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Passive acoustic surveys demonstrate high densities of sperm whales off the mid-Atlantic coast of the USA in winter and spring

Oliver Boisseau [a,*], Doug Nowacek [b], D. Ann Pabst [c], Jason Roberts [d], Ashley Blawas [b,e], Anna Clabaugh [b], Richard McLanaghan [a], Anna Moscrop [a], J. Jacob Levenson [f]

[a] Marine Conservation Research International, R/V Song of the Whale Team, 94 High Street, Kelvedon, CO5 9AA, UK
[b] Duke University Marine Laboratory, Nicholas School of the Environment, Duke University, Beaufort, NC, 28516, USA
[c] Department of Biology and Marine Biology, University of North Carolina Wilmington, 601 S. College Rd, Wilmington, NC, 28403, USA
[d] Marine Geospatial Ecology Laboratory, Duke University, Durham, NC, 27708, USA
[e] Hopkins Marine Station, Oceans Department, Stanford University, Pacific Grove, CA, 93950, USA
[f] Environmental Studies Program, Bureau of Ocean Energy Management, U.S. Department of the Interior, Washington DC, 20240, USA

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ABSTRACT

Oceans are increasingly crowded by anthropogenic activities yet the impact on Outer Continental Shelf (OCS) marine life remains largely unquantified. The MAPS (Marine Mammal Acoustic and Spatial Ecology) study of 2019 included passive acoustic and visual vessel surveys over the Mid-Atlantic OCS of the USA to address data gaps in winter/spring for deep-diving cetaceans, including sperm whales. Echolocation clicks were used to derive slant ranges to sperm whales for design- and model-based density estimates. Although more survey effort was realised in the spring, high densities of whales were identified in both winter and spring (10.46 and 8.89 per 1000 km^2 respectively). The spring model-based abundance estimate of 1587 whales (CI 946–2663) was considered the most representative figure, in part due to lower coefficients of variation. Modelling suggested that high densities of whales were associated with warm core rings, eddies and edges. As OCS waters provide an important foraging habitat for North Atlantic sperm whales, appropriate mitigation is required to ensure commercial pressures to develop offshore energy do not negatively affect this endangered species.

1. Introduction

Ocean waters are becoming increasingly crowded by anthropogenic activities. These can include fisheries, shipping, resource extraction, dredging, offshore dumping of waste and munitions, aquaculture, tourism and recreational activities (USCOP, 2004). Human activities such as these have the potential to introduce pollutants into the marine environment, including underwater noise (Williams et al., 2015). Underwater noise levels have been increasing globally due to these activities (McDonald et al., 2008; Hildebrand, 2009; Chapman and Price, 2011; Miksis-Olds and Nichols, 2016) and this trend is predicted to continue (Jerem and Mathews, 2021; Vagle et al., 2021). Energy extraction, whether from fossil fuels or renewable sources, can generate significant noise from exploration, construction, extraction, maintenance and decommissioning phases (Nedwell and Howell, 2004; Blackwell and Greene Jr, 2006; Erbe et al., 2013; Kyhn et al., 2014; Nowacek et al., 2015). Technical innovations have increased the reach of viable energy extraction to deeper waters (Randolph et al., 2011; Kaiser and Narra, 2018) where significant unexploited reserves of fossil fuels or renewable energy may now be accessible. Despite this extension of spatial reach, the potential for these activities to impact marine life in Outer Continental Shelf (OCS) waters remains largely unquantified. This deficit is in part due to a paucity of knowledge on marine biodiversity in the outer waters of the continental shelf, as these regions are relatively inaccessible compared to coastal waters and have thus received relatively little research effort. The gaps in our understanding of the offshore distribution of marine organisms exposed to anthropogenic noise are most pronounced for winter months when survey effort is heavily constrained by poor weather (Roberts et al., 2016; Mannocci et al., 2018).

The sperm whale (*Physeter macrocephalus* Linnaeus, 1758) is the largest species of toothed-whale and is found in all ice-free oceanic waters (approximately 80°N to 70°S; Whitehead, 2018). Although mature males may be found at extreme high latitudes, they move to warmer waters with unknown frequency to breed with adult females

* Corresponding author.
E-mail address: oboisseau@mcr-team.org (O. Boisseau).

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that are typically restricted to latitudes below 40°, corresponding roughly to sea surface temperatures greater than 15° (Rice, 1989). Whaling efforts targeting sperm whales peaked in the mid-nineteenth century, and during this period the whaling industry accumulated a significant understanding of sperm whale distribution and migratory patterns (Bannister et al., 2008). The American 'Yankee' sperm whale fishery constituted the dominant global hunt (Ellis, 2018), and the catches from their logbooks from 1761 to 1920 were summarized by Townsend in 1935. The "Southern", "Hatteras" and "Charleston" grounds (28°-41°N, 60°-78°W) were important areas for hunting sperm whales in the western Atlantic from the mid-18th century to the early 20th century (Townsend, 1935; Bannister et al., 2008). In part due to intensive whaling effort, sperm whales are currently listed as Endangered under the U.S. Endangered Species List and depleted under the Marine Mammal Protection Act (Hayes et al., 2020).

Building on this early understanding of sperm whale distribution have been several efforts to quantify the number of sperm whales utilising the OCS of the USA. Recent summer abundance estimates have been made for surveys conducted north of North Carolina (36–42°N) in June–August 2011 (Palka, 2012) and August–September 2016 (Palka, 2020; Westell et al., 2022), from Florida to Maryland (28–38°N) in June–August 2016 (Garrison, 2020) and from Florida to Maine (25–45°N) in March–November 2010–2013 (Chavez-Rosales et al., 2019). However, only one estimate of abundance is available for winter months. This was made using density-habitat models derived from visual line transect data collected by aerial and vessel surveys from 2010 to 2017 along the eastern seaboard of the U.S. (Palka et al., 2021); only aerial survey data could be used for the winter estimates (December to March) due to a lack of vessel effort. Despite the paucity of winter density estimates, recordings collected year-round from static acoustic recorders suggest sperm whale are present off the eastern seaboard of the U.S. in all calendar months (Cohen et al., 2022; Kowarski et al., 2022). There is even evidence of a winter peak in occurrence off North Carolina (35°N), with a subsequent peak in detections further north (37–40°N) in spring (Stanistreet et al., 2018; Cohen et al., 2023). Winter research effort may therefore be viewed as a priority for refining sperm whale density estimates for the eastern seaboard of the U.S.

Sperm whales routinely dive to depths greater than 200 m on long foraging dives (Miller et al., 2004; Fais et al., 2016a; Westell et al., 2022). As deep-diving cetaceans such as sperm whales spend proportionally little time at the surface, their availability to observers in traditional visual surveys is limited (Barlow and Taylor, 2005). Passive acoustic techniques can offer several advantages over visual methods for detecting cetaceans, including extended strip widths, detection at night and detection during periods of bad weather (Leaper et al., 1992; Barlow and Taylor, 2005). Sperm whales are well suited for acoustic detection as they generate regular loud clicks (apparent source levels up to 236 dB re: 1 μPa rms; Møhl et al., 2003; Zimmer et al., 2005) that can be detected reliably up to 10 km away with a towed hydrophone array in pelagic waters (Lewis et al., 2018). Furthermore, they typically vocalise throughout 60–80% of their dive cycles (Douglas et al., 2005; Watwood et al., 2006; Miller et al., 2008; Teloni et al., 2008; Fais et al., 2016b). The rapid rise time of sperm whale clicks (<1ms) allows time-of-arrival differences between two or more hydrophone elements to be estimated and subsequently used to derive bearing information; by triangulating the bearing lines to successive clicks in a click train, robust estimates of distance can be made (Leaper et al., 1992; Lewis et al., 2007; Matthews, 2014). These acoustic estimates of slant range, or straight line distance between two points, can be translated to perpendicular distances from a survey transect for subsequent use in a distance sampling framework to estimate density (e.g. Leaper et al., 1992; Leaper et al., 2000; Hastie et al., 2003; Barlow and Taylor, 2005; Ward et al., 2012; Fais et al., 2016b; Lewis et al., 2018; Gordon et al., 2020; Westell et al., 2022). Where possible, corrections should be made for acoustic availability, as individual whales may be silent for 20–40% of the time (Douglas et al., 2005; Miller et al., 2008; Teloni et al., 2008; Fais et al., 2016b), during which they cannot be detected by passive acoustic sensors.

Considering the lack of winter data on deep-diving cetaceans of the U.S. OCS, the Marine Mammal Acoustic and Spatial Ecology (MAPS) research programme prioritised survey effort in winter and spring months in offshore waters deeper than 1000 m. The study area, which incorporated the OCS of North and South Carolina and southern Virginia, was selected due to the growing commercial pressure to develop offshore energy infrastructure in a region that provides an important habitat for multiple species of deep-diving odontocetes (Roberts et al., 2016; McLellan et al., 2018; Stanistreet et al., 2018; Boisseau et al., 2023). The region also sees a dramatic spatial oceanographic shift, as the warm, high salinity waters of the Gulf Stream diverge from the shelf break near Cape Hatteras, North Carolina, to leave shelf waters that are both cooler and of lower salinity than the adjacent slope water (Schmitz, 1996; Fratantoni and Pickart, 2007). This paper presents the results of the line-transect surveys used to investigate the distribution of sperm whales in the mid-Atlantic OCS using passive acoustic and visual techniques in winter and spring, and subsequently derive local density and abundance estimates for this species.

