showed that capelin was most positively associated with the two baleen whale species. The largest occurrences of capelin were found in the largest continuous hotspot area of the baleen whales (between Svalbard and mainland Norway) (**Figure 4**). For fin whales, a strong association between blue whiting and a hotspot area southwest of the Faroe Islands was also detected. This association was due to an observation of a large gathering of fin whales in 2016 together with a school of blue whiting. The strong association between fin whales and blue whiting may thus be over-inflated, due to the high numbers of fin whales recorded off the Faroes in 2016. The killer whale kernel area was more spread out throughout the study area and overlapped in large part with mackerel catches (**Figure 5**).

The hypothesis that fin and humpback whales avoid areas where mackerel normally is most abundant was supported

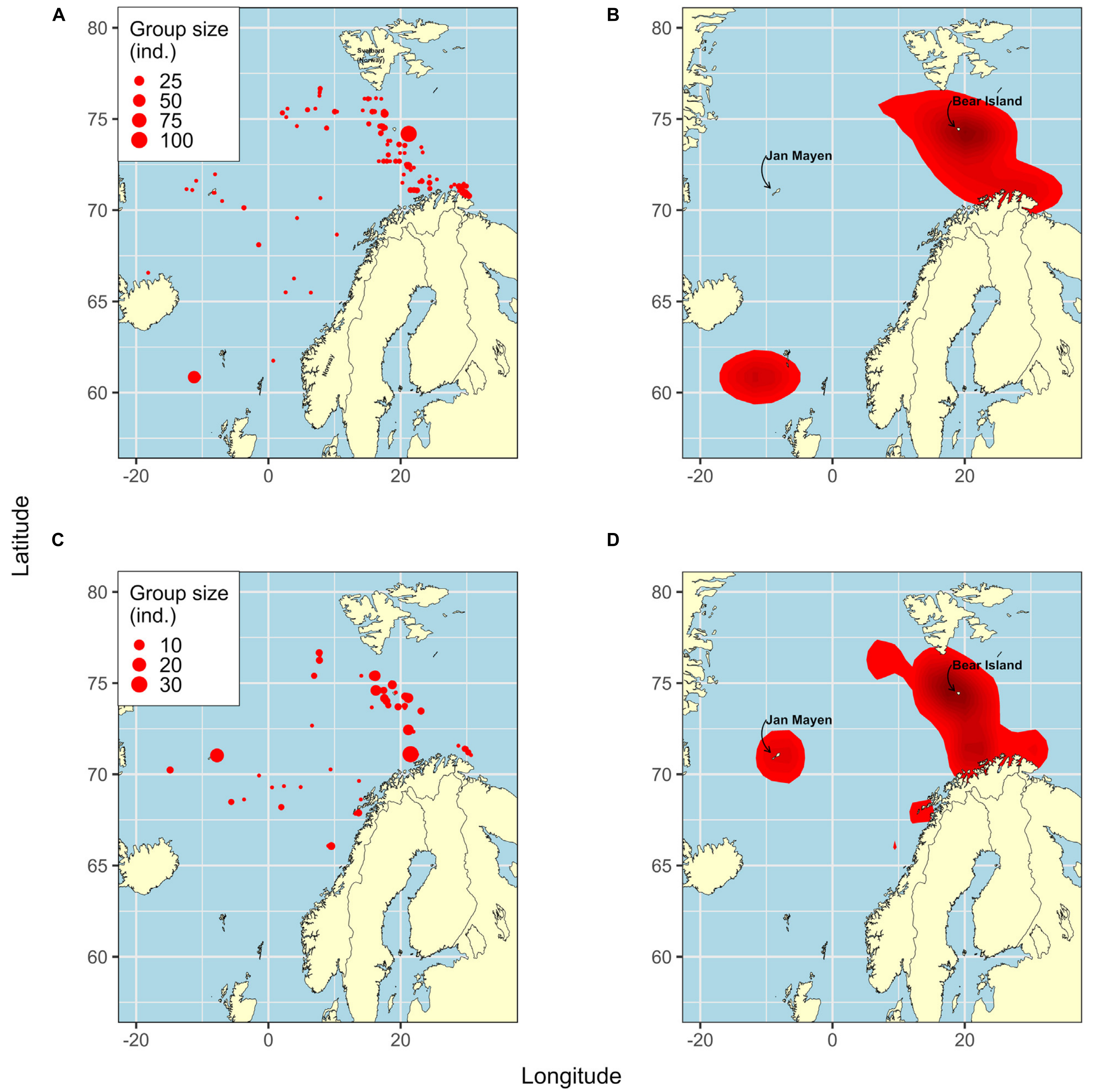

FIGURE 2 | Fin **(A,B)** and humpback **(C,D)** whale distribution. Size of red points (left panels) represents the number of individuals from sightings from the IESSNS, 2013–2018. Red areas (right panels) represent kernel areas determined by two-dimensional kernel density estimation. Within each area, darker red denotes a higher probability of observing whales.

by the significant lack of high catch samples of mackerel in the whales' kernel areas than what was hypothesized under H_0 (**Figure 5**, binomial tests; $p < 0.001$ for both species). Of the total number of high catch samples, only 4.66% and 5.54% were found within the kernel areas of fin and humpback whales, respectively. For killer whales, however, high catch samples of mackerel occurred significantly more often within the kernel areas than what was hypothesized under H_0 (**Figure 5**, binomial tests; $p < 0.001$). Of the total number of high catch samples, 76.72% were found within the kernel areas of killer whales.

The tests of spatial overlap between killer and fin whales and between killer and humpback whales showed that significantly fewer sightings of killer whales were made within the kernel areas of the two baleen whale species than what was hypothesized under H_0 (**Figure 6**, binomial tests; $p < 0.001$ for both species). Of the total number of killer whale sightings, 5.54% were made within the kernel areas of the two baleen whale species.

