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ORIGINAL PAPER

Spatiotemporal occurrence of northern bottlenose whales (*Hyperoodon ampullatus*) within the Nordic Seas based upon passive acoustic monitoring

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Abstract

Northern bottlenose whales (*Hyperoodon ampullatus*) are echolocating, deep-diving beaked whales found primarily in arctic and sub-arctic offshore waters. In the eastern North Atlantic, the species has been suggested to undergo seasonal north–south migrations, however, previous whaling data and more recent sighting surveys insufficiently covered the winter months. To address this data gap, bottom-moored hydrophone deployments (n = 8) were conducted at three locations in the Nordic Seas: off Jan Mayen (Norway; 2015–2017), north-east Iceland (2020–2022) and east Iceland (2020–2023). Automated click detection allowed identification of species-specific clicks. Detector precision and recall were manually evaluated using subsets of the data and precision was used to correct the weekly proportion of snapshots that contained clicks. Generalized additive mixed models were used to investigate whether environmental variables associated with prey availability explained occurrence patterns. Results revealed near year-round presence of northern bottlenose whales in the Nordic Seas with a gradual northward shift in spring between Iceland and Jan Mayen. The lowest numbers of detections occurred from July into September, contradicting the long-standing hypothesis of north–south migrations to enable overwintering at lower latitudes. The observed seasonal occurrence patterns were stable across years and associated with higher sea surface height variation, indicative of eddy activity. We interpreted this as support of a prey-driven distribution, as eddies characterize the spawning grounds of northern bottlenose whales' main squid prey in the Nordic Seas, *Gonatus fabricii*. The observed occurrence patterns can inform planning of future anthropogenic activities in these waters to avoid habitat degradation and reduce stressors on this species.

Keywords Beaked whale · Distribution · Eastern North Atlantic · Environmental modelling · Conservation

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Introduction

Animal movements are commonly driven by environmental conditions, predator avoidance, and the availability of resources needed to maintain basic life functions and maximise fitness. Such resources include availability of food, access to mating partners, and appropriate shelter (Dingle and Drake 2007). The spatial and temporal scale over which animals move to obtain access to resources relates to a species' life history and ecological needs (Bräger and Bräger 2019) but can also vary between individuals and populations of the same species (Shaw 2020). Within cetaceans, small populations of many species are considered resident, i.e. they only move within a limited range (e.g. Indo-Pacific bottlenose dolphins (*Tursiops aduncus*): Chabanne et al.

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2012; fin whales (*Balaenoptera physalus*): Falcone et al. 2022; goose-beaked (*Ziphius cavirostris*) and Blainville's beaked whales (*Mesoplodon densirostris*): McSweeney et al. 2007). At the other extreme are migratory species. For instance, grey whales (*Eschrichtius robustus*) spend the summer months on their feeding grounds in Alaska and along the Canadian west-coast, and travel over 7600 km south to their winter breeding and birthing grounds along the Mexican coast (Swartz 1986). On a smaller spatial scale, fish-eating Norwegian killer whales (*Orcinus orca*) seasonally migrate between feeding grounds, following the movement of their herring prey (Vogel et al. 2021).

Understanding a species' movement patterns and their underlying drivers are crucial aspects in conservation as knowledge of habitat use is helpful to mitigate potential threats. For instance, resident populations can greatly benefit from the establishment of a localised protected area, whereas this might have less conservation benefit for a migratory population (Reynolds et al. 2017). Nevertheless, if a migratory species is known to seasonally return to the same areas for specific behaviours relevant to species survival (e.g. breeding grounds, feeding hotspots) the protection of such areas can have positive effects on species conservation (Lascelles et al. 2014), especially if the migration routes connecting them are also considered (Hooker et al. 2011). Key habitats may also shift over time and can result in temporal and spatial shifts of cetacean ranging behaviour (Hooker et al. 2011; Lascelles et al. 2014), for instance due to climate change induced ocean warming (Lambert et al. 2014; MacLeod 2009).

A key driver of animal movements is food availability (Stern and Friedlaender 2018; Bräger and Bräger 2019), both on short and small (e.g. immediate foraging, diel movements) as well as long and large (e.g. migratory) temporal-spatial scales. Distributions of marine mammals are typically closely linked to the availability and distribution of their prey; therefore, many studies have investigated the relationship of environmental proxies for prey availability with visual or acoustic detections of cetaceans to understand and predict their movements (e.g. Feyrer et al. 2024; Pirotta et al. 2011; Ramirez-Martinez et al. 2024).

Northern bottlenose whales (*Hyperoodon ampullatus*) are deep-diving beaked whales found primarily in arctic and sub-arctic offshore waters (Gray 1882; Whitehead and Hooker 2012), feeding mainly on deep-sea squid. Fish is also part of their diet, though with some regional variation (Murray and Hjort 1912; Hooker et al. 2001; Fernández et al. 2014). Northern bottlenose whales are believed to follow the distribution of their main prey, cephalopods of the genus *Gonatus* (Bjørke 2001; Hooker et al. 2001). *Gonatus fabricii* is the most abundant squid in arctic and sub-arctic waters of the North Atlantic with a range from the central Polar Basin in the north, as far south as the North Sea in the east and Cape Cod (USA) in the west (Golikov et al. 2013). The species undergoes life history related vertical migrations from an epipelagic distribution of paralarvae and juveniles, to a meso- and bathypelagic distribution of immature and mature specimens (Bjørke and Gjøsæter 1998). Mature *Gonatus fabricii* undergo sex-specific developments: while males remain active swimmers, spawning females become gelatinous and immobile serving as positively buoyant floats for their eggs until paralarvae hatches (Arkhipkin and Bjørke 1999; Golikov et al. 2019). Northern bottlenose whales have been suggested to feed primarily on easier to catch gelatinous females as they aggregate on breeding and spawning grounds (Bjørke and Gjøsæter 1998; Arkhipkin and Bjørke 1999). This hypothesis has been confirmed for the small northern bottlenose whale population on the Scotian Shelf (Canada) based upon comparisons of fatty-acid compositions (Hooker et al. 2001). The Scotian Shelf waters, as well as the Central Polar Basin, southwestern and northern Davis Strait, southeastern Greenland Sea, northern Icelandic Sea, waters southwest of Svalbard, and northeastern and southern Norwegian Sea have to date been suggested to be *Gonatus fabricii* breeding and spawning grounds (Wiborg et al. 1984; Arkhipkin and Bjørke 1999; Golikov et al. 2019). These areas are characterized by a highly productive epipelagic layer providing food for juvenile specimens and strong surface currents contributing to dispersal (Golikov et al. 2019). It has further been suggested that eddies, frontal activities and retention processes locally concentrating nutrient rich waters attract *Gonatus* to such areas due to high food availability (Wiborg et al. 1982; Semmens et al. 2007). Remotely sensed environmental variables on ocean surface conditions can be useful proxies for identifying such oceanographic processes and thus for inferring the distributions of cephalopods and their specialist predators.

The hypothesis that the distribution of northern bottlenose whales follows that of its squid prey stems from research that focused on either *Gonatus fabricii* (Bjørke and Gjøsæter 1998; Arkhipkin and Bjørke 1999) or the well-studied Scotian Shelf population of northern bottlenose whales (Hooker et al. 2001). However, the Scotian Shelf population is considered resident, with individuals only moving across few adjacent underwater canyons (Wimmer and Whitehead 2004), and is genetically distinct from populations further north off Canada and in the eastern North Atlantic (Dalebout et al. 2001; Feyrer et al. 2019; de Greef et al. 2022). In contrast, the distribution of bottlenose whales in the eastern North Atlantic is believed to change seasonally. It has been a long-standing hypothesis that these whales migrate north to sub-arctic and arctic feeding grounds in spring and move southwards in late summer or early autumn to overwinter in

more temperate waters (Gray 1882; Murray and Hjort 1912; Benjaminsen and Christensen 1979). Southward migrations were indeed observed using Argos-linked satellite tags by Miller et al. (2015a, b, 2016a, b), as two whales tagged off Jan Mayen in June of 2015 and 2016 travelled south to an area close to the Azores (Portugal) before the tags stopped transmitting. The dive behaviour of these and eight other individuals tagged off Jan Mayen in 2014–2016 suggested that the Iceland and Norwegian Seas are important foraging areas for the population (Neubarth et al. 2025). Three northern bottlenose whales tagged off north-east Iceland in June 2023 were tracked following an almost identical route, and then only spent about two weeks near the Azores before quickly heading back northwards in late July or early August (Wensveen et al. 2025).

These recent findings from satellite telemetry are consistent with visual sightings of northern bottlenose whales in the Azores peaking in July and August (Silva et al. 2003), but contradict the whalers' belief that bottlenose whales overwintered in more temperate Central Atlantic waters (Gray 1882; Murray and Hjort 1912; Benjaminsen and Christensen 1979). Low numbers of bottlenose whale sightings in Icelandic and Norwegian waters throughout the winter months (Gunnlaugsson and Víkingsson 2014; Øien and Hartvedt 2015) may be due to a lack of scientific sighting surveys (Øien and Hartvedt 2015; Pike et al. 2019, 2020a; Leonard and Øien 2020) or, historically, whaling activities (Benjaminsen and Christensen 1979) in the rough and dark Nordic winter. Thus, the currently available evidence on northern bottlenose whale distribution and movement contains a summer bias in sampling effort and, in the case of tagging studies, stems from few individuals.

Here we address this data gap on the winter distribution of eastern North Atlantic bottlenose whales using multi-year passive acoustic monitoring (PAM) data collected with bottom-moored hydrophones. Northern bottlenose whales are suitable for PAM methods (Moors 2012; Kowarski et al. 2018; Delarue et al. 2024) as they produce species-specific echolocation clicks at high rates (Wahlberg et al. 2011; Baumann-Pickering et al. 2013) throughout much of their dive cycle (Haas et al. 2025). Hydrophones were deployed at three locations within the Nordic Seas, situated within different water masses. Deployments to the east of Jan Mayen Island were located close to the Jan Mayen Front where warmer and more saline waters originating from the North Atlantic encounter colder and fresher waters of polar origin (Erga et al. 2014; Drinkwater et al. 2020). The north-east Iceland deployments were located within the East Icelandic Current originating from the Arctic Sea carrying colder less saline water (Jónsson 2007; Macrander et al. 2014), and the east Iceland deployments were between the East Icelandic Current to the north and the warmer North Atlantic Current to the south (Semper et al. 2020, 2022). This might result in different environmental conditions and prey availability at the monitored locations. Thus, we investigated whether observed occurrence patterns of northern bottlenose whales simply follow a seasonal trend independent of environmental conditions (HP0) or can be explained by environmental variables that may be indicative of high prey abundance (HP1). We addressed this objective by modelling the relationship between bottlenose whale acoustic detections and environmental data on ocean surface conditions indicating biomass aggregation, frontal activities and eddies, which locally attract *Gonatus* squid (Wiborg et al. 1982; Semmens et al. 2007). We hypothesized that higher occurrence and acoustic detections of northern bottlenose whales occur due to increased prey availability as indicated by oceanographic variables.

Materials and methods

Acoustic data collection

Acoustic data were collected with bottom-moored hydrophones (Loggerhead Instruments, autonomous recorder, models DSG-ST, LS1X-AL and LS2X-AL) at three offshore sites in the Nordic Seas: Jan Mayen, Norway (71.03°N 7.03°W), north-east Iceland (67.27°N 13.63°W) and east Iceland (64.89°N 9.05°W; Fig. 1). The deployment site off Jan Mayen was approximately 493 km and 685 km from the north-east and east Iceland location, respectively, and the two Icelandic deployment sites were about 335 km apart. Recorders were equipped with either one (DSG-ST, LS1X-AL) or two (LS2X-AL) HTI-96-MIN hydrophones, though in the latter case only the channel with less frequency dependent interference was analysed for consistency across deployments. Hydrophone sensitivity at 27.4 kHz, the centre frequency of northern bottlenose whale clicks (Clarke et al. 2019), was similar across instruments, with clipping levels of 166.8 dB re 1 µPa for the DSG-ST, and 166.6 dB re 1 µPa for the two LSX-AL models.

