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Habitat utilization by beaked whales in the western North Atlantic Ocean using passive acoustics

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ABSTRACT: Beaked whales (family Ziphiidae) are cryptic, deep-diving cetaceans found offshore. Passive acoustic monitoring of this family allows identification to species level and is instrumental in expanding knowledge of their behavior, distribution, and habitat use. From 28 June to 25 August 2016, 2 broadscale shipboard surveys towed a hydrophone array in the western North Atlantic. Concurrently, 11 bottom-mounted recorders collected continuous passive acoustic data along the 1000 m contour during July and August 2016. Five beaked whale species (goose-beaked, *Ziphius cavirostris*; Gervais', *Mesoplodon europaeus*; True's, *M. mirus*; Sowerby's, *M. bidens*; and Blainville's, *M. densirostris*) were present in both data sets. Beaked whales were commonly detected at the bottom-mounted sites (71% total days present), with sites off the US Mid-Atlantic Bight containing the greatest species diversity. Overall, daily co-occurrence was uncommon (35% of study period). Using the towed array, Blainville's and Gervais' beaked whales were found in the Gulf Stream, True's beaked whales were more common in abyssal waters, and Sowerby's beaked whales were more common on the continental slope. Goose-beaked whales were present throughout. Using multipath reflections, click depths were examined for 192 beaked whale detection events. Among 3 species tested (goose-beaked, Gervais', and True's), only goose-beaked whales were found to significantly forage in proximity to the seafloor. This is the first study of its kind to provide a comprehensive overview of how these whales utilize their habitat across latitudes, longitudes, and depths.

KEY WORDS: Beaked whales · Ziphiidae · Passive acoustic monitoring · PAM · Distribution · Gulf Stream · Shelf break front

1. INTRODUCTION

Cetaceans play diverse roles in marine ecosystems. For example, many baleen whale species are primary consumers (e.g. Würsig 1988), many toothed whales function as top predators, feeding on a diverse assortment of prey (Estes et al. 2016) (e.g. killer whales *Orcinus orca*, Estes et al. 1998, Matthews et al. 2020), some cetaceans also act as ecosystem engineers (e.g. Roman & McCarthy 2010, Roman et al. 2014), and almost all are important vertical integrators either through whale falls or by deep-sea foraging (Estes et

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al. 2016). While most cetaceans forage at relatively shallow depths (i.e. within the top 200 m of the water column, Panigada et al. 1999, Stewart 2009), cetaceans that forage at meso- and bathypelagic depths, such as the family of beaked whales (Ziphiidae), avoid competition and thereby decrease overlap with shallow-foraging species.

Beaked whales comprise the largest number of deep-diving cetacean species, with 24 confirmed species at present (IUCN 2022). The time they spend at the surface tends to be short (minutes), likely to avoid predation while recovering from deep foraging dives that extend past their aerobic dive limit (Tyack et al. 2006, Aguilar de Soto et al. 2020). While at the surface and during shallow dive sequences, many beaked whale species are cryptic, rarely vocalizing to avoid detection (e.g. Aguilar de Soto et al. 2012, Alcázar-Treviño et al. 2021, Visser et al. 2021). In contrast, they emit regular echolocation clicks below the thermocline during their deep foraging dives (Johnson et al. 2004, Tyack et al. 2006, Visser et al. 2021). These echolocation clicks have been well-characterized in the literature, are distinctly different in comparison to other odontocete species, and have been found to be species-specific (e.g. Baumann-Pickering et al. 2013, Stanistreet et al. 2017). Partly due to their anti-predator diving behavior, studying beaked whales using traditional visual surveys is challenging. They are visually inconspicuous at the surface, requiring low sea states (Beaufort <2) to be sighted without significant bias and highly experienced observers to identify them reliably to species (Barlow et al. 2006). Passive acoustic monitoring (PAM) approaches are able to bypass many of these issues and have become a highly effective methodology for documenting the spatio-temporal occurrence and densities of distinct beaked whale species, especially in remote areas (e.g. Hildebrand et al. 2015, Stanistreet et al. 2017, Barlow et al. 2021, McCullough et al. 2021, Rice et al. 2021, Cohen et al. 2022, Kowarski et al. 2023).

