

# DISTRIBUTION AND HABITAT USE OF DEEP-DIVING CETACEANS IN THE CENTRAL AND NORTH-EASTERN NORTH ATLANTIC

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## ABSTRACT

Major changes in the distribution of some cetaceans have been observed coincident with changing oceanography of the North Atlantic in the last 30 years. This study aimed to improve understanding of the underlying ecological drivers of any changes in deep-diving cetacean distribution. We used data from two series of summer surveys (in Iceland-Faroes and Norway) to model density of sperm (*Physeter macrocephalus*), long-finned pilot (*Globicephala melas*) and northern bottlenose (*Hyperoodon ampullatus*) whales as a function of static (relief), physical, and biological oceanographic covariates using GAMs. The best models, based on a robust model selection framework, were used to predict distribution. The study period was divided into two periods, 1987-1989 and 1998-2015, based on environmental changes in the area and data availability. The common covariates that best explained these three species' distributions (in both periods) were bathymetric variables and SST. The selected dynamic temperature-related covariates for sperm and pilot whales were for spring, but for bottlenose whales were for summer. Summer relationships were also found for the three species for the other dynamic variables, except spring chlorophyll-a for bottlenose whales. The difference in seasonal relationships for bottlenose whales may be related to a previously suggested north-south summer migration. As expected, the predicted high-use areas for all three species were deep waters, with some overlap among them in the central Norwegian Sea, and the Central North Atlantic, including the Irminger Sea. Differences in distribution likely reflect differences in prey. Changes in distribution between the two periods appear more as a range expansion than a shift, which could result from an increase in suitable habitat due to warming waters. This new knowledge will help improve understanding of how these species may respond over this wide area to a changing environment and inform their conservation.

**Keywords:** deep-diving cetaceans, habitat use, North Atlantic, summer distribution

## INTRODUCTION

An important goal in ecology is to understand the underlying processes driving animal distribution and how animals use their habitat; this knowledge also provides scientific advice for management and conservation (Redfern et al., 2006). Physical changes during the last decades in the North Atlantic (e.g. warmer temperatures) have been linked to biological changes, which have been detected in fish species such as mackerel, herring, capelin, and blue whiting (Astthorsson et al., 2012; Hátún et al., 2009; Huse et al., 2015; Trenkel et al., 2014; Valdimarsson et al., 2012). The main goal of this study was to improve understanding of the environmental factors that influence the distribution and habitat use of deep diving cetaceans in the central and north-eastern North Atlantic over a period of three decades by modelling their relative abundance as a function of a series of static and dynamic variables.

The three main species of deep diving cetaceans commonly observed in the central and north-eastern North Atlantic are

sperm, long-finned pilot, and northern bottlenose whale. Each of these species are known to feed on squid, other cephalopods and less commonly fish (Bjørke, 2001; Bloch et al., 1996; Desportes & Mouritsen, 1993; Whitehead et al., 2003), accounting for a substantial proportion of cetacean food consumption in this area (Sigurjónsson & Víkingsson, 1997; Skern-Mauritzen et al., 2022).

This group of cetaceans is or has been subject to a range of pressures, including whaling and ocean noise. Abundance estimates for the entire central and north-eastern North Atlantic come from four different series of surveys: the Norwegian Independent Line-transect Surveys (NILS), the North Atlantic Sightings Surveys (NASS), Small Cetacean Abundance in European Atlantic waters and the North Sea (SCANS), and Aerial Surveys of Cetaceans and Seabirds in Irish waters (ObSERVE) where these species were not the main target. Globally, the sperm whale, the long-finned pilot whale, and the northern

bottlenose whale are listed by the IUCN as Vulnerable, Least Concern, and Data Deficient, respectively.

### **Sperm whale distribution and habitat use**

The sperm whale (*Physeter macrocephalus*) is the most sexually dimorphic of whale species, and this is reflected in their seasonal distribution. Females are generally found in latitudes lower than 40-50° and in equatorial waters, in the company of other females; in sperm whale societies the basic family unit is around 10 females and their young (Whitehead, 2003). Young male sperm whales stay in the family unit in tropical and subtropical waters until moving gradually to higher latitudes. Mature male sperm whales are distributed at high latitudes up to the ice-edge in both hemispheres. They return to lower latitudes to breed but the exact timing is unknown (Whitehead, 2018). In the eastern part of the North Atlantic, there were no reports of females and young north of the Azores (Clarke, 1956 In: Christensen et al., 1992), except in Ireland where less than 20 reports of strandings or sightings have been made since 1910 (O'Callaghan et al., 2024). In Norway, there have not been reports until 2020 when a female sperm whale carcass was found stranded in Saltfjorden, Bodø (D. Leonard & N. Øien, personal communication, February 7, 2024). Although no females were reported in the area from whaling, in the 1989 NASS females were believed to have been observed around 55°N (Gunnlaugsson, et al., 2009). As sperm whale female occurrence seems to be exceptional in the study area, it is assumed that mainly or only males were observed.

Globally, sperm whales of both sexes and all age classes are more commonly found in deep waters and along the continental slope (Christensen et al., 1992; Gunnlaugsson et al., 2009; Roberts et al., 2016; Rogan et al., 2017; Virgili et al., 2019; Whitehead, 2018). Females are almost always found exclusively in waters deeper than 1,000 m (Rice, 1989), while males are generally found in deep waters but in some areas such as off New York and Nova Scotia have been seen in waters less than 300 m deep (Whitehead, 2018). In the central and north-eastern North Atlantic, sperm whales have been observed most frequently in deep waters (Christensen et al., 1992; Gunnlaugsson et al., 2009; Rogan et al., 2017). In Icelandic waters (Denmark Strait) the species depth range, based on existing knowledge from whaling and some of its prey, is between 400 and 1,200 m but can extend to depths of 2,000-3,000 m (Martin & Clarke, 1986). Rogan et al. (2017) found that sperm whale group abundance was highest in waters between 1,000 and 4,000 m, while group size was larger in waters <2,000 m. Slope consistently seems to be an important feature influencing sperm whale distribution (Rogan et al., 2017; Virgili et al., 2019); especially in Norwegian waters where most whales have been observed along the continental slope (Christensen et al., 1992; Øien, 2009).

Globally, the relationship between sperm whale distribution and water temperature varies between the sexes. Females, calves and juveniles seem to be concentrated in waters of around 15 °C (Rice, 1989), while males occur in a wider range of temperatures because of their broader distribution (Baumgartner et al., 2001; Pirotta et al., 2011; Rogan et al., 2017). In the southern part of the central and north-eastern North Atlantic, estimated abundance was found to be highest between sea surface temperatures (SST) of 10 °C and 20 °C, while group size was predicted to increase with increasing SST (Rogan et al., 2017). Overall, the relationship between sperm

whale density and water temperature seems to be linked to the presence of thermal fronts. Some studies have found sperm whale occurrence to be related to upwelling zones but others have found a relationship with downwelling zones (Baumgartner et al., 2001; Pirotta et al., 2011). Fronts are areas with density gradients in physical features such as temperature; this favours the accumulation of nutrients and plankton, which in turn attracts higher trophic level species such as sperm whales.

Sperm whale diet has been mainly described as consisting of squid and other cephalopods, and males are more likely than females to consume demersal fish (Bjørke, 2001; Sigurjónsson & Víkingsson, 1997; Whitehead, 2018). Diet analysis from 221 sperm whales caught in the Denmark Strait had fish remains in 87% and cephalopod remains in 68% of stomachs. The main fish species contributing to the diet was lumpsucker (*Cyclopterus lumpus*). The most important families of cephalopods were Histiotteuthidae, Cranchiidae, Ommastrephidae, and Gonatidae (Martin & Clarke, 1986). In Norwegian waters, studies have shown a mainly squid-based diet (Hjort and Ruud, 1929, as cited in Bjørke, 2001; Clarke, 1996; Santos et al., 1999). The squid *Gonatus fabricii* has been suggested to represent the main cephalopod species consumed and, in some studies, the main prey for sperm whales in the Norwegian Sea (Clarke, 1996; Santos et al., 1999). However, summer distribution of sperm whales in the Norwegian Sea in 2009, 2010, and 2012 was found not to be related to the distributions of herring, mackerel, blue whiting, capelin, krill or *Gonatus* spp. (Nøttestad et al., 2015).

### **Pilot whale distribution and habitat use**

The two pilot whale species, long-finned (*Globicephala melas*) and short-finned (*G. macrorhynchus*) pilot whale, are wide-ranging species found along coasts and far offshore (Abend & Smith, 1999; Buckland et al., 1993; Olson, 2018; Pike, Gunnlaugsson, Desportes et al., 2019). Pilot whales are believed to be nomadic; few resident populations have been identified (Abend & Smith, 1999). However, in the North Atlantic, Alves et al. (2013) and Servidio et al. (2019) found evidence for different levels of site fidelity in short-finned pilot whales: transient, temporary migrants and resident (island associated) animals in Madeira and the Canary Islands, respectively. Photo-identification studies of long-finned pilot whales in the Strait of Gibraltar have suggested that some whales are seasonal (summer) residents (Verborgh et al., 2009).

Long-finned pilot whales are broadly distributed in coastal and oceanic waters in the west and east of the North Atlantic: in the western part from around 35° to 65° N and in the eastern part from around 40° to 75° N (Figure 1) (Abend & Smith, 1999; ICES, 1992; NAMMCO, 1997, 1998; Roberts et al., 2016). In Icelandic waters, data from whaling vessels collected during 1979 to 1988 showed an increase in long-finned pilot whale sightings after July 15<sup>th</sup>, occurring mostly in waters of 400 to 1,000 m in depth and some in waters less than 400 m, although there may be some inaccuracies, as small cetaceans were of little direct interest to whalers (Sigurjónsson & Gunnlaugsson, 1990). More recently, Rogan et al. (2017) found that long-finned pilot whale summer distribution in the north-eastern North Atlantic peaked at depths >1,000m, and was strongly associated with the 2,000 m depth contour and areas of moderate slope. Similarly, the summer distribution to the west of Scotland during 2004-2005 occurred primarily in depths between 1,370 and 1,951 m (MacLeod et al., 2007). In contrast, during the summer months

of 2009, 2010, and 2012 in the Norwegian Sea, long-finned pilot whales were associated with shallow depths, especially those shallower than 300 m (Nøttestad et al., 2015).

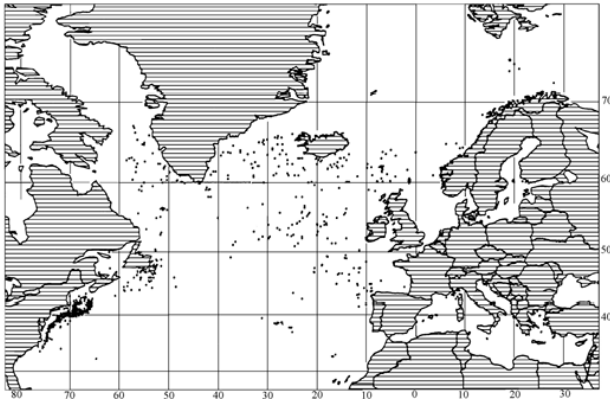


Figure 1. Distribution of long-finned pilot whales in the North Atlantic and Mediterranean Sea based on sighting data from 1952 to 1992 (Abend & Smith, 1999).

These distributional differences may relate to a wide water temperature range, but there is little information directly relating pilot whale occurrence to water temperature. Because they are considered deep divers, sea surface temperature is not thought to directly influence, or act as a direct proxy of their presence. However, observations do seem to be associated with warmer surface temperatures. For example, long-finned pilot whales west of Scotland were only recorded in warmer waters at SST >10.9 °C (MacLeod et al., 2007). Analysis of whaling data from the north-eastern region of the Faroe Islands found large catches associated with warmer water temperatures (Hátún et al., 2009), suggesting a possible relationship between pilot whale distribution and water temperature.

Long-finned pilot whale distribution changes seasonally. In the summer, whales in the North Atlantic occur more in slope and/or shelf waters, while in the winter it is believed that they move southward and into deeper waters (Abend & Smith, 1999; IWC, 1990; Nøttestad et al., 2015; Roberts et al., 2016; Rogan et al., 2017). Long-finned pilot whales in the central and north-eastern North Atlantic occur in offshore and in coastal waters (Nøttestad et al., 2015; Pike, Gunnlaugsson, Desportes, et al., 2019). In Icelandic waters, opportunistic sightings made from whaling vessels during 1979 to 1988 occurred west-northwest of the island (Sigurjónsson & Gunnlaugsson, 1990). Abend and Smith (1999) compiled data from the 1950s to 1992; their summary of Icelandic sightings indicates that long-finned pilot whales regularly occurred off the southern coast and did not occur on the northern side of the island (Figure 1). Pike, Gunnlaugsson, Desportes, et al. (2019) evaluated long-finned pilot whale relative abundance using the Icelandic and Faroese NASS data (1987 to 2015), concluding that they were broadly spread offshore but that their distribution varied among survey years. The year with broadest southern coverage was 1989, revealing an area of high density south of 56° N but this area was not covered by any other survey. The peak in the number of whale drives in July-August in the Faroe Islands is indicative of seasonal movements (Zachariassen, 1993). In Norwegian waters, long-finned pilot whales seem less common (Abend & Smith, 1999), but the catch history also showed a high July-August peak along the coasts of Lofoten and Møre (ICES, 1992).

The most northerly records of long-finned pilot whales are from opportunistic observations from whaling boats during the summer of 1973 to 1975 in the Barents Sea (Christensen, 1977, as cited in: Abend & Smith, 1999).

Changes in distribution and movements of long-finned pilot whales are assumed to be linked to the abundance of their prey, which are mainly various squid species. The species consumed seem to vary depending on the area, and small pelagic fish are also consumed. They are believed to be opportunistic feeders, exploiting any locally abundant prey in oceanic and coastal waters; ecological tracers show this dietary plasticity (Desportes & Mouritsen, 1993; Méndez-Fernandez et al., 2013; Santos et al., 2014).

In Faroese waters, their preferred prey seems to be the European flying squid (*Todarodes sagittatus*). If this species is abundant, the diet seems to be nearly mono-specific (Desportes & Mouritsen, 1993). Other prey species around the Faroes include the harmhook squid (*Gonatus* spp.), fish such as greater argentine (*Argentina silus*), blue whiting (*Micromisistius poutassou*), Greenland halibut (*Reinhardtius hippoglossoides*), and pandalid shrimps. Other common fish species in the area are cod, herring, and mackerel, but they have not been reported as prey despite being preyed upon by long-finned pilot whales in other areas (Desportes & Mouritsen, 1993). In other areas of the north-eastern and central North Atlantic, information regarding long-finned pilot whale prey preferences is less complete than the Faroes. Limited stranding data from Iceland in the 1980s also indicated the European flying squid as the main prey (Sigurjónsson, Vikingsson, & Lockyer, 1993). In the Norwegian Sea, long-finned pilot whale summer distribution in 2009, 2010, and 2012 seemed to be highly correlated with high concentrations of Norwegian spring-spawning herring (Nøttestad et al., 2015).

#### **Northern bottlenose whale distribution and habitat use**

The northern bottlenose whale (*Hyperoodon ampullatus*) is the least known among the deep diving species in this study. Northern bottlenose whales are found in temperate, subarctic, and Arctic waters of the North Atlantic, extending from the ice edge to approximately 30° N (Taylor et al., 2008). They are usually found in waters deeper than 500 m with the highest occurrences at depths between 750 and 1,800 m and along the continental shelf edge (Figure 2) (Benjaminsen & Christensen, 1979; Compton, 2004; Hooker, Whitehead, & Gowans, 1999; Whitehead & Hooker, 2010, 2012a). In the north-western North Atlantic, Compton (2004) found the core predicted area to be characterised by an aspect of 142° (south-east facing slopes). The broad latitudinal occurrence implies a wide temperature range for the species. Benjaminsen and Christensen (1979) summarised reports from whaling data in the northeast Atlantic, where animals were reported in surface water temperatures from -2 °C to +17 °C, but in the northwest Atlantic the core predicted area had an average surface temperature of 2.7 °C (Compton, 2004).

In the north-eastern North Atlantic, the northern bottlenose whale is the only deep diving species for which a specific summer north-south migration has been suggested (Benjaminsen & Christensen, 1979; Benjaminsen, 1979, as cited in: NAMMCO, 2019; Reeves et al., 1993). However, the evidence for this is limited. Some information from whaling and tagged animals suggests that August is the month when animals are

moving south (Benjaminsen & Christensen, 1979; Bloch et al., 1996; Miller et al., 2015; Reeves et al., 1993). However, there are also records of animals year-round in Faroese and Norwegian waters (Bloch et al., 1996; IWC, 2012). An alternative hypothesis is that there is an inshore–offshore movement (Whitehead & Hooker, 2012a).

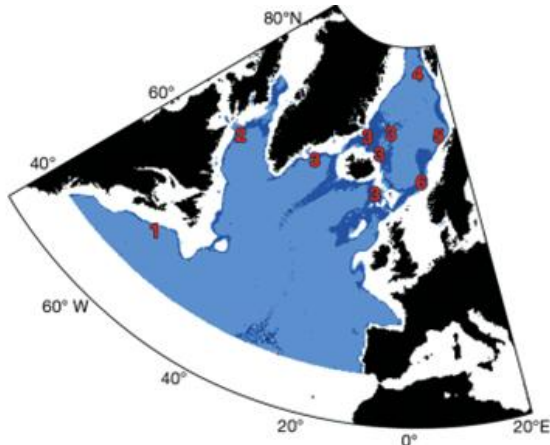


Figure 2. General distribution of northern bottlenose whales in the North Atlantic (light blue), defined as waters greater than 500 m deep and north of 37.5° N. Preferred habitat (800–1800 m deep) is shown in dark blue. The six centres of whaling operations are shown: (1) Scotian Shelf; (2) Labrador and southern Baffin Bay; (3) East Greenland, Iceland, Jan Mayen and the Faroe Islands; (4) Svalbard; (5) Andenes; and (6) Møre (Whitehead & Hooker, 2012a).

Several studies suggest that the main prey of northern bottlenose whales are *Gonatus* spp. In the Norwegian Sea, *Gonatus fabricii* and northern bottlenose whales have a similar distribution (Bjørke, 2001). In the western North Atlantic off Baffin-Labrador, the primary prey is also *G. fabricii* (Mead, 1989) while on the Scotian Shelf it is *G. steenstrupi* (Hooker et al., 2001). In the North Sea, stomach content analysis of two stranded whales showed that *Gonatus* spp. comprised greater than 98% of the estimated prey weight (Santos et al., 2001). Other squid species also taken include *Teuthowenia* spp., *Taonius pavo* and *Histioteuthis reversa* (Hooker et al., 2001). Fernández et al. (2014), analysing the stomach contents of 10 stranded whales from the North Sea, found *Gonatus* spp., *Teuthowenia* spp. and *Taonius pavo* to comprise greater than 90% of the total prey weight and number. Fish and occasionally benthic organisms have also been found in stomachs (Benjaminsen & Christensen, 1979; Reeves et al., 1993; Taylor et al., 2008). From whaling data there appear to be differences in the amount of fish consumed between areas: 53% of stomachs off Labrador but only 13% off Iceland (Benjaminsen & Christensen, 1979). There is also evidence of a mixed diet in the north-western North Atlantic where the core predicted area depth (1,780 m) matched with the maximum depth of Greenland halibut (Compton, 2004).