2. Material and methods

2.1. Survey design

The study area incorporated 220,605 km^2 of heterogeneous habitats, including continental shelf, steep slope waters and canyon systems, in the Northwest Atlantic (Fig. 1) between the approximate latitudes of 32°N and 38°N. The oceanography of the region is driven by the

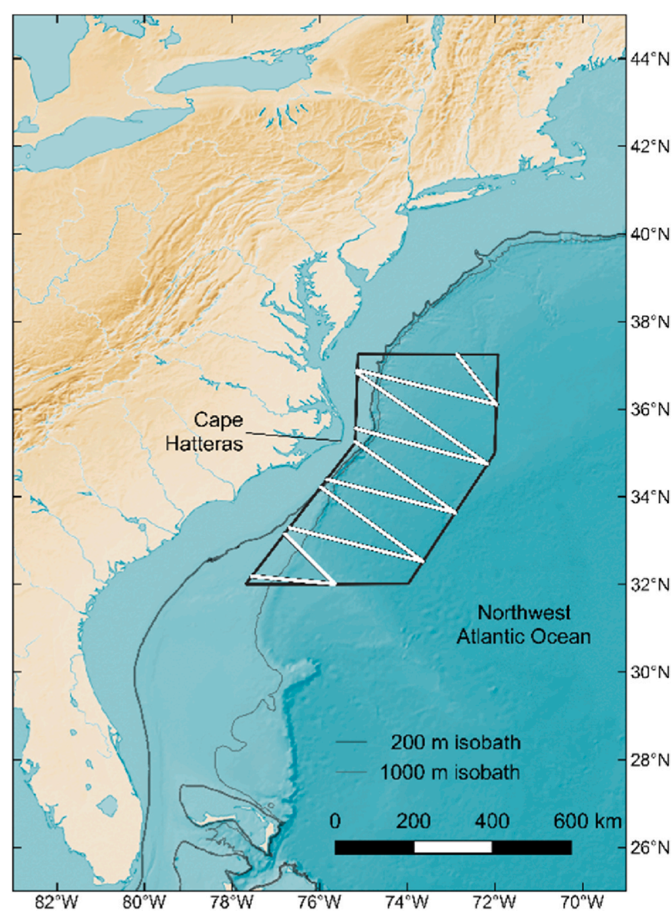

Fig. 1. The study area with equal-spaced zigzag transects providing coverage of the Outer Continental Shelf off North and South Carolina and Virginia in the USA. Topography and bathymetry from naturalearthdata.com.

interaction between local topography and the convergence of two major water masses, the Gulf Stream from the south and Labrador Current from the north (McLellan, 1957; Savidge and Bane, 2001; Fratantoni and Pickart, 2007). The same study area was surveyed twice in 2019 to capture seasonal variation between winter and spring; the first cruise was conducted in winter (17th January to 24th February), the second in spring (6th April to 19th May). Transects were designed using the software Distance 7.3 (Thomas et al., 2010) as equal-spaced zigzags to provide almost uniform coverage probability. Ten transects with a total length of 3005 km were designed to provide an acoustic coverage of at least 10% based on a maximum likely half strip width of 10 km for sperm whale clicks (Lewis et al., 2018). The intention was to survey the same transects in both cruises and thus derive separate winter and spring density estimates. Both passive acoustic and visual data were collected from RV Song of the Whale, a 21 m auxiliary-powered cutter-rigged sailing research vessel. All research was conducted under NOAA permits 14809–03 and 16473.

2.2. Passive acoustic surveys

A passive acoustic linear towed hydrophone array was used to detect sperm whale vocalisations and consisted of a 400 m tow cable attached to multiple hydrophone elements in an oil-filled tube. These included a pair of low-frequency AQ-4 elements (Teledyne Benthos) with a flat frequency response (±1.5 dB) from 1 Hz to 30 kHz and receiving sensitivities of −201 dB re 1V/μPa. Pre-amplifiers with 39 dB gain were used to prevent voltage drop between the array and research vessel. The elements were 3 m apart to provide optimal spacing for localising sperm whale clicks. Array outputs were digitised at 500 kHz by a SAIL DAQ card (SA Instrumentation) and subsequently down-sampled to 48 kHz with a 4th order Chebyshev low-pass filter set to cut-off at 19.2 kHz. The two elements were monitored in real-time using a click detector module in PAMGuard (Gillespie et al., 2008) configured to detect potential sperm whale clicks and plot their bearing relative to the array. Raw audio was also recorded continuously to hard disk as 16-bit wav files. In addition to the survey transects, acoustic effort was maintained continuously in waters deeper than 50 m. R/V Song of the Whale maintained survey speeds of 5–8 knots to ensure the array was streamed behind the vessel without the introduction of cable strum and to avoid biases related to animal movement; vessels should travel at least 2–3 times faster than the focal animals during distance-sampling surveys (Buckland et al., 2015), the mean speed of sperm whales being approximately 2.1 knots (Whitehead, 2018).

2.3. Visual surveys

Visual searching was conducted by two dedicated observers on an elevated platform (eye height of 5.4 m). One observer scanned the sector from 270 to 360° and the other from 0 to 90°. Observers were rotated every hour, with at least 2 h between consecutive watches. Details of encounters were clarified with 7x50 binoculars and observers reported species identity, range (subjective estimation by eye), bearing (from angle boards) and group size to another team member acting as a dedicated data recorder. The data recorder logged sighting time, species, distance, relative bearing and number of animals to a survey database using Logger software (marineconservationresearch.org). The vessel's position was logged to the same database every second from the shipboard GPS.

2.4. Click train identification and localisation

Recordings made in the field were re-examined through post-processing in PAMGuard (Gillespie et al., 2008) to identify candidate sperm whale click trains. Regular sperm whale clicks have distinctive waveforms (rapid onset/offset and evidence of multiple pulses within each click), spectral properties (most energy at or below 12 kHz) and inter-click intervals (a regular click being produced every 0.46–2.00 s) (Leaper et al., 1992; Møhl et al., 2003; Solsona Berga et al., 2022). Candidate clicks were further identified as being part of a click train if they displayed at similar bearings with regular inter-click intervals (Fig. 2). Differences in bearing were used to identify unique click trains, therefore allowing detections to be made at the individual rather than the group level (Lewis et al., 2018). Estimates of slant range to individual whales were made in PAMGuard using the Target Motion Analysis (TMA) module's 2D simplex optimization algorithm. A towed hydrophone array will detect a series of clicks from a focal animal; if the source is assumed to be stationary then each click will be detected with a time differential on the two elements. Successive sets of time delays can be visualised as 2D bearings converging on the likely location of the source. To differentiate between left and right convergence points, PAMGuard calculates a chi-squared goodness of fit between the simulated and observed bearings and the side with the smaller value is considered the best convergence point (Boisseau et al., 2023).

2.5. Acoustic density estimation

Density was estimated both with a traditional design-based approach (Buckland et al., 2015) and with two-stage density surface modelling (DSM; Miller et al., 2013). First, a detection function was developed from the acoustically-localised sperm whale detections. For those whales detected on a transect when the research vessel was following the survey protocol (i.e. traveling at 5–8 knots), slant ranges were imported into Distance 7.3 to generate candidate detection functions using multiple covariate distance sampling (MCDS; Marques and Buckland, 2003). To avoid the need for extra adjustment terms to fit a long tail to the detection function (Buckland et al., 2001), the slant range data were right truncated at 8000 m prior to the analysis, excluding 3% of the largest distance estimates. 'Effort covariates' that could modify the noise field around the hydrophone elements, and thus the likelihood of detecting clicks, were included in the analysis to modify the scale of candidate detection functions without affecting their shapes. These effort covariates were logged at least every hour in the field and included sea state (Beaufort scale), wave height (m), swell height (m) and rain condition (heavy, light or none); in addition, instruments on the research vessel logged wind speed (knots), sea surface temperature (SST; °C), engine speed (rpm), vessel heading (° true) and vessel speed (knots) every second. These covariates were investigated for collinearity using Pearson's correlation coefficient to remove any redundancy; all remaining covariates were subsequently incorporated into candidate detection functions. Initial exploration considered cruise identity (winter vs. spring) to ascertain whether the same detection function could be used for both cruises. Subsequent candidates were initially generated with single effort covariates; following this, candidates combining up to three effort covariates were generated. The best-fitting candidate was selected using Akaike's Information Criterion (AIC). Densities were then estimated using a design-based approach (Marques et al., 2013; Boisseau et al., 2023) with a correction for availability (see below).

The second analytical stage assumed sperm whale density varied across the survey block in response to specific environmental covariates. To investigate these relationships, survey transects were divided into short segments of homogeneous effort type and a density surface model was developed. The segment lengths were approximately similar to the lowest resolution of the environmental covariates (i.e. 8 km). Counts were summarized per segment and then a generalised additive model (GAM; Wood, 2006) was constructed with the per-segment counts as the response, as corrected for detectability using the detection function selected in the MCDS procedure. Several bathymetric and oceanographic covariates (Table 1) were obtained for each segment, based on their potential to influence sperm whale distribution (e.g. Waring et al., 1993; Praca et al., 2009; Pirotta et al., 2011; Tepsich et al., 2014; Mannocci et al., 2015; Breen et al., 2016; Claro et al., 2020; Vachon