At present, there are 5 known beaked whale species which appear to exhibit latitudinal segregation in the western North Atlantic: northern bottlenose whales *Hyperoodon ampullatus* and Sowerby's beaked whales *Mesoplodon bidens* are found in cold temperate/subarctic waters, True's beaked whales *M. mirus* often inhabit warm temperate waters, and Blainville's *M. densirostris* and Gervais' beaked whales *M. europaeus* occur between warm temperate and tropical waters (MacLeod et al. 2006, Hayes et al. 2022). A sixth species, the goose-beaked whale *Ziphius cavirostris*, has a cosmopolitan distribution (MacLeod et al. 2006, Hayes et al. 2022), with PAM detections expanding the range observed through visual survey data to span Florida (USA) to Newfoundland (Canada) (Cohen et al. 2022, Kowarski et al. 2023, Delarue et al. 2024). The greatest presence of goose-beaked whales is off of Cape Hatteras, North Carolina, where a resident population occurs (Stanistreet et al. 2017, McLellan et al. 2018, Foley et al. 2021, Cohen et al. 2022). In PAM studies, Blainville's beaked whales were acoustically detected primarily off the coasts of Georgia and Florida, making this species the most southerly of all North Atlantic beaked whale species (Cohen et al. 2022, Kowarski et al. 2023), with few detections as far north as Cape Hatteras (Stanistreet et al. 2017). Northern bottlenose whales, in contrast, have only been acoustically detected in Canadian waters, although to date, no effort has been made to identify them acoustically in US waters (Stanistreet et al. 2017, Delarue et al. 2024). They have been sighted in US waters as far south as the abyssal waters off of Rhode Island. Sowerby's beaked whales were also detected and sighted in the more northerly regions, with elevated presence from Norfolk, Virginia, to Delaware, off of Georges Bank and the Scotian Shelf, with their presence extending as far north as Newfoundland (Stanistreet et al. 2017, Cohen et al. 2022, Hayes et al. 2022, Delarue et al. 2024).

In addition to the visual difficulties in distinguishing between *Mesoplodon* species, there are also difficulties with passive acoustics in distinguishing between Gervais' and True's beaked whales, especially if few clicks are detected, due to the similarities in the spectral content of their clicks (DeAngelis et al. 2018). If enough clicks are detected to calculate a 'stable' inter-click interval (ICI), distinguishing between the 2 species becomes possible. Stanistreet et al. (2017) found Gervais'-like clicks from Florida to Georges Bank, with the majority occurring off Onslow Bay, North Carolina. Kowarski et al. (2023) used a Gervais'/True's beaked whale class and found that this signal type predominantly occurred off of Savannah, Georgia. Cohen et al. (2022) used the ICI to distinguish between Gervais' and True's beaked whales and found the former to occur predominantly off the Carolinas, extending as far north as Cape Hatteras and within the Gulf Stream, and the latter northward of Cape Hatteras, outside of the Gulf Stream. These studies are all restricted to the slope waters of the western north Atlantic, and at present, there is little/no PAM effort published for the abyssal plain region further offshore; thus, longitudinal segregation has yet to be examined.

Many studies have examined the relationship between beaked whales and environmental variables through various species distribution models across the world over various timescales. These range from visual surveys (e.g. Virgili et al. 2021, Woo et al. 2023) or PAM-only studies (e.g. Hazen et al. 2011, McCullough et al. 2021) to ones that combine the 2 data sources (e.g. Feyrer et al. 2024). As summarized by Feyrer et al. (2024), despite the high number of environmental covariates that are included in the models, the most significant covariates are water depth, sea surface temperature (SST), and chlorophyll *a* concentration. Other covariates trying to encapsulate the bottom conditions experienced by beaked whales (e.g. temperature at depth, thermocline) or prey fields (e.g. backscatter) are important variables retained in these models, but do not contribute as much towards model significance. Which covariates to use in models and model selection are important questions to consider, and in general statistical models follow the principle of parsimony, selecting the lowest number of covariates without compromising model significance (Kuhn & Johnson 2013, Chowdhury & Turin 2020).