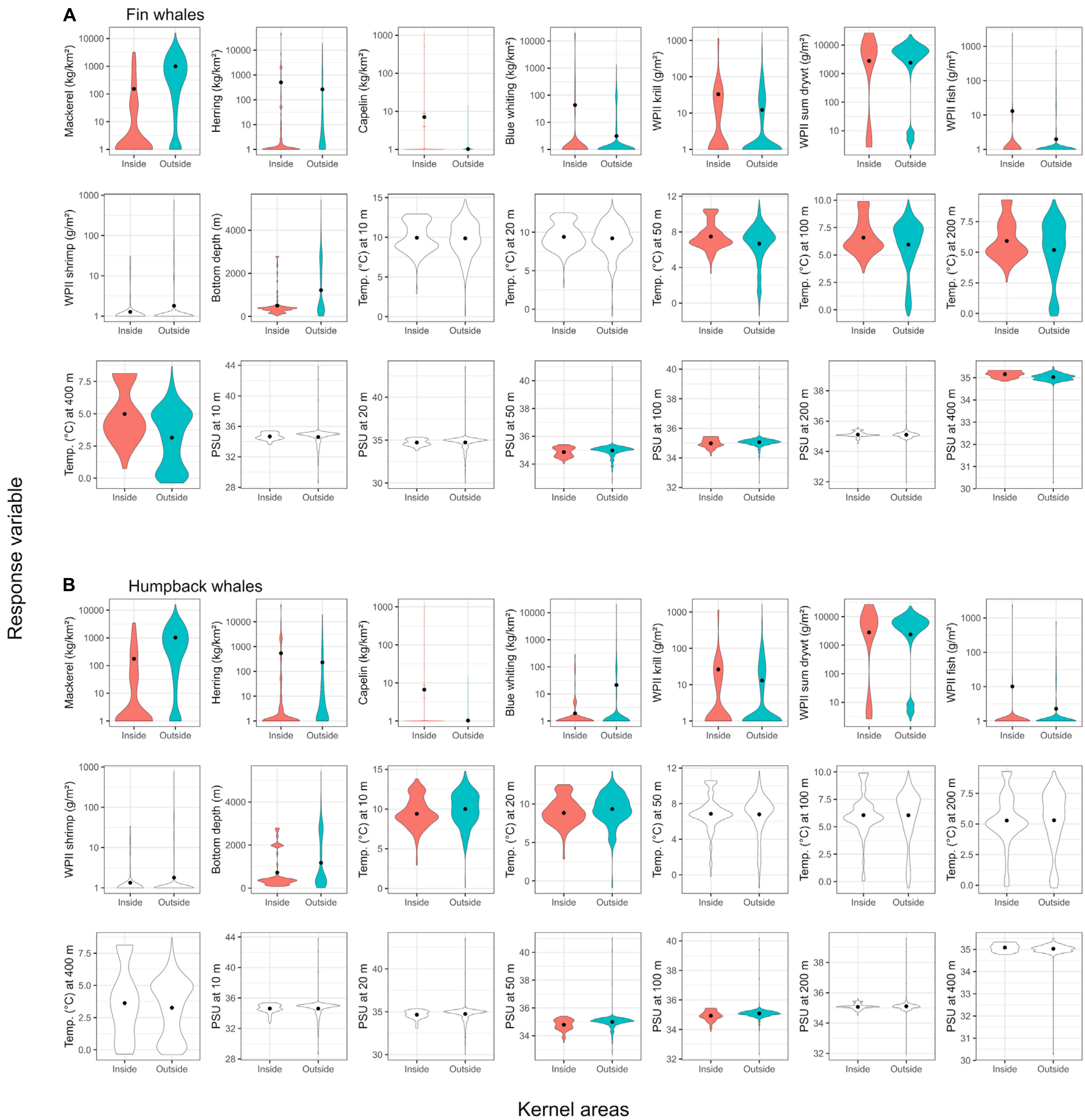

FIGURE 3 | Violin plots of biotic and abiotic variables from sampling stations inside versus outside kernel areas of fin (**A** panels) and humpback (**B** panels) whales. Different colors within a plot indicate significant differences determined by a generalized linear mixed-effects model (catch data and depth) or a linear mixed-effects model (CTD data). Solid circles represent predicted mean values from the models for which the random effect of year was taken into account. A violin plot is a mirrored density plot displayed in the same way as a boxplot (i.e., it illustrates data density along the *y*-axis). WPII is the plankton net for sampling meso- and macro-zooplankton.

DISCUSSION

This large-scale multi-species field study conducted in the Norwegian Sea during the summers of 2013 through 2018 documents an interesting northern displacement trend of fin and humpback whales compared to previous relevant available ecological studies within this productive marine ecosystem (Nøttestad and Olsen, 2004; Skjoldal et al., 2004). A predictable distributional pattern of fin and humpback whales within the Norwegian Sea ecosystem as well as within the southwestern part of the Barents Sea was described for the late 1980s until 2006–2007 based on previous sighting and ecological studies

TABLE 2 | Test statistics for biotic and abiotic factors compared between inside and outside the kernel areas of fin whales: glmm refers to the generalized linear mixed-effects model and lme refers to the linear mixed-effects model.