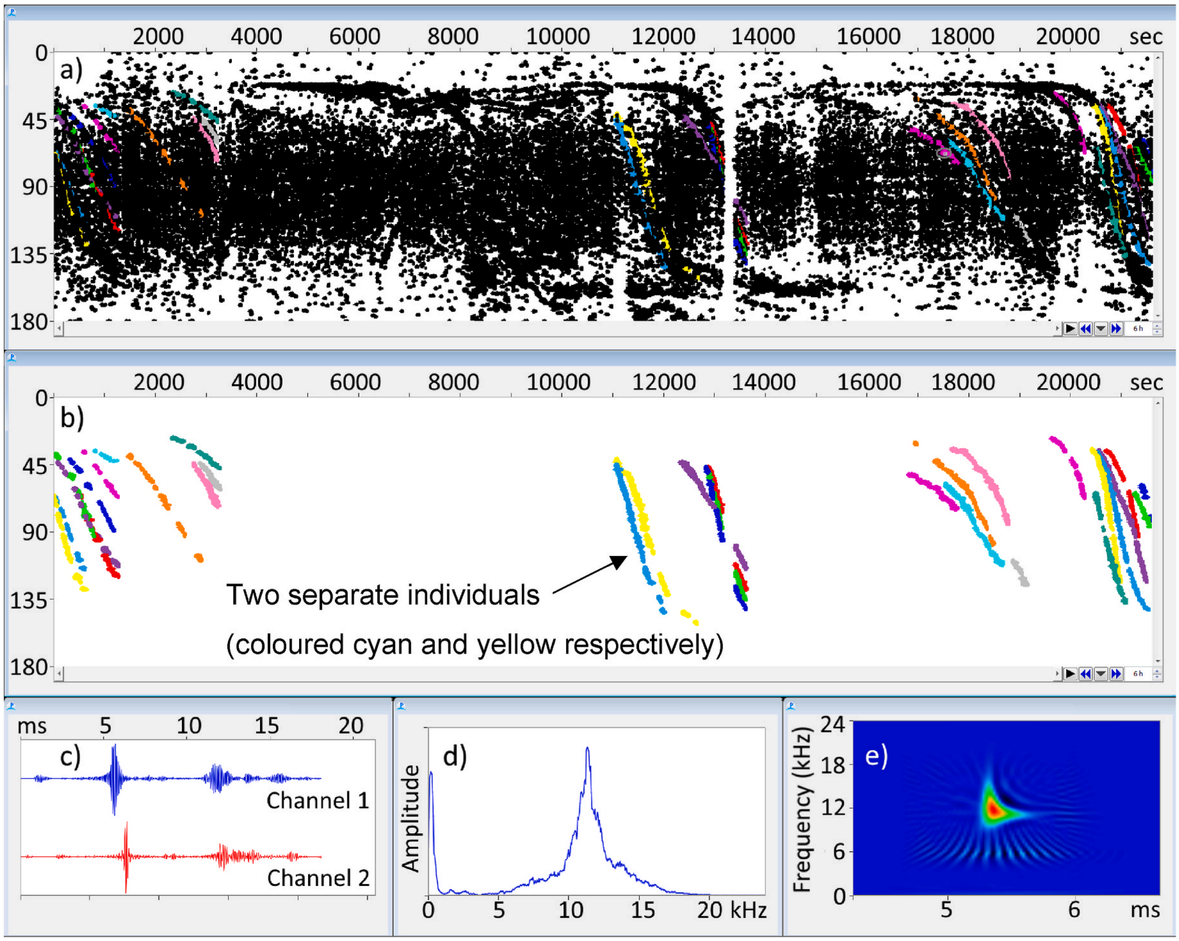

Fig. 2. An example of click train identification and localisation in PAMGuard from 6 h of data, where a) shows the original bearing/time plot with candidate sperm whale clicks marked with sequential colours (x-axis = time, y-axis = bearing relative to array), and b) shows just candidate click trains with extraneous detections removed. Clicks with a similar rate of bearing change are deemed to be from a single individual and are grouped together with the same colour. The lower panels represent a typical sperm whale click as, c) a waveform (showing a characteristic pulsed structure), d) a power spectrum (with peak frequency close to 12 kHz) and e) a flat Wigner-Ville distribution.

et al., 2022). Salinity was not included due to its close relationship with temperature in the Gulf Stream (Pauthenet et al., 2022) and its likely correlation with SST. Smooth functions of the environmental covariates were constructed using thin plate regression splines with shrinkage, except for the circular variables aspect and water direction, which used cyclic cubic regression splines (Wood, 2006). The Tweedie distribution with a logarithmic link function was assumed for the response variable, as this approach adequately handles zero-inflated spatial models (Miller et al., 2013). GAMs were fitted using the "dsm" R package (Miller et al., 2013). Model selection was conducted by adding one candidate explanatory variable at a time in a forward approach. The model selected at each step was chosen based on AIC score and percentage of deviance explained; QQ and residual plots were also examined for normality, auto-correlation and homoscedasticity. A prediction grid was generated by dividing the study area into 2980 cells with a cell size of 8 × 8 km (Albers equal conic area projection); the grid resolution was selected to correspond with the length of segments. Horizontal and spatial locations in the projected coordinate system were used as candidate covariates both separately (as univariate smooths) and together (as a bivariate smooth); the remaining covariates in Table 1 were averaged over each grid cell. Grids of predicted density were created in Quantum GIS 3.18.2 (QGIS, 2021) by predicting the final spatial model across grids of the covariates.

2.6. *Acoustic availability*

Availability for acoustic detection is influenced by both whale behaviour (the proportion of time sperm whales spend clicking) and survey protocol (as survey speed affects the time window during which whales can be detected). To quantify the vocal output of local sperm whales, attempts were made to attach digital acoustic recording tags (DTAG version 3; Johnson and Tyack, 2003) to adult whales during the MAPS surveys; we were successful in one such effort. The DTAG was attached with suction-cups to the back of the focal animal using a 10 m carbon-fibre pole from a 4.2 m Grand Raid Mk2 Zodiac. The DTAG provided 16-bit acoustic recordings (sampling rate 500 kHz) with a flat frequency response (62 dB) from 0.5 to 50 kHz. Additionally, the DTAG collected data on tag depth and orientation throughout its deployment (via a pressure sensor, tri-axial accelerometer and magnetometer sampled at 50 Hz). The tag remained on the subject whale for 6.5 h and was retrieved using a VHF radio signal. Clicks recorded on the DTAG were used to estimate the acoustic *g* (0), the probability of detecting sperm whales at zero metres from the trackline. Although acoustic *g* (0) for sperm whales is often assumed to be unity (e.g. Barlow and Taylor, 2005; Lewis et al., 2018), individuals are known to spend prolonged periods silent, for example during short reoxygenation dives at the surface (Douglas et al., 2005; Miller et al., 2008; Teloni et al., 2008; Fais et al., 2016b). We therefore estimated the acoustic availability of sperm whales using a Monte Carlo simulation (following Fais et al., 2016b).

Table 1
Summary of all bathymetric and oceanographic covariates used in DSM. Dynamic variables denoted by asterisk are averaged over February (for cruise 1) and April (for cruise 2).

Parameter	Source	Resolution (km)
Latitude/longitude	PAMGuard	0.1
Water depth (m)	NOAA ETOPO1 (ice)	1.4
Slope (°horizontal)	NOAA ETOPO1 (ice)	1.4
Aspect (°magnetic)	NOAA ETOPO1 (ice)	1.4
Distance to shore (m)	NOAA ETOPO1 (ice)	0.1
Distance to 125 m contour (m)	QGIS	0.1
Distance to 200 m contour (m)	QGIS	0.1
Distance to 1000 m contour (m)	QGIS	0.1
Distance to 5000 m contour (m)	QGIS	0.1
SST (°C)	NASA MODIS (Moderate Resolution Imaging Spectroradiometer)*	4.0
Chlorophyll A (mg m^{-3})	NASA MODIS (Moderate Resolution Imaging Spectroradiometer)*	4.0
Ocean mixed layer thickness (m)	CMEMS GLORYS2V4 GLOBAL-REANALYSIS-PHY-001-031*	27.8
Water layer velocity (ms^{-1})	CMEMS GLORYS2V4 GLOBAL-REANALYSIS-PHY-001-031*	27.8
Water layer direction (−180°–180°)	CMEMS GLORYS2V4 GLOBAL-REANALYSIS-PHY-001-031*	27.8
Distance to nearest canyon (m)	www.bluehabitats.org	1.0
Distance to nearest escarpment (m)	www.bluehabitats.org	1.0
Distance to nearest ridge (m)	www.bluehabitats.org	1.0
Distance to nearest seamount (m)	www.bluehabitats.org	1.0
Distance to nearest shelf (m)	www.bluehabitats.org	1.0
Distance to nearest shelf valley (m)	www.bluehabitats.org	1.0
Distance to nearest slope (m)	www.bluehabitats.org	1.0
Distance to nearest terrace (m)	www.bluehabitats.org	1.0
Distance to nearest trough (m)	www.bluehabitats.org	1.0

This approach assumed the survey vessel was moving along a transect of a random length between 100 and 1000 km at the average on-track survey speed (5.6 knots). A random number of stationary whales (N = 1–300) were randomly distributed along the trackline, each undertaking virtual dives. A virtual dive incorporated a period spent echolocating, t_e, defined as the interval between the start and end of clicking within a dive, followed by a period not echolocating at the surface, t_{ne}, the interval between the end of clicking and the subsequent resumption on the following dive. For each virtual dive, values of t_e and t_{ne} were selected randomly from a distribution of t_e and t_{ne} values derived from the DTAG dataset. Virtual whales on the trackline were considered detected if they were vocalising at any point within the effective strip half-width (EShW, estimated during the MCDS procedure) of the vessel as it travelled at the average survey speed. Acoustic g (0) was estimated by dividing the number of detected whales n by the total number of whales present in the simulation. The simulation was performed 2000 times to estimate mean availability and its standard deviation.

3. Results

The first cruise in winter 2019 (17th January to 24th February) incorporated 1733 km of on-track passive acoustic effort; poor weather conditions meant only 58% of the designed transects could be surveyed. All transects were surveyed in the subsequent spring cruise (6th April to 19th May) with 2829 km of on-track acoustic effort. A total of 238 individual sperm whales were acoustically detected on the transects during the two surveys (Fig. 3); of these, 115 were detected in the winter cruise (with a further 65 off-track detections) and 123 in the spring cruise (with a further 99 off-track detections). In addition to these acoustic detections, there were four visual sightings of sperm whale groups (from 1 to 20 individuals) in the winter cruise, of which three were on-track (761 km of on-track visual effort), and eight (1–16 individuals) in the spring cruise, of which three were on-track (1246 km of on-track visual effort). The sightings were not used for density estimation due to the low sample size. All sightings were preceded by acoustic detections. For four of the on-track sightings, there was agreement between the number of animals seen and the number of animals detected acoustically; for the two remaining on-track sightings, the estimates of group size (one animal seen in each encounter) was notably lower than the corresponding acoustic estimate (11 and 13 individuals respectively). As these two encounters occurred close to dusk, it seems likely that failing light conditions prevented subsequent sightings that may have allowed an accurate estimate of group size. It was thus deemed that there were not enough robust estimates of group size from the visual encounters to adequately 'ground truth' any acoustic estimations of cluster size. Subsequent density estimations were therefore made to the individual level rather than the cluster level.