It is difficult to study the temporal partitioning of beaked whales as it requires long-term data sets. Visual data are typically collected during times of good weather (e.g. summer months) and thus have the capacity to provide inter-annual trends over set months. PAM can provide continuous yearly coverage, but requires periodic maintenance trips that are often in remote areas. Accruing PAM data results in large data sets that require refined automatic detection and classification systems (or manual analysis) to extract ephemeral beaked whale echolocation clicks to at least a daily resolution (e.g. Cohen et al. 2022, Solsona-Berga et al. 2024). Additionally, beaked whale echolocation clicks need to be abundant enough at a particular location such that seasonal models can converge (e.g. Cohen et al. 2023). Early PAM studies in the western North Atlantic and the North Pacific found limited temporal patterning of beaked whale presence, and no coordinated migratory movements as seen in baleen whale species (Baumann-Pickering et al. 2014, Stanistreet et al. 2017). A more recent PAM study in the North Atlantic did find localized areas of seasonality across the beaked whale species, with relatively high temporal co-occurrence between goose-beaked and Sowerby's beaked whales at Heezen Canyon at the northern tip of Georges Bank and at 2 sites in the mid-Atlantic, as well as between Blainville's and Gervais' beaked whales at Blake Spur in the southeastern US (Cohen et al. 2023). Thus, there appears to be spatio-temporal segregation of beaked whale species, though knowledge is restricted to areas along the shelf break.

This study coalesces data from 2 separate PAM efforts that occurred along the western North Atlantic waters off the USA, one using stationary bottom-mounted acoustic recorders placed along the North Atlantic shelf break and the other using a linear towed hydrophone array as part of a vessel-based line transect cetacean survey that covered both shelf break and abyssal waters. To date there has been limited coverage of the abyssal region of the western North Atlantic; this study will provide insights into the longitudinal distribution of multiple beaked whale species. In addition, this study will expand our knowledge of beaked whale ecology to species other than Blainville's and goose-beaked whales, along with identifying areas with more than 2 beaked whale species present, which could represent areas with more deep-sea resources that can support more nuanced segregation. Together these 2 methodologies provide new information on the temporal and spatial distribution of beaked whales, as well as their foraging depths, yielding a more comprehensive look at beaked whale ecology in this large region.

2. MATERIALS AND METHODS

2.1. Study area description

The study area encompassed the offshore waters (200–4000 m water depth from the shelf break to the US exclusive economic zone [EEZ]) of the western North Atlantic extending from Florida to just southeast of Nova Scotia. In this region, the Gulf Stream is an important current that influences the oceanography of the offshore region, flowing from the southern tip of Florida along the shelf break until Cape Hatteras, where it proceeds to flow further offshore (Fig. 1B; Atkinson 1977, Fratantoni & Pickart 2007). Along the shelf break north of Cape Hatteras flows a southward cool shelf break current (Fig. 1A). Between the Gulf Stream and the shelf break current is the slope water, which is a mixture of warm, salty slope water from the south and cool, less saline water from the north (McLellan 1957, Fratantoni & Pickart 2007). Additionally, the slope water can contain many warm core rings that branch off from the Gulf Stream, or cool, less saline incursions of shelf water that push the shelf break front further offshore. South of Cape Hatteras, many meanders and frontal eddies from the Gulf Stream occur, bringing upwelling and localized areas of high productivity to the South Atlantic Bight (Xue & Mellor 1993, Gula et al. 2016).