Response variable	Type of model	Model intercept	Model contrast for outside kernel area	Predicted mean inside kernel area	Predicted mean outside kernel area	Unit	df	*t*-value	*p*-value
Mackerel catch	glmm	4.954	1.901	141.682	948.152	Kilogram	1088	7.4806693	<0.001
Herring catch		6.223	−0.638	504.405	254.721	Kilogram	1088	1.947685	0.052
Capelin catch		1.829	−5.910	6.225	0.017	Kilogram	1090	6.930824	<0.001
Blue whiting catch		3.767	−2.927	43.235	2.316	Kilogram	1087	8.800952	<0.001
Krill catch from WPII plankton net		3.507	−1.076	33.347	11.369	Milligram	741	3.77221	<0.001
Total catch from WPII plankton net		7.944	−0.145	2819.954	2438.992	Milligram	739	2.568913	0.010
Fish catch from WPII plankton net		2.479	−2.544	11.932	0.937	Milligram	739	4.633633	<0.001
Shrimp catch from WPII plankton net		−1.352	1.109	0.259	0.785	Milligram	739	1.265312	
Bottom depth		6.218	0.880	501.561	1209.500	Meter	936	8.80529	<0.001
T10	lme	9.938	−0.040	9.389	9.898	°C	744	0.2046419	0.837
T20		9.377	−0.151	9.377	9.226	°C	744	0.81412	0.416
T50		7.460	−0.766	7.460	6.695	°C	743	3.752973	<0.001
T100		6.572	−0.608	6.572	5.964	°C	723	2.84159	0.005
T200		5.912	−0.717	5.912	5.195	°C	653	2.95556	0.003
T400		5.038	−1.913	5.038	3.125	°C	447	5.170627	<0.001
S10		34.666	−0.073	34.666	34.593	PSU	744	0.7958	0.426
S20		34.714	0.012	34.714	34.726	PSU	744	0.1539	0.878
S50		34.865	0.107	34.865	34.972	PSU	743	2.3254	0.020
S100		34.984	0.084	34.984	35.069	PSU	723	2.34	0.020
S200		35.105	−0.005	35.105	35.100	PSU	653	0.1653	0.869
S400		35.159	−0.137	35.159	35.021	PSU	446	3.1684	0.002