Deployments off Jan Mayen were conducted between June 2015 to June 2017 as part of international research projects on body condition (Miller et al. 2016a, b) and the effects of naval sonar on cetacean behaviour (Miller et al. 2015a, b; Wensveen et al. 2019). We deployed the instruments to the east of the island within the Jan Mayen Fracture Zone from aboard the sailing vessel Donna Wood. Water depths at deployment locations ranged between 2000–2300 m (Table 1) and the hydrophones were mounted on the mooring line at approximately 115 m above the seafloor. Recordings were conducted at 144 kHz sampling rate and

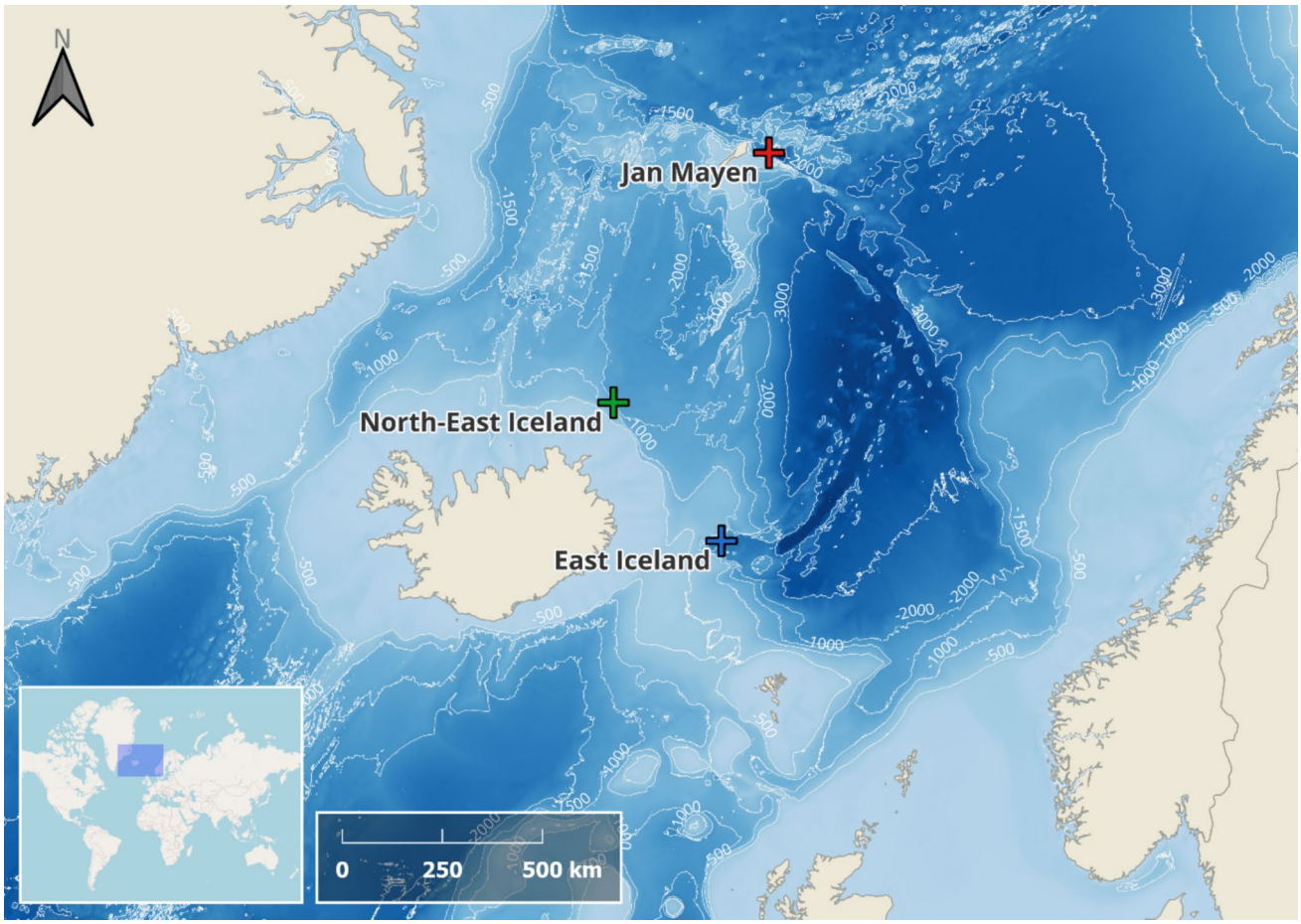

Fig. 1 Hydrophone deployment locations in the Nordic Seas. Seafloor depth is based on GEBCO 2024 gridded bathymetry data (https://doi.org/10.5285/1c44ce99-0a0d-5f4f-e063-7086abc0ea0f)

Table 1 Detailed overview of autonomous acoustic recorder deployments including location, approximate hydrophone and seafloor depth, deployment time and duration, duty-cycle (as recording duration/cycle duration) and sample rate of each deployment

Location	Deployment ID	Recorder model	Latitude (°N)	Longitude (°W)	Hydrophone depth (m)	Seafloor depth (m)	Deployment start (UTC)	Deployment end (UTC)	Deployment duration (hours)	Duty cycle (min/min)	Sample rate (kHz)
Jan Mayen	JM3	DSG-ST	71.03203	7.02855	2185	2300	30/06/2015 23:12	09/06/2016 20:12	8277	2.5/45	144
	JM7	DSG-ST	70.85213	6.13852	1885	2000	23/06/2016 06:52	14/06/2017 21:07	8558	2.5/45	144
North-east Iceland	LNE1	DSG-ST	67.26558	13.63352	1470	1510	07/11/2020 06:45	14/08/2021 00:30	6714	5/15	96
	LNE2	DSG-ST	67.26783	13.62633	1440	1480	27/10/2021 00:30	16/08/2022 09:00	7041	5/15	96
East Iceland	KRA1	DSG-ST	64.88870	9.04570	2540	2580	21/02/2020 00:00	16/08/2020 23:45	4272	5/15	96
	KRA2	LS1X-AL	64.88805	9.04593	2520	2560	24/02/2021 16:55	14/08/2021 18:25	4106	5/15	96
	KRA3	LS1X-AL	64.88600	9.04650	2600	2640	28/10/2021 11:25	25/05/2022 05:40	5010	3/15	96
	KRC3	LS2X-AL	64.91900	9.04517	2300	2340	19/08/2022 16:00	10/08/2023 12:30	8541	2.5/30	96

16-bits resolution, with a duty-cycle of 2.5/45 min, i.e. recording 2.5 min snapshots every 45 min.

Deployments off the Icelandic shelf were carried out in collaboration with the Icelandic Marine and Freshwater Research Institute from aboard the research vessel Bjarni Sæmundsson. Off north-east Iceland, we collected data between November 2020 and August 2022 near the continental shelf edge at bottom depths of approximately 1500 m (Table 1). Off east Iceland, hydrophones were deployed between February 2020 and August 2023 at water depths between 2300–2650 m on the northern side of the Iceland-Faroe Ridge. The hydrophones at these two sites were deployed around 40 m above the seafloor. At the two sites in Icelandic waters, data were recorded at 96 kHz sampling rate and 16-bits resolution though at variable duty-cycles, recording either 5/15 min, 3/15 min or 2.5/30 min (Table 1).

Spatiotemporal acoustic occurrence patterns

All acoustic recordings were processed and analysed in MATLAB (Version 9.12.0 R2022a; The MathWorks Inc., (2022). Automated detection and classification of echolocation clicks was performed using the SPICE detector plugin (Frasier 2020) in the software Triton (Wiggins et al. 2010). We used a peak-to-peak received level threshold of 120 dB re 1 µPa (for details on detector tuning, see supplementary information S1). A peak-to-peak level threshold provides an absolute detection criterion for calibrated hydrophones and was chosen to ensure consistent detection probability across seasons and recording locations, regardless of background noise level. Click classification was based on known time, frequency and energy characteristics of northern bottlenose whale echolocation clicks (Wahlberg et al. 2011; Clarke et al. 2019) (Fig. 2, Table 2). Manual evaluation of detections was carried out using the MATLAB interface detEdit (Solsona-Berga et al. 2020) customised to work with duty-cycled recordings and with an additional Wigner-Ville time–frequency display. The tool displayed received level and time–frequency characteristics (supplementary information S2) averaged over all, or a manual selection of, detected clicks inside a detection positive snapshot (each corresponding to a recording file of 2.5, 3 or 5 min depending on the respective duty-cycle). Those files containing a minimum of two click detections were classified as detection positive snapshots.

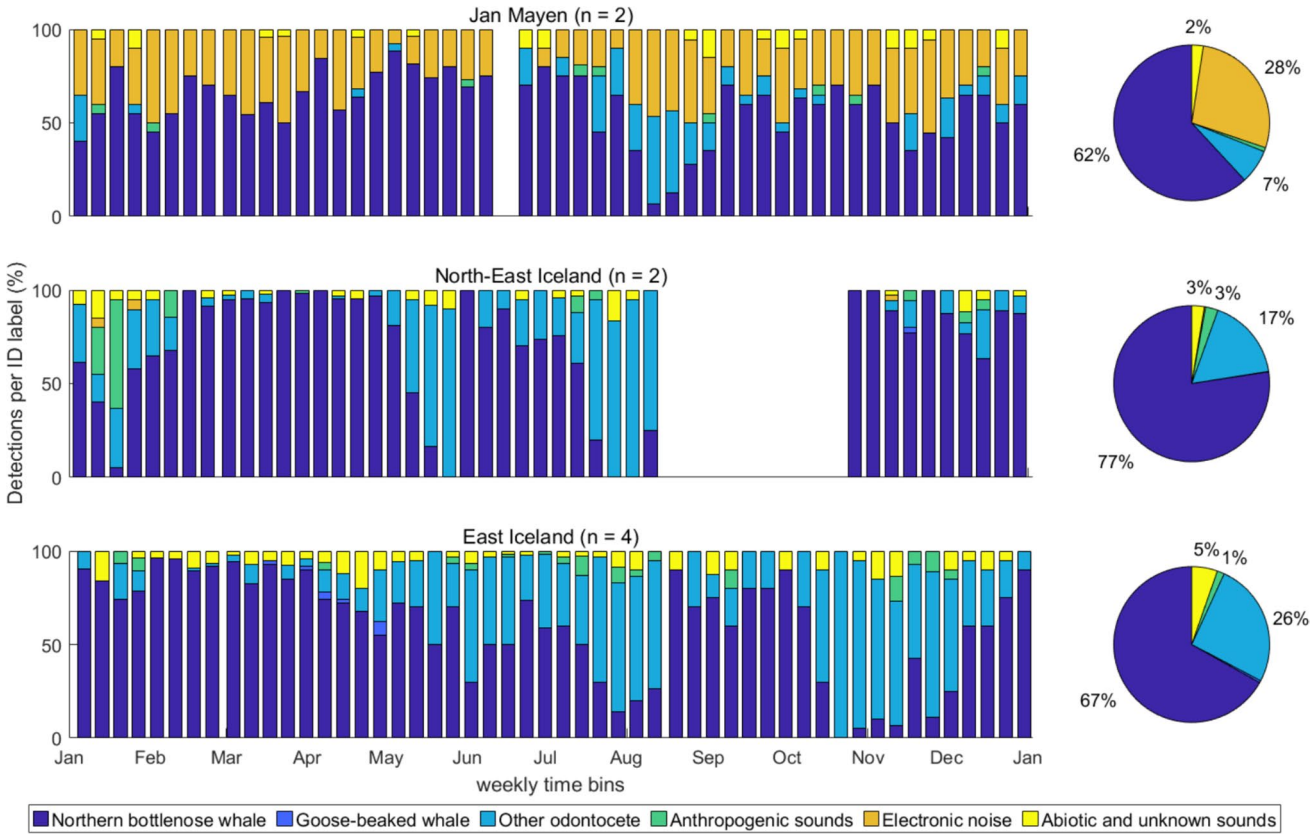

Fig. 2 Seasonal (bar graphs) and geographic variability (bar and pie graphs) in detector precision for northern bottlenose whales (i.e. the proportion of detections that were true positive detections), and proportions of false positive detections per different annotated category. Results are averaged across deployments at the respective monitoring location based on the manually evaluated subset of ~ 10% of detection positive snapshots per deployment