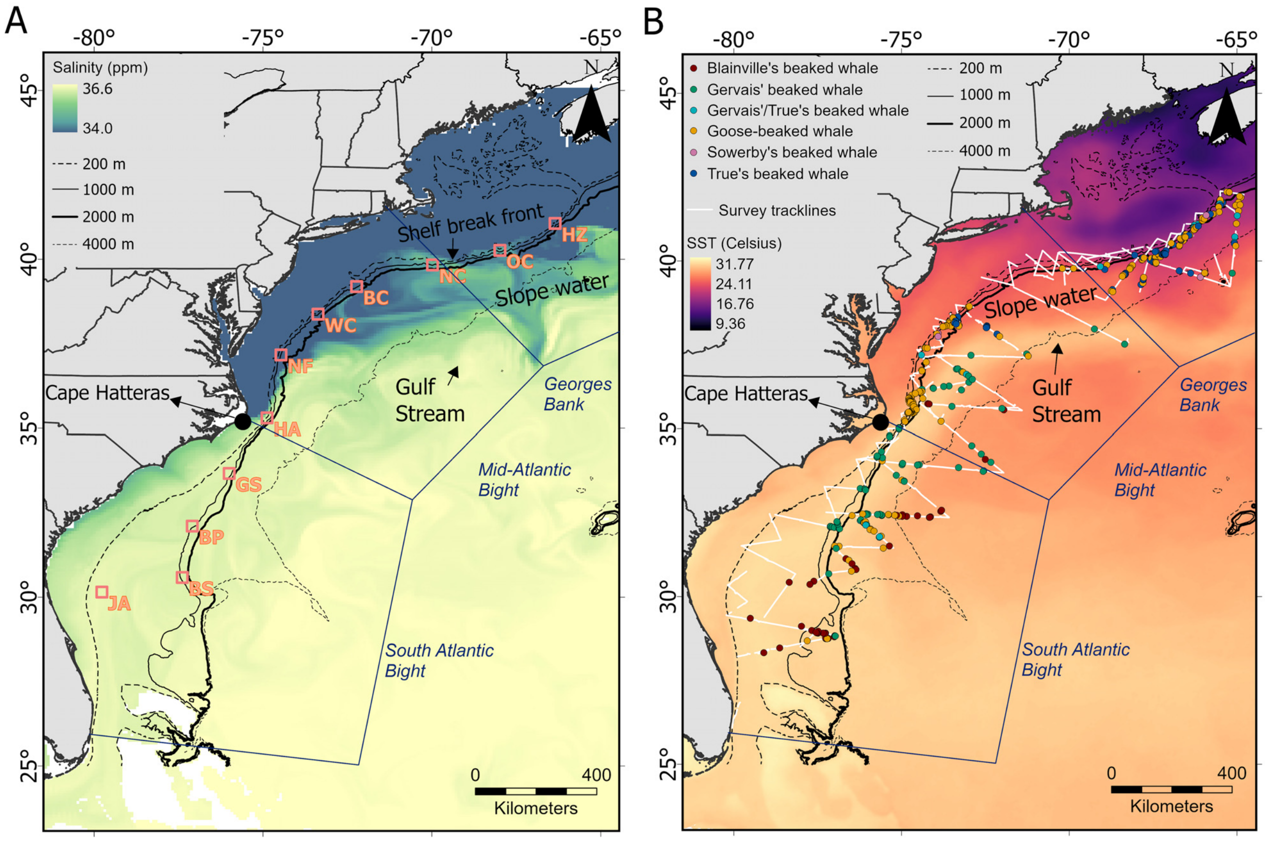

Fig. 1. Key features of the study area in the western North Atlantic. (A) The Gulf Stream is visible by salinity, shown in yellow, as well as the shelf break front, shown as the offshore edge of the dark blue area. Salinity for mapping purposes was extracted for the surface layer for 10 July 2016 from the Naval Research Laboratory's HYCOM+NCODA model from ERDAPP. The high-frequency acoustic recording package (HARP) sites are shown as squares; site abbreviations as in Table 1. (B) Sea surface temperature (SST) also shows the general path of the Gulf Stream. SST was extracted from ERDADPP from the NOAA ERD and CoastWatch West Coast Regional Node, jplMURSST41mday 0.01°for the month of July 2016. The beaked whale species-specific detections from the towed hydrophone array are overlaid as color-coded circles. In this map, the tracklines for both northern and southern surveys are combined as white lines and simplified to only show tracklines when the echosounders were in passive mode (off)