## MATERIALS AND METHODS

### Data preparation

Ship-based survey data collected in summer (7.3% in June, 79.7% in July, 13% in August) were made available by the governments of Norway, Iceland, and Faroe Islands. The data from Iceland and the Faroes cover the period 1987–2015, when

surveys were conducted in 1987, 1989, 1995, 2001, 2007, and 2015; details about these surveys are given by Víkingsson et al. (2009), Pike, Gunnlaugsson, Mikkelsen, et al. (2019), and Pike et al. (2020). The data from Norway cover the period 1987–2013 with broad coverage in the earlier years 1987, 1988, 1989 and 1995. After 1995, Norway introduced a protocol to survey parts of the northeastern Atlantic each year to cover the whole area every 6 years in a so-called mosaic survey. Three series of these rotations were included in this study 1996–2001, 2002–2007 and 2008–2013; details about these surveys can be found in Øien and Bøthun (2009), Solvang et al. (2015), and some generalities in Víkingsson et al. (2009). Focal species of the surveys were the common minke whale for Norway and fin, minke, long-finned pilot, humpback, sperm and northern bottlenose whales for Iceland and the Faroes. There were differences in data collection protocols between the two datasets (Iceland-Faroes and Norway) and between survey years, which required the implementation of a series of data processing steps to create consistent datasets appropriate for modelling. All data processing was conducted in R (version 4.0.5; R Core Team, 2021). In summary, six steps were followed.

1. Survey data were standardised (e.g. consistent column names) for each survey year or rotation (Norway) and off-effort data were excluded. For Norwegian data, duplicate identification data were not available for deep-diving species, thus only sightings from the primary platform were included in analysis. By the end of this step, annual-rotation data were consistent within each year.

2. All annual survey effort and sightings data (recorded independently in the field) were merged by associating sightings with effort within each dataset (Iceland-Faroes and Norway). Inconsistencies in data and measurement units were standardised so that all distances were expressed in nm.

3. Effort and associated sightings were cut into segments of a target length suitable for modelling (maximum length 25 km; see also below under Prediction). In the Iceland-Faroes data some very small effort legs (<4 km) that could be problematic for modelling were combined. Any duplicate sightings made between platforms were removed, so that only unique individual sightings were used.

4. The effective search area (calculated as twice the estimated effective strip half width (see Appendix A) multiplied by the segment length) for each covariate combination in the detection-function for each species was estimated and added to the working datasets.

5. The Iceland-Faroes and Norway datasets were joined.

6. Values of environmental variables (Table 1) were extracted for the mid-location of each segment using package 'raster' (version 2.6-7; Hijmans, 2017). The extraction was a weighted mean over circular buffers of 10 km radius around the mid-location at each segment, where data points closer to the segment's mid-location were given higher weight. For the oceanographic dynamic covariates (SST, Chl, PP, MLD, SSH, BT and Sal), data were extracted for the month in which the segment was surveyed, and also for each of the spring and summer months (April–August) of that year to allow evaluation of time-lagged relationships (see below).

In this paper, we present analyses for two time periods (1987–1989 and 1998–2015). The data were split in this way primarily

Table 1. Environmental variables, description, source and abbreviation used in modelling.

Name	Description	Source
Depth	Weighted mean depth in the grid cell	1-Minute Gridded Global Relief Data (ETOPO1). NOAA Satellite and Information Service. Extracted using 'marmap' R package.
Slope	Slope of the sea floor in degrees	Derived from ETOPO1 bathymetric data. Extracted using 'marmap' R package. Computed using 'raster' R package, function terrain.
Aspect	Direction of slope of the sea floor in degrees	Derived from ETOPO1 bathymetric data. Extracted using 'marmap' R package. Computed using 'raster' R package, function terrain.
Sea surface temperature (SST)	Weighted mean sea surface temperature (°C) for the months of April to August 1998 to 2015	Data were processed by NEODAAS from NOAA L3 data. Sensor: Advanced Very High Resolution Radiometer (AVHRR); Resolution: 9 km, monthly composite.
Chlorophyll a (Chl)	Weighted mean Chlorophyll a concentration [ $\text{mg m}^{-3}$ ] for the months of April to August 1998 to 2015	Data products generated by the Ocean Colour component of the European Space Agency Climate Change Initiative project. Data were processed by NEODAAS (NERC Earth Observation Data Acquisition and Analysis Service) from ESA Ocean Colour CCI L3 data. Sensor: (MERIS, MODIS Aqua, SeaWiFS LAC and GAC, VIIRS); Resolution: 9 km, monthly composite.
Primary productivity (PP)	Weighted mean primary production [ $\text{mg C m}^{-2} \text{day}^{-1}$ ] for the months of March to August 1998 to 2015	A derived covariate of Chlorophyll a, processed by NEODAAS where chlorophyll profile parameters and photosynthesis parameters were used in conjunction with the remotely-sensed chlorophyll data from the OC-CCI v2.0 products (Sathyendranath et al., 2016). Average sea-surface irradiance (Photosynthetically Active Radiation, PAR) for each month was taken from the NASA MODIS and SeaWiFS PAR products (OBPG, 2014). Resolution: 9 km, monthly composite
Density ocean mixed layer depth (MLD)	Weighted mean ocean mixed layer depth (m) for the months of April to August 1998 to 2015	Global reanalysis, GLORYS2V4. It relies on three main components, 1) the ocean model (including the surface atmospheric boundary condition, 2) the data assimilation method and 3) the assimilated observations. Resolution: 0.25 degree, monthly composite.
Sea surface height (SSH)	Weighted mean sea surface height (m) for the months of April to August 1998 to 2015	Global reanalysis, GLORYS2V4 as in MLD. Resolution: 0.25 degree, monthly composite.
Sea floor potential temperature (BT)	Weighted mean bottom temperature (Kelvin) for the months of April to August 1998 to 2015	Global reanalysis, GLORYS2V4 as in MLD. Resolution: 0.25 degree, monthly composite.
Salinity (Sal)	Weighted mean salinity (PSU) for the months of April to August 1998 to 2015	Global reanalysis, GLORYS2V4 as in MLD. Resolution: 0.25 degree, monthly composite.

because the limited availability of environmental variables in 1987–1989 (Table 1) meant that only relatively simple models including relief-related variables and SST could be fitted for this period. A broader suite of environmental variables was available for the period 1998–2015. Although 1995 was the year with the broadest survey coverage (Pike, 2009), it was not included in analysis due to the low quality of the environmental data available, including SST, in that year.

The effort and sightings used for modelling are shown in Figure 3. The numbers of individuals sighted during this effort are summarized in Table 2. For the earlier period (1987–1989), modelling of northern bottlenose whales and long-finned pilot whales was conducted using only data from Icelandic and

Faroese surveys because there were too few sightings of these species from Norwegian surveys.

#### Analytical methods

Relative abundance of each of the species along the transect line was modelled as a function of explanatory environmental covariates given in Table 1. The response variable was the estimated number of individuals in each effort segment. An offset of log (effective area searched) was included to account for differences in area effectively searched among segments. Generalized Additive Models (GAMs) were fitted in R (version 4.0.5; R Core Team, 2021) using the package mgcv (version 1.8.22; Wood, 2017).

Table 2. Annual summary of Norway (left) and Iceland-Faroes (right) shipboard surveys, including searching effort and the number of individuals of the studied species PM- sperm, GM- long-finned pilot, and HA- northern bottlenose whales.

year	Norway				year	Iceland-Faroes			
	Effort (nm)	PM	GM	HA		Effort (nm)	PM	GM	HA
1987	4,193.069	17	0	0	1987	16,653.393	107	3,953	220
1988	7,722.76	47	0	41					
1989	15,893.06	83	75	2	1989	10,704.762	161	3,488	53
1995	14,571.31	54	326	0	1995	7,862.246	90	1,448	169
1996	3,910.452	78	0	0					
1997	2,577.05	12	0	0					
1998	3,449.854	4	30	0					
1999	3,461.254	5	0	4					
2000	2,942.249	10	31	0					
2001	1,767.432	16	0	8	2001	9,892.699	198	1,240	386
2002	3,286.552	80	0	1					
2003	2,362.99	22	0	2					
2004	1,977.867	2	0	11					
2005	2,138.439	20	0	9					
2006	2,259.906	53	0	0					
2007	2,243.245	0	0	0	2007	7,260.555	99	893	84
2008	2,760.412	2	0	34					
2009	2,347.127	0	0	0					
2010	2,521.187	27	0	2					
2011	3,716.717	45	20	1					
2013	4,735.535	10	0	0					
2015					2015	9,748.588	134	4,235	188
Total	90,838.47	587	482	115	Total	62,122.243	789	15,257	1,100

### Model Fitting

GAMs were fitted using a similar framework to that used by Rogan et al. (2017). The error distribution of the response variable was evaluated by comparing the Poisson, quasi-Poisson, negative binomial, and Tweedie distributions (e.g., Víkingsson et al., 2015). For all species, the error structure that best described the data was either the negative binomial or Tweedie distribution. The link function used was logarithmic. The general formulation of the model was:

$$E[n_i] = \exp \left[ \ln(a_i) + \beta_0 + \sum_k f_k(z_{ik}) \right]$$

Where  $n_i$  is the number of individuals in the  $i^{\text{th}}$  segment,  $a_i$  is the effective search area for the  $i^{\text{th}}$  segment,  $\beta_0$  is the intercept,  $f_k$  is the smooth function of the explanatory covariates, and  $z_{ik}$  is the value of the  $k^{\text{th}}$  explanatory covariate in the  $i^{\text{th}}$  segment.

All static and dynamic environmental variables (Table 1) were considered for modelling as smooth terms. Dynamic drivers of cetacean distribution could have different temporal signals. Some dynamic variables are expected to have a longer temporal signal or lags, while others are not (e.g. Drinkwater et al., 2003; Greene & Pershing, 2004; Hátún et al., 2009; Houghton et al.,

2020; Silva et al., 2014). We interpret this as the signals of seasonal progression, spring months signal, versus proxies of more direct prey aggregation, summer months signal. Given that the surveys were only performed during the summer months, the lagged relationships were evaluated only in the direction of spring towards summer.

To account for any systematic differences in the two datasets, Iceland-Faroes or Norway, a categorical variable identifying dataset/survey was included in base models.

The degree of smoothness was estimated as part of the model fitting procedure in which the smooth functions are treated as random effects, so that variance parameters could be estimated by restricted maximum likelihood (REML), in which the smoothing parameter selection penalises the terms in the model so it can shrink the function to a linear function, as appropriate. Here double penalisation (select=True) was used so that covariates could be completely removed from the model if appropriate (Wood, 2011).

### Model selection

Model selection following an automatic stepwise approach cannot be implemented in the mgcv package, so models were selected manually after penalisation. To account for temporal

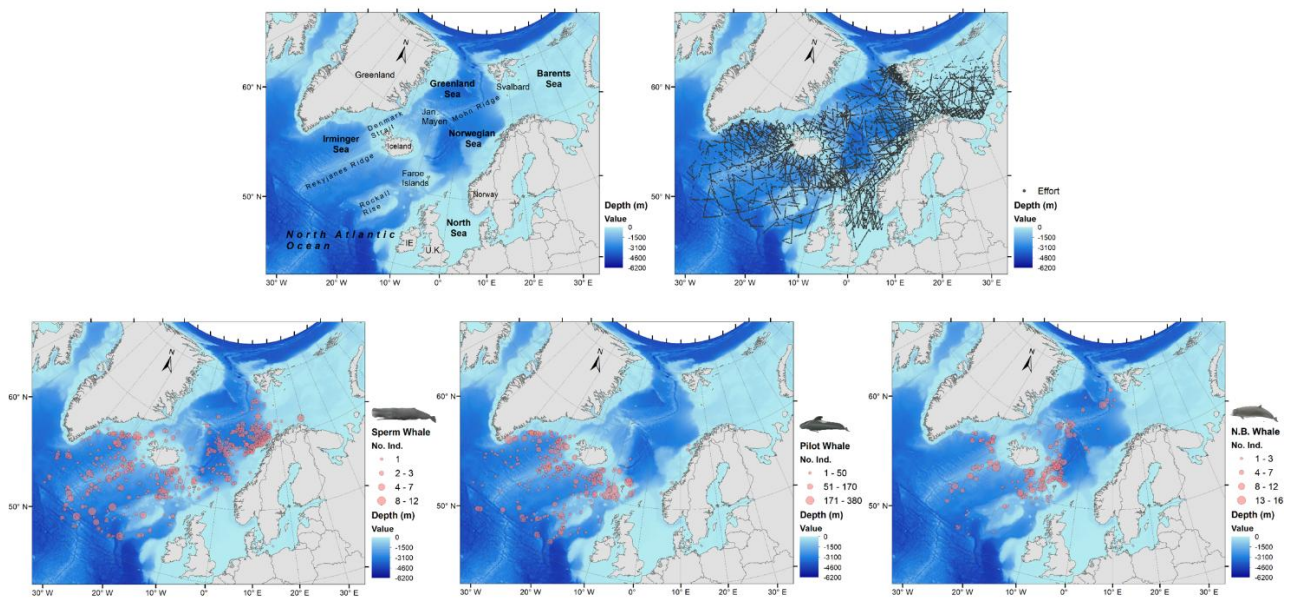


Figure 3. Overview map of the study area and summary of 1987–2015 Norway & Iceland-Faroes survey effort and sightings of long-finned pilot, northern bottlenose, and sperm whales used for modelling. Effort is depicted by segment mid-points as grey-dots. Sightings are shown as coloured dots, the size of which indicates group size. The map was plotted using the geographic coordinate system WGS84 and overlaid over the bathymetry of the area (ETOPO).

variation resulting from time lag and without any time lag assessments (from April to August) in the oceanographic dynamic covariates (SST, Chl, PP, MLD, SSH, BT, and Sal; Table 1) an important first step was to select the month that explained the most deviance for each covariate. To avoid correlation, only one month per covariate was included in any model. For each temporally varying covariate, the month that resulted in the best model improvement was selected as representative of that particular covariate. Then, all the temporally varying (selected month for each covariate) and non-temporally varying covariates were fitted in a full model. Terms that were penalised were taken out of the model.

All the remaining variables were retained as candidate covariates in the model, unless they had Pearson correlation coefficients larger than 0.7 and therefore covariance with other variables in the ‘penalised full model’. Because concurvity and collinearity are analogues, and both were evaluated in the model smooth terms, all the pairs of terms that had collinearity and concurvity were identified in the ‘penalised full model’. A model was run with each of the terms within a pair plus the rest of the terms already selected in the ‘penalised full model’. Selection between the models considering each of the concurvity/collinearity pairs was based on AIC (Akaike’s Information Criterion). Other criteria considered in model selection were the percentage of deviance explained by the models, and the probability that the variables selected were included in the model by chance (p-values).

**Prediction**

To predict the model results spatially, the whole study area was overlaid by a spatial grid of resolution 25 km x 25 km. This grid resolution was selected to be the same as the resolution of most of the covariates and also the radius at which the environmental covariates were extracted from the mid-point of each segment when covariates were added to the effort data. The grid was

built using QGIS software using the vector grid function (QGIS Desktop 2.18.15; QGIS Development Team, 2018). Each grid cell was populated with the environmental variables described in Table 1. Using the best model for each period, predictions were generated by averaging values of the selected month for each dynamic covariate over period years.

**Estimation of uncertainty**

The uncertainty of the prediction was estimated by calculating the coefficient of variation (CV) using a posterior simulation as in Schleimer et al. (2019). A matrix that produces a vector of linear predictor values for each grid cell was generated using the R package mgcv, function predict (type=‘lpmatrix’) (Wood, 2017). Model coefficients were extracted from the posterior distribution and 1,000 samples were produced using the R package MASS, function ‘mvrnorm’ (Venables & Ripley, 2002). Then both calculations were used to generate 1,000 predictions from which the CV was calculated and plotted.

**RESULTS**

**Sperm whales**

**Distribution and habitat use models: 1987–1989**

The covariates selected in the best 1987–1989 model for sperm whales included: depth, slope, aspect, and April SST. It had a

Table 3. Summary of sperm whale 1987-1989 best model.

Model: Survey +	Best model
Deviance	630.72
Deviance explained (%)	32.33
REML	1038.77
n	6,695
Error structure (theta)	Negative Binomial (0.045)

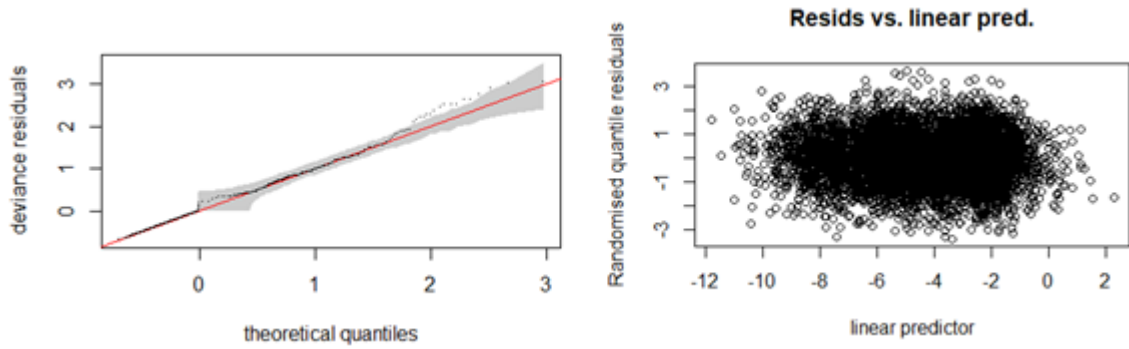


Figure 5. GAM diagnostics for the sperm whale 1987–1989 best model. In the Q-Q plot (left) the shaded area represents 95% confidence interval, the circles represent the data, the line is the expected data distribution if the model fits the data perfectly. The residual versus linear predictor (right) does not show any patterns or presence of heteroscedasticity.