Predicted mean values from the glmms are back-transformed values to the response scale from the log link function used in the models.

TABLE 3 | Test statistics for biotic and abiotic factors compared between inside and outside the kernel areas of humpback whales.

Response variable	Type of model	Model intercept	Model contrast for outside kernel area	Predicted mean inside kernel area	Predicted mean outside kernel area	Unit	df	*t*-value	*p*-value
Mackerel catch	glmm	5.045	1.849	155.172	986.010	Kilogram	1088	8.749474	<0.001
Herring catch		6.306	−0.909	547.782	220.777	Kilogram	1088	2.748509	0.006
Capelin catch		1.768	−5.235	5.857	0.031	Kilogram	1090	5.10857	<0.001
Blue whiting catch		−0.021	3.102	0.979	21.768	Kilogram	1087	2.0606536	0.040
Krill catch from WPII plankton net		3.255	−0.749	25.931	12.263	Milligram	741	2.594601	0.010
Total catch from WPII plankton net		7.960	−0.173	2863.643	2408.340	Milligram	739	3.218343	0.001
Fish catch from WPII plankton net		2.193	−1.964	8.966	1.258	Milligram	739	3.443147	0.001
Shrimp catch from WPII plankton net		−1.230	0.984	0.292	0.782	Milligram	739	1.353895	0.176
Bottom depth		6.567	0.496	711.153	1167.760	Meter	936	5.87804	<0.001
T10	lme	9.366	0.677	9.938	10.043	°C	744	3.776942	<0.001
T20		8.811	0.554	9.377	9.365	°C	744	3.178365	0.002
T50		6.835	−0.011	7.460	6.824	°C	743	0.055735	0.956
T100		6.034	0.045	6.572	6.079	°C	723	0.219419	0.826
T200		5.262	0.064	5.912	5.326	°C	653	0.277601	0.781
T400		3.621	−0.366	5.038	3.254	°C	447	1.108851	0.268
S10		34.626	−0.025	34.66	34.601	PSU	744	0.2892	0.773
S20		34.666	0.072	34.714	34.738	PSU	744	1.013	0.311
S50		34.793	0.202	34.865	34.995	PSU	743	4.7031	<0.001
S100		34.928	0.159	34.984	35.087	PSU	723	4.7238	<0.001
S200		35.068	0.040	35.105	35.109	PSU	653	1.3507	0.177
S400		35.083	−0.056	35.159	35.026	PSU	446	1.4764	0.141