2.2. Acoustic data collection

From April 2016 to June 2017, 11 high-frequency acoustic recording packages (HARPs, Wiggins & Hildebrand 2007) were deployed near the 1000 m isobath along the western North Atlantic Ocean shelf break at 130–230 km intervals from the northern tip of Georges Bank, south to Florida (Fig. 1A, Table 1). These HARPs were placed at Heezen Canyon (HZ), Oceanographer Canyon (OC), Nantucket Canyon (NC), Babylon Canyon (BC), Wilmington Canyon (WC), Norfolk Canyon (NF), off of Cape Hatteras, North Carolina (HA), within the Gulf Stream (GS), Blake Plateau (BP), Blake Spur (BS), and off of Jacksonville, Florida (JA). Each HARP was bottom-mounted with a hydrophone located 10–30 m off the seafloor, depending on the mooring design. All HARPs recorded continuously at a sample rate of 200 kHz, and each hydrophone sensor was connected to custom-built preamplifier boards that were calibrated to achieve a flat (±2 dB) sensitivity of −200 dB re V/µPa from 10 Hz to 100 kHz.

In a separate effort from June through August of 2016, 2 shipboard surveys that were part of the Atlantic Marine Assessment Program for Protected Species spanned the east coast of the US shelf break to abyssal waters out just beyond the US EEZ (Fig. 1B, Table 1). These surveys were conducted concurrently on 2 NOAA vessels. The NOAA Ship 'Henry B. Bigelow' covered northern tracklines, from the southern tip of Nova Scotia, Canada, to waters off of Maryland, USA, and the NOAA Ship 'Gordon Gunter' covered southern tracklines, from

Table 1. Deployment information for both high-frequency acoustic recording package (HARP) and towed array data sets. The full HARP deployment timeframe is shown, although for analyses the data were truncated from 1 July to 31 August 2016. The Southeast Fisheries Science Center (SEFSC) survey data were downsampled from 500 to 192 kHz to make them comparable with the towed array data collected by the Northeast Fisheries Science Center (NEFSC). Dates are given as d.mo.yr

Site	Recorder type	Latitude	Longitude	Depth (m)	Sample rate (kHz)	Data start	Data end	Analysis days (n)
Heezen Canyon (HZ)	HARP	41.0618	−66.3516	845	200	22.04.16	19.06.17	62
Oceanographer Canyon (OC)	HARP	40.2633	−67.9862	450	200	24.04.16	18.05.17	62
Nantucket Canyon (NC)	HARP	39.8324	−69.9821	977	200	21.04.16	24.05.17	62
Babylon Canyon (BC)	HARP	39.1911	−72.2287	1000	200	20.04.16	10.06.17	62
Wilmington Canyon (WC)	HARP	38.3742	−73.3707	1000	200	20.04.16	29.06.17	62
Norfolk Canyon (NF)	HARP	37.1665	−74.4666	968	200	30.04.16	28.06.17	62
Cape Hatteras (HA)	HARP	35.3018	−74.8790	1021	200	29.04.16	06.02.17	62
Gulf Stream (GS)	HARP	33.6656	−76.0014	953	200	29.04.16	27.06.17	62
Blake Plateau (BP)	HARP	32.1060	−77.0943	945	200	28.04.16	27.06.17	62
Blake Spur (BS)	HARP	30.5838	−77.3907	1005	200	27.04.16	26.06.17	62
Jacksonville (JA)	HARP	30.1518	−79.7702	736	200	26.04.16	25.06.17	62
NEFSC HB1603 Leg1	Towed array				192	28.06.16	13.07.16	6
NEFSC HB1603 Leg2	Towed array				192	19.07.16	03.08.16	8
NEFSC HB1603 Leg3	Towed array				192	11.08.16	24.08.16	7
SEFSC GU1605 Leg1	Towed array				500	01.07.16	14.07.16	5
SEFSC GU1605 Leg2	Towed array				500	20.07.16	04.08.16	16
SEFSC GU1605 Leg3	Towed array				500	10.08.16	24.08.16	14