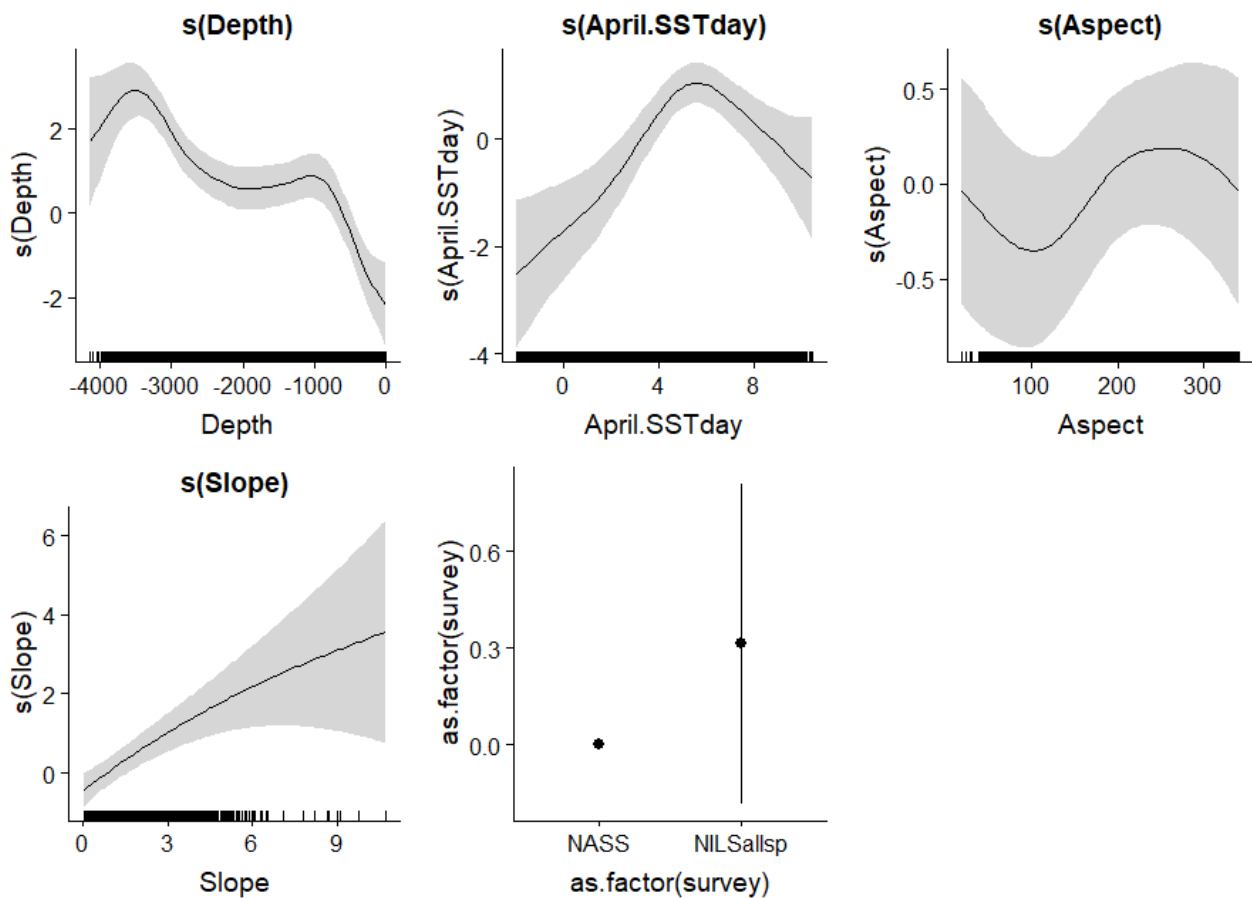


Figure 4. Relative density of sperm whales as a smooth function of depth, April SST, aspect, and slope. Zero on the vertical axes corresponds to no effect of the covariate on the relative density of sperm whales. Shaded areas represent 95% confidence intervals. The scales on each y-axis vary among plots. Data points are represented as rug plots on the horizontal axes.

deviance explained of 32.3% (Table 3) and adequate fit as shown in Figure 4.

The smooth functions show a predicted positive effect on sperm whale density of depths greater than 800 m and a negative effect in waters 500 m or shallower. Slopes below 1° had a negative effect, while slopes of 1.5° to 9° had a positive effect. Cold SST in April from -2 °C to 2 °C had a negative effect, while

warmer waters between 4°C to around 8°C had a positive effect (Figure 5).

Predictions of sperm whale density in 1987–1989 are shown in Figure 6. The model prediction was consistent with the patterns of observations in the Norwegian Sea, Denmark Strait, Irminger Sea and around the Charlie-Gibbs fracture zone. Predictions showed the highest precision in the areas of highest predicted sperm whale density (Figure 7). There was less confidence in



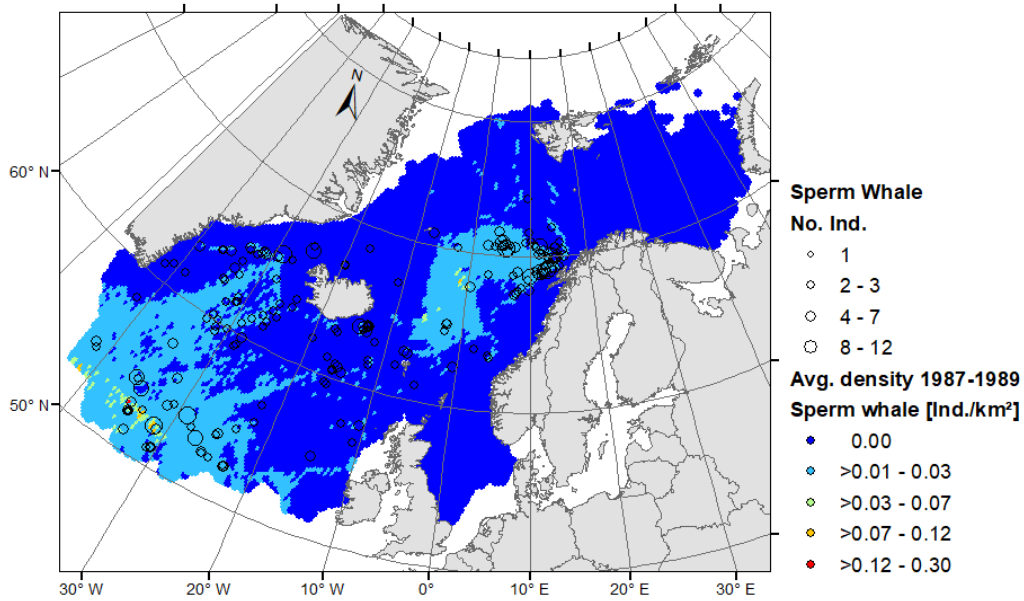


Figure 7. Predicted density of sperm whales for the best-fitting model for 1987–1989, which included depth, slope, aspect and April SST. The map shows sperm whale observations as grey circles, the size of which indicates the group size.

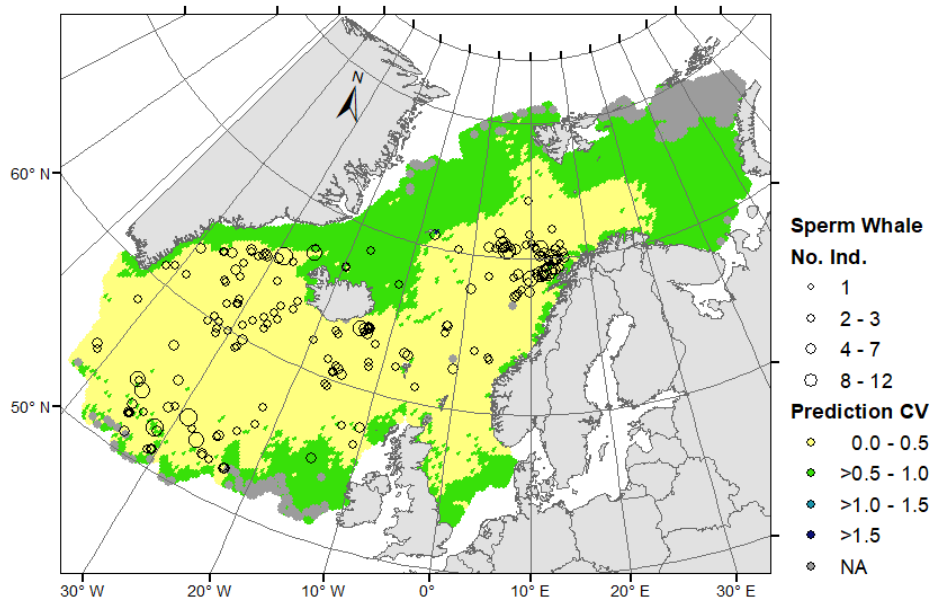


Figure 6. Coefficient of variation of the average predicted density of sperm whales best-fitting model for 1987–1989. Yellow areas show the highest precision. Sperm whale observations are indicated as grey circles and scaled for the group size.

predictions in the Barents and Greenland Sea, southern North Sea and in the south-eastern North Atlantic, areas in which there were no or very few sperm whale sightings.

**Distribution and habitat use models: 1998–2015**

The best sperm whale model for 1998–2015 included: depth, aspect, slope, April SST, August SSH, July MLD, and July PP. The model fitted the data adequately, as shown in Figure 8. The best model explained 33.9% of the deviance in the data (Table 4).

The model predicted a positive effect on sperm whale density of depths greater than 800 m and a negative effect of waters of 500 m or shallower. April SST had a negative effect between -1 °C and 1 °C and also greater than 8 °C, and a positive effect between 3 °C and 7 °C. July MLD showed positive peaks around 12 m and 18 m, with a dip in between around 15 m. August SSH

Table 4. Summary of the best model for sperm whales 1998–2015. The best model included: depth, aspect, slope, April SST, August SSH, July MLD, and July PP. The covariates April BT, May Sal, and May Chl were removed by penalisation.

Model: Survey +	Best model
Deviance	1024.78
Deviance explained (%)	33.91
REML	1496.16
n	7,361
Error structure (theta)	Negative Binomial (0.10)

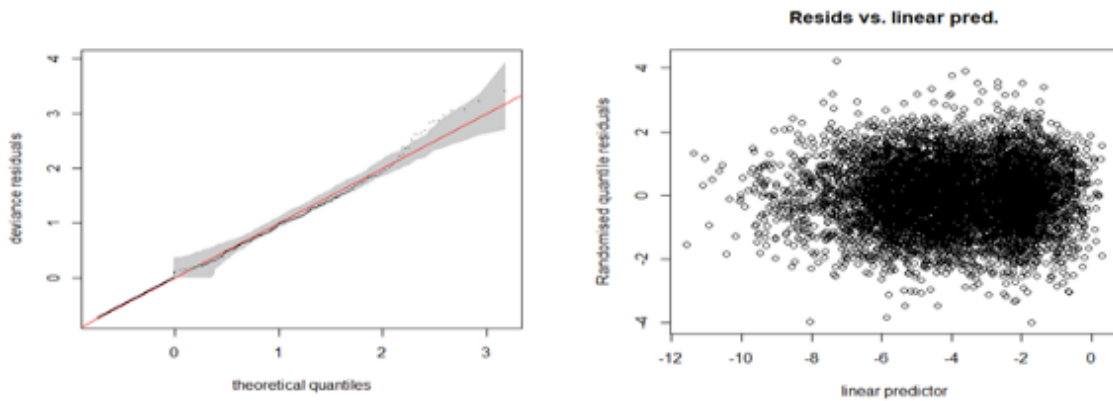


Figure 8. GAM diagnostics for the best sperm whale model for 1998–2015. In the Q-Q plot (left) the shaded area represents 95% confidence interval, the circles represent the data, the line is the expected data distribution if the model fits the data perfectly. The residual versus linear predictor (right) does not show any patterns or presence of heteroscedasticity.

had a negative effect between -1 m and -0.7 m and a positive effect at less negative values between -0.7 m and -0.4 m (Figure 9).

The prediction of sperm whale density for 1998–2015 (Figure 10) is consistent with the observations in the Norwegian Sea, the Irminger Sea and Icelandic Basin, and around the Denmark Strait. High predicted density also occurred around the Rockall Trough and Charlie-Gibbs fracture zone, where there were fewer observations but also less effort. Predictions showed the

highest precision in areas of highest predicted sperm whale density. At the southern edge of the study area, including the Charlie-Gibbs fracture zone, confidence in predictions was lower than in the other areas, again likely due to a low number of sightings in the area. There was also low prediction confidence in the Barents, Greenland, and North Sea, where there were no sightings (Figure 11).

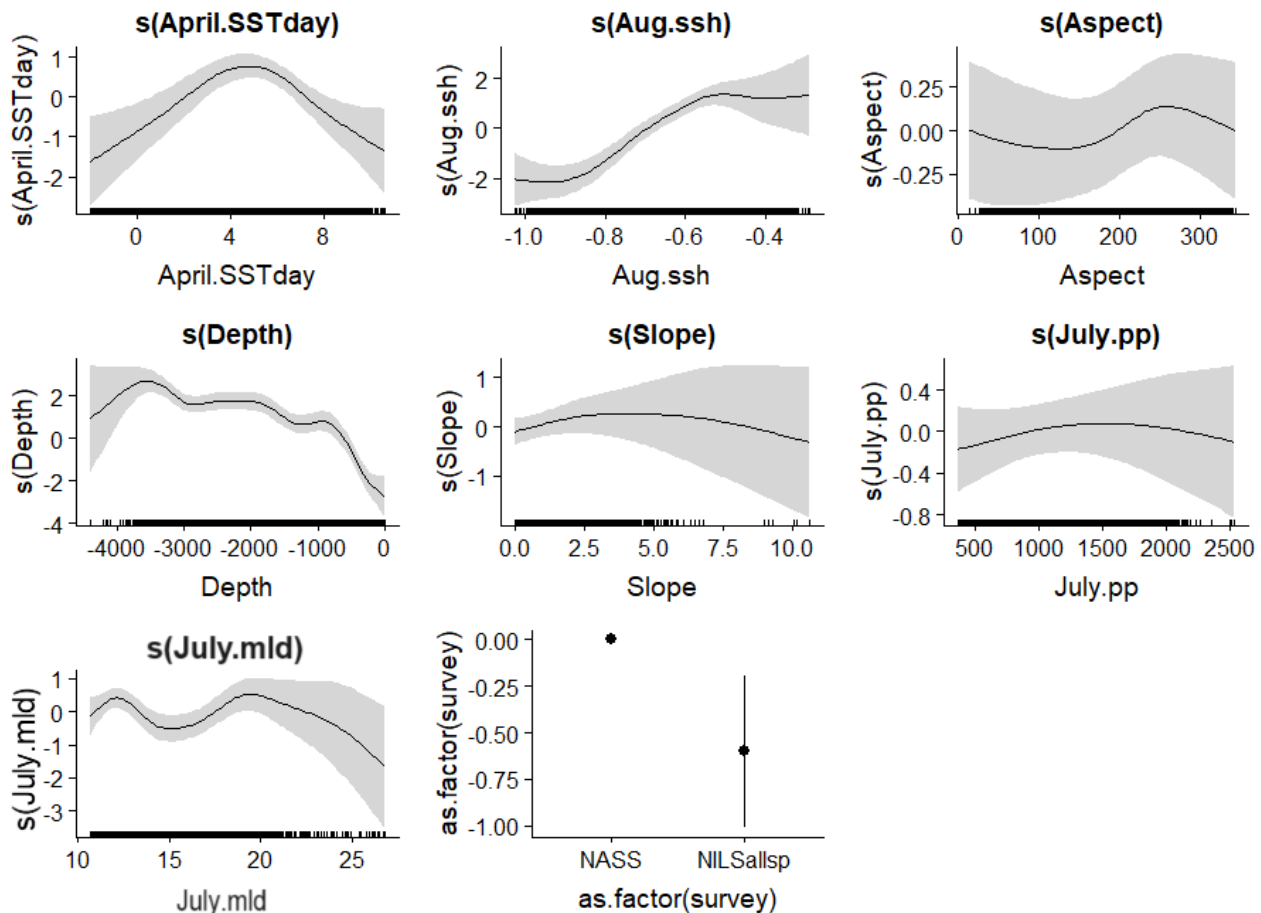


Figure 9. Relative density of sperm whales as a smooth function of April SST, August SSH, aspect, depth, slope, July PP, and July MLD. Zero on the vertical axes corresponds to no effect of the covariate on the relative density of sperm whales. Shaded areas represent 95% confidence intervals. The scales on each y-axis vary among plots. Data points are represented as rug plots on the horizontal axes.

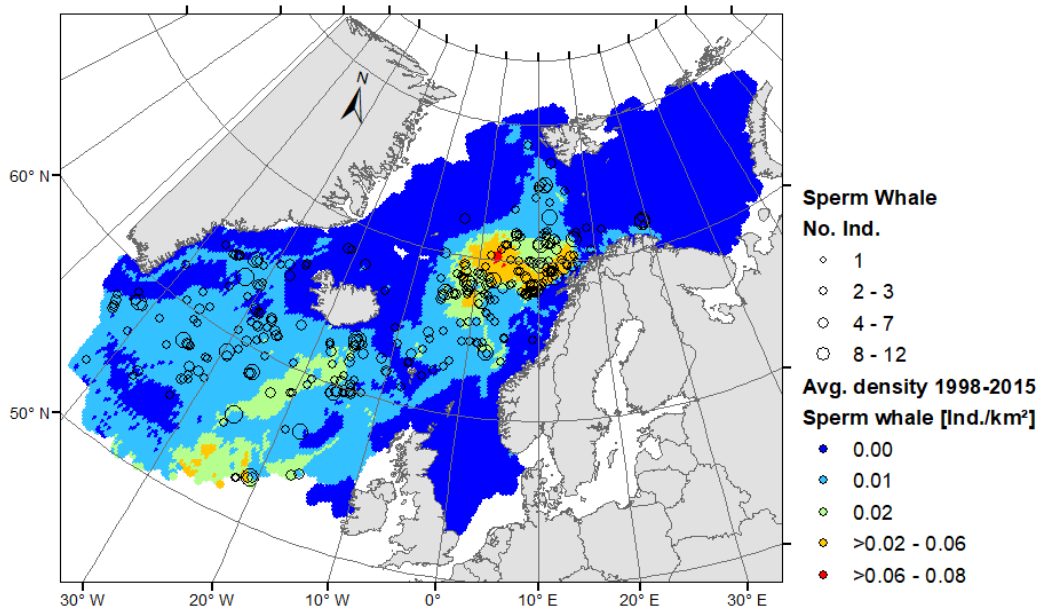


Figure 10. Predicted density of sperm whales for the best-fitting model for 1998–2015 including aspect, April BT, April SST, July Sal, and July MLD. Sperm whale observations are shown as grey circles, the size of which indicates the group size.

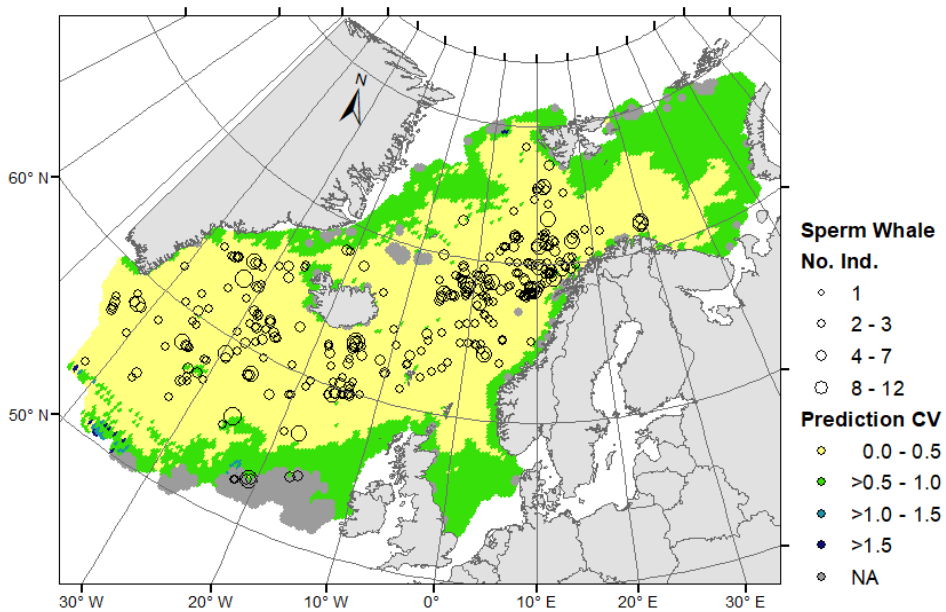


Figure 11. Coefficient of variation of the average predicted density of sperm whales best-fitting model for 1998–2015. Yellow areas show the highest precision. Sperm whale observations are indicated as grey circles and scaled for the group size.

**Long-finned pilot whales**

**Distribution and habitat use models: 1987–1989**

The covariates selected in the best 1987–1989 long-finned pilot whale model included: depth, slope, and May SST. The model fitted the data adequately, as shown in Figure 12. The best model explained 14% of the deviance in the data (Table 5).