3.1. Estimation of acoustic availability

Only one DTAG was successfully deployed and recovered during the MAPS surveys, for 6.5 h on May 16, 2019. The tagged individual was believed to be male based on surface observations of the genital slit. Ongoing efforts to estimate the length of sperm whales encountered during the MAPS surveys derived total body length estimates of 10.5 m (via photogrammetry) and 11.2 m (via acoustic length estimation) for this individual (A. Clabaugh, pers. comm. December 2022). The tagged whale undertook four deep foraging dives with three corresponding silent inter-dive periods spent at the surface; the focal animal then stayed at or near the surface for approximately 3 h 13 min without vocalising before the tag detached (Fig. 4). The tag sensors suggest that during one of these shallow dives the whale initially dropped to 12 m deep with a head-down orientation before drifting at 6–8 m deep with a head-up orientation. This latter behaviour is analogous to the 'head-down' drift-dives reported from various parts of the world (Miller et al., 2008), whereby a sperm whale will descend head-down to 1–2 body lengths below the surface, before passively turning head-up and remaining in that position for some time. Although drift-dives were identified in 53 % of the tags investigated by Miller et al. (2008), they typically only accounted for 7.1 % of recording time. The drift-dive shown in Fig. 4 accounted for 4.3% of the total tag deployment. As it is not clear if this short tag deployment provides a representative characterisation of sperm whale diving behaviour in this region, acoustic availability was estimated both without the silent surface behaviour (termed here the "typical" estimate, using only the first 3h 18 m of the deployment) and with it (termed here the 'atypical' estimate using the full 6h 31m dataset).

Estimates of acoustic g (0) were calculated for a representative survey-wide EShW of 3.5 km (see below) and the average on-track survey speed of 5.6 knots for both cruises. The Monte Carlo simulation exercise estimated typical g (0) as 0.872 (sd = 0.069) and atypical g (0) as 0.600 (sd = 0.099). Both estimates were used to scale subsequent density and abundance estimates. The issues relating to estimating g (0) with only one tag deployment are given further consideration in the

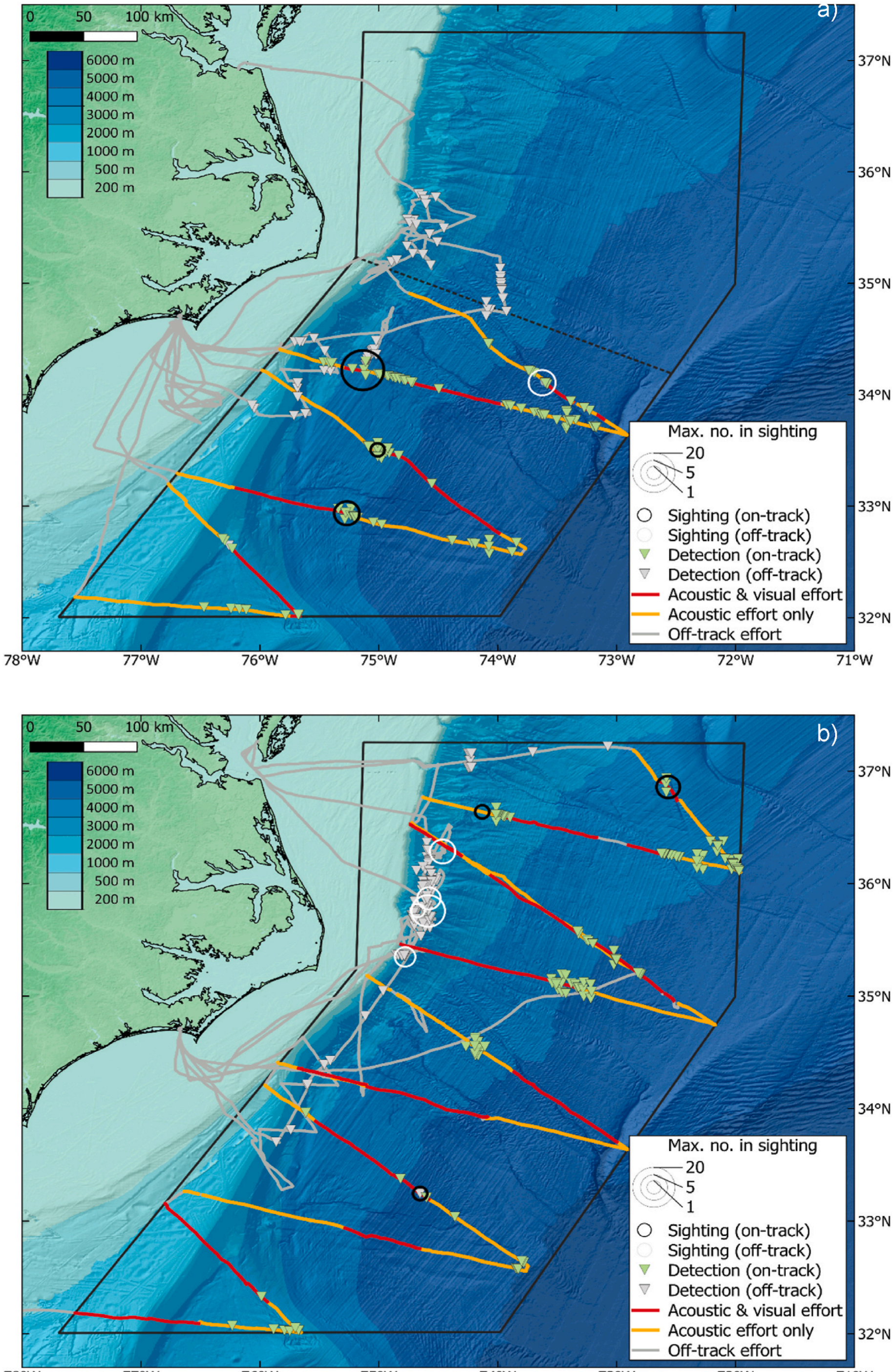

Fig. 3. Acoustic detections of individual sperm whales (on-track = green triangles; off-track = grey triangles) during a) the winter cruise and b) the spring cruise. Sightings of sperm whale groups are shown as black (on-track) or white (off-track) circles (areas proportional to the maximum estimates of group size). The off-track sighting in the winter survey was made after the vessel had broken from the transect to approach a group of beaked whales. Survey effort on transects is categorised as either joint acoustic-visual or acoustic-only. The dotted line in the winter plot (a) shows the truncated study area used for the subsequent estimate of winter abundance.

Discussion.

3.2. Acoustic density estimation of sperm whales

All on-track detections of sperm whales ($n = 238$) were included in subsequent estimation of encounter rate. Initial investigation comparing a MCDS model without covariates to a model containing cruise identity improved the fit of the model, suggesting the detection probability of sperm whales varied between winter and spring. Detections functions were therefore fitted to each cruise independently. Of the eight ‘effort covariates’ initially considered for improving of the detection function, four were excluded for being significantly correlated ($p < 0.05$) with at least one other, leaving swell height, engine revs, vessel heading and SST as candidates for the detection function. For the winter cruise, a half-normal key function without adjustment provided the closest fit to slant range estimates based on AIC scores; for the spring cruise, a hazard

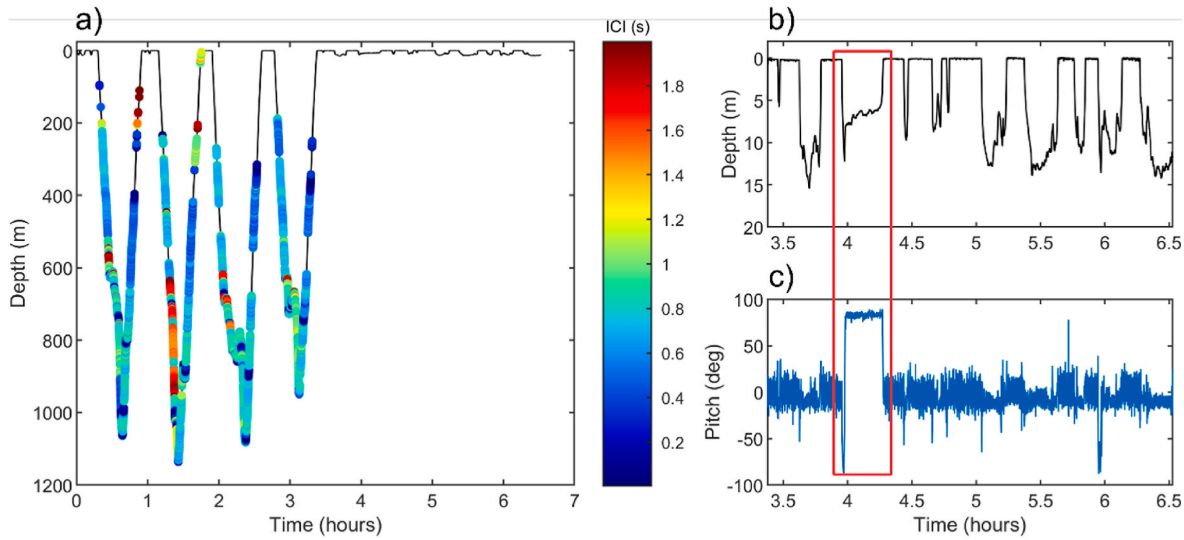

Fig. 4. Summary of the single DTAG deployed and recovered during the MAPS cruises on May 16th’ 2019. The plot on the left (a) shows the changing depth of the focal animal over time; vocalisations are represented by thicker traces with colours relating to inter-click interval, feeding buzzes appearing as dark blue regions. The plots on the right show the whale’s silent surface behaviour, including a stereotypical drift-dive outlined in red, with the animal staying within 15 m of the surface for ~3h13m (b). The plot of animal pitch (c) suggests the focal animal was mostly head-up throughout the drift-dive (i.e. positive pitch).

rate key function without adjustment was selected (Fig. 5). Parameter estimates were σ > 457,700 for the winter model, and σ > 3200 and β = 3.4 for the spring model. Inclusion of SST had the most pronounced effect on the detection function for the winter cruise, with lower sea surface temperatures associated with an increased likelihood of detecting sperm whales (i.e. a broadening of the detection function). Only swell height was included in the spring detection function, as a decrease in swell height tended to be linked to a broadening of the detection function. The estimated EShW for the winter cruise was 4258 m with a CV of 7.0 % (CI 3710–4888); for the spring cruise it was 3190 m with a CV of 7.5 % (CI 2750–3670).

The estimates of both typical and atypical *g* (0) described above (0.87 and 0.60 respectively) were used as multipliers in the design-based density and abundance estimates to correct for availability (Table 2). As only the six southernmost of the ten survey transects were fully surveyed in the winter cruise, winter estimates were made only for this smaller study block. During the spring survey, all ten transects were fully surveyed, and thus estimates made for the entire study area. However, to provide a seasonal comparison, spring estimates were also made for the smaller block containing only the six southernmost transects (Table 2).