the area south of Maryland to Florida. Both vessels surveyed at a speed of 10 knots. Linear towed hydrophone arrays were deployed from both vessels to collect passive acoustic data primarily during daylight hours (06:00−18:00 h EDT), with some opportunistic sampling during the night. The array towed in the northern survey was comprised of 2 modular oil-filled tubes with 3 hydrophones at the fore separated by 30 m of cable, followed by an aft tube containing 5 hydrophones and a Keller PA7FLE depth sensor (Keller America), as described by DeAngelis et al. (2018). The last 2 hydrophones in the aft section of the array were used for data analysis. These were HTI-96-Min hydrophones (High Tech, Inc.) with a flat frequency response from 1 to 30 kHz (−167 dB re V/μPa ± 1.5 dB) and a heightened sensitivity of 6 dB from 30 to 70 kHz (see 'standard hydrophone' curve in Wildlife Acoustics 2017). These hydrophones sampled at 192 kHz and were spaced 1 m apart. The array in the southern survey was similar in most aspects except for the hydrophone models, which were Teledyne RESON TC4013 sensors with a flat frequency response from 5 to 160 kHz (−212 dB re V/μPa ± 2.0 dB) that sampled at 500 kHz. The northern towed array data set was digitized using a National Instruments USB-6356 A/D card while the southern towed array data set was digitized using a custom 12-channel SailDAQ A/D card (SA Instrumentation), and both data streams recorded directly to a computer using the acoustical software PAMGuard (Gillespie et al. 2009). A high-pass filter set at 1 kHz (northern) and 5 kHz (southern) was used by the recording system to reduce the amount of ship and flow noise in the recordings, and 10 dB gain was added to the HTIs and 50 dB gain added to the RESONs by each respective system (Palka 2016).

Visual data were collected using high-powered binoculars (25 × 150), and oceanographic and prey data collection included bongo tows, CTD casts, midwater trawls, and echosounders, the latter of which are used to map prey fields used as a covariate in the modeling of cetacean abundance (Palka et al. 2021). These consisted of multiple frequencies pinging in sync every 6 s as described by Cholewiak et al. (2017). On the northern survey, the echosounders were switched into active mode (on) every other day during daylight hours and were in passive mode (off) during opportunistic night-time passive acoustic sampling. On the southern survey, echosounders were only switched into active mode at night when no passive acoustic recordings were collected. As echosounders have been shown to elicit an acoustic behavioral response from beaked whales in our survey area (Cholewiak et al. 2017), we have only included time periods and corresponding tracklines for when the echosounders were in passive mode (Fig. 1B). Besides logging sightings information on cetaceans, the marine mammal observers recorded environmental conditions (e.g. sea state) every 30 min while they were surveying (Beaufort <6 and no rain or fog).

2.3. Acoustic data processing

2.3.1. Species classification

Beaked whale echolocation clicks can be easily distinguishable from other odontocete echolocation clicks by the presence of a frequency-modulated upsweep (Baumann-Pickering et al. 2013). The echolocation clicks of most known North Atlantic beaked whale species have their main energy between 30 and 50 kHz, except for northern bottlenose whales (20–40 kHz) and Sowerby's beaked whales (60–80 kHz, DeAngelis et al. 2018); discriminating between species was done by examining the spectral content of their clicks along with their ICI (Table S1 in the Supplement at www.int-res.com/articles/suppl/m754p137_supp.pdf). Most species' clicks are distinguishable by reviewing these features; however, in cases where few clicks are detected, there is some ambiguity in the spectral content between True's and Gervais' beaked whales due to variability caused by the directionality of their clicks (e.g. Zimmer et al. 2005), combined with an unreliable modal ICI (see DeAngelis et al. 2018). In these instances, a joint Gervais'/True's beaked whale classification category was used.