*See **Table 2** for more details.*

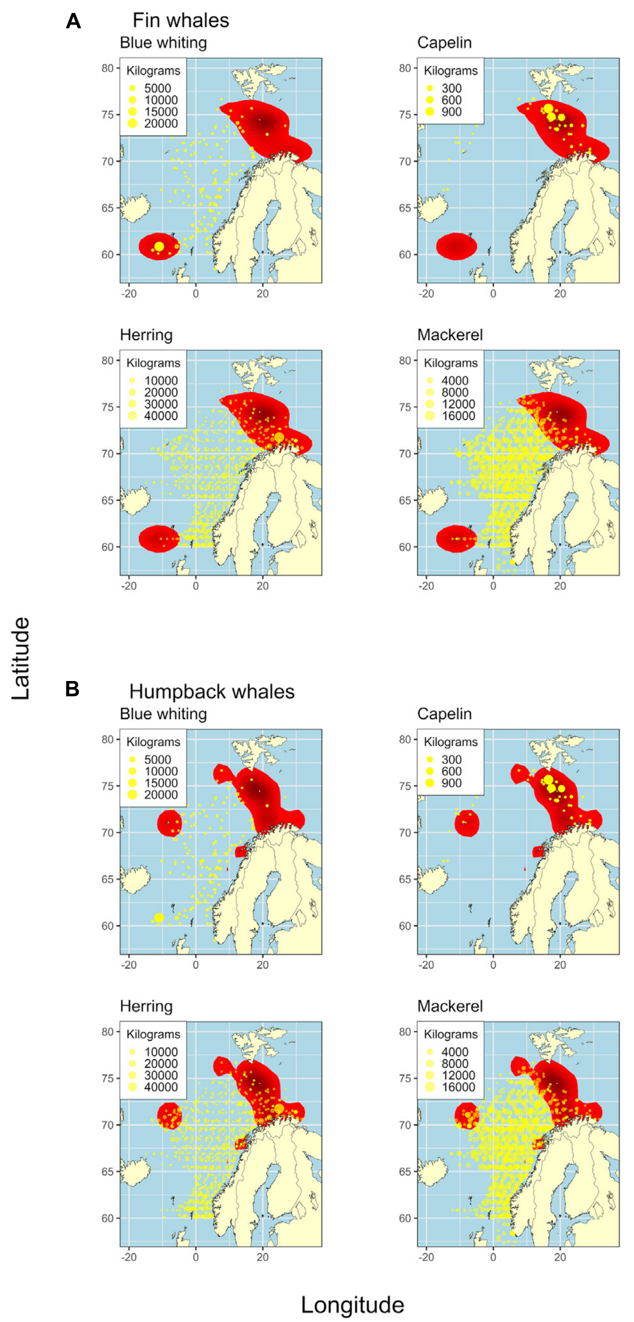

FIGURE 4 | Fin (**A** panels) and humpback (**B** panels) whale kernel areas (red) and catch of potential prey fish at each sampling station (yellow points). Each cluster of four panels **(A,B)** shows the catch of blue whiting, capelin, herring, and mackerel, respectively.

(Christensen et al., 1992; Øien, 2009; Skern-Mauritzen et al., 2011; Nøttestad et al., 2014c). However, a distributional shift for these species occurred during 2009–2012 (Nøttestad et al., 2015b).

In our survey, the highest number of sightings of fin and humpback whales occurred north of 70°N and along shelf areas. Their distribution was linked to the available prey (several pelagic fish and macro-zooplankton species) in this highly productive area. Humpback whales were more abundant than fin whales in the area around Jan Mayen. The shelf area around Jan Mayen has traditionally been considered a highly productive area, with cold Arctic water providing high densities of herring, capelin, krill, amphipods, and other zooplankton species (Blindheim, 2004; Melle et al., 2004; Skjoldal, 2004). Earlier studies of fin and humpback whales describe these areas as important feeding grounds during the summer season (Christensen et al., 1992; Nøttestad and Olsen, 2004; Nøttestad et al., 2014c, 2015b). Fin whales depend on dense aggregations of prey due to their energetically costly method of lunge feeding; this also applies to humpback whales, although they use more diverse in feeding tactics (Piatt and Methven, 1992; Croll et al., 2001; Acevedo-Gutiérrez et al., 2002; Croll et al., 2005; Goldbogen et al., 2012, 2013).