Sperm whale detections were evident on 44 of 183 segments in the winter cruise, and 37 of 320 segments in the spring cruise. As the MCDS analysis suggested different detection functions should be used for each cruise (Fig. 5), the DSM procedure was also conducted separately for each. As for the MCDS analysis, the estimates of both typical and atypical g (0) were used as multipliers in the model-based density and abundance estimates to correct for availability (Table 3). The final DSM model selected for the winter cruise included location (as a bivariate term) and mean slope (° horizontal); both covariates were considered significant ($p < 0.05$) and together explained 32 % of the deviance (Fig. 6). Densities were highest towards the centre of the study block in regions of low slope (<2°; Fig. 7). The final DSM model selected for the spring cruise included a bivariate of location and mean SST; both covariates were considered significant ($p < 0.001$) and together explained 54 % of the deviance (Fig. 8). Densities were highest towards the northeast of the study block and in regions of low SST (<23°; Fig. 9).

4. Discussion

Sperm whale vocalisations were recorded on all but one of the transects surveyed in the winter and spring cruises in 2019, suggesting the study area is used routinely by sperm whales from January to May. Of the 238 on-effort acoustic detections of sperm whales in this study, 99% occurred in waters greater than 2000 m deep. A previous study using a static High-frequency Acoustic Recording Package (HARP) off Cape Hatteras also documented peak levels of clicking during winter and

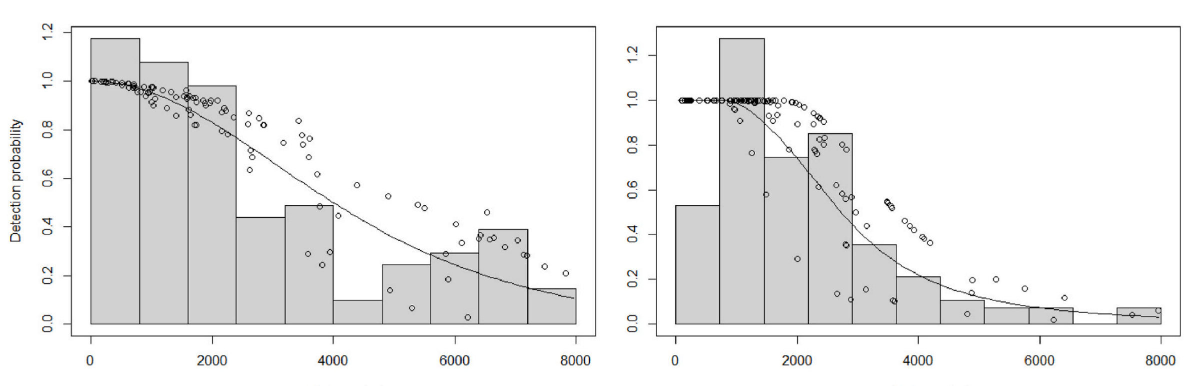

Fig. 5. Detection functions used in MCDS for winter (a; half-normal key function with SST) and spring (b; hazard rate key function with swell height). The open circles represent the probability of detection for individual encounters.

Table 2
Density (*D*) and abundance (*N*) estimates derived using MCDS for both cruises. Estimates are corrected for both typical acoustic availability (*g* (0) = 0.872) and atypical availability (*g* (0) = 0.600). Densities presented as individuals per 1000 km^2; values in parentheses represent 95% confidence limits. For comparative purposes, a reduced analysis is presented for the spring survey using the same six transects surveyed in winter.

Cruise	Area (km^2)	CV %	*D* (typical)	*N* (typical)	*D* (atypical)	*N* (atypical)
1: winter (six transects)	99,300	28.9	10.46 (5.17–21.14)	1038 (514–2099)	15.20 (7.52–30.73)	1509 (747–3051)
2: spring (six transects)	99,300	38.9	3.70 (1.52–8.99)	367 (151–893)	5.38 (2.21–13.07)	524 (220–1297)
2: spring (all transects)	181,190	30.7	8.89 (4.35–17.31)	1610 (827–3137)	12.92 (6.63–25.17)	2341 (1202–4560)

Table 3
Density (*D*) and abundance (*N*) estimates derived from DMS for both cruises. Estimates are corrected for both typical acoustic availability (*g* (0) = 0.872) and atypical availability (*g* (0) = 0.600). Densities presented as individuals per 1000 km^2; values in parentheses represent 95% confidence limits. For comparative purposes, a reduced analysis is presented for the spring survey using the same six transects surveyed in winter.

Cruise	Area (km^2)	CV %	*D* (typical)	*N* (typical)	*D* (atypical)	*N* (atypical)
1: winter (six transects)	99,300	28.6	9.22 (5.32–15.97)	915 (528–1586)	13.40 (7.73–23.21)	1330 (768–2305)
2: spring (six transects)	99,300	34.1	3.94 (2.06–7.54)	391 (204–749)	5.72 (2.99–10.96)	568 (297–1088)
2: spring (all transects)	181,190	26.9	8.76 (5.22–14.70)	1587 (946–2663)	12.73 (7.59–21.37)	2307 (1375–3871)

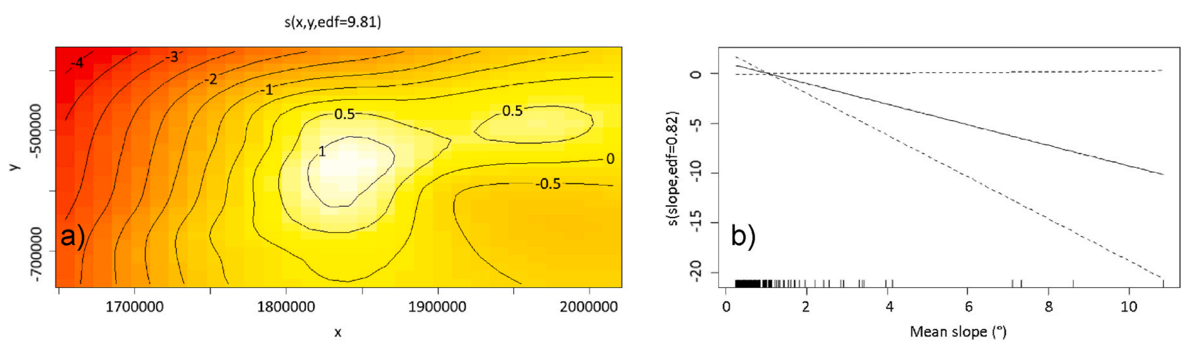

Fig. 6. Plot of the GAM smooth fit of density across (a) position and (b) mean slope (°) in the winter cruise. The solid line represents the best fit, with the dashed lines representing 95% confidence intervals. Vertical lines on the x-axis in (b) are observed data values.

spring, followed by consistently low levels during the late summer and fall (Stanistreet et al., 2018). The same study described a seasonal peak in sperm whale click occurrence being evident later in the year at HARPs North of Cape Hatteras. Cohen et al. (2022, 2023) also used HARPs in similar positions but over a different timeframe (2016–2019 cf. 2011–2015 in Stanistreet et al., 2018), and with more units deployed. They did not find evidence of a winter peak off North Carolina, and acoustic presence here was noticeably lower than for the recorders positioned further north. Rather, Cohen et al. (2022) identified the highest acoustic presence of sperm whales off the eastern seaboard at Hatteras in summer months. This pattern was also evident in another contemporary study using different recording units (Autonomous Multichannel Acoustic Recorders, AMARs) in slightly shallower waters (Kowarski et al., 2022). This study documented only an intermittent presence of sperm whales off Hatteras in winter months from 2017 to 2020. However, the authors note that overall, Stanistreet et al. (2018) detected whales in more months, a variation attributed to the fact that the recorders in that study were in deeper waters (800–970 m deep) compared to the study by Kowarski et al. (e.g. 300 m deep off Hatteras). Some of these differences may be due to inter-annual variation. However, the static acoustic recorders in all of the studies above were typically in waters shallower than those shown to have high sperm whale densities (Roberts et al., 2016; this study) and thus they may not fully capture the local prevalence of sperm whale clicks. A DSM modelling exercise using multiple datasets from shipboard and aerial surveys from 1998 to 2019 confirms a winter peak in March to May off Hatteras, moving northwards from June to November (Roberts et al., 2016, 2022).

Efforts to estimate the length of sperm whales encountered during the MAPS surveys, using both acoustic and photogrammetric techniques, suggest the total body length of most individuals was between 3.8 and 12.9 m (A. Clabaugh, pers. comm. December 2022). Only three individuals were estimated to be longer (14.4, 15.0 and 17.8 m respectively, derived using photogrammetry). Although the sex of these animals was not identified in the field, it would appear most encounters were of large aggregations of adult females, immature males, and calves that were occasionally visited by large males, as has been recorded in