2.3.2. HARP analyses

HARP data were truncated to span July and August 2016 to overlap with the towed array data. Data from 3 of the 11 HARP sites (NC, HA, and JA) were analyzed using a 2-stage detection and validation process as described by Baumann-Pickering et al. (2013). A click detector was run to extract candidate beaked whale clicks and the output from the click detector was manually validated using the process described by Stanistreet et al. (2017), where clicks that matched the spectral characteristics of beaked whales and were no more than 5 min apart were grouped together into detection events. Acoustic data from the 8 other HARP sites were run through the SPICE detector (https://github.com/MarineBioAcousticsRC/Triton/wiki/SPICE-Detector) using MATLAB (MathWorks) (Frasier 2021). The difference between the 2 detectors was negligible, as subsequent criteria (requirement of >7 clicks in 1 min) excluded low-amplitude, off-axis clicks that were few in number. The output from the SPICE detector was then run through a custom MATLAB script that extracted all likely beaked whale clicks based on spectral and temporal characteristics (Baumann-Pickering et al. 2013). The resulting clicks were manually reviewed using the MATLAB-based program DetEdit (https://github.com/MarineBioAcousticsRC/DetEdit/wiki), which allows an analyst to review detections using figures displaying long-term spectral averages, waveforms, power spectral density, ICI, and measures of received level versus peak frequency (Solsona-Berga et al. 2020), which are similar reviewing displays to those used by Stanistreet et al. (2017). A threshold was set to display and review clicks that met or exceeded 118 $\mathrm{dB_{pp}}$ re V/μPa. Beaked whale clicks that matched the species-specific characteristics as described in the literature (Table S1) were then manually classified and grouped into detection events using a method similar to that of Stanistreet et al. (2017). Thus, while the 2 detection methods differed slightly, the subsequent grouping of closely spaced beaked whale clicks into detection events ensured compatibility between the 2 methods.

2.3.3. Towed array analyses

Towed hydrophone array data collected on the northern survey were processed using PAMGuard v.1.15.09 (Gillespie et al. 2009) and later updated to the newer PAMGuard v.2.00.14 for subsequent depth analysis. Data collected on the southern survey were processed using PAMGuard v.2.00.14 and were downsampled within PAMGuard to 192 kHz to mirror the sample rate used in the north. For both data sets, a basic click detector within PAMGuard was used, with a pre-filter and trigger filter set from 16 to 90 kHz. A trigger of 10 dB was used for the northern data set whereas a trigger of 8 dB was used for the southern data to account for the fact that the RESON hydrophones had a lower sensitivity than the HTIs. The data were reviewed using PAMGuard's Bearing-Time plot with a 2 min page window, where signals at 0° = forward of the array, 90° = in line with the array, and 180° = behind the array. As both the northern and southern arrays were linear, for beaked whales these angles represent conical angles. Clicks along similar bearings with a similar rate of change were grouped together into 'events', as these most likely represented a track of one echolocating animal. These events were classified to species using the ICI, waveform, power spectral density, and Wigner plots. Each event was labeled based on the total duration of the event, with '<2 min' not being suitable for depth estimation, and 'BWE2' being a beaked whale detection event ≥2 min long and therefore suitable for depth estimation (DeAngelis et al. 2017). All events, regardless of event duration, were localized using PAMGuard's Target Motion Analysis Module, 2D simplex optimization algorithm when possible, where the algorithm selects the location with the best chi-squared goodness of fit (DeAngelis et al. 2017). Those events labeled 'BWE2' were further analyzed for whale depth (see Section 2.6). If PAMGuard could not localize an event, then the GPS position of the vessel at the start of the event was used as its location.