The model predicted a positive effect on long-finned pilot whale density of depths greater than 1,500 m and a negative effect of waters shallower than that. Slopes below 1° had a negative effect, while slopes of 1° to 6° had a positive effect. There was a

generally increasing positive effect as May SST increased, with peaks around 8 °C and around 11 °C (Figure 13).

Table 3. Summary of long-finned pilot whale 1987–1989 best model.

Model: Survey +	Best model
Deviance	33375.02
Deviance explained (%)	14.01
REML	1297.34
n	3,491
Error structure (theta)	Tweedie (p=1.586)

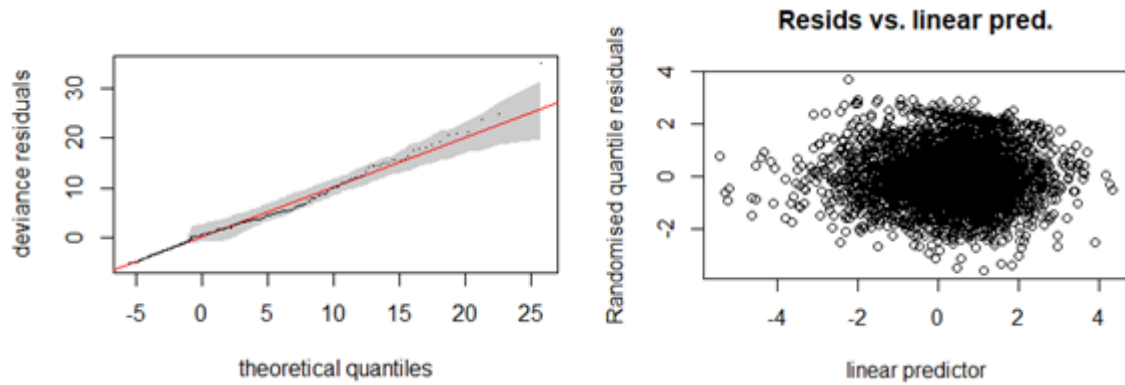


Figure 13. GAM diagnostics for the long-finned pilot whale 1987–1989 best model. In the Q-Q plot (left) the shaded area represents 95% confidence interval, the circles represent the data, the line is the expected data distribution if the model fits the data perfectly. The residual versus linear predictor (right) does not show any patterns or presence of heteroscedasticity.

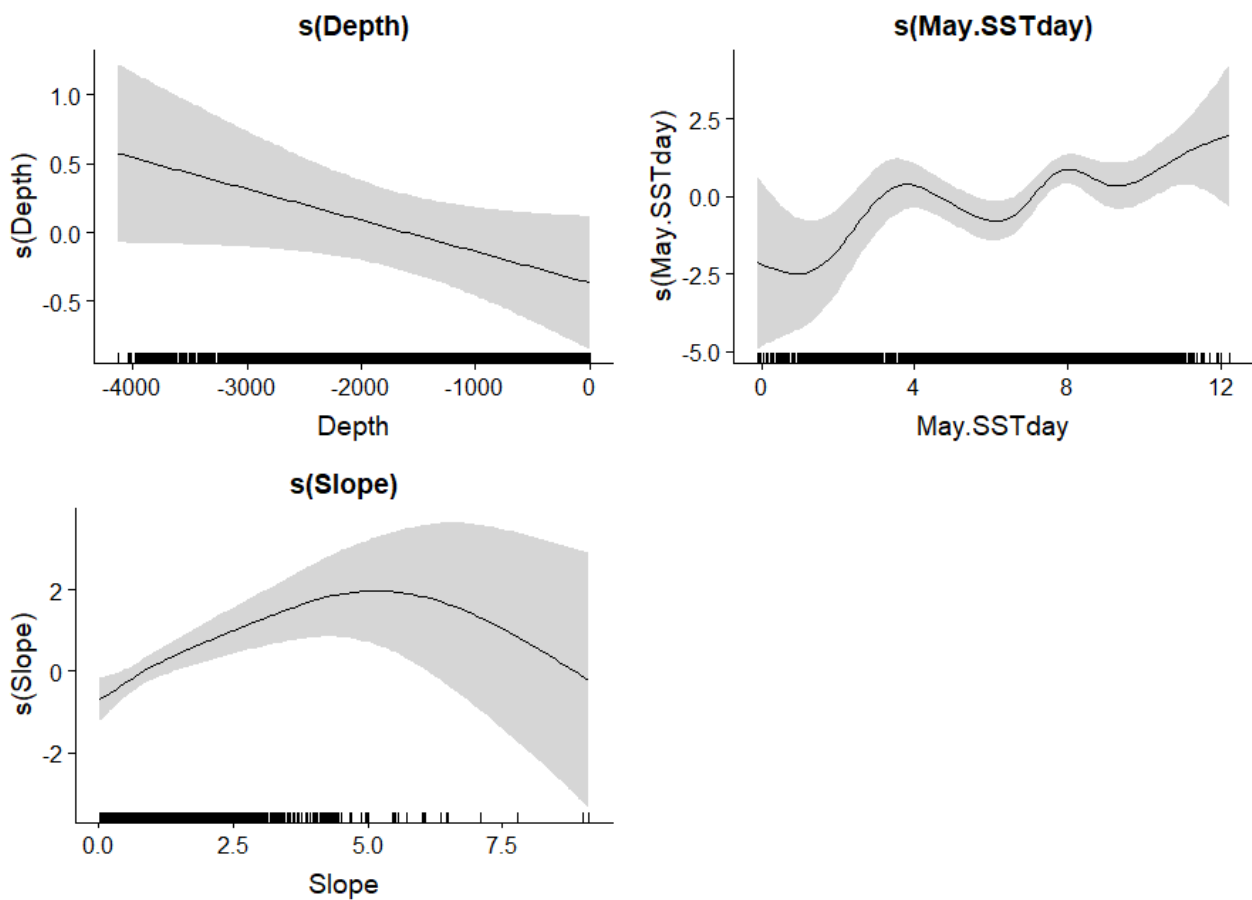


Figure 12. Relative density of long-finned pilot whales as a smooth function of depth, slope, and May SST. Zero on the vertical axes corresponds to no effect of the covariate on the relative density of long-finned pilot whales. Shaded areas represent 95% confidence intervals. The scales on each y-axis vary between plots. Data points are represented as rug plots on the horizontal axes.

Predictions of long-finned pilot whale density (from 1987 and 1989) are shown in Figure 14. The model predicted the highest densities in the southern part of the study area, where there was less survey effort (See Figure 3). Further north, the observations around the Faroe Islands were reflected by relatively high predicted density in this area. Prediction precision was highest in the areas where long-finned pilot whales were observed. Generally, there was less confidence in

predictions around the edge of the study area and off north-eastern Iceland (between Iceland and Jan Mayen), where no animals were recorded (Figure 15).

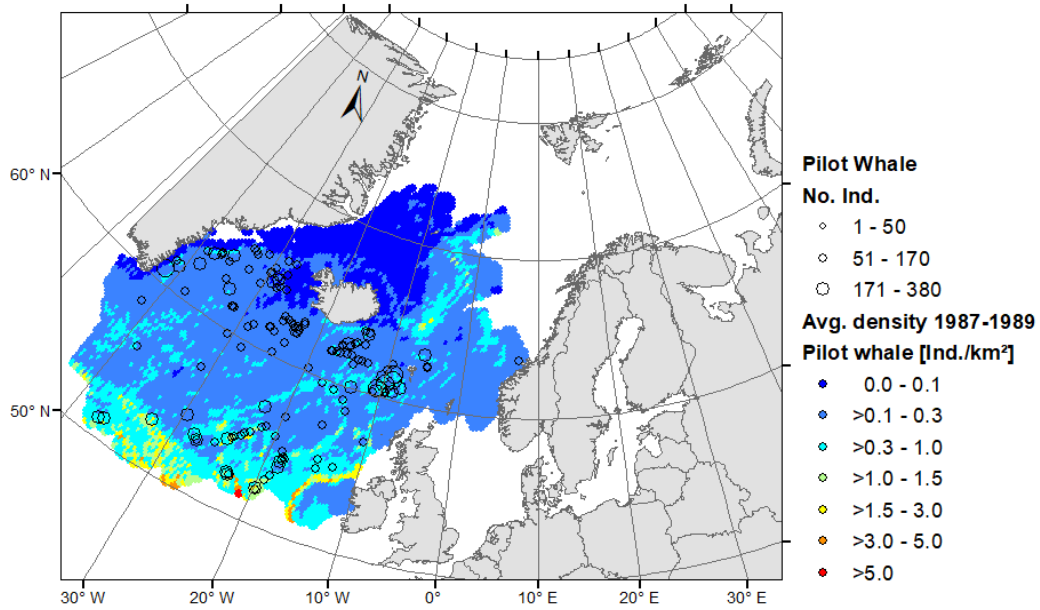


Figure 14. Predicted density of long-finned pilot whales for the best-fitting model in 1987 and 1989 including depth, slope, and May SST. The map shows long-finned pilot whale observations as grey circles, the size of which indicates the group size.

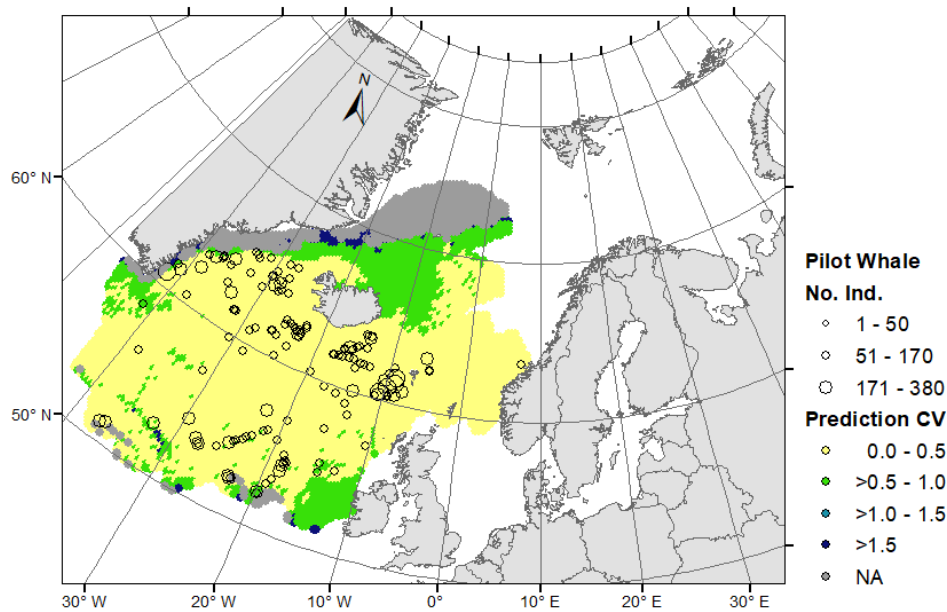


Figure 15. Coefficient of variation of the average predicted density of long-finned pilot whales best-fitting model for 1987 and 1989. Yellow areas show the highest precision. Long-finned pilot whale observations are indicated as grey circles and scaled for the group size.

**Distribution and habitat use models: 1998–2015**

The covariates selected in the best long-finned pilot whale model for 1998–2015 included: aspect, April BT, April SST, July Sal, and July MLD. The model fitted the data adequately (Figure 16). The best model explained 50.4% of the deviance in the data (Table 6).

The model predicted a positive effect on long-finned pilot whale density at aspects towards the west around 275°. A negative effect was found at angles around 180° (south). April BT had a negative effect at warmer temperatures around 7 °C and a tendency to have a positive effect, but no clear signal, at greater temperatures. April SST had a positive effect at temperatures

Table 4. Summary of the best model for long-finned pilot whales 1998–2015. The best model included: April BT, April SST, July Sal, and July MLD. The covariates July SSH, July Chl, July PP, and depth were removed by penalisation and concurrency penalisation.

Model: Survey +	Best model
Deviance	397.06
Deviance explained (%)	50.39
REML	1424.62
n	7,361
Error structure (theta)	Negative Binomial (0.011)

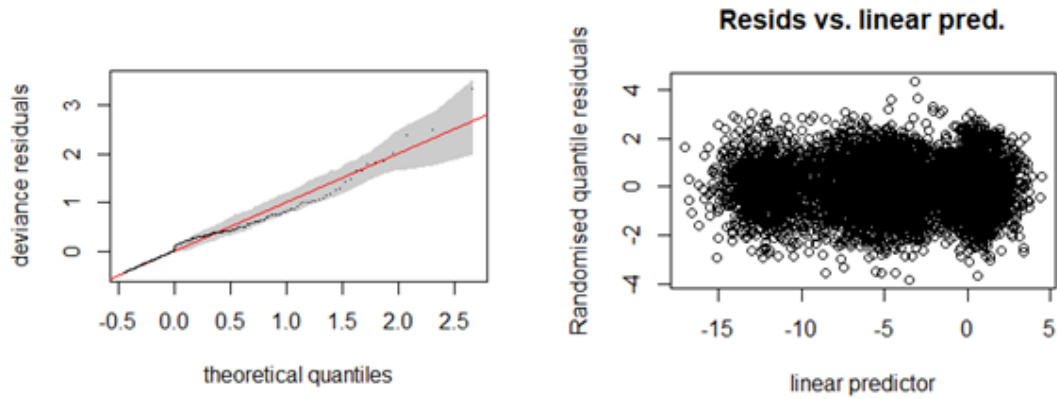


Figure 16. GAM diagnostics for the long-finned pilot whale 1998–2015 best model. In the Q-Q plot (left) the shaded area represents 95% confidence interval, the circles represent the data, the line is the expected data distribution if the model fits the data perfectly. The residual versus linear predictor (right) does not show any patterns or presence of heteroscedasticity.

greater than 4 °C and a negative effect below this temperature. Saltier waters greater than 35 PSU in July had a negative effect while waters between 32 and 34 PSU had a positive effect. Mixed layer depths between 17 and 25 m had a positive effect while shallower depths did not show a clear signal (Figure 17).

Predictions of long-finned pilot whale density for average values across 1998–2015 are shown in Figure 18. The model predicted

fairly well the sightings around the Denmark Strait, Faroe Islands, the Irminger Sea, and the Icelandic Basin. However, higher densities were predicted in a number of areas with few observations, including some Norwegian waters, and across most of the southern part of the study area, where there was less effort (see Figure 3). There was higher confidence in predictions in the areas where most of the long-finned pilot

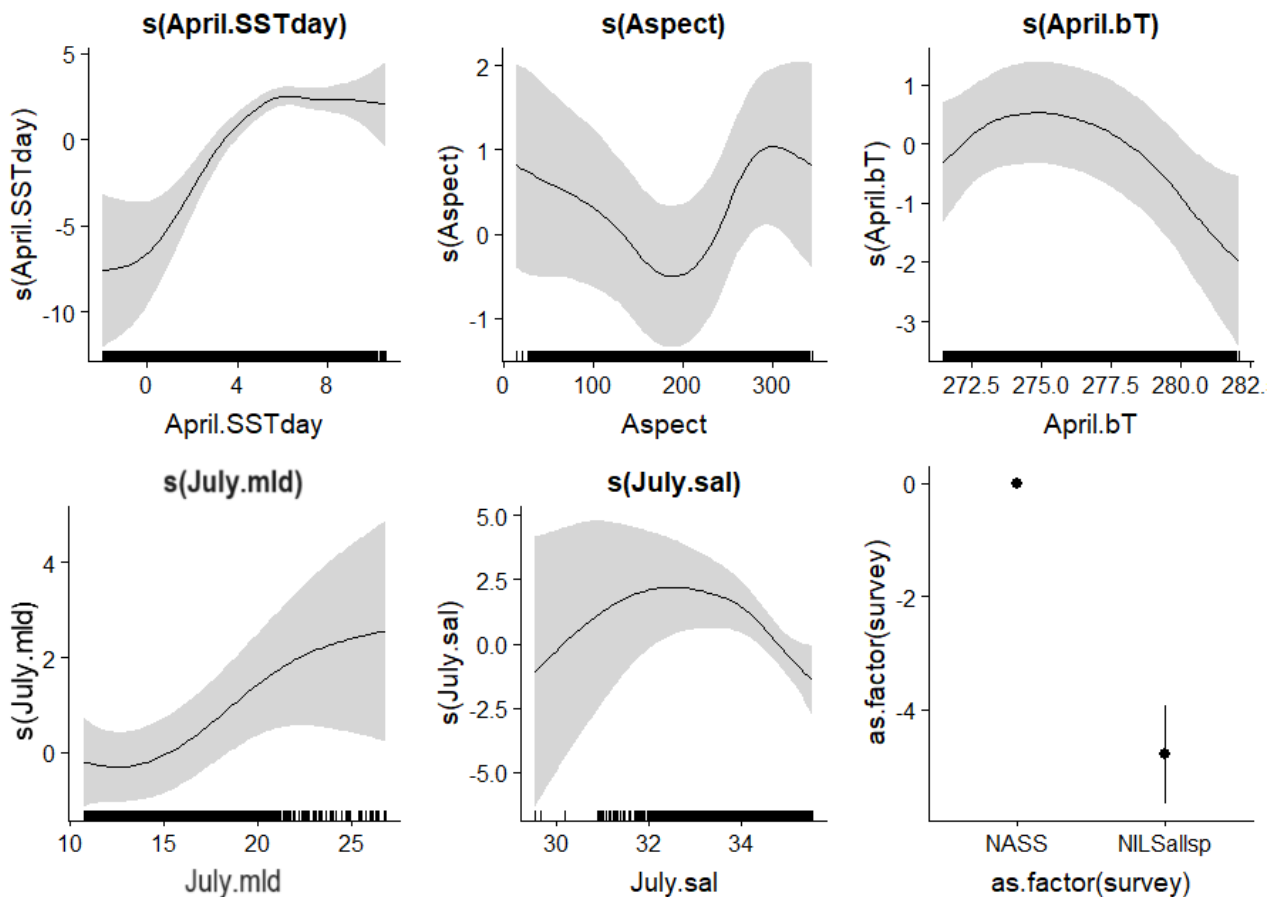


Figure 17. Relative density of long-finned pilot whales as a smooth function of April SST, aspect, April BT, July MLD, and July Sal. Zero on the vertical axes corresponds to no effect of the covariate on the relative density of long-finned pilot whales. Shaded areas represent 95% confidence intervals. The scales on each y-axis vary between plots. Data points are represented as rug plots on the horizontal axes. BT is shown in the original scale, Kelvin degrees.

whales were observed (Figure 19). There was less confidence in general around the edge of the study area, and in the Greenland and Barents Sea.

**Northern bottlenose whales**

**Distribution and habitat use models: 1987–1989**

The covariates selected in the northern bottlenose whale best model for 1987–1989 included: depth, aspect, and August SST. The model fitted the data quite well as shown in Figure 20. The best model explained 24.2% of the deviance in the data (Table 7).

Table 7. Summary of northern bottlenose whale 1987–1989 best model.