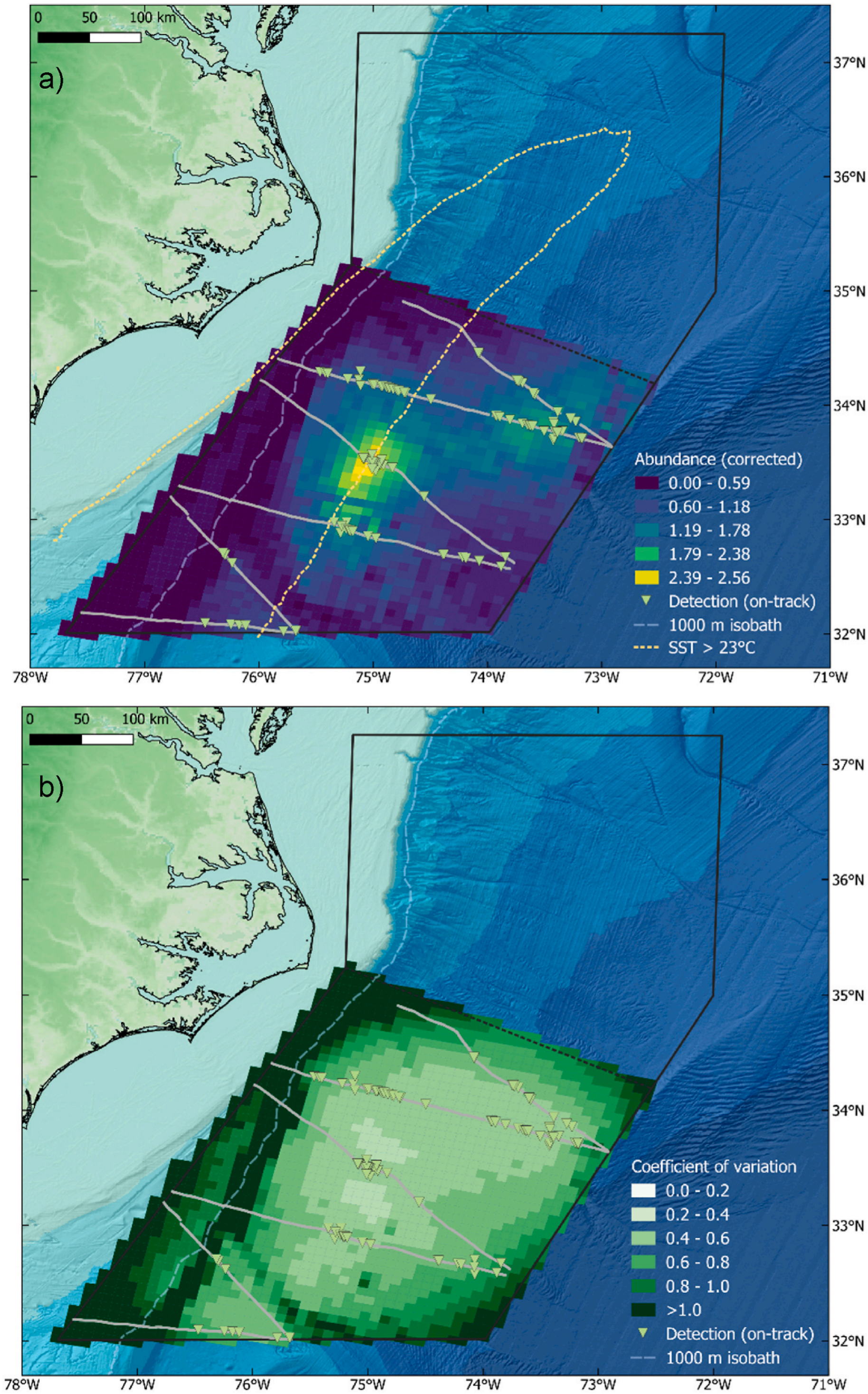

Fig. 7. Density surface map showing corrected abundance (above) and corresponding coefficients of variation (below) for the winter cruise. Abundances were corrected using the estimate of typical g (0). On-track sperm whale individuals are shown as green triangles (n = 115), segments with on-track acoustic effort are shown as grey lines. The Gulf Stream, shown as a dashed yellow line, is defined here as surface waters warmer than 23 °C.

other temperate areas (Whitehead, 2003).

4.1. Design-based abundance estimates

On-track acoustic detections of sperm whales far outnumbered on-track sightings in both cruises, with 115 vs. 25 individual whales in the winter cruise and 123 vs. 5 in the spring cruise, respectively. These results highlight the value of using acoustical methods to detect and quantify the presence of deep diving cetaceans, especially under inclement weather conditions. Because of the small number of visual sightings, only the acoustic detections were used for subsequent density estimation. Due to the uncertainty associated with estimating cluster size for widespread whales that are likely to be in acoustic range of one another, density estimation was made to the level of individual, rather than cluster. Including cruise identity in MCDS analysis suggested the detection probability of sperm whales varied between winter and spring;

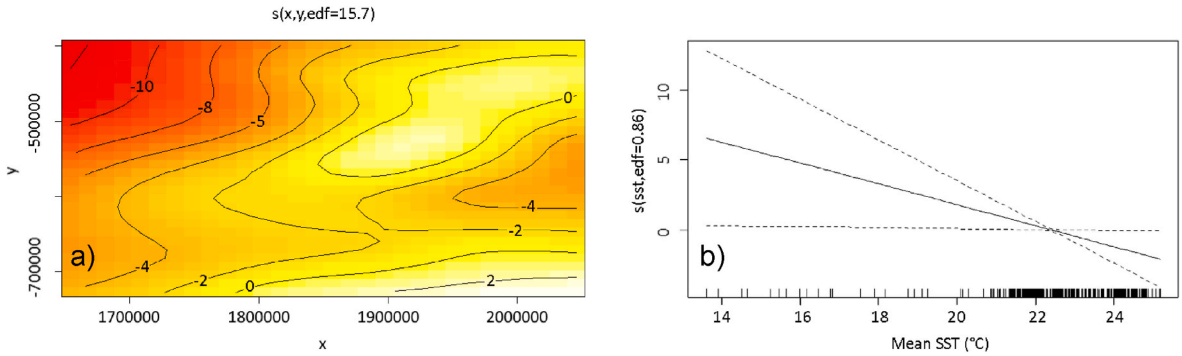

Fig. 8. Plot of the GAM smooth fit of density across (a) location and (b) mean SST (°C) in the spring cruise. The solid line represents the best fit, with the dashed lines representing 95% confidence intervals. Vertical lines on the x-axis are observed data values.

therefore, separate estimates were made for each cruise. A robust abundance estimate for the entire study area was only possible for the spring cruise, as not all ten designed transects were surveyed in winter. The spring abundance was 1610 whales (CV 0.31; CI 827–3137), when corrected with the 'typical' scenario for acoustic availability (see Table 2 for all results). However, if the density estimated for the first cruise were assumed to be representative of the whole study area, the winter abundance would be approximately 18 % higher, i.e. 1895 whales (CV 0.29; CI 915–3924).

Separate detection functions were fitted for each survey, in part because of the peak in the 730–1460 m bin evident in winter in Fig. 5; this peak necessitated a hazard rate key to ensure a wide shoulder that provided detection probabilities close to 1 for small distances. The under-representation of small distances is likely caused by the use of slant ranges in the analysis rather than corrected perpendicular distances (see below). In winter, lower SSTs were associated with an increased likelihood of detecting sperm whales (i.e. a broadening of the detection function). As the Gulf Stream interacts with cooler underlying waters in winter, it is possible that warmer surface waters cause the development of a more pronounced thermocline that could affect the acoustic pathway for near-surface sensors, as soundwaves refract towards slower (cooler) waters (Kinsler et al., 1982). Thus, SST had the potential to modify the scale of the winter detection function. In spring, a decrease in swell height was associated with a broadening of the detection function. The swell height estimates when sperm whales were encountered were typically higher in the spring survey (mean 0.63 m; CI 0.51–0.76) compared with the winter survey (mean 0.36 m; CI 0.27–0.44 m); elevated swell can increase surface 'heave', and subsequent changes in array depth will create hydrostatic pressure fluctuations that can increase background noise levels on near-surface sensors (Urick, 1983). Thus, swell had the potential to modify the scale of the spring detection function.

4.2. Model-based abundance estimates

The DSM procedure also generated abundance estimates but assumed sperm whale density varied across the survey area in response to specific environmental covariates. In addition to location (i.e. x-y bivariate), the final models for winter and spring incorporated mean slope and mean SST respectively. In winter, the model used accounted for only 32 % of deviance in the model (compared with 54 % in the spring) which may in part relate to only six of the ten transects being fully surveyed (generating 183 segments vs. 320 in the spring cruise). Despite not all transects being fully surveyed, the corrected winter DSM abundance estimate of 915 whales (CI 528–1586) was similar to that estimated using MCDS (1038; CI 514–2099). Likewise, the corrected spring DSM estimate of 1587 (CI 946–2663) was similar to the MCDS estimate (1610; CI 827–3137). When using the delta method to combine the uncertainties in the detection function and the GAM, the DSM estimates had slightly greater precision than the MCDS estimates (CVs of 0.286 vs. 0.289 in winter and 0.269 vs. 0.307 in spring, respectively), in part because they were able to provide density information at a finer spatial resolution. The DSM procedure also allows density heterogeneity along each transect to be considered, whereas the design-based approach treated each of the transects as equivalent. As the transects were typically long (108–354 km), the assumption that each transect is directly equivalent (in terms of sperm whale habitat provided) is unlikely to be valid and between-transect variation is often a large component of the variance in design-based estimate (Miller et al., 2013). Therefore, the DSM estimates may be considered more appropriate than the design-based estimates in this study.

4.3. Sperm whale habitat use

The DSM for the winter cruise suggested mean slope had a significant effect ($p < 0.05$) on the model, in addition to a bivariate of location, with detections typically made in regions of low slope (<2°; Fig. 10). Although not included in the spring DSM model, whales in the second cruise also tended to be detected in regions of low slope; the mean slope for detections made in spring (0.66°) was not significantly different to the mean slope in winter (0.61°) ($t_{236} = 1.43, p = 0.16$). Although steep slope has been found to be a key driver for sperm whale presence in other regions (Praca et al., 2009; Mannocci et al., 2015; Tepsich et al., 2014), the MAPS surveys support the findings from other studies that have not found such a strong influence (Waring et al., 1993; Pirotta et al., 2011; Breen et al., 2016; Claro et al., 2020; Vachon et al., 2022). However, it should be noted that several sperm whales were detected during MAPS on the continental slope during off-effort surveying, and as relatively little dedicated on-effort surveying was dedicated to that region, more effort should be spent there before concluding that the region only supports low densities of sperm whales.