Table 2 Parameter thresholds used by the detector for automated detection and classification of northern bottlenose whale clicks. Thresholds were based on previous knowledge (Wahlberg et al. 2011; Clarke et al. 2019) and recommended SPICE detector settings for beaked whales

Parameter	Minimum	Maximum
Peak-to-peak received level threshold (dB re 1 µPa)	120	-
Bandpass filter edges (kHz)	15	45
Click duration (µs)	100	1000
Peak frequency limits (kHz)	20	45
Click energy envelope ratio	−0.8	0.8
Clip threshold (0–1)	-	0.98
Time between detections (sec)	0.07	-

Detections were annotated as (1) northern bottlenose whale, (2) goose-beaked whale, (3) other odontocete, (4) anthropogenic sound, (5) electronic noise, or (6) abiotic and unknown sounds. Goose-beaked whales were in a separate category due to the similarity of their clicks with those of northern bottlenose whales (Stanistreet et al. 2017). Other odontocete species that frequent the monitored waters off Iceland and Jan Mayen and can produce clicks within the recording bandwidth are primarily the sperm whale (*Physeter macrocephalus*), killer whale, long-finned pilot whale (*Globicephala melas*) and white-beaked dolphin (*Lagenorhynchus albirostris*) (Pike et al. 2019, 2020b; Leonard and Øien 2020). Both killer whales and long-finned pilot whales can be acoustically distinguished from bottlenose whales as their clicks are unmodulated in frequency and shorter in duration (Eskesen et al. 2011) and often accompanied by burst-pulse calls and whistles (Bellon et al. 2024), whereas sperm whales produce clicks at lower frequencies (Goold and Jones 1995). Detector performance was evaluated on the level of the detection snapshots as opposed to individual clicks. If detections were caused by multiple sources, the majority category was assigned unless the snapshot included northern bottlenose whale clicks, in which case it was considered a true positive snapshot.

Detector performance is commonly described considering two statistics, *precision* and *recall* (Knight et al. 2017):

$$Precision = \frac{true\ positives}{true\ positives + false\ positives} \quad (1)$$

$$Recall = \frac{true\ positives}{true\ positives + false\ negatives} \quad (2)$$

with false positives referring to detections caused by anything other than northern bottlenose whales, and false negatives referring to missed detections. Recall was evaluated for a 1% subset from three deployments, using the longest deployment per monitoring location (JM7, LNE2, KRC3; see Table 1) to cover all seasons. Within the initial 100 detection negative files, a random starting point was chosen and subsequently every 100th file manually inspected for missed detections using frequency and time-domain plots similar to those in detEdit. When the LTSA of the detection negative file showed click-like sound energy at the frequencies of interest (20–45 kHz; Table 4.2), the recording was inspected further in Raven Pro 1.6, (Lisa Yang K. Center for Conservation Bioacoustics at the Cornell Lab of Ornithology 2021) to determine the origin of the sound.

Detector precision was evaluated for each deployment and calculated per week, using a subset of detection positive snapshots (~10% per deployment). This subset was chosen to cover the deployments' distribution of detections across time of year and time of day (for details see supplementary information S2 and Figure S1).

The weekly proportions of detection positive snapshots were calculated from the raw detector output, correcting for the monitoring effort, i.e. recording proportion, based on the respective duty-cycle. Each weekly presence proportion was then multiplied with its detector precision estimate to obtain the weekly proportion of northern bottlenose whale acoustic presence. We did not correct for recall in the calculation of northern bottlenose whale acoustic presence since the detector showed a near perfect recall (>99%) at all three monitoring sites. The 95% confidence intervals were calculated per week by correcting the standard error with the finite population correction factor (Cochran 1977), accounting for the size of the manually evaluated subsample for that week.

Environmental covariates

The relationship between northern bottlenose whale acoustic detections and environmental variables was investigated using generalised additive mixed models (GAMMs). The variables considered were: chlorophyll (*chl a*) sea surface concentration as phytoplankton biomass indicator; mean sea surface height (*SSH*) and deviations from it (*sdSSH*), indicating eddy formations potentially associated with cephalopod distribution (Wiborg et al. 1982; Semmens et al. 2007); mean sea surface temperature (*SST*), previously associated with bottlenose whale distribution (Woo et al. 2023; Feyrer et al. 2024; Ramirez-Martinez et al. 2024) and deviations from it (*sdSST*) as an indicator of frontal activities; and *sea ice* concentration since the geographical range of northern bottlenose whales extends to the pack ice edge (Gray 1882; Whitehead et al. 2021).

Choosing the appropriate temporal and spatial scales can impact predictions of species occurrence by an environmental covariate model. We therefore followed a multi-scale approach and statistically selected variables to create the best fitting model (Jaquet 1996; Goh et al. 2024). Environmental covariates were considered at weekly and monthly

time resolutions and at multiple spatial resolutions ranging from 0.1° × 0.1° to 0.5° × 0.5° latitude × longitude (subject to availability; Table S1). The highest considered spatial resolution for acoustic studies should be equivalent to the species' acoustic detection range to ensure inclusion of environmental conditions at all possible whale locations. Thus, the smallest grid cell considered was 0.1° × 0.1° around the mooring location, equivalent to approximately 4 km longitude × 10 km latitude at the monitoring sites, latitudinally matching the 5-km maximum acoustic detection range estimated for northern bottlenose whales (Moors 2012).

Chl a data were obtained from the Copernicus Marine Service at a daily temporal resolution and multiple spatial resolutions (Table S1). The data were downloaded using the Copernicus Marine Toolbox in Python (Version 3.9) for a grid cell centred around each deployment's mooring location. Chlorophyll (*chl a*) surface concentration has been hypothesized to translate into prey biomass after a time lag, and cephalopod abundance is estimated to peak 3–4 months after surface *chl a* peaks (Jaquet 1996; Pirotta et al. 2011). Thus, we averaged daily *chl a* concentration over 7 and 30 days centred around a time lag of 90 days prior to the start of a weekly detection bin. However, our approach does not account for ocean currents, thus surface *chl a* at the mooring locations could have resulted in time lagged increases in biomass at other locations rather than locally. *SSH*, *SST* and *sea ice* data were downloaded from the NOAA ERDDAP data servers using the *rerddap* (Chamberlain 2024) and *rerddapXtracto* (Mendelssohn 2024) packages in R (Version 4.3.2; R Core Team 2023). These data were obtained at daily temporal resolution and different spatial scales (Table S1). Mean values were calculated as 7-day averages corresponding to the weekly detection bins, and monthly averages comprised the weekly detection bins plus 23 days before the bin start date. Similarly, *sdSSH* and *sdSST* were calculated as the standard deviations of the respective variable over these time windows. Due to the remoteness of the study area and to ensure consistency in data source across deployment sites, the environmental variable datasets considered here were either assimilations and interpolations of sparsely sampled data or stemmed from oceanographic models.

Modelling of environmental distribution drivers

The relationship between environmental covariates and marine mammal occurrence has often been shown to be non-linear (e.g. Barile et al. 2021; Pirotta et al. 2011) thus to investigate said relationships, we used generalized additive mixed models (GAMM). Models were fitted in R (version 4.3.2) using the *mgcv* package (Wood 2004) with an autoregressive order 1 correlation structure per deployment to control for temporal autocorrelation (supplementary information S3). Since the response variable was a proportion bound between 0 and 1 calculated from binomial data, we used a quasibinomial error family and logit link function. Additionally, weights corresponding to the amount of data points inside each bin were included in the model to account for differences in the number of available recordings across different duty-cycle settings. The base model was fitted with week of year as a smooth cyclic cubic regression spline per deployment location to account for simple temporal patterns in the acoustic detections of northern bottlenose whales at each location.

Selection of the best-fitting temporal and spatial scales was done manually by maximising adjusted R^2 values as indicator of model fit. Therefore, each covariate at each temporal and spatial scale was added individually to the base model to avoid correlation due to adding the same variable but at different scales. Covariates were fitted as thin plate regression splines using restricted maximum likelihood (REML) estimation to allow smooths to shrink to linear terms if suitable. The selected covariates were then assessed for collinearity and for any pair with a Pearson correlation coefficient greater than 0.7, only the variable with the better individual model fit was retained. All remaining variables were then added to the base model as thin plate regression splines with a shrinkage base, allowing smooth penalization towards zero (bs = 'ts'), and using REML. Smooths that were penalized to zero and those with p-values above the significance level ($\alpha = 0.05$) were removed to reduce model complexity.

Results

Detector performance

The detector showed a near perfect recall based on the 1% subset evaluated for three deployments, with a recall of 100% off Jan Mayen (JM7), 99.2% off north-east Iceland (LNE2), and 100% off east Iceland (KRC3). Thus, recall was considered neglectable and not evaluated further in the remaining deployments.

Detector precision varied with deployment ID, location and week of year (Fig. 2, S4). The first deployment off Jan Mayen (JM3), between June 2015 and 2016, had the lowest overall precision (41%) because of electronic noise (Figure S4). Its temporal detection pattern corrected for detector precision nevertheless showed great similarity with the deployment off Jan Mayen in the subsequent year (JM7, June 2016–2017; Fig. 3A) which had the highest overall detector precision (83%) of all deployments.

Detector precision for the deployments off north-east (November 2020 – August 2022) and east Iceland (February 2020 – August 2023) ranged between 61–78% (Figure S4) and varied greatly with time of year, showing highest precision in the winter months (Fig. 2). The most common cause of false positive detections in these Icelandic waters were other odontocetes, with higher false positive rates in the east Iceland location, followed by abiotic and unknown sounds, and anthropogenic noise.

Spatiotemporal acoustic occurrence patterns

Acoustic detection patterns for northern bottlenose whales were relatively stable across years but showed strong seasonal variations at all three recording sites (Fig. 3). Around Jan Mayen, bottlenose whales were largely acoustically absent in mid-August, followed by a gradual increase in detections from September onward which reached its weekly maxima (58%) between the following April to early June. After that, detections in Jan Mayen dropped rapidly in late June, followed by short detection peaks in Icelandic waters, and low numbers of acoustic detections for all three locations throughout late July, August and September (Fig. 3). Northern bottlenose whales were acoustically present off north-east and east Iceland throughout the year, though weeks of acoustic absence occurred at both recording sites at different times of year (Fig. 3). Detections around Iceland were highest in March (57% off north-east Iceland) and around the short detection peaks in late June and early July (approx. 50% at both sites).