Model: Survey +	Best model
Deviance	161.82
Deviance explained (%)	24.18
REML	416.88
n	3,491
Error structure (theta)	Negative Binomial (0.012)

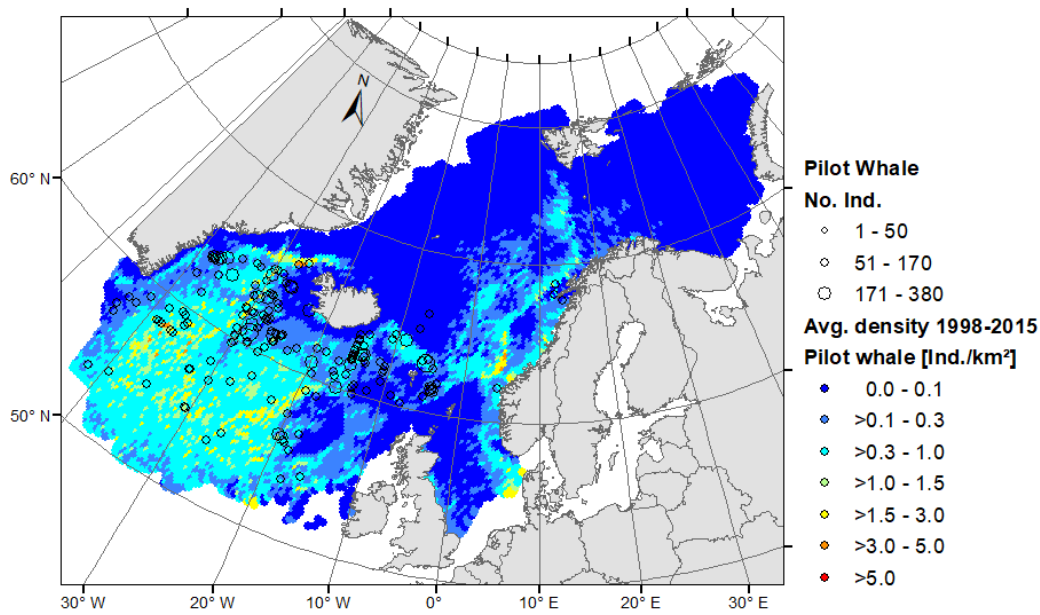


Figure 18. Predicted density of long-finned pilot whales for the best-fitting model across 1998-2015 including aspect, April BT, April SST, July Sal, and July MLD. Long-finned pilot whale observations are shown as grey circles, the size of which indicates the group size.

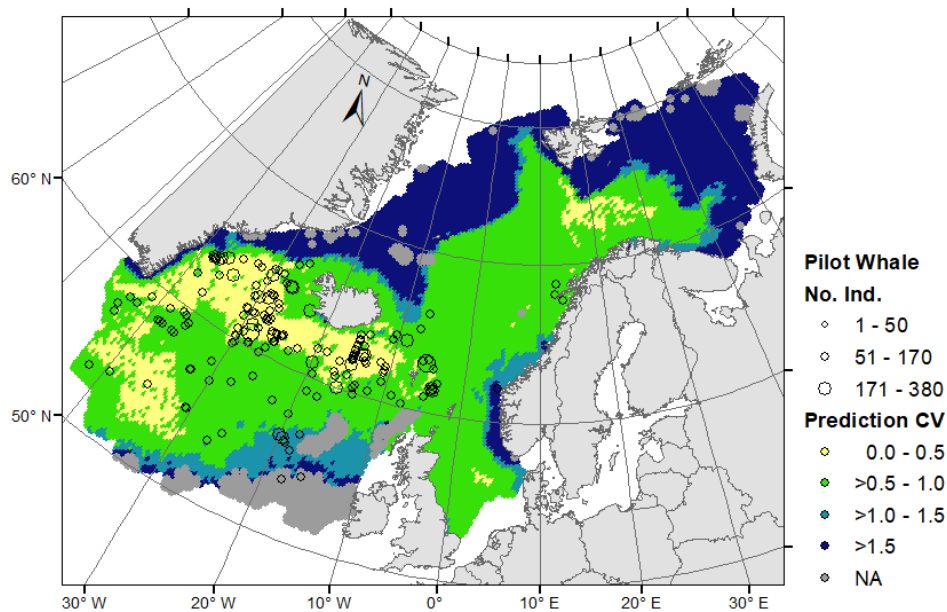


Figure 19. Coefficient of variation of the average predicted density of long-finned pilot whales best-fitting model for 1998-2015. Yellow areas show the highest precision. Long-finned pilot whale observations are indicated as grey circles and scaled for the group size.

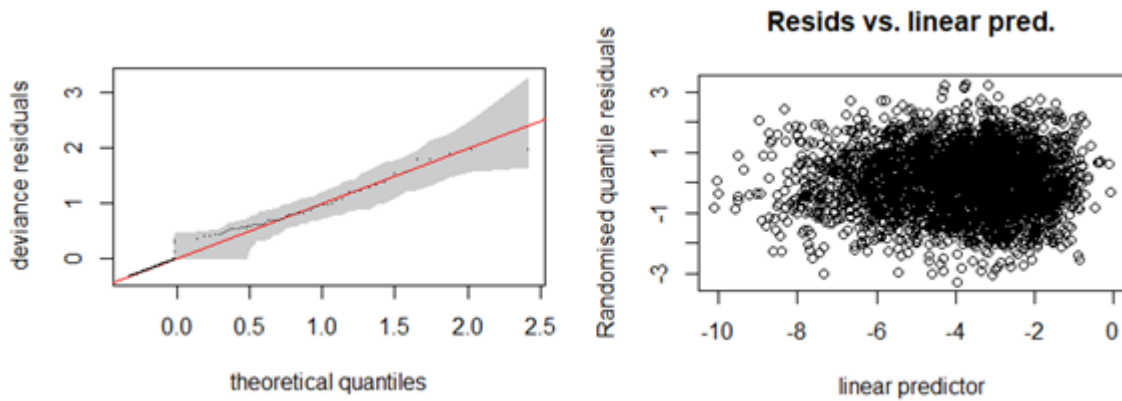


Figure 21. GAM diagnostics for the northern bottlenose whale 1987–1989 best model. In the Q-Q plot (left) the shaded area represents 95% confidence interval, the circles represent the data, the line is the expected data distribution if the model fits the data perfectly. The residual versus linear predictor (right) does not show any patterns or presence of heteroscedasticity.

The model predicted a positive effect on northern bottlenose whale density at depths between 1,000 m and 2,000 m and a much greater positive effect in waters greater than 3,500 m, and a negative effect in waters of 500 m or shallower. August SST was predicted to have a positive effect at temperatures between 9 °C to 11 °C (Figure 21).

along the Reykjanes ridge, an area with some sightings. There was generally less confidence in predictions around the edge of the study area, southeast of Jan Mayen and in the western Charlie-Gibbs fracture zone, all areas with no or very few observations (Figure 23).

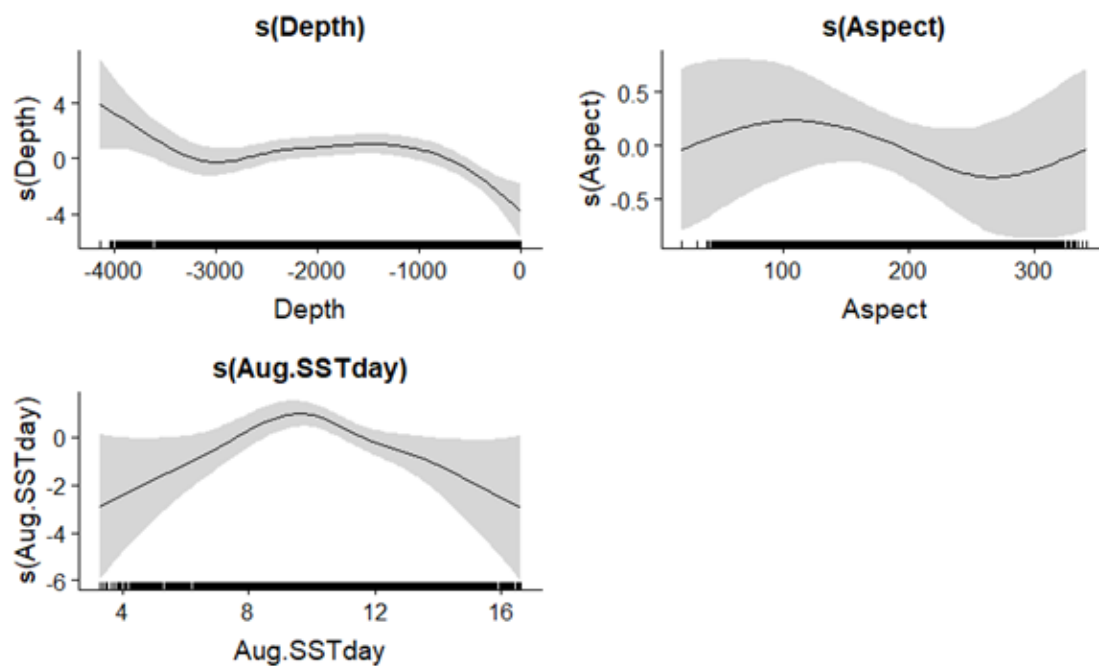


Figure 20. Relative density of northern bottlenose whales as a smooth function of depth, aspect, and August SST. Zero on the vertical axes corresponds to no effect of the covariate on the relative density of northern bottlenose whales. Shaded areas represent 95% confidence intervals. The scales on each y-axis vary between plots. Data points are represented as rug plots on the horizontal axes.

Predictions of northern bottlenose whale density from 1987 and 1989 are shown in Figure 22. The model predictions reflected well the clusters of observations north of the Faroe Islands, in the Irminger Sea and Icelandic Basin, and in the mid-Atlantic (eastern Charlie-Gibbs fracture zone). However, the model also predicted high densities in areas which were without any sightings, including southeast of Jan Mayen, along the Reykjanes ridge and western Charlie-Gibbs fracture zone. Prediction precision was generally higher in the central area where most of the northern bottlenose whales were observed (Figure 23). Higher predicted density and precision were found

**Distribution and habitat use models: 1998–2015**

The covariates selected in the best northern bottlenose whale model for 1998–2015 included: depth, aspect, June SST, August Sal, July SSH, June MLD, and April Chl. The model fitted the data quite well (Figure 24) and explained 53.7% of the deviance in the data (Table 8).

The model predicted a positive effect on northern bottlenose whale density of depths between 2,000 m and 800 m, while shallow waters from 500 m had a negative effect. For aspect,



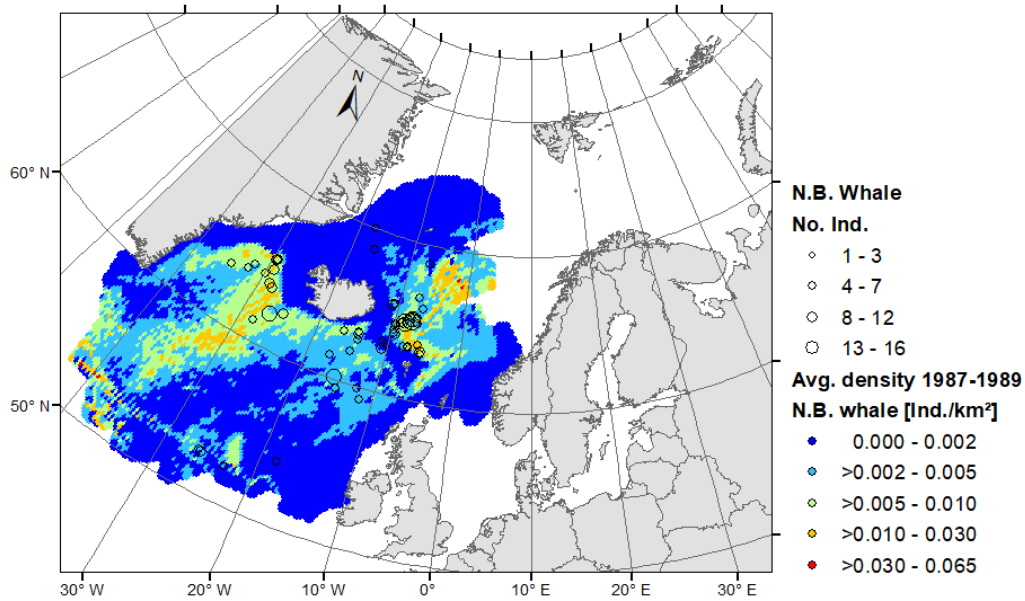


Figure 22. Predicted density of northern bottlenose whales for the best-fitting model in 1987 and 1989 including depth, aspect, and August SST. The map shows northern bottlenose whale observations as grey circles, the size of which indicates the group size.

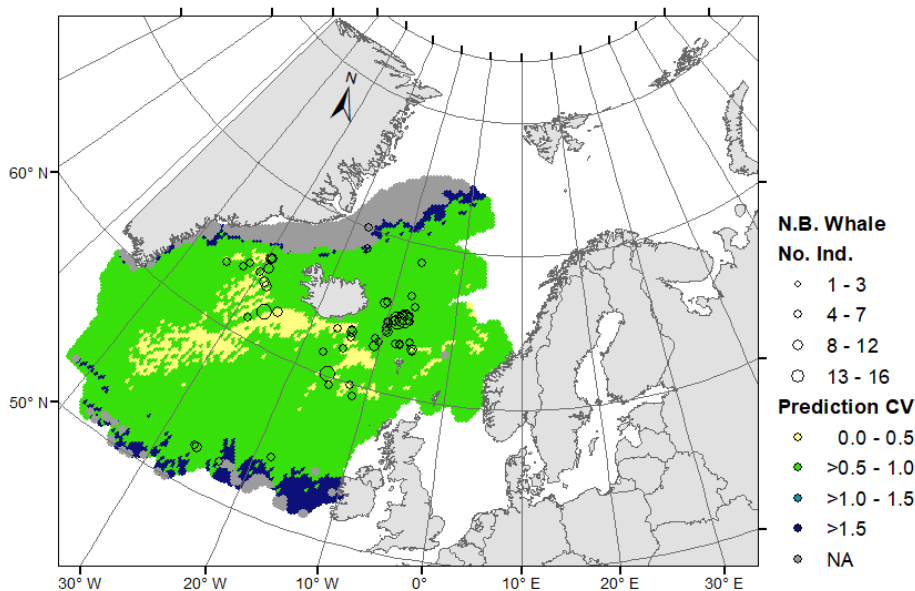


Figure 23. Coefficient of variation of the average predicted density of northern bottlenose whales best-fitting model for 1987 and 1989. Yellow areas show the highest precision. Northern bottlenose whale observations are indicated as grey circles and scaled for the group size.

the effects were weak, but angles from 90° to 120° (east) had a positive effect while angles from 250° to 310° (west) had a negative effect on density. June SST had a positive effect for temperatures around 5 °C but a negative effect in warmer waters around 12.5 °C. Saltier waters around 35 PSU in August had a slight positive effect while waters around 34 PSU had a slight negative effect. July SSH showed a negative effect around -1 m but a positive effect around -0.85 m. June MLD did not show a clear signal, mainly due to the limited amount of data at depths greater than 100 m. April Chl had a clear negative effect as the concentration increased (Figure 25).

Predictions of northern bottlenose whale density for average values across 1998-2015 are shown in Figure 26. The model predicted well the clusters of observations around west of

Table 5. Summary of the best model for northern bottlenose whales 1998-2015. The best model included: depth, aspect, June SST, August Sal, July SSH, June MLD, and April Chl. The covariates slope, April PP, and April BT were removed by penalisation and concavity penalisation.

Model: Survey +	Best model
Deviance	343.65
Deviance explained (%)	53.72
REML	949.91
n	7,361
Error structure (theta)	Negative Binomial (0.016)

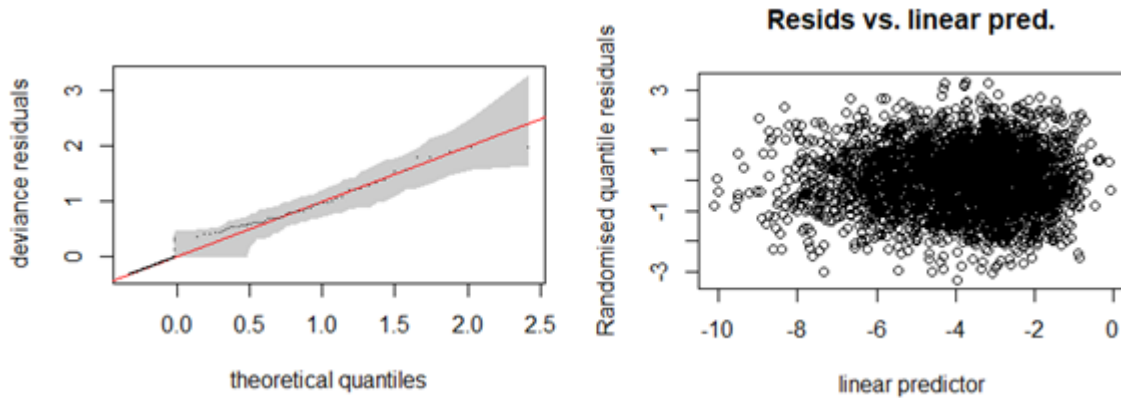


Figure 24. GAM diagnostics for the northern bottlenose whale 1998–2015 best model. In the Q-Q plot (left) the shaded area represents 95% confidence interval, the circles represent the data, the line is the expected data distribution if the model fits the data perfectly. The residual versus linear predictor (right) does not show any patterns or presence of heteroscedasticity.

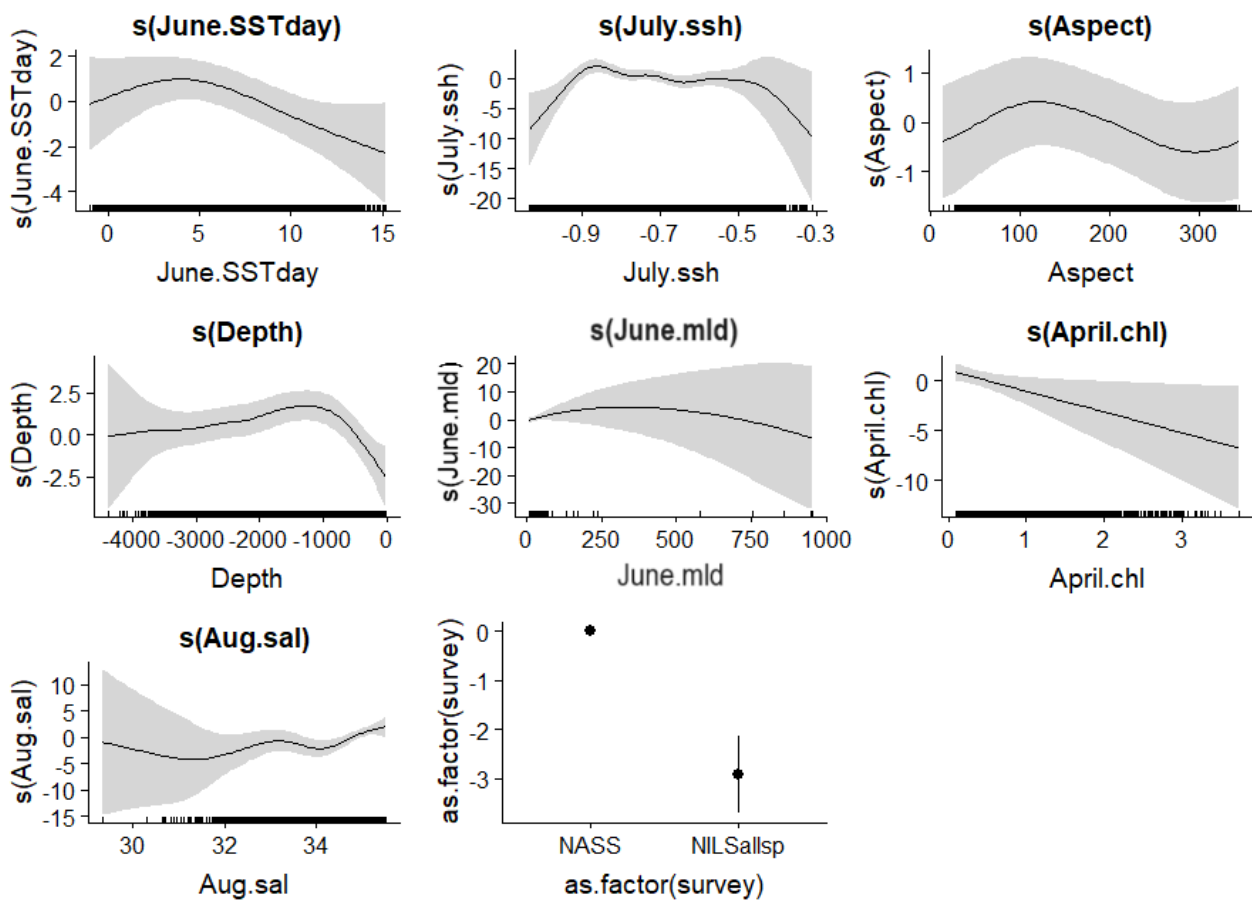


Figure 25. Relative density of northern bottlenose whales as a smooth function of June SST, July SSH, aspect, depth, April Chl, June MLD, and Aug Sal. Zero on the vertical axes corresponds to no effect of the covariate on the relative density of northern bottlenose whales. Shaded areas represent 95% confidence intervals. The scales on each y-axis vary among plots. Data points are represented as rug plots on the horizontal axes.