Capelin appears to be an important and preferred prey species for humpback whales despite its decreasing abundance. Capelin stocks were relatively stable from the mid-2000s until 2013, when a decline began, and by 2016 the stock had collapsed (Hjermann et al., 2004; Huse et al., 2012; ICES (International Council for the Exploration of the Sea), 2017a,b). In our study, humpback whale distribution was positively correlated with capelin distribution, and humpbacks were more often found in large aggregations and annually in areas with high capelin catches. A large group of up to 100 fin whales was observed to be feeding on capelin, and a few other observations also noted feeding on capelin. The catches of capelin and the fin whale hotspot overlapped, indicating that they occurred in the same area. These findings indicate that capelin is an important prey species for both fin and humpback whales, which is supported by results of earlier studies (Piatt et al., 1989; Piatt and Methven, 1992; Aguilar, 2009; Clapham, 2002). Several cetacean species were observed in the Norwegian Sea, and many observations were near fin and humpback whales.

We also found significant negative spatial correlations between both fin and humpback whales and mackerel. These large baleen whales predominantly avoided overlap with the widely expanding mackerel population. Mackerel have been present in high abundance throughout the entire Norwegian Sea from around 2010 and onward (Nøttestad et al., 2016a; ICES (International Council for the Exploration of the Sea), 2019). One potential reason for the observed negative correlation is that although mackerel have the highest fat content among the available prey species, they also are faster swimmers and have advanced and highly dynamic anti-predator maneuvers (Iversen, 2004; Nøttestad et al., 2004, 2014b), which make them difficult for fin and humpback whales to catch during attacks. The active anti-predator maneuvers also inevitably increase energy costs for feeding fin and humpback whales (Acevedo-Gutiérrez et al., 2002; Nøttestad et al., 2004, 2014c, 2015b). Another potential explanation for the negative correlation is that important prey species, such as herring, capelin, and copepod feeding krill, may have been outcompeted for preferred food or displaced by hunting schools of hungry mackerel. Another plausible explanation is that killer whales exploiting mackerel as prey (Nøttestad et al., 2014b) pose a predation threat, especially to humpback whales and their calves (Ford and Reeves, 2008;

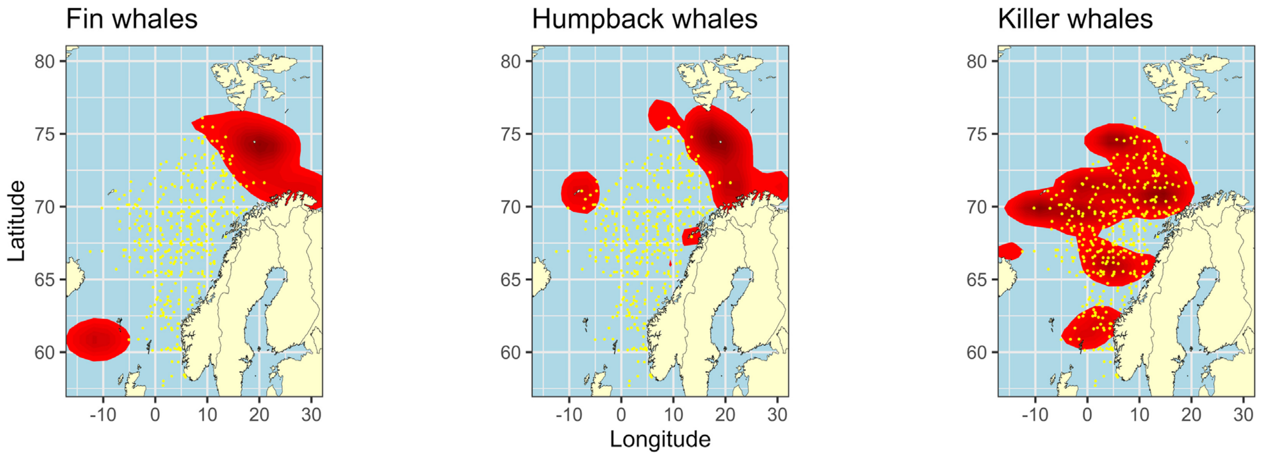

FIGURE 5 | Overall spatial overlap between fin, humpback, or killer whale kernel areas (red) and high catches (≥median) of mackerel (yellow data points) from data collected in July and August, 2013–2018.