It is possible that the presence of warmer Gulf Stream waters over the regions of steepest slope in the study area did not provide ideal habitat for sperm whales. This hypothesis is supported by the spring DSM, where mean SST was found to have a pronounced effect on ($p < 0.001$) sperm whale density, with most detections being made with SSTs lower than 23 °C (Fig. 10). Although not included in the winter DSM model, whales in the first cruise were also typically encountered in regions of lower SST; the mean SST for detections made in spring (22.2 °C) was not significantly different to the mean SST in winter (22.1 °C) ($U = 6{,}644$, $p = 0.42$). The sperm whales in the MAPS survey typically avoided regions of warmer water, preferring to forage in the cooler waters marginal to the Gulf Stream. Other studies in the west Atlantic have had similar findings. For example, sperm whales from 36 to 42°N were typically seen close to the edges of warm core rings (Waring et al., 1993, 2001). Sperm whale habitat between 38 and 42°N has been described as being offshore of surface temperature fronts associated with the Gulf Stream (LaBrecque, 2016). A significant, positive relationship between sperm

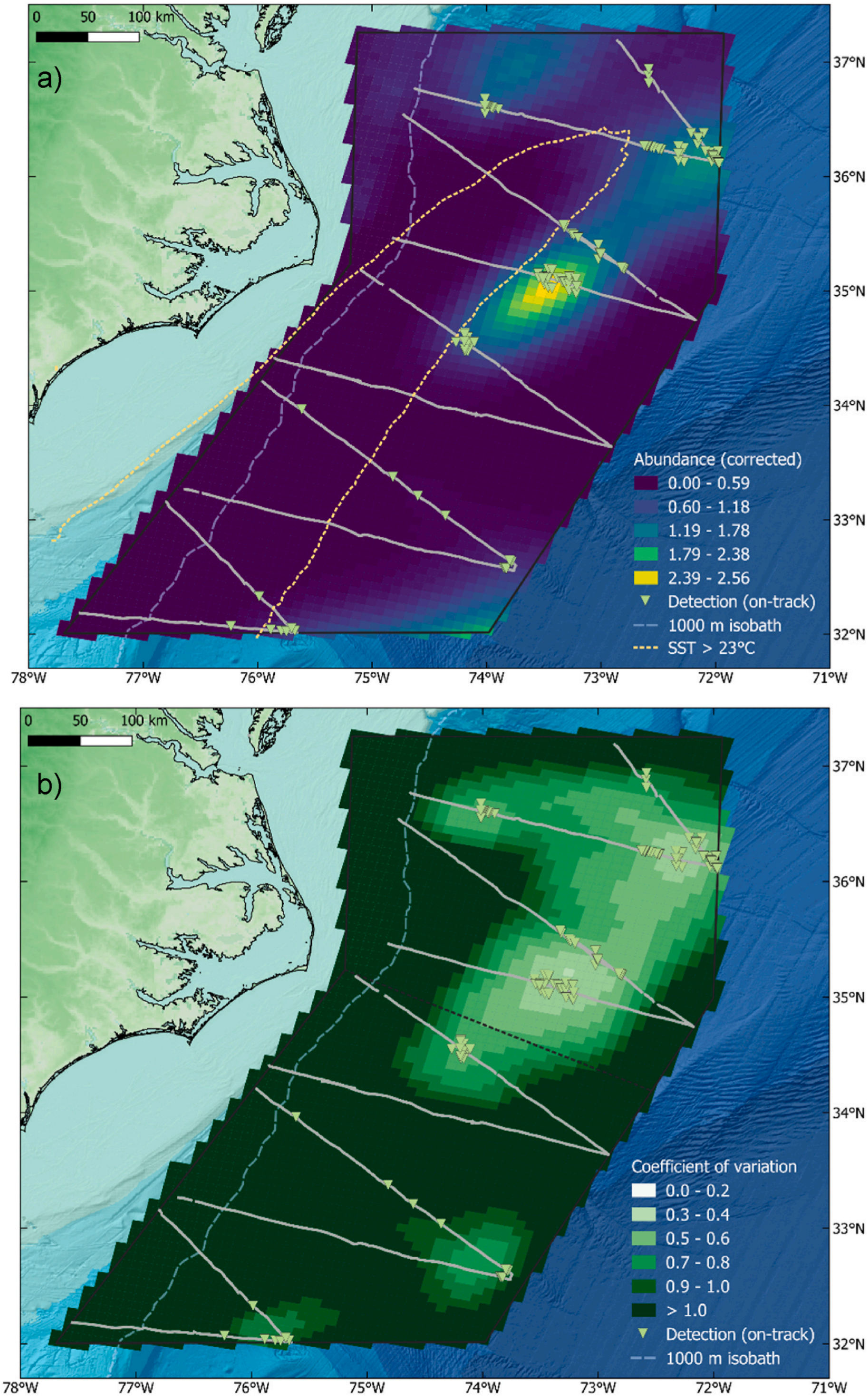

Fig. 9. Density surface map showing corrected abundance (above) and corresponding coefficients of variation (below) for the spring cruise. Abundances were corrected using the estimate of typical *g* (0). On-track sperm whale individuals are shown as green triangles (n = 123), segments with on-track acoustic effort are shown as grey lines. The Gulf Stream, shown as a dashed yellow line, is defined here as surface waters warmer than 23 °C.

whale prevalence and eddy kinetic energy (EKE) was noted for a nearby seamount (approximately 850 km to the northeast at 39°N 064°W), with high EKE being indicative of turbulence associated with eddies, fronts and Gulf Stream meanders (Wong and Whitehead, 2014). In the MAPS study area, the Gulf Stream off Cape Hatteras starts to meander at larger amplitudes and forms rings that have the capacity to transport their distinct biological, chemical, and physical properties to the new waters into which they travel (Schmitz, 1996), with the transport of the Gulf Stream nearly doubling downstream of Cape Hatteras (Knauss, 1969).

The MAPS surveys support other local studies by demonstrating that warm core rings, eddies and edges associated with the Gulf Stream attract sperm whales, as upwelling associated with turbulent boundary areas may attract and concentrate a wide range of prey. This pattern is reflected in the June 2022 update to the Habitat-based Marine Mammal Density Models for the U.S. Atlantic curated by the Marine Geospatial Ecology Laboratory, Duke University (Roberts et al., 2016) that

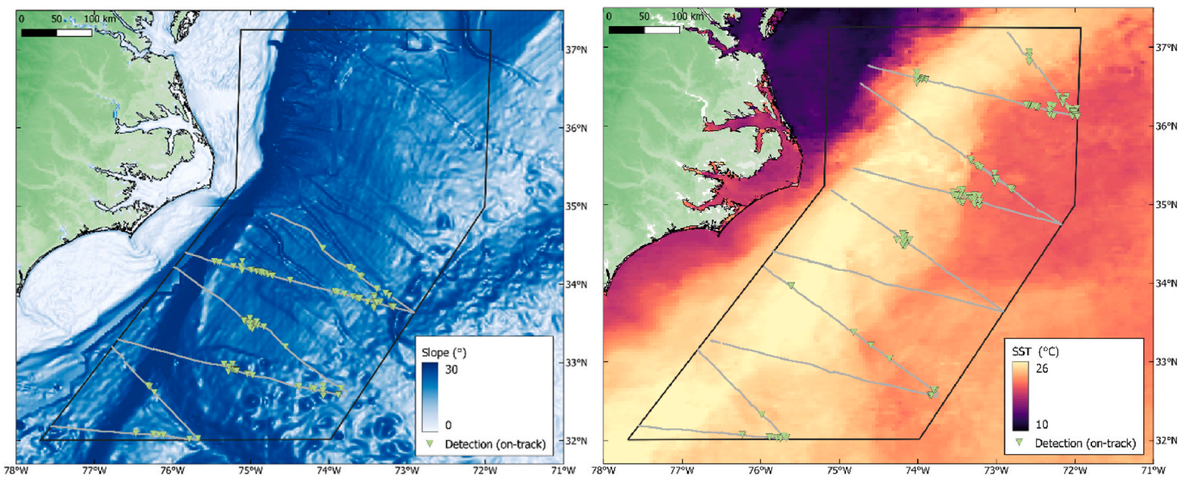

Fig. 10. Plots representing mean slope (°) throughout the study area (left) and mean SST (°C) in April 2019 (right). On-track acoustic effort is shown as a grey line for winter (left) and spring (right); on-track sperm whale detections are shown for each cruise as green triangles. Slope information provided by NOAA ETOPO1 (1.4 km resolution) and SST values provided by NASA MODIS (4 km resolution).

incorporates the MAPS data and shows high densities of sperm whales in the MAPS study area from February to May (Roberts et al., 2022).

4.4. Comparison of densities with other studies

Although comparisons of density estimates between studies using different methodologies and corrections for availability can be challenging, the approach can be useful for identifying seasonal trends or regions with unexpectedly high densities. The MAPS density and abundance estimates for winter and spring were typically higher than other estimates made from the eastern seaboard of the U.S. in summer months (Table 4). Sperm whale numbers for the northern sector (from approximately 36-42°N) of the Atlantic Marine Assessment Program for Protected Species project (AMAPPS) have been estimated as 1593 to 3321 (corrected for availability) in 2011 and 2016 respectively (Palka, 2012, 2020). Westell et al. (2022) used passive acoustic data from the same AMAPPS surveys to give a corrected estimate of 2199 whales. For the southern AMAPPS region (from approximately 28-38°N), uncorrected summer sperm whale abundances of 1028 to 2455 animals have been presented for 2016 (Garrison, 2020) and 2004 (Garrison et al., 2010) respectively. Combining the AMAPPS estimates, the 'best' recent estimate for the entire eastern seaboard has been 4349 whales for June–August 2016 (Hayes et al., 2020). A DSM analysis of the 2010 to 2013 AMAPPS surveys (Palka et al., 2017; Chavez-Rosales et al., 2019) gave a corrected summer abundance of 3667 sperm whales for the eastern seaboard; numbers were found to be higher in the spring (4,766) and not much lower in the fall (3,557). Due to low effort, winter data were not included in model development (Palka et al., 2017; Chavez-Rosales et al., 2019). Palka et al. (2021) used a similar DSM analysis of the AMAPPS eastern seaboard-wide data to give corrected abundances in spring of 2,536, in summer of 4,073, in fall of 3098 and in winter of 1778; the winter estimate was made with aerial effort only (i.e. no shipboard effort available) and effort was noticeably lower than other seasons (~10 % of total aerial effort).

The corrected DSM estimates presented in this study for both winter (915 whales) and spring (1587 whales) were high compared to the 'best' estimate of 4349 whales for summer along the entire US Atlantic coast (Hayes et al., 2020); if corrected for the area of each survey, the MAPS densities (measured as whales per 1000 km^2) were 10.46 in winter and 8.89 in spring, compared to AMAPPS global estimate of 3.64. The MAPS estimates for the two cruises are also high when compared to approximately equivalent time periods presented for the eastern seaboard from 1998 to 2019 (Roberts et al., 2022), namely a February estimate of 5516 whales (density = 4.33 per 1000 km^2) and an April estimate of 5776

Table 4
Summary of previous abundance (*N*) estimates derived for sperm whales of the eastern seaboard of the US.