Svalbard, Jan Mayen, Faroe Islands, East Greenland in the Irminger Sea and Icelandic Basin, and along the Reykjanes ridge. Predicted density was also high southwest of Svalbard where there were fewer observations. Prediction precision (Figure 27) was higher in the central area where most of the northern bottlenose whales were observed. Higher predicted density and precision were also found along the Reykjanes ridge and Irminger Sea (by the East Greenland Current), also areas with numerous observations. There was generally less confidence in predicted density around the edge of the study area, the North

Sea and west of UK and Ireland, areas with no or very few observations (Figure 27).

## DISCUSSION AND CONCLUSIONS

### Sperm whales

Male sperm whales have been suggested to have a wide distribution but in general occur in deep water and along the continental shelf (Christensen et al., 1992; Gunnlaugsson et al.,

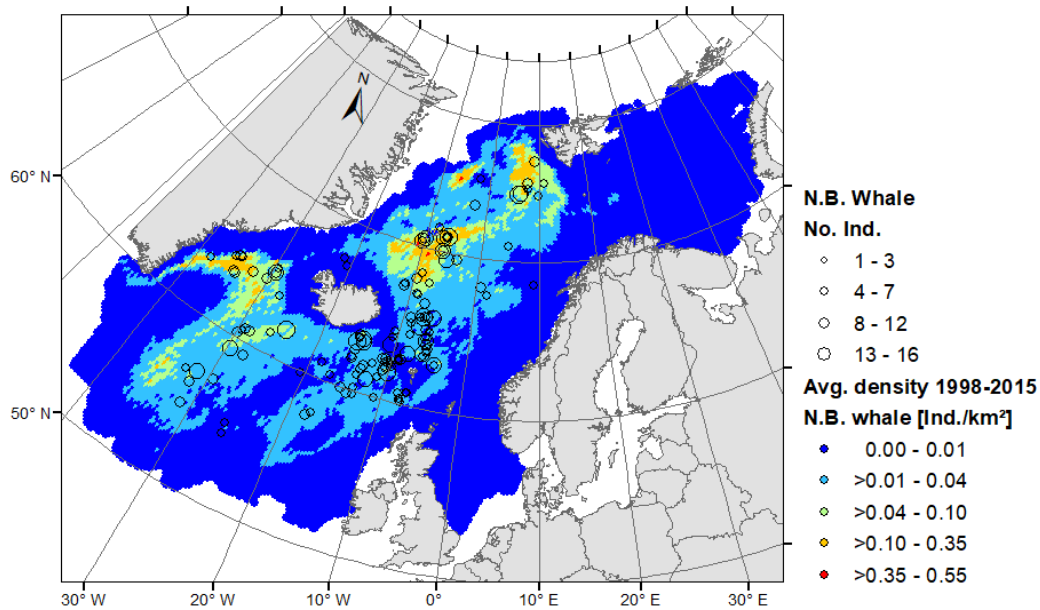


Figure 26. Predicted density of northern bottlenose whales for the best-fitting model across 1998-2015 including depth, aspect, June SST, August Sal, July SSH, June MLD, and April Chl. The map shows northern bottlenose whale observations as grey circles, the size of which indicates the group size.

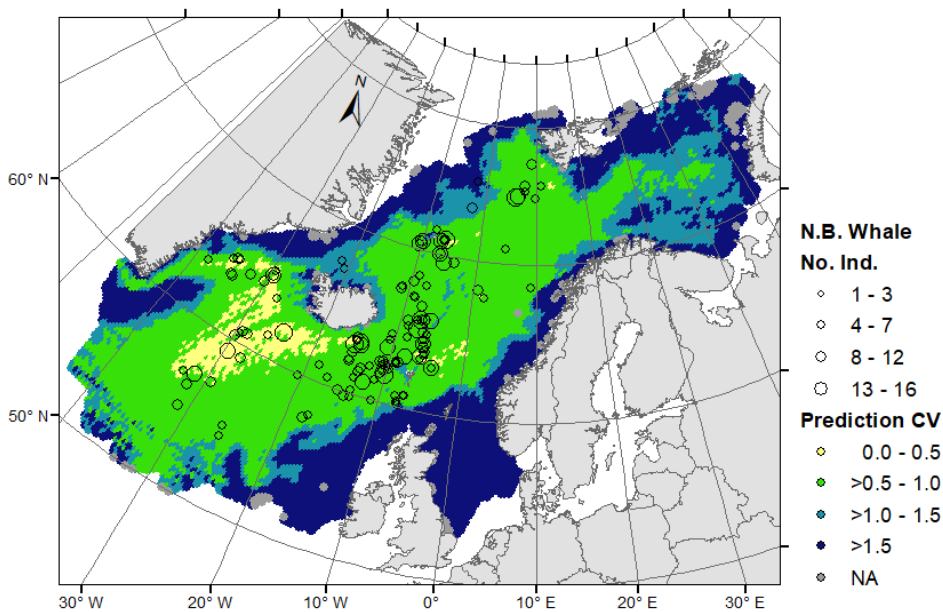


Figure 27. Coefficient of variation of the average predicted density of northern bottlenose whales best-fitting model for 1998-2015. Yellow areas show the highest precision. Northern bottlenose whale observations are indicated as grey circles and scaled for the group size.

2009; Rogan et al., 2017). Modelling results for the two periods evaluated, 1987–1989 and 1998–2015, show a consistent relationship between sperm whale density and depth. Shallower waters of  $\leq 500$  m have a negative effect on density, while waters  $>800$  m have a positive effect. Slope and aspect did not show this consistency or a clear signal over time, suggesting that these variables are not informative predictors of sperm whale density. The consistent relationship with depth indicates that it is likely a strong proxy for sperm whale prey occurrence. However, in light of ocean warming and changes in some pelagic fish distributions in the area (Astthorsson et al., 2012; Hátún et al., 2009; Huse et al., 2015; Trenkel et al., 2014), it is possible that sperm whales are adapting to environmental change by staying in the same area but consuming different prey.

The relationship between sperm whale occurrence and sea surface temperature has been suggested to have a broad range due to the species' wide distribution, especially for males (Baumgartner et al., 2001; Pirotta et al., 2011; Rogan et al., 2017). Because sperm whales dive deeply to find their prey (Whitehead, 2018), SST is not expected to be a strong predictor of prey abundance. However, the modelling results from both periods, 1987–1989 and 1998–2015, show a similar and consistent signal. In both periods, SST in April best explained sperm whale density, and the fitted smooth relationships were also similar for both periods. Very cold temperatures of  $-1^{\circ}$  to  $2^{\circ}$  °C and the warmest temperatures  $\geq 8^{\circ}$  °C had a negative effect on sperm whale density. In both sets of years, a temperature range between  $4^{\circ}$  °C to  $7^{\circ}$  °C had a positive effect. These temperatures are within the range found by Rogan et al., (2017)

in the north-western part of their area. In summary, SST in April shows a consistent signal and is a good predictor of sperm whale densities in the area.

Considering the physical variables in the 1998–2015 model, SST was the only one with a spring signal, while mixed layer depth and sea surface height both had summer signals in July and August, respectively. Although only 13% of the survey data were collected in August, this study focuses on broadly comparing spring versus summer signals. Therefore, any model retaining an August covariate should be interpreted as a summer signal. SST is expected to have a more lagged relationship with density, because it is assumed to affect the subsequent seasonal progression of productivity up the trophic levels. MLD and SSH are expected to have shorter lagged relationships because they may be more related to water masses and prey aggregation. Generally, SSH values are negative in the North Atlantic. Negative values are associated with cyclonic circulation or cold-core rings (Leterme & Pingree, 2008) and, in the model, the least negative SSH values from approximately -0.7 m to 0.4 m had a positive effect on sperm whale densities. The strongest negative SSH anomaly was in the Irminger Sea, where sperm whales were observed and predicted but not in great densities. The highest densities were predicted around the Norwegian Sea where the SSH seems on average to be less negative; here anticyclonic eddies are known to form. Anticyclonic eddies, where the MLD is shallow and there are high nutrient levels, can support phytoplankton blooms (Hansen, et al., 2010), which attract higher trophic levels including the prey of sperm whales. The biological covariate primary productivity did not show a clear signal, which was expected because of the trophic level difference between this and sperm whales, which feed high in the trophic web (Whitehead, 2018).

Sperm whales were predicted to be widely distributed in the area and no major change in distribution was seen between the two periods (Figure 28). In the later period, the model predicted a slightly higher density than in 1987–1989 along the Norwegian Sea, west of Svalbard, along the Denmark Strait, southeast Greenland, and offshore southeast Iceland. This could indicate a slight expansion in distribution in areas such as the Denmark

Strait where sperm whales were previously caught (Martin & Clarke, 1986).

Overall, these summer models for sperm whales show some clear and consistent relationships with depth and SST over the area during the two periods studied. Moreover, it seems that sperm whale distribution has not shifted but rather has slightly expanded over time, including into areas where they were previously caught. It is unknown if the prey of sperm whales in the entire central and north-eastern North Atlantic is the same. Therefore, two alternate hypotheses about the consistency of the influential variables in the model and their use as proxies for the sperm whale prey arise. Firstly, sperm whales are feeding on the same prey over the entire study period and study area, meaning that sperm whales from Iceland to Norway feed on a mixture of fish and cephalopod species such as lumpsucker and *Gonatus* sp, respectively (Bjørke, 2001; Clarke, 1996; Martin & Clarke, 1986; Santos et al., 1999; Sigurjónsson & Víkingsson, 1997). Secondly, the distribution of the prey may have changed as reported for some pelagic fish species in the area (Astthorsson et al., 2012; Hátún et al., 2009; Huse et al., 2015; Trenkel et al., 2014; Valdimarsson et al., 2012) and sperm whales are now feeding on different prey. Future research could compare historical samples with current biopsy samples to understand the foraging ecology of the animals better and how well this reflects the results of the present models.

#### Long-finned pilot whales

Modelling results show the expected effect of relief variables on long-finned pilot whale density; these whales are generally associated with deeper water because they dive deeply for their prey (MacLeod et al., 2007; Rogan et al., 2017). However, results were not completely clear or consistent between the models for the two time periods. In the 1987–1989 model, depth and slope were selected as the best covariates. Depth did show the expected relationship with a positive effect in deeper waters and a negative effect in shallower waters, but this relationship had high variability. Slope also had the expected effect with steeper slopes having a positive effect. However, in the 1998–2015 models the only covariate selected from the

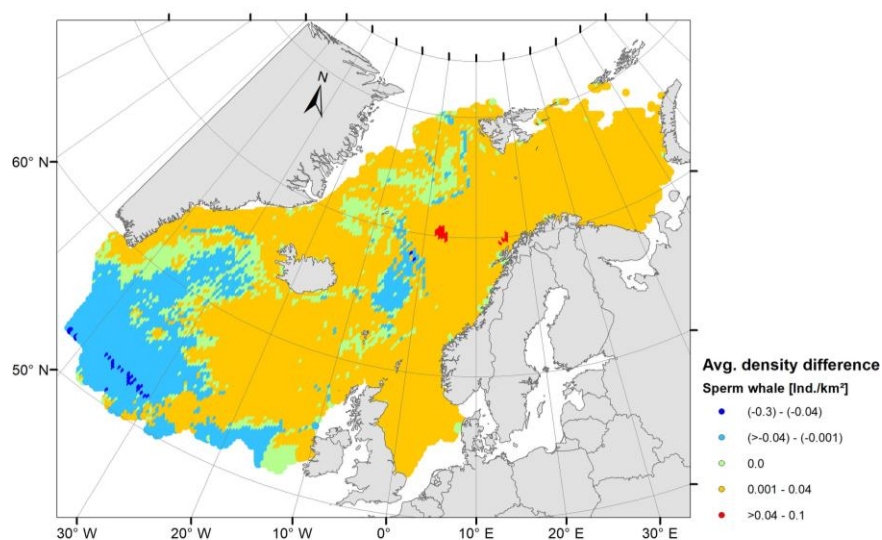


Figure 27. Difference in sperm whale predicted density between the best-fitting models from 1987–1989 and 1998–2015. The coloured prediction scale refers to the density (whales/km<sup>2</sup>) difference between 1998–2015 and 1987–1989; a recent increase in density is depicted by positive values, while a decrease by negative values

relief variables was aspect with positive west/northwest effects and negative southerly effects, all with high variability. These findings may reflect the previously suggested high foraging plasticity in long-finned pilot whales (Desportes & Mouritsen, 1993; Miller et al., 2015; Pike, Gunnlaugsson, Desportes, et al., 2019; Sigurjónsson et al., 1993; Zachariassen, 1993).

Spring sea surface temperature was selected in both models, and the relationship with density generally described a positive effect of warmer waters and a negative effect of colder waters. Although the general pattern was similar, the slightly greater 'wiggleness' in the fitted smooth relationship in the 1998–2015 model could be due to the inclusion of Norwegian waters, where the relationship between long-finned pilot whale density and temperature may be different. A similar general relationship was also described for long-finned pilot whales in Scottish and Faroese waters, where higher sightings/catches were associated with warmer summer waters (Hátún et al., 2009; MacLeod et al., 2007). Although it is not expected that SST has a direct influence on long-finned pilot whales, the pattern found in this study appears similar to those previously found. The previous studies did not evaluate lagged relationships, but it is possible that temperature in the spring months was also important. This relationship with temperature in general could be related to warmer water favouring early stages of planktonic production that link with higher trophic levels such as fish and squid.

Of the physical covariates selected in the 1998–2015 model, sea surface and bottom temperature showed a spring signal, while mixed layer depth and salinity showed a summer signal. This may be related to foraging and the trophic level at which long-finned pilot whales feed. As described above, temperature most likely influences phytoplankton productivity, which would thus lead to a lagged relationship with long-finned pilot whale density. Summer MLD and Sal relate to water masses that could be linked to summer prey availability/aggregation. The biological covariate chlorophyll a concentration was not retained in the final model, which could be expected because long-finned pilot whales feed at a higher trophic level.

There seems to be no major change in the predicted distribution between the two modelled periods (1987–1989 and 1998–2015) (Figure 29). A wide distribution is predicted in the study area in both periods, notwithstanding that there is no prediction in Norwegian waters in the earlier period because of lack of data. Predicted density was higher around the southern edge of the area, and north of Iceland during the earlier years compared with the later years when high density was predicted in the Irminger Sea, north of the Faroes, and in the Norwegian Sea. One problematic area in the 1998–2015 model is the North Sea, where long-finned pilot whales are not commonly seen either historically (Figure 1) or from this study (Figure 3). Models were fitted to data collected mostly in deeper waters, and may thus predict poorly in the North Sea.

Overall, relating the summer distribution of long-finned pilot whales to information about their prey appears difficult with the available covariates. The main reason seems to be the inter-annual variation in distribution (Hoydal & Lastein, 1993; Pike, Gunnlaugsson, Desportes, et al., 2019), which is likely linked to changes in their prey distribution. Long-finned pilot whales are plastic in their diet and hence opportunistic feeders and their main prey may vary among areas (Desportes & Mouritsen, 1993; Nøttestad et al., 2015; Sigurjónsson et al., 1993).

The most consistent feature in the models over time and over the whole study area was the spring SST signal, where warmer water had a positive effect on long-finned pilot whale density. This has previously been described in the area and also in Scotland (Hátún et al., 2009; MacLeod et al., 2007) but the mechanisms underlying these relationships are unknown. Future research could focus on investigating this relationship in the context of ocean warming. If there is strong interannual variation in distribution, models fitted to data from each year separately may reveal relationships that may help explain distribution annually. It may also be informative to develop separate models for different regions, such as around Iceland, the Faroes, and Norway.

#### **Northern bottlenose whales**

As expected, model results show that the effect of depth on northern bottlenose whale density did not change between the 1980s and 1998–2015. The positive effects were in deeper waters around 1,000–2,000 m and greater than 3,500 m, and negative effects were found in shallower waters of 500 m or less (Figure 21 and Figure 25). These relationships and approximate ranges support the findings in other studies in the Western Atlantic (Compton, 2004; Whitehead & Hooker, 2012a). They are also supported by whaling data in the Eastern Atlantic (Benjaminsen & Christensen, 1979) and in a recent study in a small area around Jan Mayen (Woo, Isojunno, & Miller, 2023), both suggesting that this whale species is quite restricted in the habitat it uses in terms of depth.

Regarding the relationship with depth, bottlenose whales prey on different deep-water fishes and squid (Mead, 1989); *Gonatus* spp seem to be common prey items (Bjørke, 2001; Fernández et al., 2014; Mead, 1989; Whitehead et al., 2003), especially in the Northeast Atlantic (Benjaminsen & Christensen, 1979; Bjørke, 2001; Santos et al., 2001). For example, in the Norwegian Sea, northern bottlenose whale distribution seems to match the distribution of *Gonatus fabricii* (Bjørke, 2001).

The month selected for sea surface temperature in the 1980s was August with positive effects between 9 °C and 11 °C, while the month selected for the period 1998–2015 was June with positive effects around 5 °C (Figure 21 and Figure 25). The difference in both the month selected and the temperature exerting a positive effect are not readily explained. The 1980s model includes a later summer signal compared to the 1998–2015 model. An explanation may lie in the combination of the southward 'migration' movement of the animals as summer progresses (Benjaminsen & Christensen, 1979; Bloch et al., 1996; Miller et al., 2015; Reeves et al., 1993; Whitehead & Hooker, 2012a) and the fact that Norwegian (north-eastern) data were not included in the 1980s model. A way to evaluate differences in both the month selected and the effect of different coverage could be to model only the Iceland-Faroese data for both periods.