Environmental distribution drivers

The base model, fitted with week of year as cyclic cubic regression spline per location and an autoregressive order 1 correlation structure per deployment, had an adjusted R^2 value of 0.52 (n = 315). Following stepwise selection and backwards reduction of environmental covariates, *sdSSH* and *SST* were retained in the final model (Fig. 4; adjusted $R^2 = 0.65$, n = 315), both selected at the largest considered temporal (monthly) and spatial (0.5° × 0.5° latitude and longitude) scale (Fig. 5). *Chl a* and mean *SST* showed moderate correlation (Pearson's r = 0.70) and comparison of base model fits when either one of the two covariates was added revealed a better fit with *SST* (adjusted $R^2 = 0.61$) than *chl a* (adjusted $R^2 = 0.56$); thus, *chl a* data was removed from further analysis. *Sea ice* and *sdSST* did not improve model fit, and mean *SSH* had no significant effect (p = 0.15) on the proportion of northern bottlenose whale presence, thus these covariates were removed.

In the final model, the effect of time (*week of year*) on northern bottlenose whale acoustic presence depended on the location (Fig. 4A). A positive effect with higher than average northern bottlenose whale presence was predicted for Jan Mayen (edf = 5.40, F = 5.89, p < 0.001) from February until early June, for north-east Iceland (edf = 5.46, F = 3.80, p < 0.001) during mid-February into April, and for east Iceland (edf = 5.26, F = 6.78, p < 0.001) from late December to the beginning of April. Negative effects of week of year, i.e. northern bottlenose whale presence expected to be below the yearly average, were most pronounced from late June to early October for Jan Mayen and north-east Iceland when data were available, and from September to November off east Iceland. The *sdSSH* smooth was shrunk to a linear term (edf = 1, F = 14.48, p < 0.001), thus *sdSSH* had a linearly increasing positive effect on the probability of bottlenose whale presence for *sdSSH* values greater than 0.2 m, and a negative effect below that (Fig. 4B). The *SST* thin plate regression spline (edf = 6.90, F = 7.39, p < 0.001) predicted minimal effects of surface water temperatures below 5.0 °C on bottlenose whale presence, and a positive effect at temperatures between 5.0–7.5°C (Fig. 4C). Overall, the model showed a moderately good fit to the data (adjusted $R^2 = 0.65$, n = 315) but predictions of northern bottlenose whale acoustic presence were overestimated at low and underestimated at high observed presence (Fig. 4D).

Discussion

Acoustic occurrence of northern bottlenose whales in the Nordic Seas differed seasonally between monitored locations but was notably stable across years. There was a substantial northwards shift in bottlenose whale occurrence from February to May, with the highest proportions of detections in Jan Mayen throughout May and early June, coinciding with fewer detections off north-east and east Iceland (Fig. 3). Detections off Jan Mayen suddenly dropped in late June to early July, coinciding with short detection peaks in Icelandic waters which were followed by fewer detections at all three locations throughout late July and August. This pattern matches the historical observation by whalers of the species moving south in summer; however, the increase in detections across all locations from September onwards contradicts the hypothesis that these animals overwinter at more southern latitudes and would only return north in spring (Gray 1882; Murray and Hjort 1912; Benjaminsen and Christensen 1979). Instead, our observations included only a short period of low acoustic occurrence from late July into October, providing evidence of a near year-round presence of northern bottlenose whales in the Nordic Seas.

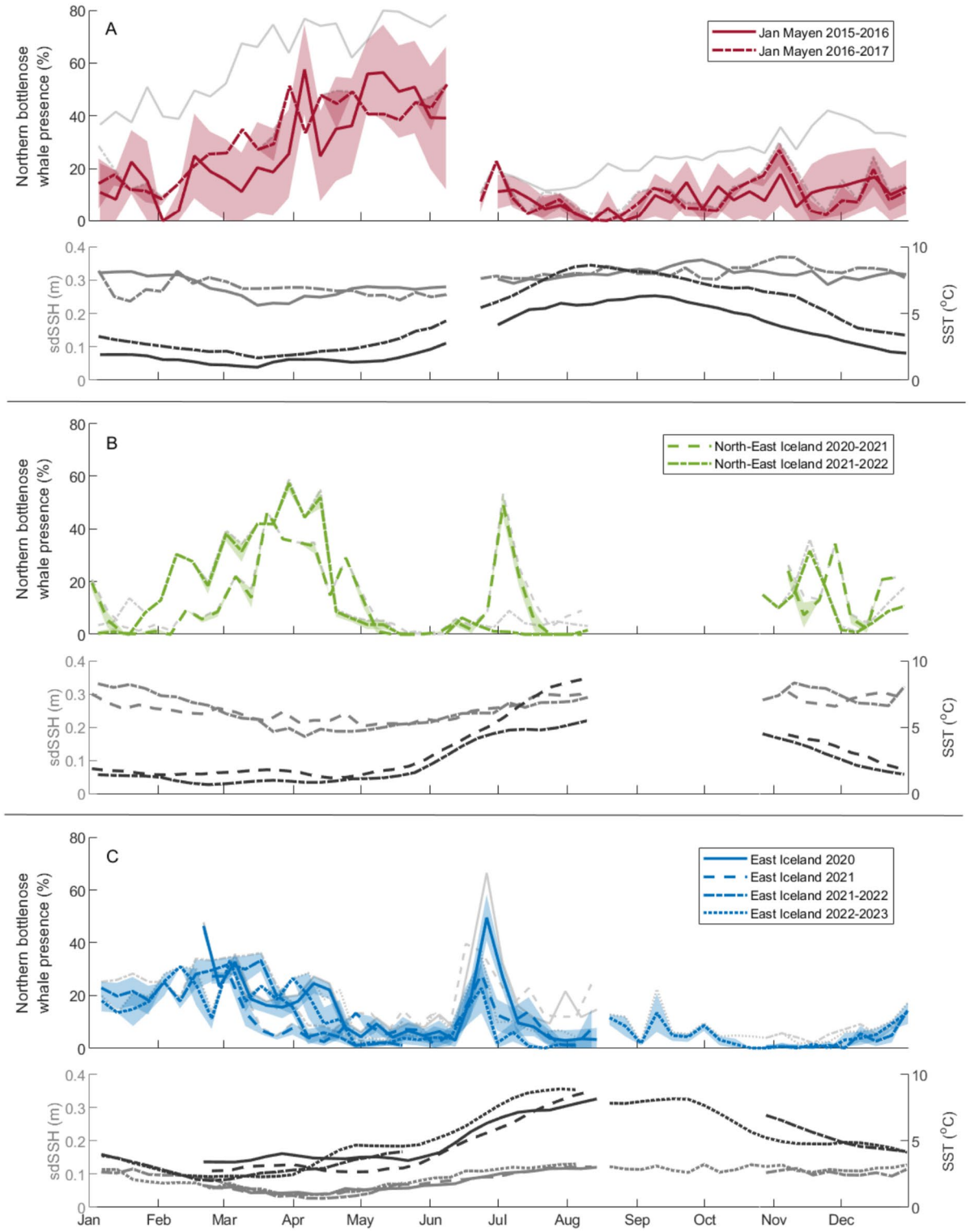

Fig. 3 Temporal acoustic detection patterns of northern bottlenose whales (colour) with corresponding sea surface height deviations (*sdSSH,* grey, left y-axis) and mean sea surface temperature (*SST*, black, right y-axis). Northern bottlenose whale presence is presented as the weekly proportion of recording files containing true positive detections of bottlenose whale clicks (coloured lines, 95% confidence interval shaded) and grey lines correspond to raw detector output before correcting for precision. Data were separated by deployment (line style) and monitoring site (**A**: Jan Mayen, **B**: North-east Iceland, **C**: East Iceland)

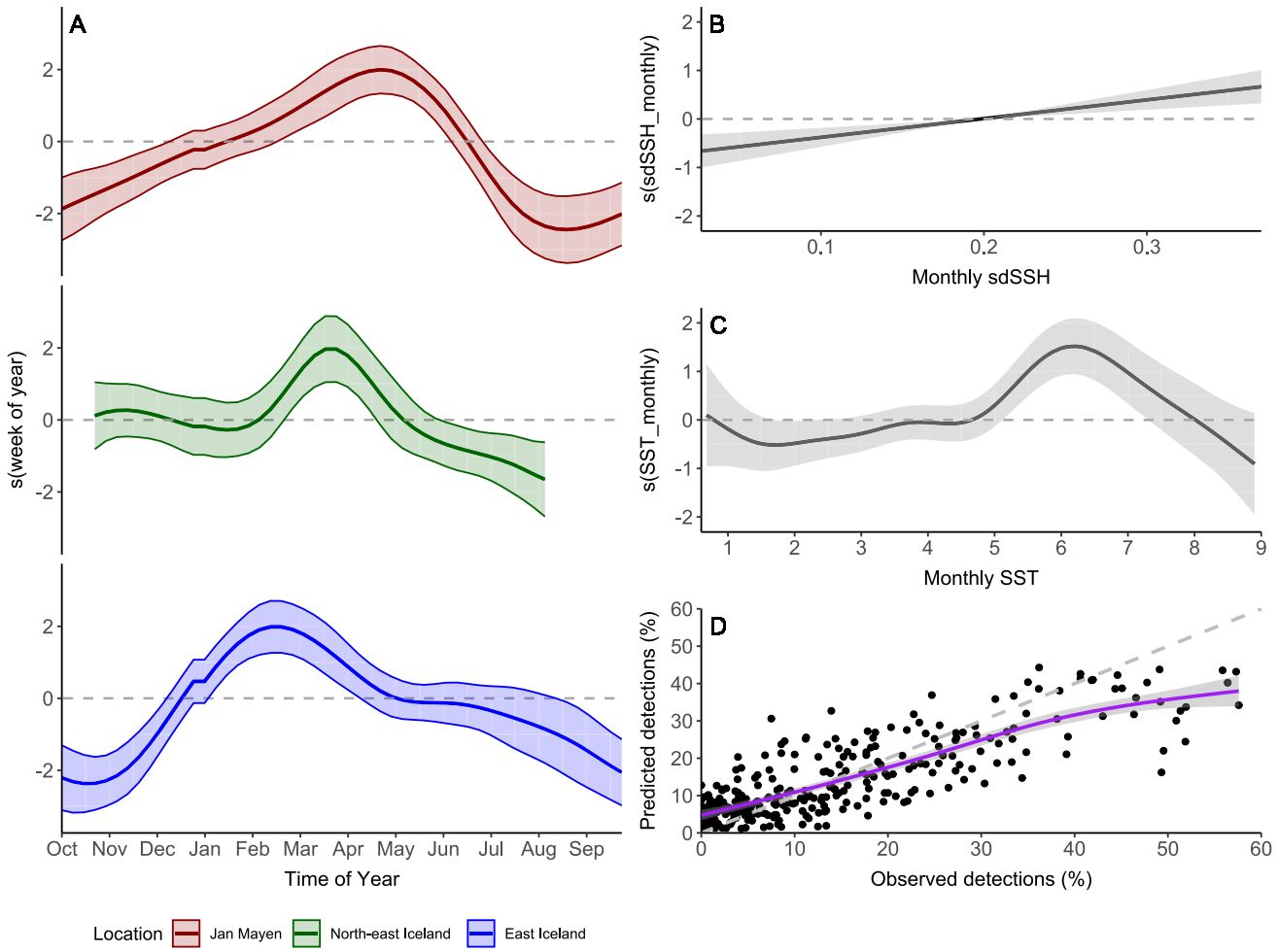

Fig. 4 (**A, B, C**) Estimated smooth terms ± 95% confidence intervals from the selected generalized additive mixed model, showing the relationship between the weekly proportion of northern bottlenose whale detections (response variable) and (**A**) week of year per location, (**B**) sea surface height deviations (*sdSSH*), and (**C**) mean sea surface temperature (*SST*) on a logit scale. (**D**) Observed proportions of northern bottlenose whale detection positive snapshots plotted against predicted proportions, illustrating model fit. The grey dashed line indicates a perfect linear agreement between observed and predicted values, whereas the purple line shows a GAM smooth fit to the observed and predicted proportions

Detector performance

The precision of the northern bottlenose whale detector varied temporally and across deployment locations. Thus, to allow for valid comparisons of northern bottlenose whale occurrence across space and time, the raw detector output was corrected for detector precision at weekly resolution. False positive detections were primarily annotated as stemming from other odontocetes, which showed spatiotemporal differences in their acoustic occurrence (Fig. 2). Off Iceland, these detections of other odontocetes appeared to be primarily caused by killer whales or long-finned pilot whales, and occasionally sperm whales, and were in line with reports on the seasonal presence of these species to the north and east of Iceland (Pike et al. 2019, 2020a; Leonard and Øien 2020; Bellon et al. 2024). Around Jan Mayen, occurrence of killer and sperm whales has also been visually confirmed (Leonard and Øien 2020; Ramirez-Martinez et al. 2024). Both species caused false positive detections annotated as 'other odontocetes' in this location, which were fewer than in Icelandic waters. Compared to the Icelandic monitoring sites, the more remote location off Jan Mayen resulted in fewer detections of anthropogenic activities (i.e. ship noise) and an overall higher detector precision for the deployment not affected by electronic noise (Fig. 2; Figure S4).