Survey	Season	Year(s)	Latitude	Type	Analysis	N	g (0)	cv	Citation
MGEL	Jan	1998–2020	25-44°N	Visual/acoustic	DSM	5516	0.1–0.87	0.11	Roberts et al. (2022)
MGEL	April	1998–2019	25-44°N	Visual/acoustic	DSM	5776	0.1–0.87	0.11	Roberts et al. (2022)
AMAPPS	Jun–Aug	2004	28-38°N	Visual	MRDS	2455	Assumed 1	0.42	Garrison et al. (2010)
AMAPPS	Jun–Aug	2011	36-42°N	Visual	MRDS	1593	0.803	0.36	Palka (2012)
AMAPPS	Mar–May	2010–2014	25-44°N	Visual	DSM	4766	0.613	0.33	Palka et al. (2017); Chavez-Rosales et al. (2019)
AMAPPS	Jun–Aug	2010–2014	25-44°N	Visual	DSM	3667	0.613	0.14	Palka et al. (2017); Chavez-Rosales et al. (2019)
AMAPPS	Sep–Nov	2010–2014	25-44°N	Visual	DSM	3557	0.613	0.15	Palka et al. (2017); Chavez-Rosales et al. (2019)
AMAPPS	Mar–May	2010–2017	25-44°N	Visual	MRDS	2536	0.613	0.33	Palka et al. (2021)
AMAPPS	Jun–Aug	2010–2017	25-44°N	Visual	MRDS	4073	0.613	0.28	Palka et al. (2021)
AMAPPS	Sep–Nov	2010–2017	25-44°N	Visual	MRDS	3098	0.613	0.29	Palka et al. (2021)
AMAPPS	Dec–Feb	2010–2017	25-44°N	Visual	MRDS	1778	0.613	0.31	Palka et al. (2021)
AMAPPS	Jun–Aug	2016	36-42°N	Visual	MRDS	3321	0.613	0.35	Palka (2020)
AMAPPS	Jun–Aug	2016	36-42°N	Visual	MRDS	1028	Assumed 1	0.35	Garrison (2020)
AMAPPS	Jun–Aug	2016	25-44°N	Visual	MRDS	4349	Variable	0.28	Hayes et al. (2020)
AMAPPS	Jun–Aug	2016	36-42°N	Acoustic	CDS	2199	Assumed 1	0.15	Westell et al. (2022)
MAPS	Winter	2019	32-38°N	Acoustic	MCDS	1038	0.872	0.29	This study
MAPS	Winter	2019	32-38°N	Acoustic	DSM	1055	0.872	0.29	This study
MAPS	Spring	2019	32-38°N	Acoustic	MCDS	1610	0.872	0.31	This study
MAPS	Spring	2019	32-38°N	Acoustic	DSM	1587	0.872	0.27	This study

whales (density = 4.54 per 1000 km^2). However, as much of the offshore January–May survey effort (i.e. from the 1000 m isobath to the EEZ limit) used in the Roberts et al. models was derived from the MAPS surveys, it is likely that this region still remains underrepresented by winter/spring survey effort. In a much broader geographical context, Whitehead and Shin (2022) presented a corrected estimate of 92,085 sperm whales (CV 0.38; density = 2.47 per 1000 km^2) for the entire North Atlantic (37,229 km^2) in 1993. A similar analysis reported highest global densities (17.0 per 1000 km^2) in the western North Atlantic between the edge of the continental shelf and the Gulf Stream (Whitehead, 2002). Although much higher than the MAPS density estimates, this number highlights the continued importance of the 'Hatteras Ground' as a key sperm whale habitat in the global context.

4.5. Availability & slant range biases

It is essential to correct for availability if study animals are routinely absent from the surface (e.g. deep-diving cetaceans in visual surveys) or vocalise intermittently (e.g. most cetaceans in passive acoustic surveys). To correct for acoustic availability, the single DTAG deployed in the MAPS surveys was used to estimate the total click rate of sperm whales in the study area. Over four dives, deemed 'typical' diving behaviour, the focal whale produced regular echolocation clicks for 75 % of the tag deployment (the remaining time being silent). This is similar to other estimates that have suggested sperm whales vocalise throughout 60–80% of their dive cycles (Douglas et al., 2005; Miller et al., 2008; Teloni et al., 2008; Fais et al., 2016b). However, as the whale exhibited silent surface behaviour for more than half of the total tag deployment, an 'atypical' assessment characterised the whale as echolocating for only 38 % of the time. These parameters had a subsequent impact on the estimation of acoustic availability (0.872 vs. 0.600 for the typical and atypical scenarios). The estimates of density and abundance were therefore ~50 % higher if using the atypical correction in lieu of the typical scenario. A previous study investigating the foraging behaviour of six sperm whales in the western Atlantic did not present evidence of significant silent periods and/or drift-dives (Watwood et al., 2006), with the tagged animals vocalising for 68 % of dive cycles. As Miller et al. (2008) found only 53 % of tagged sperm whales performed drift-dives, it is not clear how often individuals perform acoustically inactive dives in the western North Atlantic, nor whether this is influenced by sex, age class or any other parameters. Until further robust estimates are made of vocalisation rate in the region, it is most prudent to use the density and abundance estimates corrected with the typical g (0) value.

Another potential bias in the analysis is the use of slant ranges rather than perpendicular distances to derive density estimates; a mismatch between slant ranges and perpendicular distances was evident in the spring detection function (Fig. 5), with small distances being underrepresented. A passive acoustic survey of the AMAPPS region in 2016 used depth estimates to correct slant ranges, with the subsequent perpendicular distances used in conventional distance sampling (Westell et al., 2022). Westell et al. (2022) found the use of corrected perpendicular distances resulted in a better fitting detection function that increased the abundance estimate by 12 %. However, other studies have suggested that when the perpendicular distances to detections are typically greater than the likely depth of the animal, the 'vertical ambiguity' can be accounted for by the detection function and has little impact on density estimation (Leaper et al., 1992, 2000; Lewis et al., 2018). The tagged whale in the MAPS study typically started vocalising at depths between 200 and 300 m, before reaching maximum bottom depths of approximately 1000 m (maximum depths for the four deep dives were 1065 m, 1136 m, 1083 m and 949 m respectively). Whales tagged by Watwood and colleagues (2006) in the western North Atlantic were typically in the 'bottom' phase of their dives at depths of 636–985 m. As mean slant ranges were 2937 m (CI 2466–3408) in winter and 2233 m (CI 1895–2570) in spring, the use of slant ranges as proxies for perpendicular distance may not introduce too much distortion into the detection functions. A previous modelling exercise for Mediterranean sperm whales found that for hazard-rate detection functions with high values (i.e. > 1000) of the scale parameter, σ, and values of the power parameter, β, between 1 and 5, the bias introduced by using slant ranges in lieu of perpendicular distances was negligible (Lewis et al., 2018). As the hazard rate detection function used in the spring model had parameter estimates of $\sigma > 3200$ and $\beta = 3.4$ respectively, it is likely that any bias introduced into the estimate of detection probability were minimal. It should be noted that Lewis et al. (2018) analysed data collected in European waters, and it is possible that the assumption of minimal bias may not be true for every population or habitat (Westell et al., 2022). As the study area considered by Westell et al. (2022) was in the north of the OCS of the United States, further consideration should be given to any bias introduced by the use of slant ranges in acoustic density estimation for this region.

5. Conclusions

The MAPS cruises found high densities of sperm whales in both winter and spring across the Outer Continental Shelf (OCS) of the U.S. Mid-Atlantic. As not all of the designed transects could be surveyed in winter, the spring abundance estimate is more likely to be a representative value for this region. As the DSM procedure provided estimates with smaller coefficients of variation and allowed heterogeneity in the environment to influence density estimation, it may provide a more robust approach than MCDS. Confidence in the density estimates could be further increased by correcting slant ranges with the depth of the vocalising animals (as in Westell et al., 2022). The spring DSM abundance estimate was 1587 (CI 946–2663), when corrected for 'typical' acoustic availability. The DSM results suggested that the high densities documented in spring were related to interactions between bathymetry and dynamic oceanographic variables, with sperm whales being most prevalent in marginal regions of the Gulf Stream characterised by warm core rings, eddies and edges. In terms of management, the International Whaling Commission recognizes one sperm whale stock for the North Atlantic; whether the west North Atlantic population is discrete from eastern North Atlantic whales is currently unresolved. Engelhaupt et al. (2009) found no differentiation in mtDNA between samples taken from the west North Atlantic and the North Sea, but did find significant differentiation between the Gulf of Mexico and from the Atlantic region just outside the Gulf of Mexico. These findings, and those from other studies, indicate stable social groups, site fidelity, and latitudinal range limitations may foster a predominance of female and juvenile groups in the region (Whitehead 2002), with more solitary adult males migrating out of the area to feed or moving among social groups to breed. As the OCS waters in the study area appear to provide an important foraging habitat for North Atlantic sperm whales, appropriate mitigation is required to ensure growing pressures to develop offshore energy infrastructure in the region do not negatively affect a species listed as Endangered under the U.S. Endangered Species Act.

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CRediT authorship contribution statement

Oliver Boisseau: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Doug Nowacek:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **D. Ann Pabst:** Writing – review &

editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Jason Roberts:** Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Ashley Blawas:** Writing – review & editing, Writing – original draft, Visualization, Validation, Formal analysis. **Anna Clabaugh:** Writing – review & editing, Writing – original draft, Project administration, Funding acquisition, Conceptualization. **Richard McLanaghan:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Anna Moscrop:** Writing – review & editing, Supervision, Project administration, Investigation, Funding acquisition, Conceptualization. **J. Jacob Levenson:** Writing – review & editing, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data associated with the project can be found at seamap. env.duke.edu/dataset/1999, seamap. env.duke.edu/dataset/ 2001, seamap. env.duke.edu/dataset/2055 & seamap. env.duke.edu/ dataset/2056.

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