All the physical covariates selected in the 1998–2015 model show a summer signal and it is likely that this may be related to foraging. Regarding the biological covariates, specifically chlorophyll a concentration, the signal was from spring and we cannot offer an explanation for the apparent negative effect of increasing chlorophyll a concentration on density. Woo, Isojunno, & Miller (2023) found a similar negative effect of

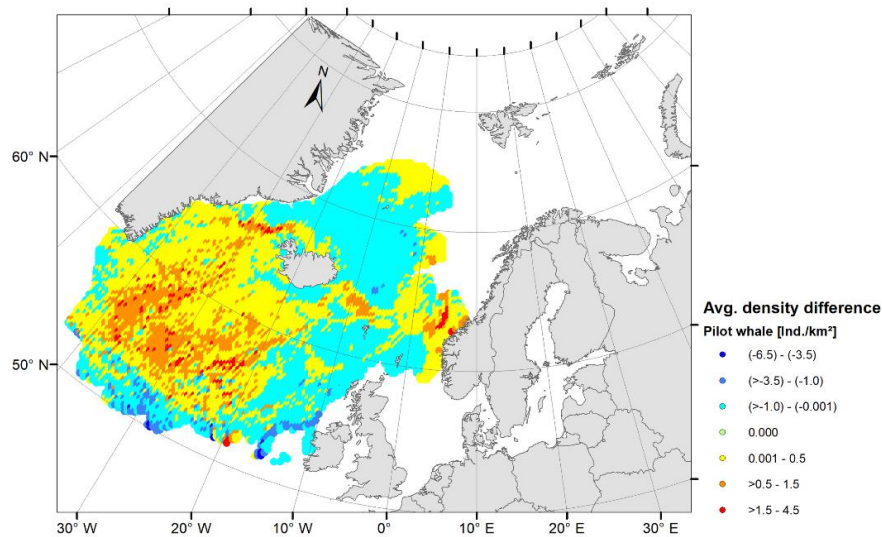


Figure 29. Difference in long-finned pilot whale predicted density between the best-fitting models from 1987–1989 and 1998–2015. The coloured prediction scale refers to the density (whales/km<sup>2</sup>) difference 1998–2015 1987–1989, a recent increase density is depicted by positive values, while a decrease by negative values.

spring chlorophyll on northern bottlenose whale occurrence around Jan Mayen.

In terms of modelled distribution, in north-eastern waters in 1998–2015 there were high density areas predicted southwest of Svalbard and around Jan Mayen, but in the 1980s there were few sightings around Jan Mayen and too few sightings in northern areas to include in the models (Figure 30). There is no reason to believe that northern bottlenose whales would have been missed by the Norwegian surveys in the 1980s, so the increase in sightings in 1998–2015 may indicate an increase in density.

in density since whaling ceased almost 50 years ago. However, the very low predicted density in waters off the coast of Andenes (around 69.3° N) and Møre (around 62.9° N) where whales were previously hunted, implies that whales have not returned to these areas following former exploitation (Figure 30 and Figure 31) (Benjaminsen & Christensen, 1979).

Northern bottlenose whales were observed in the southern areas in both periods studied. Results indicate that there has been an increase in density over time, particularly between Greenland and Iceland. Indeed, the available abundance estimates for the species show an increase from the initial

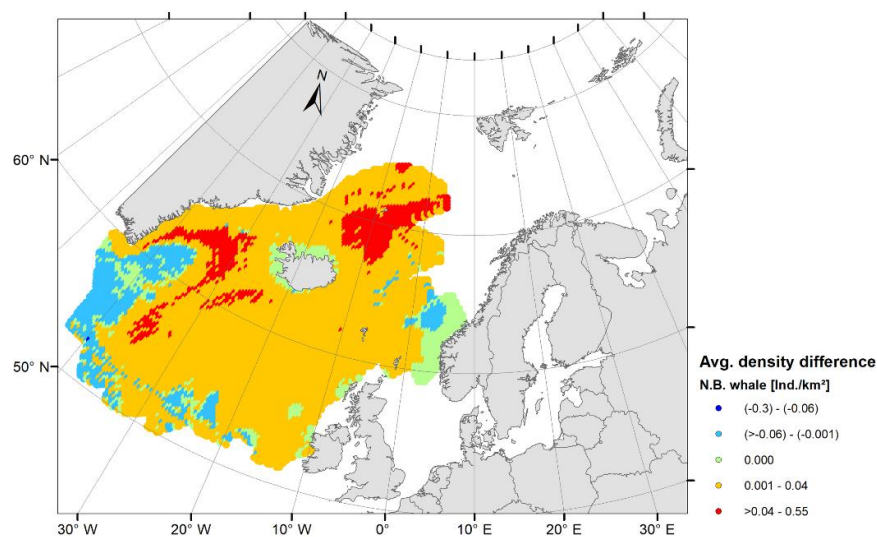


Figure 30. Difference in northern bottlenose whale predicted density between the best-fitting models from 1987–1989 and 1998–2015. The coloured prediction scale refers to the density (whales/km<sup>2</sup>) difference between 1998–2015 and 1987–1989 period, a recent increase in density is depicted by positive values, while a decrease by negative values.

The lower predicted densities north of Iceland in the 1980s may be a result of population reduction due to whaling, which continued until 1972 (Whitehead & Hooker, 2012a). Data from the whaling period 1938–1972 show that northern bottlenose whales historically occupied waters southwest of Svalbard and around Jan Mayen (Figure 31). Thus, the higher densities predicted in these areas in 1998–2015 may reflect an increase

estimates in the 1980s of 4,925 (CV = 0.16) off Iceland and 902 (CV = 0.45) off the Faroes (Gunnlaugsson & Sigurjónsson, 1990, as cited in: NAMMCO, 2019) to the combined estimates for Iceland and the Faroes of 24,561 (CV = 0.23) in 2001 (Pike et al. 2003, as cited in: NAMMCO, 2019) and the latest combined estimate of 19,975 (CV = 0.06) (Pike, Gunnlaugsson, Mikkelsen, et al., 2019).

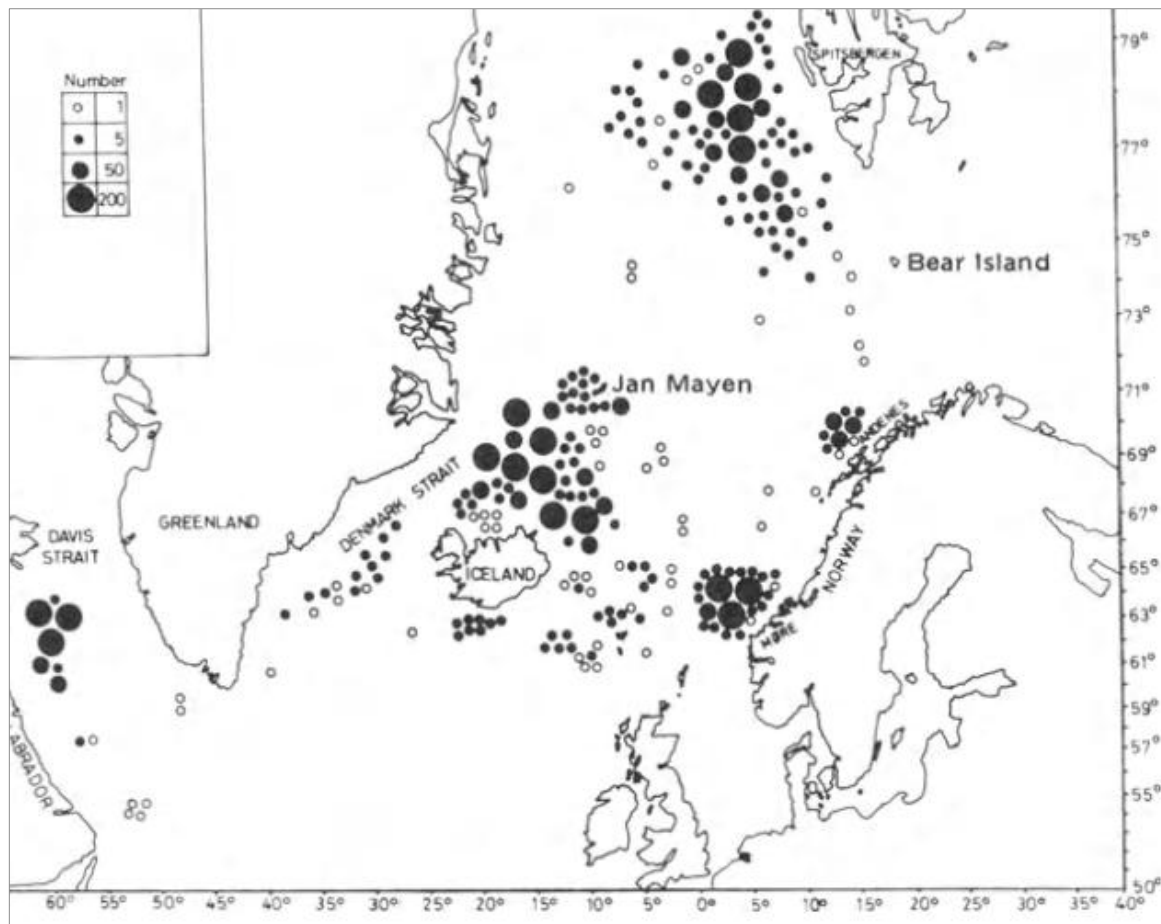


Figure 31. Localities of bottlenose whale caught by Norwegian whalers in the period 1938–1972 (Modified from Benjaminsen, 19722, as cited in: Benjaminsen & Christensen, 1979).

It is difficult to provide a clear explanation of northern bottlenose whale habitat use and the relationship with its prey. Prey is expected to be one of the main drivers of distribution and depth seems to be the best covariate explaining this relationship for northern bottlenose whales. Nevertheless, the extent to which possible north-south summer “migration” is also a driver of distribution is unclear, as is how such possible migration may be related to prey distribution. Overall, this study indicates a general increase in density through the study period perhaps caused by the post-whaling return of whales to some areas but not to others, as mentioned above.

#### **Deep-diving species concluding remarks**

The predicted high-use areas for all three species were deep waters, as expected (Christensen et al., 1992; Gunnlaugsson et al., 2009; Hooker et al., 1999; MacLeod et al., 2007; Roberts et al., 2016; Rogan et al., 2017; Virgili et al., 2019; Whitehead, 2018; Whitehead & Hooker, 2010, 2012b), with some overlap among them in the central Norwegian Sea (e.g. Nøttestad et al., 2015), and the central North Atlantic (e.g. Rogan et al., 2017), including the Irminger Sea (Abend & Smith, 1999; Gunnlaugsson et al., 2009; Whitehead & Hooker, 2012a). Looking more closely at each species in the Norwegian Sea, pilot whales tended to be closer to the coast, while sperm whales were in the central Norwegian Sea and northern bottlenose whales were more towards the Greenland-Norwegian Seas. Similar differentiation can be observed around the Faroe Islands, where all three species use the area with only some overlap in distribution. These differences in distribution likely reflect species-specific

differences in preferred prey and variation in these preferences according to the area (Benjaminsen & Christensen, 1979; Bjørke, 2001; Desportes & Mouritsen, 1993; Fernández et al., 2014; Martin & Clarke, 1986; Méndez-Fernandez et al., 2013; e.g. Nøttestad et al., 2015; Santos et al., 2014; Sigurjónsson & Víkingsson, 1997; Zachariassen, 1993). This study helps to understand the niche partitioning of the three deep diving species in the area.

In terms of predicted distribution of the deep diving species, changes in distribution between the two periods appear more as a range expansion than a shift, with generally higher predicted densities in northern waters in recent years. Changes in the distribution patterns of these and other species of cetaceans are expected to be mediated by variation in the availability and distribution of their prey; in other words the result of food-web interactions linked strongly to prey-environment relationships (Hastie, Wilson, Wilson, Parsons, & Thompson, 2004; Laran & Drouot-Dulau, 2007; Moore, 2008; Moore & Huntington, 2008).

This work provides a better understanding of the ecology of the three most common deep-diving cetacean species in the central and north-eastern North Atlantic by identifying key factors that have influenced their summer distribution and habitat use in the last 30 years. This information could also inform assessments of human pressures on these species and provide clues about how environmental changes including climate change may affect deep-diving species in the future.

## ADHERENCE TO ANIMAL WELFARE PROTOCOLS

The research presented in this article has been undertaken in accordance with the institutional and national laws and protocols for animal welfare that are applicable in the jurisdictions where the work was conducted.

## AUTHOR CONTRIBUTION STATEMENT

**NCRM:** Conceptualisation, data curation, formal analysis, funding acquisition, investigation, methodology, software, visualization, writing-original draft, review and editing; **GAV:** Data curation, funding acquisition, investigation, resources, writing-reviewing and editing; **NIØ:** Data curation, funding acquisition, investigation, resources, writing-reviewing and editing; **BM:** Data curation, funding acquisition, investigation, resources, writing-reviewing and editing; **TG:** Data curation, funding acquisition, investigation, resources, writing-reviewing and editing; **PSH:** Conceptualisation, funding acquisition, project administration, resources, supervision, writing-reviewing and editing.

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## REFERENCES

- Abend, A. G., & Smith, T. D. (1999). Review of Distribution of the Long-finned Pilot Whale (*Globicephala melas*) in the North Atlantic and Mediterranean. NOAA Technical Memorandum NMFS-NE, (117), 22. Retrieved from <http://www.nefsc.noaa.gov/nefsc/publications/tm/tm117/tm117index.htm>
- Alves, F., Quérouil, S., Dinis, A., Nicolau, C., Ribeiro, C., Freitas, L., ... Fortuna, C. (2013). Population structure of short-finned pilot whales in the oceanic archipelago of Madeira based on photo-identification and genetic analyses: Implications for conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 23(5), 758–776. <https://doi.org/10.1002/aqc.2332>
- Astthorsson, O. S., Valdimarsson, H., Gudmundsdottir, A., & Óskarsson, G. J. (2012). Climate-related variations in the occurrence and distribution of mackerel (*Scomber scombrus*) in Icelandic waters. *ICES Journal of Marine Science*, 69(7), 1289–1297. <https://doi.org/10.1093/icesjms/fss084>
- Baumgartner, M. F., Mullin, K. D., May, L. N., & Leming, T. D. (2001). Cetacean habitats in the northern Gulf of Mexico. *Fishery Bulletin*, 99(2), 219–239.
- Benjaminsen, T., & Christensen, I. (1979). The natural history of the bottlenose whale, *Hyperoodon ampullatus* (FORSTER). In H. E. Winn & B. L. Olla (Eds.), *Behaviour of marine animals* (3rd ed., pp. 143–164). Boston, MA: Springer US. [https://doi.org/10.1007/978-1-4684-2985-5\\_5](https://doi.org/10.1007/978-1-4684-2985-5_5)
- Bjørke, H. (2001). Predators of the squid *Gonatus fabricii* (Lichtenstein) in the Norwegian Sea. *Fisheries Research*, 52(1–2), 113–120. [https://doi.org/10.1016/S0165-7836\(01\)00235-1](https://doi.org/10.1016/S0165-7836(01)00235-1)
- Bloch, D., Desportes, G., Zachariassen, M., & Christensen, I. (1996). The northern bottlenose whale in the Faroe Islands, 1584–1993. *Journal of Zoology*, 239(1), 123–140. <https://doi.org/10.1111/j.1469-7998.1996.tb05441.x>
- Buckland, S. T., Bloch, D. R., Cattanach, K. L., Gunnlaugsson, T., Hoydall, K., Lens, S., & Sigurjónsson, J. (1993). Distribution and abundance of long-finned pilot whales in the North Atlantic, estimated from NASS-87 and NASS-89 data. Reports of the International Whaling Commission, 14(special issue), 33–49. Retrieved from <https://www.semanticscholar.org/paper/Distribution-and-abundance-of-long-finned-pilot-in-Buckland-Bloch/cc753bbd6396b2046fee3f0fe37ee7802f4162fe>
- Christensen, I., Haug, T., & Øien, N. I. (1992). Seasonal distribution, exploitation and present abundance of stocks of large baleen whales (Mysticeti) and sperm whales (*Physeter macrocephalus*) in norwegian and adjacent waters. *ICES Journal of Marine Science*, 49(3), 341–355. <https://doi.org/10.1093/icesjms/49.3.341>
- Clarke, M. R. (1996). Cephalopods as prey. III. Cetaceans. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 351(1343), 1053–1065. <https://doi.org/10.1098/rstb.1996.0093>
- Compton, R. C. (2004). *Predicting key habitat and potential distribution of northern bottlenose whales (Hyperoodon ampullatus) in the Northwest Atlantic Ocean*. University of Plymouth.
- Desportes, G., & Mouritsen, R. (1993). Preliminary results on the diet of long-finned pilot whales off the Faroe Islands. Reports of the International Whaling Commission, 14(special issue), 305–324.
- Drinkwater, K. F., Belgrano, A., Borja, A., Conversi, A., Edwards, M., Greene, C. H., ... Walker, H. (2003). The response of freshwater ecosystems to climate variability associated with the North Atlantic oscillation. In J. W. Hurrell, Y. Kushnir, G. Ottersen, & M. Visbeck (Eds.), *Geophysical Monograph Series* (pp. 211–234). Washington, D. C.: American Geophysical Union. <https://doi.org/10.1029/134GM12>
- Fernández, R., Pierce, G. J., MacLeod, C. D., Brownlow, A., Reid, R. J., Rogan, E., ... Santos, M. B. (2014). Strandings of northern bottlenose whales, *Hyperoodon ampullatus*, in the north-east Atlantic: Seasonality and diet. *Journal of the Marine Biological Association of the UK*, 94(6), 1109–1116. <https://doi.org/10.1017/S002531541300180X>
- Greene, C., & Pershing, A. J. (2004). North Atlantic right whales: the right whale at the wrong time? *Frontiers in Ecology and the Environment*, 2(1), 29–34. Retrieved from <http://www.jstor.org/stable/3868292>
- Gunnlaugsson, T., Víkingsson, G. A., & Pike, D. G. (2009). Combined line-transect and cue-count estimate of sperm whale abundance in the North Atlantic, from Icelandic NASS-2001 shipboard survey. *NAMMCO Scientific Publications*, 7, 73. <https://doi.org/10.7557/3.2706>
- Hansen, C., Kvaleberg, E., & Samuelson, A. (2010). Anticyclonic eddies in the Norwegian Sea; their generation, evolution and impact on primary production. *Deep-Sea Research Part I: Oceanographic Research Papers*, 57(9), 1079–1091. <https://doi.org/10.1016/j.dsr.2010.05.013>
- Hastie, G. D., Wilson, B., Wilson, L. J., Parsons, K. M., & Thompson, P. M. (2004). Functional mechanisms underlying cetacean distribution patterns: Hotspots for bottlenose dolphins are linked to foraging. *Marine Biology*, 144(2), 397–403. <https://doi.org/10.1007/s00227-003-1195-4>
- Hátún, H., Payne, M. R., Beaugrand, G., Reid, P. C., Sandø, A. B., Drange, H., ... Bloch, D. (2009). Large bio-geographical shifts in the north-eastern Atlantic Ocean: From the subpolar gyre, via plankton, to blue whiting and pilot whales. *Progress in Oceanography*, 80(3–4), 149–162. <https://doi.org/10.1016/j.pocean.2009.03.001>
- Hijmans, R. J. (2017). Raster: Geographic data analysis and modeling (Vol. 1). Vol. 1. version 2.6-7. <https://cran.r-project.org/package=raster>. Retrieved from <https://cran.r-project.org/package=raster>