Echolocation clicks with a beaked whale-specific frequency upsweep, but with a higher peak frequency and increased lower frequency bandwidth cutoff than northern bottlenose whale clicks (Figure S5), were identified and matched, with low confidence, to goose-beaked whales (Zimmer et al. 2005; Baumann-Pickering et al. 2013). These detections occurred only off east Iceland between April to

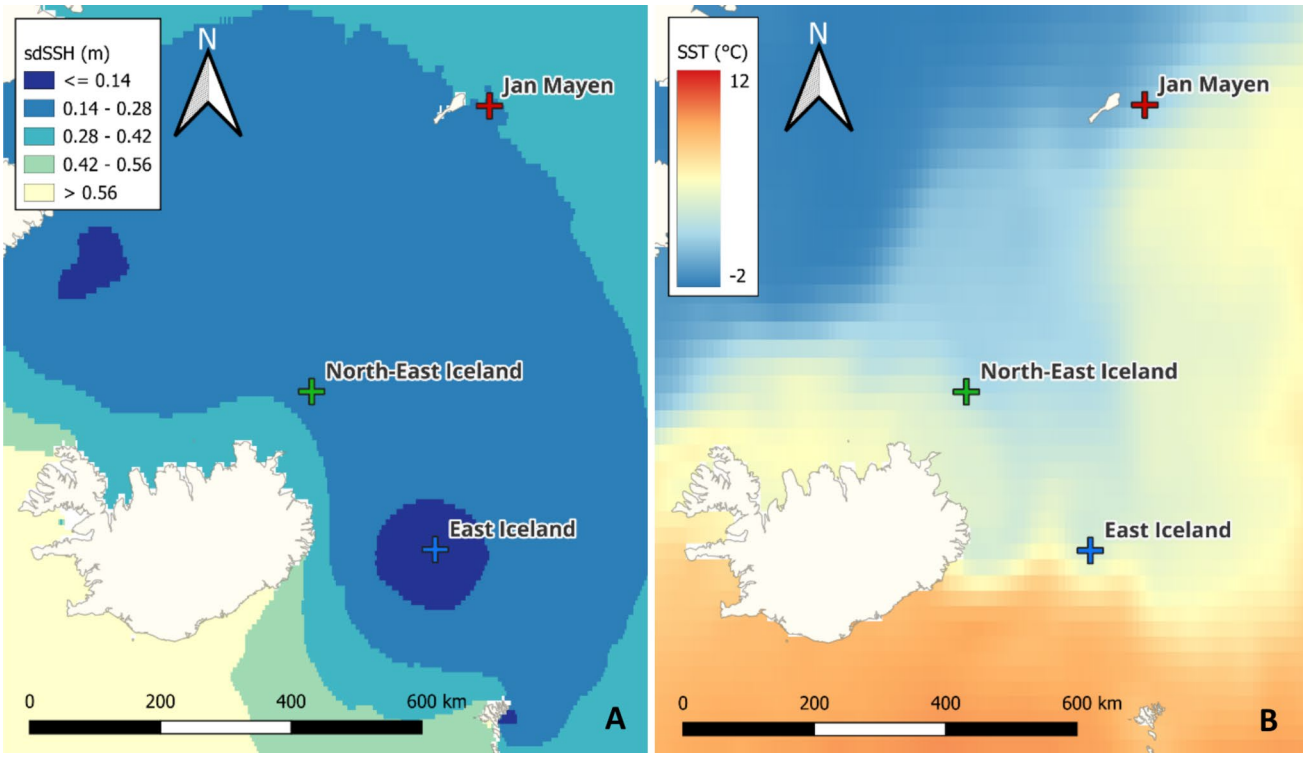

Fig. 5 Example of monthly (**A**) sea surface height deviations (*sdSSH*) and (**B**) mean sea surface temperature (*SST*) during May 2020. The month of May was chosen as an example as northern bottlenose whale detections greatly varied across monitoring locations during this time of year, reflecting a northwards shift in acoustic occurrence (Fig. 3)

May of 2022 and 2023 (Fig. 2, S4). Strandings of goose-beaked whales have, amongst other locations, been reported along the Icelandic east coast (Halldórsson et al. 2019), which is considered the most northern extent of their range in the eastern North Atlantic (Baird et al. 2018). However, the species' presence in the Nordic Seas has yet to be confirmed through visual sightings. Based on the present data, we cannot confirm the acoustic presence of goose-beaked whales with certainty, since the acoustic sample rate of the Icelandic deployments (96 kHz) was too low to capture the full bandwidth of the species' echolocation clicks (Zimmer et al. 2005).

Seasonal distribution drivers

The whales' weekly presence data were associated with time of year (Fig. 4A) but also with deviations in sea surface height (*sdSSH* Fig. 4B), a proxy for frontal activities and eddy formation. This supports our hypothesis (HP1) that environmental variables associated with *Gonatus* occurrence (Wiborg et al. 1982; Semmens et al. 2007) also explain northern bottlenose whale occurrence due to increased prey availability. Low *sdSSH* values east of Iceland throughout the year (Fig. 3C, Fig. 5A) and temporarily reduced *sdSSH* values north-east of Iceland between March to June (Fig. 3B) suggested reduced eddy activity at these locations and times, indicating low upwelling and associated productivity. This might indicate lower densities of prey, possibly causing the whales to leave these areas and forage elsewhere. The consistently higher values in *sdSSH* around Jan Mayen (Fig. 3A, Fig. 5A) – known to be a key habitat for northern bottlenose whales (Woo et al. 2023) – indicate dynamic movements of water masses and high productivity in the area. Dynamic surface conditions have also been identified as a common characteristic across *Gonatus fabricii* breeding grounds (Golikov et al. 2019), which constitute suitable feeding grounds for bottlenose whales due to the aggregation of gelatinous spawning females (Bjørke and Gjøsæter 1998; Arkhipkin and Bjørke 1999). *Gonatus fabricii* spawns over several months throughout winter to spring, with the spawning peak in the Norwegian Sea between April to June (Wiborg 1979). This could explain the gradual increase of northern bottlenose whale detections off Jan Mayen during this time (Fig. 3) and supports a prey-driven distribution of the whales with an underlying seasonal pattern.

Sea surface temperatures (*SST*) between 5.0–7.5°C had a positive effect on northern bottlenose whale detections (Fig. 4C), however, this appeared to be driven solely by the short detection peaks recorded north-east and east of Iceland between late June to early July (Fig. 3). Previous studies that had associated bottlenose whale occurrence

with *SST* also did not yield clear results as the effect varied depending on the considered monitoring period (Ramirez-Martinez et al. 2024), was of small predictive power (Feyrer et al. 2024) or unstable between models (Woo et al. 2023). Surface water temperatures change with season because of solar heating, yet northern bottlenose whales spend most time at meso- and bathypelagic depths (Neubarth et al. 2025), and deeper waters (> 800–1000 m) remain at more stable temperatures between −1 to 0°C throughout the year (Drinkwater et al. 2020; Semper et al. 2020). Thus, surface water temperatures are unlikely to directly impact northern bottlenose whale occurrence or availability of deep-sea squid but could point towards a seasonal distribution trend. Overall, our GAMM performed better in predicting low to moderate proportions of northern bottlenose whale detections, likely driven by prey distribution, compared to higher levels in detections (Fig. 4D), some of which were caused by movements through an area (Fig. 3) possibly due to long-distance migrations (Wensveen et al. 2025).

The environmental covariates considered here were largely derived from oceanographic models to ensure consistency across monitored locations and seasons but might therefore not fully capture the true environmental states. In situ measurements are available for part of the Nordic Seas across seasons and research efforts have been increasing in recent years (Renfrew et al. 2019; Semper et al. 2025; Euro-Argo https://www.euro-argo.eu/; Icelandic Marine and Freshwater Research Institute data available through www.seadatanet.org). However, temporal and spatial coverage is not uniformly available for the monitored locations and timeframes. Moreover, the scarcity of light during the polar and sub-polar winter further hinders the acquisition of remotely sensed data through satellite imagery. Thus, modelling data or assimilating modelled and in situ measured data are the only means of getting year-round environmental data coverage at the required temporal and spatial scales. The interpretation of these environmental drivers should therefore be viewed with caution and might yield different results depending on the considered environmental datasets and underlying modelling methods.

Despite our results supporting a prey driven distribution of northern bottlenose whales within the Nordic Seas, the low numbers of acoustic detections during part of the summer months, which are considered a productive period of the Arctic (Pabi et al. 2008), raises the question of where the whales might go and what drives their movement away from feeding grounds. Northern bottlenose whales around Jan Mayen in June were found to spend more time performing foraging dives (Siegal 2020) and had larger lipid stores (Miller et al. 2016a, b) compared to the resident animals on the Scotian Shelf off Nova Scotia (Canada), possibly in preparation for migrations. Seasonal migrations between higher latitude productive feeding grounds and less productive lower latitude breeding grounds are common among baleen whales (Swartz 1986; Evans 1987), but the increase of bottlenose whale detections throughout autumn and winter (Fig. 3) contradicts such a seasonal feeding-breeding migration.

Recently, short-term moulting migrations have been proposed for northern bottlenose whales. A whale tagged in the Canadian Arctic travelled over 2500 km southwards in July but was back north already in early September (Lefort et al. 2025). Similarly, three bottlenose whales tagged off Iceland moved to the Azores and back within few weeks between June to August 2023 (Wensveen et al. 2025). This behaviour appears to be similar to Antarctic killer whales' short and directional roundtrips to subtropical waters (Durban and Pitman 2012; Levin et al. 2016; Pitman et al. 2020), and these rapid migrations into warmer waters are thought to support skin maintenance by encouraging increased blood flow to the skin (Pitman et al. 2020). The pattern of northern bottlenose whale acoustic presence observed in this study, with lower detections off Jan Mayen from late June, followed by short detection peaks at the lower latitude Icelandic deployment locations and low detections throughout July, August and September, supports such short-term moulting migrations over seasonal north–south migrations for overwintering in warmer waters. This migratory behaviour differs from the movement behaviour of several other beaked whale species, which typically includes high residency or site fidelity with consistent usage of the same habitats year-round (McSweeney et al. 2007; Stanistreet et al. 2017; Dinis et al. 2017; Foley et al. 2021).