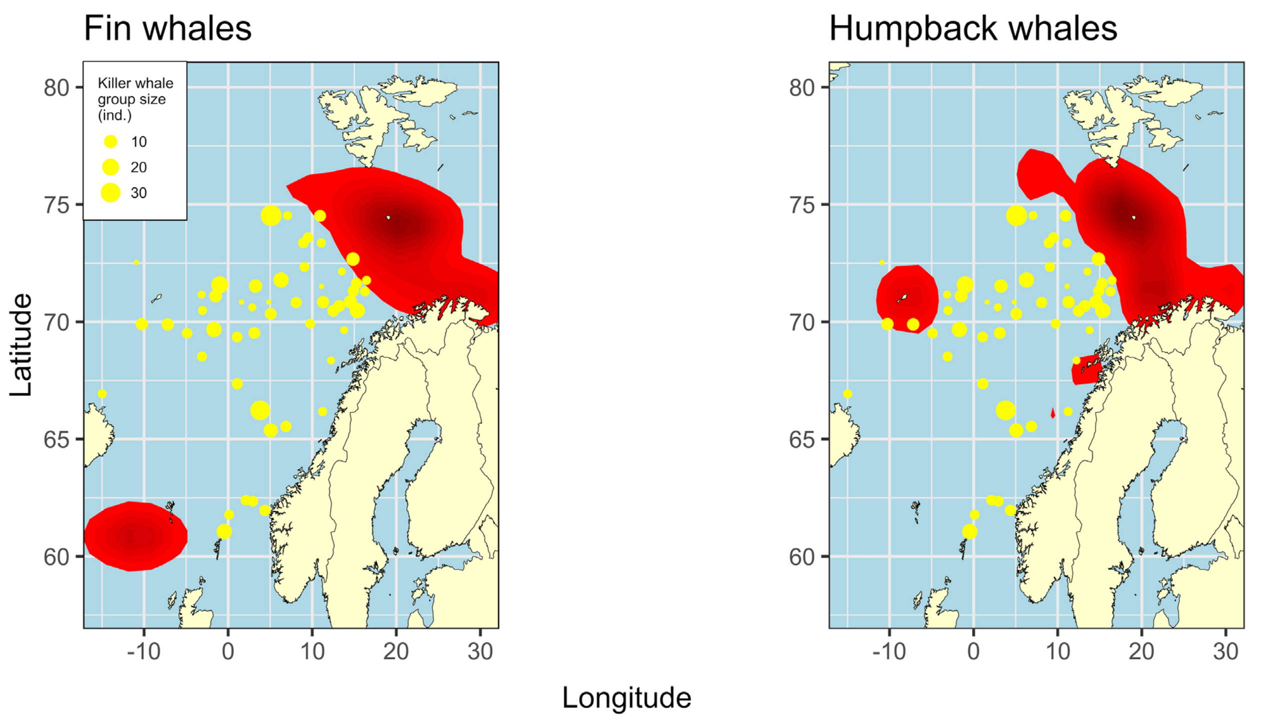

FIGURE 6 | Fin or humpback whale kernel areas (red) and sightings of killer whales (yellow points) from data collected in July and August, 2013–2018.

Aguilar, 2009). This threat likely would cause fin and humpback whales to avoid the areas where killer whales forage on mackerel (Ford and Reeves, 2008). Observations of pods of killer whales overlapping significantly in space and time with mackerel in the Norwegian Sea during the summers from 2013 to 2018 confirms the patterns described previously by Nøttestad et al. (2014b). Furthermore, since we found a positive association between killer whales and mackerel, but not between mackerel and fin- and humpback whales, mackerel may simply not be a preferred prey species by fin- and humpback whales in the Norwegian Sea during summer.