- Hooker, S. K., Iverson, S. J., Ostrom, P., & Smith, S. C. (2001). Diet of northern bottlenose whales inferred from fatty-acid and stable-isotope analyses of biopsy samples. *Canadian Journal of Zoology*, 79(8), 1442–1454. <https://doi.org/10.1139/z01-096>
- Hooker, S. K., Whitehead, H., & Gowans, S. (1999). Marine Protected Area Design and the Spatial and Temporal Distribution of Cetaceans in a Submarine Canyon (Diseño de Areas Marinas Protegidas y la Distribución Espacial y Temporal de Cetaceos en un Cañón Submarino). *Conservation Biology*, 13(3), 592–602. <https://doi.org/10.1046/j.1523-1739.1999.98099.x>
- Houghton, L., Ramirez-Martinez, N., Mikkelsen, B., Vikingsson, G., Gunnlaugsson, T., Øien, N. I., & Hammond, P. (2020). Oceanic Drivers of Sei Whale Distribution in the North Atlantic. *NAMMCO Scientific Publications*, 11, 1–10. <https://doi.org/10.7557/3.5211>
- Hoydal, K., & Lastein, L. (1993). Analysis of Faroese catches of pilot whales (1709-1992), in relation to environmental variations. *Reports of the International Whaling Commission*, 14(special issue), 89–106.
- Huse, G., MacKenzie, B. R., Trenkel, V., Doray, M., Nøttestad, L., & Oskarsson, G. (2015). Spatially explicit estimates of stock sizes, structure and biomass of herring and blue whiting, and catch data of bluefin tuna. *Earth System Science Data*, 7(1), 35–46. <https://doi.org/10.5194/essd-7-35-2015>
- ICES. (1992). Report of the study group on pilot whales. In ICES C.M. Montreal, 3-4 December 1991.
- IWC. (1990). Report to the Scientific Committee. *Reports of the International Whaling Commission*, 40, 39–80.
- IWC. (2012). Report of the Scientific Committee. *Journal of Cetacean Research and Management*, 13 SUPPL.(SUPPL.), 1–405.
- Laran, S., & Drouot-Dulau, V. (2007). Seasonal variation of striped dolphins, fin- and sperm whales' abundance in the Ligurian Sea (Mediterranean Sea). *Journal of the Marine Biological Association of the United Kingdom*, 87(1), 345–352. <https://doi.org/10.1017/S0025315407054719>
- Leterme, S. C., & Pingree, R. D. (2008). The Gulf Stream, rings and North Atlantic eddy structures from remote sensing (Altimeter and SeaWiFS). *Journal of Marine Systems*, 69(3–4), 177–190. <https://doi.org/10.1016/j.jmarsys.2005.11.022>
- MacLeod, C. D., Weir, C. R., Pierpoint, C., & Harland, E. J. (2007). The habitat preferences of marine mammals west of Scotland (UK). *Journal of the Marine Biological Association of the UK*, 87(1), 157–164. <https://doi.org/10.1017/S0025315407055270>
- Martin, A. R., & Clarke, M. R. (1986). The Diet of Sperm Whales (*Physeter Macrocephalus*) Captured Between Iceland and Greenland. *Journal of the Marine Biological Association of the UK*, 66(4), 779–790. <https://doi.org/10.1017/S0025315400048426>
- Mead, J. G. (1989). Bottlenose Whales – *Hyperoodon ampullatus* (Forster, 1770) and *Hyperoodon planifrons* (Fowler, 1882). In S. H. Ridgway & S. R. Harrison (Eds.), *Handbook of marine mammals. Volume 4: River dolphins and the larger toothed whales* (First, pp. 321–348). London, UK: Academic Press.
- Méndez-Fernandez, P., Pierce, G. J., Bustamante, P., Chouvelon, T., Ferreira, M., González, A. F., ... Caurant, F. (2013). Ecological niche segregation among five toothed whale species off the NW Iberian Peninsula using ecological tracers as multi-approach. *Marine Biology*, 160(11), 2825–2840. <https://doi.org/10.1007/s00227-013-2274-9>
- Miller, P. J. O., Kvaldsheim, P. H., Lam, F. P. A., Tyack, P. L., Curé, C., DeRuiter, S. L., ... Hooker, S. K. (2015). First indications that northern bottlenose whales are sensitive to behavioural disturbance from anthropogenic noise. *Royal Society Open Science*, 2(6), 140484. <https://doi.org/10.1098/rsos.140484>
- Moore, S. E. (2008). Marine mammals as ecosystem sentinels. *Journal of Mammalogy*, 89(3), 534–540. <https://doi.org/10.1644/07-mamm-s-312r1.1>
- Moore, S. E., & Huntington, H. P. (2008). Arctic marine mammals and climate change: impacts and resilience. *Ecological Applications*, 18(2 Supplement), S157–S165. <https://doi.org/10.1890/06-0571.1>
- NAMMCO. (1997). Scientific Committee Report of the Working Group on Abundance Estimates. Reykjavik, 21-23 February 1997: North Atlantic Marine Mammal Commission. Retrieved from North Atlantic Marine Mammal Commission website: [https://nammco.no/wp-content/uploads/2019/02/12-sc-25\\_report\\_aewg\\_may-rev-october-2018\\_rev.pdf](https://nammco.no/wp-content/uploads/2019/02/12-sc-25_report_aewg_may-rev-october-2018_rev.pdf)
- NAMMCO. (1998). Annual Report 1997. In NAMMCO. Tromsø, Norway: North Atlantic Marine Mammal Commission. <https://doi.org/10.1037/h0090484>
- NAMMCO. (2019). Northern Bottlenose Whale. Retrieved from [https://nammco.no/topics/bottlenose\\_whale/#1478699758629-7da126c3-48a6](https://nammco.no/topics/bottlenose_whale/#1478699758629-7da126c3-48a6)
- Nøttestad, L., Krafft, B. A., Anthonypillai, V., Bernasconi, M., Langård, L., Mørk, H. L., & Fernö, A. (2015). Recent changes in distribution and relative abundance of cetaceans in the Norwegian Sea and their relationship with potential prey. *Frontiers in Ecology and Evolution*, 2(January). <https://doi.org/10.3389/fevo.2014.00083>
- OBPG. (2014). Moderate-resolution imaging spectroradiometer (MODIS) Aqua Photosynthetically Available Radiation Data: 2014 Reprocessing. NASA OB. DAAC. Greenbelt, MD: NASA Goddard Space Flight Center, Ocean Ecology Laboratory, Ocean Biology Processing Group. <https://doi.org/10.5067/AQUA/MODIS/L3B/PAR/2014>
- O'Callaghan, S. A., Griffin, B., Levesque, S., Gammell, M., & O'Brien, J. (2024). Female, juvenile, and calf sperm whale *Physeter macrocephalus* (Linnaeus 1758) records from Ireland. *Ecology and Evolution*, 14(9). <https://doi.org/10.1002/ece3.70056>
- Øien, N. I. (2009). Distribution and abundance of large whales in Norwegian and adjacent waters based on ship surveys 1995-2001. *NAMMCO Scientific Publications*, 7, 31–47. <https://doi.org/10.7557/3.2704>
- Øien, N. I., & Bøthun, G. (2009). Trends in local abundance of large whales in the Northeast Atlantic, based on Norwegian surveys 1987-2004. *IWC, SC/57/O11*, 1–7.
- Olson, P. A. (2018). Pilot Whales. In W. F. Perrin, B. Würsig, & J. G. M. Thewissen (Eds.), *Encyclopedia of Marine Mammals* (pp. 701–705). San Diego, CA: Elsevier. <https://doi.org/10.1016/B978-0-12-804327-1.00194-1>
- Pike, D. G. (2009). Introduction. In C. Lockyer & D. Pike (Eds.), *North Atlantic Sightings Surveys: Counting whales in the North Atlantic, 1987-2001* (Vol. 7, pp. 7–18). <https://doi.org/10.7557/3.7>
- Pike, D. G., Gunnlaugsson, T., Desportes, G., Mikkelsen, B., Vikingsson, G. A., & Bloch, D. (2019). Estimates of the relative abundance of long-finned pilot whales (*Globicephala melas*) in the Northeast Atlantic from 1987 to 2015 indicate no long-term trends. *NAMMCO Scientific Publications*, 11. <https://doi.org/10.7557/3.4643>
- Pike, D. G., Gunnlaugsson, T., Mikkelsen, B., Halldórsson, S. D., & Vikingsson, G. (2019). Estimates of the abundance of cetaceans in the central North Atlantic based on the NASS Icelandic and Faroese shipboard surveys conducted in 2015. *NAMMCO Scientific Publications*, 11, 1–19. <https://doi.org/10.7557/3.4941>
- Pike, D. G., Gunnlaugsson, T., Mikkelsen, B., Halldórsson, S. D., Vikingsson, G., Acquarone, M., & Desportes, G. (2020). Estimates of the Abundance of Cetaceans in the Central North Atlantic from the T-NASS Icelandic and Faroese Ship Surveys Conducted in 2007. *NAMMCO Scientific Publications*, 11. <https://doi.org/10.7557/3.5269>
- Pirrotta, E., Matthiopoulos, J., MacKenzie, M., Scott-Hayward, L., & Rendell, L. (2011). Modelling sperm whale habitat preference: A novel approach combining transect and follow data. *Marine Ecology Progress Series*, 436, 257–272. <https://doi.org/10.3354/meps09236>
- QGIS Development Team. (2018). *QGIS Geographic Information System. Open Source Geospatial Foundation Project*. QGIS Desktop 2.18.15. Retrieved from <https://www.qgis.org/de/>
- R Core Team. (2021). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Redfern, J. V., Ferguson, M. C., Becker, E. A., Hyrenbach, K. D., Good, C., Barlow, J., ... Werner, F. (2006). Techniques for cetacean – habitat modeling. *Marine Ecology Progress Series*, 310, 271–295. <https://doi.org/10.3354/meps310271>

- Reeves, R. R., Mitchell, E., & Whitehead, H. (1993). Status of the northern bottlenose whale, *Hyperoodon ampullatus*. Canadian Field-Naturalist, (107), 490–508. Retrieved from <http://whitelab.biology.dal.ca/sh/bnwstat.htm>
- Rice, D. W. (1989). Sperm whale. In S. H. Ridgway & S. R. Harrison (Eds.), *Handbook of marine mammals. Volume 4: River dolphins and the larger toothed whales* (First, pp. 177–234). London, UK.: Academic Press.
- Roberts, J. J., Best, B. D., Mannocci, L., Fujioka, E., Halpin, P. N., Palka, D. L., ... Lockhart, G. G. (2016). Habitat-based cetacean density models for the U.S. Atlantic and Gulf of Mexico. *Scientific Reports*, 6, 1–12. <https://doi.org/10.1038/srep22615>
- Rogan, E., Cañadas, A., Macleod, K., Santos, M. B., Mikkelsen, B., Uriarte, A., ... Hammond, P. S. (2017). Distribution, abundance and habitat use of deep diving cetaceans in the North-East Atlantic. *Deep-Sea Research Part II: Topical Studies in Oceanography*, 141(April), 8–19. <https://doi.org/10.1016/j.dsr2.2017.03.015>
- Santos, M. B., Monteiro, S. S., Vingada, J. V., Ferreira, M., López, A., Martínez Cedeira, J. A., ... Pierce, G. J. (2014). Patterns and trends in the diet of long-finned pilot whales (*Globicephala melas*) in the northeast Atlantic. *Marine Mammal Science*, 30(1), 1–19. <https://doi.org/10.1111/mms.12015>
- Santos, M. B., Pierce, G. J., Boyle, P. R., Reid, R. J., Ross, H. M., Patterson, I. A. P., ... Hernández-García, V. (1999). Stomach contents of sperm whales *Physeter macrocephalus* stranded in the North Sea 1990-1996. *Marine Ecology Progress Series*, 183, 281–294. <https://doi.org/10.3354/meps183281>
- Santos, M. B., Pierce, G. J., Smeenk, C., Addink, M. J., Kinze, C. C., Tougaard, S., & Herman, J. (2001). Stomach contents of northern bottlenose whales *Hyperoodon ampullatus* stranded in the North Sea. *Journal of the Marine Biological Association of the UK*, 81(1), 143–150. <https://doi.org/10.1017/S0025315401003484>
- Sathyendranath, S., Groom, S., Grant, M., Brewin, R. J. W., Thompson, A., Chuprin, A., ... Zibordi, G. (2016). ESA Ocean Colour Climate Change Initiative (Ocean\_Colour\_cci). Centre for Environmental Data Analysis. <https://doi.org/10.5285/b0d6b9c5-14ba-499f-87c9-66416cd9a1dc>
- Schleimer, A., Ramp, C., Plourde, S., Lehoux, C., Sears, R., & Hammond, P. S. (2019). Spatio-temporal patterns in fin whale *Balaenoptera physalus* habitat use in the northern Gulf of St. Lawrence. *Marine Ecology Progress Series*, 623, 221–234. <https://doi.org/10.3354/meps13020>
- Servidio, A., Pérez-Gil, E., Pérez-Gil, M., Cañadas, A., Hammond, P. S., & Martín, V. (2019). Site fidelity and movement patterns of short-finned pilot whales within the Canary Islands: Evidence for resident and transient populations. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 29(S1), 227–241. <https://doi.org/10.1002/aqc.3135>
- Sigurjónsson, J., & Gunnlaugsson, T. (1990). Recent trends in abundance of blue (*Balaenoptera musculus*) and humpback whales (*Megaptera novaeangliae*) off west and southwest Iceland with a note on occurrence of other cetacean species. Reports of the International Whaling Commission, 40, 537–551.
- Sigurjónsson, J., & Víkingsson, G. A. (1997). Seasonal abundance and estimation of food consumption by cetaceans in Icelandic and adjacent waters. *Journal of Northwest Atlantic Fishery Science*, 22, 271–287. <https://doi.org/10.2960/j.v22.a20>
- Sigurjónsson, J., Víkingsson, G. A., & Lockyer, C. (1993). Two mass strandings of pilot whales (*Globicephala melas*) on the coast of Iceland. Reports of the International Whaling Commission, 14(special issue), 407–424.
- Silva, T., Gislason, A., Licandro, P., Marteinsdóttir, G., Ferreira, A. S. A., Gudmundsson, K., & Astthorsson, O. S. (2014). Long-term changes of euphausiids in shelf and oceanic habitats southwest, south and southeast of Iceland. *Journal of Plankton Research*, 36(5), 1262–1278. <https://doi.org/10.1093/plankt/fbu050>
- Skern-Mauritzen, M., Lindstrøm, U., Biuw, M., Elvarsson, B., Gunnlaugsson, T., Haug, T., ... Víkingsson, G. (2022). Marine mammal consumption and fisheries removals in the Nordic and Barents Seas. *ICES Journal of Marine Science*, 79(May), 1583–1603. <https://doi.org/10.1093/icesjms/fsac096>
- Solvang, H. K., Skaug, H. J., & Øien, N. I. (2015). Abundance estimates of common minke whales in the Northeast Atlantic based on survey data collected over the period 2008-2013. In International Whaling Commission SC/66a/RMP/8.
- Taylor, B. L., Baird, R. W., Dawson, S. M., Ford, J., Mead, J. G., Sciara, N. G., ... Pitman, R. L. (2008). *Hyperoodon ampullatus*, North Atlantic Bottlenose Whale. The IUCN Red List of Threatened Species 2008: E.T10707A3208523., 8235. Retrieved from <http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T10707A3208523.en>
- Trenkel, V. M., Huse, G., MacKenzie, B. R., Alvarez, P., Arrizabalaga, H., Castonguay, M., ... Speirs, D. C. (2014). Comparative ecology of widely distributed pelagic fish species in the North Atlantic: Implications for modelling climate and fisheries impacts. *Progress in Oceanography*, 129(PB), 219–243. <https://doi.org/10.1016/j.pocean.2014.04.030>
- Valdimarsson, H., Astthorsson, O. S., & Palsson, J. (2012). Hydrographic variability in Icelandic waters during recent decades and related changes in distribution of some fish species. *ICES Journal of Marine Science*, 69(5), 816–825. <https://doi.org/10.1093/icesjms/fss027>
- Venables, W. N., & Ripley, B. D. (2002). *Modern applied statistics with S*. New York: Springer. <https://doi.org/10.1007/978-0-387-21706-2>
- Verborgh, P., De Stephanis, R., Pérez, S., Jaquet, Y., Barbraud, C., & Guinet, C. (2009). Survival rate, abundance, and residency of long-finned pilot whales in the strait of Gibraltar. *Marine Mammal Science*, 25(3), 523–536. <https://doi.org/10.1111/j.1748-7692.2008.00280.x>
- Víkingsson, G. A., Pike, D. G., Desportes, G., Øien, N. I., Gunnlaugsson, T., & Bloch, D. (2009). Distribution and abundance of fin whales (*Balaenoptera physalus*) in the Northeast and Central Atlantic as inferred from the North Atlantic Sightings Surveys 1987-2001. *NAMMCO Scientific Publications*, 7, 49–72. Retrieved from <https://septentrio.uit.no/index.php/NAMMCO/SP/article/view/2705>
- Víkingsson, G. A., Pike, D. G., Valdimarsson, H., Schleimer, A., Gunnlaugsson, T., Silva, T., ... Hammond, P. S. (2015). Distribution, abundance, and feeding ecology of baleen whales in Icelandic waters: have recent environmental changes had an effect? *Frontiers in Ecology and Evolution*, 3(February), 1–18. <https://doi.org/10.3389/fevo.2015.00006>
- Virgili, A., Authier, M., Boisseau, O., Cañadas, A., Claridge, D., Cole, T., ... Ridoux, V. (2019). Combining multiple visual surveys to model the habitat of deep-diving cetaceans at the basin scale: Large-scale modelling of deep-diving cetacean habitats. *Global Ecology and Biogeography*, 28(3), 300–314. <https://doi.org/10.1111/geb.12850>
- Whitehead, H. (2003). *Sperm whales: social evolution in the ocean*. University of Chicago Press.
- Whitehead, H. (2018). Sperm Whale. In *Encyclopedia of Marine Mammals* (pp. 919–925). Elsevier. <https://doi.org/10.1016/B978-0-12-804327-1.00242-9>
- Whitehead, H., & Hooker, S. K. (2010). Status of northern bottlenose whales. NAMMCO SC/63/SM4, (NAMMCO 2009), 1–11.
- Whitehead, H., & Hooker, S. K. (2012a). Uncertain status of the northern bottlenose whale *Hyperoodon ampullatus*: Population fragmentation, legacy of whaling and current threats. *Endangered Species Research*, 19(1), 47–61. <https://doi.org/10.3354/esr00458>
- Whitehead, H., & Hooker, S. K. (2012b). Uncertain status of the northern bottlenose whale *Hyperoodon ampullatus*: Population fragmentation, legacy of whaling and current threats. *Endangered Species Research*, 19(1), 47–61. <https://doi.org/10.3354/esr00458>
- Whitehead, H., Macleod, C. D., & Rodhouse, P. (2003). Differences in niche breadth among some teuthivorous mesopelagic marine mammals. *Marine Mammal Science*, 19(2), 400–406. <https://doi.org/10.1111/j.1748-7692.2003.tb01118.x>
- Woo, K., Isojunno, S., & Miller, P. (2023). Habitat use of the northern bottlenose whale *Hyperoodon ampullatus* near Jan Mayen, North

- Atlantic. *Marine Ecology Progress Series*, 718(0), 119–136.  
<https://doi.org/10.3354/meps14374>
- Wood, S. N. (2011). Fast stable REML and ML estimation of semiparametric generalized linear models. *Journal of Royal Statistical Society. Series B*, 73(1), 3–36.  
<https://doi.org/10.1111/j.1467-9868.2010.00749.x>
- Wood, S. N. (2017). *Generalized additive models: an introduction with R* (2nd ed.). Boca Raton: CRC Press/Taylor & Francis Group.  
<https://doi.org/10.1201/9781315370279>
- Zachariassen, P. (1993). Pilot whale catches in the Faroe Islands. Reports of the International Whaling Commission, 14(special issue), 69–88.