It is however likely that at least part of the northern bottlenose whale population remains in the more northern latitudes throughout the summer months based on opportunistic visual sightings from Icelandic inshore waters (Grove et al. 2020; Haas et al. 2024) and dedicated scientific surveys (Pike et al. 2019; Leonard and Øien 2020; Ramirez-Martinez et al. 2024). These surveys are typically conducted between June to August and report the highest numbers of northern bottlenose whale sightings to the north and west of the Faroe Islands and southeast of Greenland (Pike et al. 2019) on a proposed *Gonatus* breeding ground (Golikov et al. 2019). Sightings further north than Jan Mayen (Leonard and Øien 2020) or further south than the Faroe Islands (Lacey and Hammond 2023; Ramirez-Martinez et al. 2024) are rare during these sighting surveys in summer. The data presented here, however, does not allow for any conclusions on where the whales went when their detections decreased at the monitored locations. An expansion of the PAM recording locations to other bottlenose whale hotspots based on visual sightings (Pike et al. 2019; Leonard and Øien 2020) and *Gonatus fabricii* spawning grounds (Wiborg et al. 1984;

Arkhipkin and Bjørke 1999; Golikov et al. 2019) within the Nordic Seas, in conjunction with a better understanding of other prey sources and more detailed movement data from Argos-linked satellite tags, would improve our understanding of this northern bottlenose whale population's distribution and underlying drivers.

Conservation implications

Sub-arctic and arctic waters are facing an increase in ocean industrialisation because of increasing accessibility due to climate change and sea ice decline, including deep sea mineral mining (Levin et al. 2016; Gilbert 2024) and oil and gas exploration as most remaining reserves are presumed to be found in the offshore Arctic (Gautier et al. 2009; Hasle et al. 2009). The exploration and extraction of deep-sea minerals and hydrocarbons generates noise pollution that can directly impact marine mammals (Bröker 2019). They also pose the risk of long-term ecosystem impacts across trophic levels due to seafloor disturbance, wastewater discard (Levin et al. 2016) and potential oil spills at depth or during transport (Hasle et al. 2009; Barron et al. 2020).

The Dreki area at the southern end of the Jan Mayen Ridge, located between the north-east Iceland and Jan Mayen monitoring locations, has repeatedly and recently (e.g. September 18, 2025, see https://www.ruv.is/english/2025-09-18-icelands-chamber-of-commerce-urges-oil-exploration-453780, accessed October 27, 2025) been proposed as area of interest for oil and gas exploration. Such operations could affect northern bottlenose whales through noise pollution and potential long-term habitat degradation. Additionally, plans exist for the construction of an industrial harbour in Finnafjörður, north-east Iceland, to process offshore sourced resources and support future trans-arctic shipping (Bennett et al. 2020). With the retreat of sea-ice, cargo ships travelling the projected Central Arctic Shipping Route are likely to sail past Finnafjörður and along the Jan Mayen ridge, passing by Jan Mayen and Svalbard before transiting the central Polar Basin (Bennett et al. 2020). These locations between Iceland and Svalbard are considered key northern bottlenose whale habitats (Leonard and Øien 2020; Woo et al. 2023; Ramirez-Martinez et al. 2024; Neubarth et al. 2025), as confirmed by the high acoustic detection rates in this study (Fig. 3). The area between Jan Mayen and Svalbard has also been found to show the highest concentrations of juvenile *Gonatus fabricii* within the Norwegian Sea (Bjørke and Gjøsæter 2004). Extensive bottom-fishing and oil exploration have also been raised as conservation concerns for cephalopods (Hastie et al. 2009) and effects on *Gonatus fabricii* are by extension expected to affect northern bottlenose whales.

Military sonar for anti-submarine warfare constitutes a further possible threat as northern bottlenose whales were found sensitive to naval sonar, eliciting behavioural changes and displacement (Miller et al. 2015a, b; Wensveen et al. 2019). NATO anti-submarine warfare exercises occur annually within the Nordic Seas and British waters, and Russian naval activity in Norwegian waters has been reported in conjunction with such exercises in previous years (Åtland et al. 2022). The acoustic detection patterns presented here alongside visual sightings (e.g. Leonard & Øien 2020; Pike et al. 2019) and satellite tag data (Miller et al. 2015a, b, 2016a, b; Wensveen et al 2025) suggest that northern bottlenose whale distribution spatially, and at least in some years temporally (e.g. Dynamic Mongoose 2017), overlaps with these naval activities. As a result, northern bottlenose whales might cease foraging and be displaced from key habitats (Miller et al. 2015a, b; Wensveen et al. 2019) leading to a potential reduction of individual fitness and posing reason for concern.

The spatiotemporal occurrence of northern bottlenose whales in the Nordic Seas (Fig. 3, Fig. 4A), and the stability of these patterns across years, suggest a seasonal importance of Icelandic waters and the waters off Jan Mayen as northern bottlenose whale feeding grounds. The presented occurrence patterns should thus be considered in (1) the establishment of fishing regulations in bottlenose whale habitats to protect both the whales and their main cephalopod prey, (2) the planning of oil and gas exploration, deep-sea mining and future shipping routes, and (3) the timing of naval exercises in waters frequented by northern bottlenose whales at specific times of year. Activities creating noise pollution (e.g. resource exploration and extraction, naval exercises using military sonar) could be scheduled during times of low northern bottlenose whale acoustic occurrence (Fig. 3) to reduce the impact on this noise sensitive beaked whale species.

Conclusions

Using passive acoustic monitoring, this study showed a near year-round presence of northern bottlenose whales in Icelandic and Norwegian waters. Detections were lowest from July into September before increasing again throughout autumn and winter. This contradicts the previous hypothesis of seasonal north–south migrations for overwintering in lower latitudes (Benjaminsen and Christensen 1979). Distribution within the Nordic Seas between Iceland and Jan Mayen followed a gradual northward shift in spring which coincided with the proposed spawning peak of *Gonatus fabricii* in the Norwegian Sea (Wiborg et al. 1982) and overlapped with decreases in *sdSSH* at the Icelandic monitoring sites, indicative of reduced productivity, supporting a prey driven distribution. The time-delayed detection peaks from higher to lower latitudes during late June and early July,

followed by the short-term decrease in acoustic detections into September, supported a southward shift in distribution during the late summer. However, whether this shift in distribution is primarily driven by movements towards more southern feeding grounds or short-term moulting migrations requires further research. The inter-annual stability of the observed occurrence patterns has strong implications for conservation efforts and should be considered in the planning of future anthropogenic activities in these waters (e.g., by timing them during low northern bottlenose whale occurrence) to avoid habitat degradation and reduce stressors on this beaked whale species.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00227-026-04798-6.

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Author contributions C. E. Haas, P. J. O. Miller, S. K. Hooker and P. J. Wensveen conceived the ideas; C. E. Haas, P. J. O. Miller, S. K. Hooker and P. J. Wensveen designed the methodology; C. E. Haas, P. J. O. Miller, A. Macrander, F. P. A. Lam and P. J. Wensveen collected the data; C. E. Haas analysed the data; C. E. Haas wrote the initial manuscript and all authors contributed, read and approved the final version; P. J. O. Miller, S. K. Hooker, J. Svavarsson, F. P. A. Lam and P. J. Wensveen acquired funding.

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Data availability The dataset and R code generated for statistical analyses has been published in an online repository and can be accessed at https://doi.org/10.5281/zenodo.18303608

Declarations

Conflict of Interest The authors have no conflicts of interest to disclose.

Ethical note Data collection off Iceland was covered under an Institutional permit of the Marine and Freshwater Research Institute. Off Jan Mayen, data collection was approved by the University of St Andrews' Biology School Ethics committee. All data collection was non-invasive.

References

Arkhipkin AI, Bjørke H (1999) Ontogenetic changes in morphometric and reproductive indices of the squid *Gonatus fabricii* (Oegopsida, Gonatidae) in the Norwegian Sea. Polar Biol. https://doi.org/10.1007/s003000050429

Åtland K, Nilsen T, Pedersen T (2022) Military muscle-flexing as interstate communication: Russian NOTAM warnings off the coast of Norway, 2015–2021. SJMS 5:63–78. https://doi.org/10.31374/sjms.133

Baird RW, Brownell Jr. RL, Taylor BL (2018) *Ziphius cavirostris*. IUCN Red List

Barile C, Berrow S, O'Brien J (2021) Oceanographic drivers of Cuvier's (*Ziphius cavirostris*) and Sowerby's (*Mesoplodon bidens*) beaked whales acoustic occurrence along the Irish Shelf edge. J Mar Sci Eng 9:1081. https://doi.org/10.3390/jmse9101081

Barron MG, Vivian DN, Heintz RA, Yim UH (2020) Long-term ecological impacts from oil spills: comparison of *Exxon Valdez*, *Hebei Spirit*, and Deepwater Horizon. Environ Sci Technol 54:6456–6467. https://doi.org/10.1021/acs.est.9b05020

Baumann-Pickering S, McDonald MA, Simonis AE, Solsona Berga A, Merkens KPB, Oleson EM, Roch MA, Wiggins SM, Rankin S, Yack TM, Hildebrand JA (2013) Species-specific beaked whale echolocation signals. J Acoust Soc Am 134:2293–2301. https://doi.org/10.1121/1.4817832

Bellon G, Selbmann A, Wensveen P, Rasmussen M, Laute A, Mouy X, Samarra FIP (2024) Killer whale (*Orcinus orca*) occurrence in Icelandic waters revealed by passive acoustic monitoring. Mar Mamm Sci. https://doi.org/10.1111/mms.13211

Benjaminsen T, Christensen I (1979) The Natural History of the Bottlenose Whale, Hyperoodon ampullatus (Forster). Behavior of Marine Animals. Springer, US, Boston, MA, pp 143–164

Bennett MM, Stephenson SR, Yang K, Bravo MT, De Jonghe B (2020) The opening of the Transpolar Sea Route: logistical, geopolitical, environmental, and socioeconomic impacts. Mar Policy. https://doi.org/10.1016/j.marpol.2020.104178

Bjørke H (2001) Predators of the squid *Gonatus fabricii* (Lichtenstein) in the Norwegian Sea. Fish Res 52:113–120

Bjørke H, Gjøsæter H (1998) Who eats the larger *Gonatus fabricii* (Lichtenstein) in the Norwegian Sea?

Bjørke H, Gjøsæter H (2004) Cephalopods in the Norwegian Sea. In: Skjodal HR (ed) The Norwegian Sea Ecosystem. Tapir Academic Press, pp 371–394

Bräger S, Bräger Z (2019) Movement Patterns of Odontocetes Through Space and Time. In: Würsig B (ed) Ethology and Behavioral Ecology of Odontocetes. Springer Nature Switzerland AG, pp 117–144

Bröker KC (2019) An overview of potential impacts of hydrocarbon exploration and production on marine mammals and associated monitoring and mitigation measures. Aquat Mamm 45:576–611. https://doi.org/10.1578/AM.45.6.2019.576

Chabanne D, Finn H, Salgado-Kent C, Bejder L (2012) Identification of a resident community of bottlenose dolphins (*Tursiops aduncus*) in the Swan Canning Riverpark, Western Australia, using behavioural information. Pac Conserv Biol 18:247–262. https://doi.org/10.1071/pc120247

Chamberlain S (2024) rerddap: General Purpose Client for "ERDDAP" Servers.