Macro-zooplankton play a significant role as prey for large baleen whales, and we found that the distributions of humpback whales and krill were positively correlated. Krill is also associated with the shelf area in the southwestern part of the Barents Sea (Dalpadado and Skjoldal, 1991; Buchholz et al., 2010), and krill has also been shown to be an important prey species for both fin- and humpback whales in this region (Leonard and Øien, 2013 and Skern-Mauritzen et al., 2011). However, a shortcoming of this study was the lack of representative catches of macro-zooplankton, and the observed correlations likely should be higher. Macro-zooplankton included in this study, such as krill and amphipods, were sampled using vertical hauls with WPII nets from 0 to 200 m depth or by using a pelagic trawl. The WPII nets with small mesh size, a small mouth, and low hauling speed were designed to capture meso-zooplankton (Melle et al., 2004), and macro-zooplankton, such as krill, may escape or avoid the net. Additionally, the trawl used in this study was designed to catch pelagic fish. Unlike many pelagic fish species, krill are rarely herded by the side panels of the trawl when entering the mouth. Thus, using a trawl with coarse meshes in the panels near the mouth and decreasing mesh panels toward the codend provides the chance for a large proportion of krill to escape the trawl gear.

Herring is considered to be one of the most important prey species for fin and humpback whales, and a recent study of humpback whales in the Norwegian Sea positively correlated its distribution with that of herring in the northern Norwegian Sea (Aguilar, 2009; Nøttestad et al., 2002, 2015b; Nøttestad and Olsen, 2004). However, the recruitment of herring has been low since 2004, which is assumed to be partly due to the decrease and northern shift of zooplankton biomass (Melle et al., 2004; Sissener and Bjørndal, 2005; Toresen et al., 2019). Additionally, since 2009, Norwegian spring-spawning herring has been in decline (ICES (International Council for the Exploration of the Sea), 2017a). Herring catches in our study varied among the 6 years, with 2014 recording the highest catches and 2017–2018 having the lowest catches. Neither fin nor humpback whale distributions were correlated with catches of herring. In a study of the hunting tactics of fin whales on herring, Nøttestad et al. (2002) found that all interactions with herring took place at night when the schools were shallower than 200 m, which most likely is related to the energy limitations of the feeding tactics of fin whales. Herring catches in our study were not correlated with bottom depth, but the catch was spread throughout the Norwegian Sea and likely covered too great and diverse an area for the analysis to have detected a correlation. A connection between the shallow shelf area off the northern coast of Norway and the easier availability of herring for at least fin whales is plausible.

Blue whiting has also increased in abundance and distribution after around 2011 in the Norwegian Sea, but catches of this species were not correlated with distribution of either fin or humpback whales (Heino et al., 2008; Dolgov et al., 2010; Payne et al., 2012; Utne et al., 2012). However, blue whiting are not preferred prey of these whale species. Blue whiting is most often found at 100–600 m and can move up to shallower waters during its daily vertical migration (Monstad, 2004; Heino et al., 2008). A large aggregation of up to 50 fin whales was observed feeding on blue whiting in 2016 outside the Faroe Islands. This location was also where a very large catch of small juvenile blue whiting was collected at the same time. This finding suggests that fin whales are opportunistic in prey choice but are dependent on a foraging density threshold of their prey due to their energetically expensive feeding tactics.

CONCLUSION

The results of this large-scale ecosystem study suggest a northerly shift from the mid-1990s to the period 2013–2018 and pronounced hotspot feeding of fin and humpback whales off the northern coast of Norway, around Bear Island, and toward the southwestern part of Svalbard. At the same time, there has been historical spatial expansion of mackerel during summer into the northern part of the Norwegian Sea. Killer whales are a dominant predator on mackerel and may outcompete the baleen whales for this prey source, and direct interactions with these toothed whales may negatively affect fin and humpback whales. The large-scale pronounced changes in fin and humpback whale distributions confirm a high degree of plasticity for these large baleen whale species. Their response appears to be closely linked to relatively abrupt changes to the distribution, density, and behavior of available prey species. Furthermore, both fin and humpback whales seem to have shifted their distributions northwards to higher latitudes in the Norwegian Sea, probably to reduce prey competition with abundant and widely distributed pelagic schooling fish such as mackerel and/or reduce predation pressure from pods of hunting killer whales.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

SL: wrote article as master project, contributed to the analysis and writing, and data collection and quality assurance. KJ: contributed to the statistical analysis and graphical production. BK: contributed to writing and supervising of SL. VA: contributed to data collection and producing annual marine mammal overview. LN: contributed to data collection, writing, and main supervisor to SL. All authors contributed to the article and approved the submitted version.

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