Clarke E, Feyrer LJ, Moors-Murphy H, Stanistreet J (2019) Click characteristics of northern bottlenose whales (*Hyperoodon ampullatus*) and Sowerby's beaked whales (*Mesoplodon bidens*) off eastern Canada. J Acoust Soc Am 146:307–315. https://doi.org/10.1121/1.5111336

Cochran WG (1977) Sampling Techniques, 3rd edn. John Wiley & Sons Inc

Dalebout ML, Hooker SK, Christensen I (2001) Genetic diversity and population structure among northern bottlenose whales, *Hyperoodon ampullatus*, in the western North Atlantic Ocean. Can J Zool 79:478–484. https://doi.org/10.1139/cjz-79-3-478

de Greef E, Einfeldt AL, Miller PJO, Ferguson SH, Garroway CJ, Lefort KJ, Paterson IG, Bentzen P, Feyrer LJ (2022) Genomics reveal population structure, evolutionary history, and signatures of selection in the northern bottlenose whale, *Hyperoodon ampullatus*. Mol Ecol 31:4919–4931. https://doi.org/10.1111/mec.16643

Delarue J, Moors-Murphy H, Kowarski K, Maxner E, Davis G, Stanistreet J, Martin S (2024) Acoustic occurrence of beaked whales off eastern Canada, 2015–2017. Endanger Species Res 53:439–466. https://doi.org/10.3354/esr01314

Dingle H, Drake VA (2007) What is migration? Bioscience 57:113–121. https://doi.org/10.1641/B570206

Dinis A, Marques R, Dias L, Sousa D, Gomes C, Abreu N, Alves F (2017) Site fidelity of Blainville's beaked whale (*Mesoplodon densirostris*) off Madeira Island (Northeast Atlantic). Aquat Mamm 43:387–390. https://doi.org/10.1578/AM.43.4.2017.387

Drinkwater KF, Sundby S, Wiebe PH (2020) Exploring the hydrography of the boreal/arctic domains of North Atlantic seas: results from the 2013 BASIN survey. Deep Sea Res Part II Top Stud Oceanogr. https://doi.org/10.1016/j.dsr2.2020.104880

Durban JW, Pitman RL (2012) Antarctic killer whales make rapid, round-trip movements to subtropical waters: evidence for physiological maintenance migrations? Biol Lett 8:274–277. https://doi.org/10.1098/rsbl.2011.0875

Erga SR, Ssebiyonga N, Hamre B, Frette Ø, Hovland E, Hancke K, Drinkwater K, Rey F (2014) Environmental control of phytoplankton distribution and photosynthetic performance at the Jan Mayen Front in the Norwegian Sea. J Mar Syst 130:193–205. https://doi.org/10.1016/j.jmarsys.2012.01.006

Eskesen IG, Wahlberg M, Simon M, Larsen ON (2011) Comparison of echolocation clicks from geographically sympatric killer whales and long-finned pilot whales (L). J Acoust Soc Am 130:9–12. https://doi.org/10.1121/1.3583499

Evans PGH (1987) The Natural History of Whales & Dolphins. Facts on File, New York

Falcone EA, Keene EL, Keen EM, Barlow J, Stewart J, Cheeseman T, Hayslip C, Palacios DM (2022) Movements and residency of fin whales (*Balaenoptera physalus*) in the California Current System. Mamm Biol 102:1445–1462. https://doi.org/10.1007/s42991-022-00298-4

Fernández R, Pierce GJ, MacLeod CD, Brownlow A, Reid RJ, Rogan E, Addink M, Deaville R, Jepson PD, Santos MB (2014) Strandings of northern bottlenose whales, *Hyperoodon ampullatus*, in the north-east Atlantic: seasonality and diet. J Mar Biol Assoc UK 94:1109–1116. https://doi.org/10.1017/S002531541300180X

Feyrer LJ, Bentzen P, Whitehead H, Paterson IG, Einfeldt A (2019) Evolutionary impacts differ between two exploited populations of northern bottlenose whale (*Hyperoodon ampullatus*). Ecol Evol 9:13567–13584. https://doi.org/10.1002/ece3.5813

Feyrer LJ, Stanistreet JE, Gomez C, Adams M, Lawson JW, Ferguson SH, Heaslip SG, Lefort KJ, Davidson E, Hussey NE, Whitehead H, Moors-Murphy H (2024) Identifying important habitat for northern bottlenose and Sowerby's beaked whales in the western North Atlantic. Aquat Conserv. https://doi.org/10.1002/aqc.4064

Foley HJ, Pacifici K, Baird RW, Webster DL, Swaim ZT, Read AJ (2021) Residency and movement patterns of Cuvier's beaked whales *Ziphius cavirostris* off Cape Hatteras, North Carolina, USA. Mar Ecol Prog Ser 660:203–216. https://doi.org/10.3354/meps13593

Frasier K (2020) SPICE Detector · MarineBioAcousticsRC/Triton Wiki · GitHub. https://github.com/MarineBioAcousticsRC/Triton/wiki/SPICE-Detector#SP2b. Accessed 13 Jun 2022

Gautier DL, Bird KJ, Charpentier RR, Grantz A, Houseknecht DW, Klett TR, Moore TE, Pitman JK, Schenk CJ, Schuenemeyer JH, Sørensen K, Tennyson ME, Valin ZC, Wandrey CJ (2009) Assessment of undiscovered oil and gas in the Arctic. Science 324:1175–1179. https://doi.org/10.1126/science.1169467

Gilbert N (2024) First approval for sea-bed mining worries scientists. Nature 435–436.

Goh T, Jessopp M, Rogan E, Pirotta E (2024) A matter of scale: identifying the best spatial and temporal scale of environmental variables to model the distribution of a small cetacean. Ecol Evol. https://doi.org/10.1002/ece3.70102

Golikov AV, Sabirov RM, Lubin PA, Jørgensen LL (2013) Changes in distribution and range structure of Arctic cephalopods due to climatic changes of the last decades. Biodiversity 14:28–35. https://doi.org/10.1080/14888386.2012.702301

Golikov AV, Blicher ME, Jørgensen LL, Walkusz W, Zakharov DV, Zimina OL, Sabirov RM (2019) Reproductive biology and ecology of the boreoatlantic armhook squid *Gonatus fabricii* (Cephalopoda: Gonatidae). J Molluscan Stud 85:287–299. https://doi.org/10.1093/mollus/eyz023

Goold JC, Jones SE (1995) Time and frequency domain characteristics of sperm whale clicks. J Acoust Soc Am 98:1279–1291. https://doi.org/10.1121/1.413465

Gray D (1882) Notes on the characters and habits of the bottlenose whale (*Hyperoodon rostratus*). Proc Zool Soc Lond 50:726–731

Grove T, Senglat C, Petitguyot M, Kosiba D, Rasmussen MH (2020) Mass stranding and unusual sightings of northern bottlenose whales (*Hyperoodon ampullatus*) in Skjálfandi Bay, Iceland. Mar Mamm Sci 36:1033–1041. https://doi.org/10.1111/mms.12689

Gunnlaugsson Th, Víkingsson GA (2014) Winter occurrence of whales in waters around Iceland.

Haas CE, Neubarth BK, Miller PJO, Hooker SK, Svavarsson J, Wensveen PJ (2024) Acoustic behaviour of northern bottlenose whales (Hyperoodon ampullatus) in Icelandic inshore waters. In: Proceedings of the 10th Convention of the European Acoustics Association Forum Acusticum 2023. European Acoustics Association, Turin, Italy, pp 5445–5450

Haas CE, Wensveen PJ, Hooker SK, Miller PJO (2025) Acoustic characteristics and context of buzzes and rasps produced by northern bottlenose whales (*Hyperoodon ampullatus*). Bioacoustics. https://doi.org/10.1080/09524622.2025.2451955

Halldórsson SD, Gunllaugsson T, Chosson V, Víkingsson GA (2019) Cetacean strandings in Iceland 1981–2019. In: World Marine Mammal Conference. Barcelona,

Hasle JR, Kjellén U, Haugerud O (2009) Decision on oil and gas exploration in an Arctic area: case study from the Norwegian

Barents Sea. Saf Sci 47:832–842. https://doi.org/10.1016/j.ssci.2008.10.019
Hastie LC, Pierce GJ, Wang J, Bruno I, Moreno A, Piatkowski U, Robin JP (2009) Cephalopods in the North-Eastern Atlantic: species, biogeography, ecology, exploitation and conservation. Oceanogr Mar Biol 47:111–190
Hooker SK, Iverson SJ, Ostrom P, Smith SC (2001) Diet of northern bottlenose whales inferred from fatty-acid and stable-isotope analyses of biopsy samples. Can J Zool 79:1442–1454. https://doi.org/10.1139/cjz-79-8-1442
Hooker SK, Cañadas A, Hyrenbach KD, Corrigan C, Polovina JJ, Reeves RR (2011) Making protected area networks effective for marine top predators. Endanger Species Res 13:203–218. https://doi.org/10.3354/esr00322
Jaquet N (1996) How spatial and temporal scales influence understanding of sperm whale distribution: a review. Mamm Rev 26:51–65
Jónsson S (2007) Volume flux and fresh water transport associated with the East Icelandic Current. Prog Oceanogr 73:231–241. https://doi.org/10.1016/j.pocean.2006.11.003
Knight EC, Hannah KC, Foley GJ, Scott CD, Brigham RM, Bayne E (2017) Recommendations for acoustic recognizer performance assessment with application to five common automated signal recognition programs. Avian Conserv Ecol 12:art14. https://doi.org/10.5751/ACE-01114-120214
Kowarski K, Delarue J, Martin B, O'Brien J, Meade R, Ó. Cadhla O, Berrow S (2018) Signals from the deep: spatial and temporal acoustic occurrence of beaked whales off western Ireland. PLoS ONE 13:e0199431. https://doi.org/10.1371/journal.pone.0199431
Lacey C, Hammond P (2023) Distribution and abundance of beaked whales and other deep diving cetaceans in European Atlantic waters.
Lambert E, Pierce GJ, Hall K, Brereton T, Dunn TE, Wall D, Jepson PD, Deaville R, Macleod CD (2014) Cetacean range and climate in the eastern North Atlantic: future predictions and implications for conservation. Glob Chang Biol 20:1782–1793. https://doi.org/10.1111/gcb.12560
Lascelles B, Notarbartolo Di Sciara G, Agardy T, Cuttelod A, Eckert S, Glowka L, Hoyt E, Llewellyn F, Louzao M, Ridoux V, Tetley MJ (2014) Migratory marine species: their status, threats and conservation management needs. Aquat Conserv 24:111–127. https://doi.org/10.1002/aqc.2512
Lefort KJ, Storrie L, Hussey NE, Ferguson SH (2025) Aseasonal migration of a northern bottlenose whale provides support for the skin molt migration hypothesis. Ecol Evol. https://doi.org/10.1002/ece3.70921
Leonard D, Øien N (2020) Estimated abundances of cetacean species in the Northeast Atlantic from Norwegian shipboard surveys conducted in 2014–2018. NAMMCO Sci Publ Doi 10(7557/3):4694
Levin LA, Mengerink K, Gjerde KM, Rowden AA, Van Dover CL, Clark MR, Ramirez-Llodra E, Currie B, Smith CR, Sato KN, Gallo N, Sweetman AK, Lily H, Armstrong CW, Brider J (2016) Defining "serious harm" to the marine environment in the context of deep-seabed mining. Mar Policy 74:245–259
Lisa Yang K. Center for Conservation Bioacoustics at the Cornell Lab of Ornithology (2021) Raven Pro: Interactive Sound Analysis Software (Version 1.6).
MacLeod CD (2009) Global climate change, range changes and potential implications for the conservation of marine cetaceans: a review and synthesis. Endanger Species Res 7:125–136
Macrander A, Valdimarsson H, Jónsson S (2014) Improved transport estimate of the East Icelandic Current 2002–2012. J Geophys Res Oceans 119:3407–3424. https://doi.org/10.1002/2013JC009517
McSweeney DJ, Baird RW, Mahaffy SD (2007) Site fidelity, associations, and movements of Cuvier's (*Ziphius cavirostris*) and Blainville's (*Mesoplodon densirostris*) beaked whales off the island of Hawai'i. Mar Mamm Sci 23:666–687. https://doi.org/10.1111/j.1748-7692.2007.00135.x
Mendelssohn R (2024) rerddapXtracto: Extracts Environmental Data from "ERDDAPTM" Web Services.
Miller PJO, Narazaki T, Isojunno S, Hansen R, Kershaw J, Neves dos Reis M, Kleivane L (2015a) Body Condition and 3S15 Projects: 2015 Jan Mayen Trial Cruise Report.
Miller PJO, Kvadsheim PH, Lam FPA, Tyack PL, Curé C, DeRuiter SL, Kleivane L, Sivle LD, Van Ijsselmuide SP, Visser F, Wensveen PJ, Von Benda-Beckmann AM, Martín López LM, Narazaki T, Hooker SK (2015b) First indications that northern bottlenose whales are sensitive to behavioural disturbance from anthropogenic noise. R Soc Open Sci. https://doi.org/10.1098/rsos.140484
Miller PJO, Wensveen PJ, Isojunno S, Hansen R, Siegal E, Neves dos Reis M, Visser F, Kvadsheim P, Kleivane L (2016a) Body condition and ORBS Projects: 2016 Jan Mayen Trial Cruise Report.
Miller PJO, Narazaki T, Isojunno S, Aoki K, Smout S, Sato K (2016b) Body density and diving gas volume of the northern bottlenose whale (*Hyperoodon ampullatus*). J Exp Biol 219:2962–2962
Moors HB (2012) Acoustic Monitoring of Scotian Shelf Northern Bottlenose Whales (*Hyperoodon ampullatus*). PhD thesis, Dalhousie University
Murray J, Hjort J (1912) The Depths Of The Ocean. Macmillan & Co., London
Neubarth BK, Miller PJO, Roland R, Kleivane L, Wensveen PJ (2025) Long-term depth records of satellite-tagged northern bottlenose whales reveal extraordinary dive capabilities. Ecol Evol. https://doi.org/10.1002/ece3.71862
Øien N, Hartvedt S (2015) Northern bottlenose whales *Hyperoodon ampullatus* in Norwegian and adjacent waters
Pabi S, van Dijken GL, Arrigo KR (2008) Primary production in the Arctic Ocean, 1998-2006. J Geophys Res Oceans. https://doi.org/10.1029/2007JC004578
Pike DG, Gunnlaugsson T, Mikkelsen B, Halldórsson SD, Víkingsson 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 Sci Publ Doi 10(7557/3):4941
Pike DG, Gunnlaugsson T, Sigurjónsson J, Víkingsson G (2020a) Distribution and abundance of cetaceans in Icelandic waters over 30 years of aerial surveys. NAMMCO Sci Publ Doi 10(7557/3):4805
Pike DG, Gunnlaugsson T, Mikkelsen B, Halldórsson SD, Víkingsson G, Acquarone M, Desportes G (2020b) Estimates of the abundance of cetaceans in the Central North Atlantic from the T-NASS Icelandic and Faroese ship surveys conducted in 2007. NAMMCO Sci Publ Doi 10(7557/3):5269
Pirotta E, Matthiopoulos J, MacKenzie M, Scott-Hayward L, Rendell L (2011) Modelling sperm whale habitat preference: a novel approach combining transect and follow data. Mar Ecol Prog Ser 436:257–272. https://doi.org/10.3354/meps09236
Pitman RL, Durban JW, Joyce T, Fearnbach H, Panigada S, Lauriano G (2020) Skin in the game: epidermal molt as a driver of long-distance migration in whales. Mar Mamm Sci 36:565–594. https://doi.org/10.1111/mms.12661
R Core Team (2023) R: A Language and Environment for Statistical Computing.
Ramirez-Martinez NC, Víkingsson GA, Øien NI, Mikkelsen B, Gunnlaugsson T, Hammond PS (2024) Distribution and habitat use of deep-diving cetaceans in the central and north-eastern North Atlantic. NAMMCO Sci Publ Doi 10(7557/3):7416
Renfrew IA, Pickart RS, Våge K, Moore GWK, Bracegirdle TJ, Elvidge AD, Jeansson E, Lachlan-Cope T, McRaven LT, Papritz L, Reuder J, Sodemann H, Terpstra A, Waterman S, Valdimarsson H, Weiss A, Almansi M, Bahr F, Brakstad A, Barrell C, Brooke JK, Brooks BJ, Brooks IM, Brooks ME, Bruvik EM, Duscha C, Fer I, Golid HM, Hallerstig M, Hessevik I, Huang J, Houghton

L, Jónsson S, Jonassen M, Jackson K, Kvalsund K, Kolstad EW, Konstali K, Kristiansen J, Ladkin R, Lin P, Macrander A, Mitchell A, Olafsson H, Pacini A, Payne C, Palmason B, Pérez-Hernández MD, Peterson AK, Petersen GN, Pisareva MN, Pope JO, Seidl A, Semper S, Sergeev D, Skjelsvik S, Søiland H, Smith D, Spall MA, Spengler T, Touzeau A, Tupper G, Weng Y, Williams KD, Yang X, Zhou S (2019) The Iceland Greenland Seas Project. Bull Am Meteorol Soc 100:1795–1817. https://doi.org/10.1175/BAMS-D-18-0217.1

Reynolds MD, Sullivan BL, Hallstein E, Matsumoto S, Kelling S, Merrifield M, Fink D, Johnston A, Hochachka WM, Bruns NE, Reiter ME, Veloz S, Hickey C, Elliott N, Martin L, Fitzpatrick JW, Spraycar P, Golet GH, Mccoll C, Low C, Morrison SA (2017) Dynamic conservation for migratory species. Sci Adv. https://doi.org/10.1126/sciadv.1700707

Semmens JM, Pecl GT, Gillanders BM, Waluda CM, Shea EK, Jouffre D, Ichii T, Zumholz K, Katugin ON, Leporati SC, Shaw PW (2007) Approaches to resolving cephalopod movement and migration patterns. Rev Fish Biol Fish 17:401–423. https://doi.org/10.1007/s11160-007-9048-8

Semper S, Pickart RS, Våge K, Larsen KMH, Hátún H, Hansen B (2020) The Iceland-Faroe slope jet: a conduit for dense water toward the Faroe Bank Channel overflow. Nat Commun 11:5390. https://doi.org/10.1038/s41467-020-19049-5

Semper S, Våge K, Pickart RS, Jónsson S, Valdimarsson H (2022) Evolution and transformation of the North Icelandic Irminger Current along the North Iceland shelf. J Geophys Res Oceans. https://doi.org/10.1029/2021JC017700

Semper S, Våge K, Fer I, Latuta L, Skjelsvik S (2025) Formation and circulation of dense water from a two-year moored record in the Northwestern Iceland Sea. J Geophys Res Oceans. https://doi.org/10.1029/2024JC021691

Shaw AK (2020) Causes and consequences of individual variation in animal movement. Mov Ecol. https://doi.org/10.1186/s40462-020-0197-x

Siegal E (2020) The foraging behaviour and body condition of northern bottlenose whales (*Hyperoodon ampullatus*). PhD thesis, University of St Andrews

Silva MA, Prieto R, Magalhaes S, Cabecinhas R, Cruz A, Goncalves JM, Santos RS (2003) Occurrence and distribution of cetaceans in the waters around the Azores (Portugal), summer and autumn 1999–2000. Aquat Mamm 29:77–83

Solsona-Berga A, Frasier KE, Baumann-Pickering S, Wiggins SM, Hildebrand JA (2020) Detedit: a graphical user interface for annotating and editing events detected in long-term acoustic monitoring data. PLoS Comput Biol. https://doi.org/10.1371/journal.pcbi.1007598

Stanistreet JE, Nowacek DP, Baumann-Pickering S, Bell JT, Cholewiak DM, Hildebrand JA, Hodge LEW, Moors-Murphy HB, Van Parijs SM, Read AJ (2017) Using passive acoustic monitoring to document the distribution of beaked whale species in the western north Atlantic Ocean. Can J Fish Aquat Sci 74:2098–2109. https://doi.org/10.1139/cjfas-2016-0503

Stern SJ, Friedlaender AS (2018) Migration and Movement. Encyclopedia of Marine Mammals. Elsevier, pp 602–606

Swartz SL (1986) Gray whale migratory, social and breeding behavior.

The MathWorks Inc. (2022) MATLAB.

Vogel EF, Biuw M, Blanchet MA, Jonsen ID, Mul E, Johnsen E, Hjøllo SS, Olsen MT, Dietz R, Rikardsen A (2021) Killer whale movements on the Norwegian shelf are associated with herring density. Mar Ecol Prog Ser 665:217–231. https://doi.org/10.3354/meps13685

Wahlberg M, Beedholm K, Heerfordt A, Møhl B (2011) Characteristics of biosonar signals from the northern bottlenose whale, *Hyperoodon ampullatus*. J Acoust Soc Am 130:3077–3084. https://doi.org/10.1121/1.3641434

Wensveen PJ, Isojunno S, Hansen RR, von Benda-Beckmann AM, Kleivane L, van IJsselmuide S, Lam FPA, Kvadsheim PH, DeRuiter SL, Curé C, Narazaki T, Tyack PL, Miller PJO (2019) Northern bottlenose whales in a pristine environment respond strongly to close and distant navy sonar signals. Proc Biol Sci 286:20182592. https://doi.org/10.1098/rspb.2018.2592

Wensveen PJ, Miller PJO, Roland R, Neubarth BK, Svavarsson J (2025) Northern bottlenose whales (*Hyperoodon ampullatus*) make migration roundtrips between the Nordic Seas and the Azores. In: 36th Conference of the European Cetacean Society, Ponta Delgada, Azores, Portugal.

Whitehead H, Hooker S (2012) Uncertain status of the northern bottlenose whale *Hyperoodon ampullatus*: population fragmentation, legacy of whaling and current threats. Endanger Species Res 19:47–61. https://doi.org/10.3354/esr00458

Whitehead H, Reeves R, Feyrer L, Brownell RL Jr (2021) *Hyperoodon ampullatus*, northern bottlenose whale. IUCN Red List. https://doi.org/10.2305/IUCN.UK.2021-1.RLTS.T10707A50357742.en

Wiborg KF (1979) *Gonatus fabricii* (Lichtenstein), a possible fishery resource in the Norwegian Sea. Fisken Hav 33–46.

Wiborg KF, Gjøsæter J, Beck IM (1982) The squid *Gonatus fabricii* (Lichtenstein): Investigations in the Norwegian Sea and Barents Sea 1978–1981.

Wiborg KF, Gjøsæter J, Beck IM (1984) The squid *Gonatus fabricii* (Lichtenstein): investigations in the Norwegian Sea and western Barents Sea 1982–1983.

Wiggins SM, Roch MA, Hildebrand JA (2010) Triton software package: analyzing large passive acoustic monitoring data sets using MATLAB. J Acoust Soc Am 128:2299. https://doi.org/10.1121/1.3508074

Wimmer T, Whitehead H (2004) Movements and distribution of northern bottlenose whales, *Hyperoodon ampullatus*, on the Scotian Slope and in adjacent waters. Can J Zool 82:1782–1794. https://doi.org/10.1139/Z04-168

Woo KY, Isojunno S, Miller PJO (2023) Habitat use of the northern bottlenose whale *Hyperoodon ampullatus* near Jan Mayen, North Atlantic. Mar Ecol Prog Ser 718:119–136. https://doi.org/10.3354/meps14374

Wood SN (2004) Stable and efficient multiple smoothing parameter estimation for generalized additive models. J Am Stat Assoc 99:673–686

Zimmer WMX, Johnson MP, Madsen PT, Tyack PL (2005) Echolocation clicks of free-ranging Cuvier's beaked whales (*Ziphius cavirostris*). J Acoust Soc Am 117:3919–3927. https://doi.org/10.1121/1.1910225