2.4. Temporal patterns

To examine the daily co-occurrence of beaked whale species at each HARP site, individual click detections were binned to the daily level in a binary presence/absence metric by species. Only days in which at least 1 beaked whale species was detected were analyzed using conditional inference classification trees (Hothorn et al. 2006, Zeileis et al. 2008) within the statistical software R (R Core Team 2022) via the package 'partykit' (v. 1.2-20, Hothorn & Zeileis 2015). The resulting nodes of the classification tree therefore represented which species coexisted, and to what extent, at each of the HARP sites.

2.5. Spatial patterns

Using the towed array data, the acoustic presence of beaked whale species was examined relative to environmental covariates known to be significant in predicting beaked whale presence: bathymetry, SST, salinity, and chlorophyll. Using the coordinates of an event (either by localization or the GPS position of the ship), bathymetry was taken from the GEBCO bathymetric data set (https://www.gebco.net/data_and_products/gridded_bathymetry_data/) using QGIS (QGIS.org 2023). The continental slope was defined as the area between the 200 and 2000 m isobaths and the abyssal plain as the area offshore of the 2000 m isobath. The other covariates (SST, salinity, and chlorophyll) were obtained using the 'PAMpal' package (v. 0.19.1, Sakai 2023) in R, which searched the ERDAPP website (Simons & Chris 2022) for values that matched the timestamp and location of the beaked whale events. SST was gathered from the jplMURSST41 data set (daily resolution, https://www.ghrsst.org), salinity from the HYCOM models (0.125 d resolution, https://www.hycom.org/), and chlorophyll from the erdMBchla8day data set (8 d composite, coastwatch.pfeg.noaa.gov/erddap/griddap/erdMBchla8day.html). The resulting data set was then compared using conditional inference classification trees generated by the R package 'partykit,' where the resulting nodes displayed which species were associated with important delineations in the environmental variables and oceanographic features. These features can be characterized by salinity and chlorophyll, with the Gulf Stream known to contain low chlorophyll levels (<0.15 mg m^{-3}) and salinities >35 ppm (Rossby & Benway 2000, Schollaert et al. 2004, Reul et al. 2014), and the shelf break front characterized by salinities around 34.5 ppm (Linder & Gawarkiewicz 1998, Fratantoni & Pickart 2007).

2.6. Dive depth patterns

Following the methods described by DeAngelis et al. (2017), we used the presence of surface reflections of the beaked whale clicks to estimate their dive depths when detected in the towed array data sets. Only events labeled 'BWE2' were used, as those contained a long enough detection window to get reliable 2D localizations within PAMGuard. Custom scripts within the R package 'PAMpal' were used to automatically extract a waveform clip from the .wav files at the times of the annotated clicks, as well as to attribute the GPS position of the vessel, the hydrophone depth, the sea state at the time of the click (collected by the visual observers on the ship every 30 min), and PAMGuard's 2D localization positions (DeAngelis et al. 2023). These data were then imported into MATLAB to estimate the time difference of arrival between the direct click and its surface reflection, and subsequently estimate the depth of each beaked whale click. As all clicks within an event were run through this process, a filtering of the data was applied such that clicks that were within 30 s of each other had to be no more than 50 m apart (accounting for the published swim speed of ~1.5 m s^{-1} for beaked whales, e.g. Tyack et al. 2006) to minimize erroneous click depth measurements within the data. For each species, the weighted mean depth and weighted standard deviation were calculated following the equations in DeAngelis et al. (2017).

As in Westell et al. (2022), the water column was subdivided into 400 m bins down to the seafloor. For each event, the water column bin which contained the 90th percentile of the event's depths was recorded. If this bin included the depth of the seafloor, the event was labeled as 'in proximity' to the seafloor. Otherwise, the event was labeled as 'in the water column'. To test whether there was a significant difference in the number of events that were in proximity to the seafloor versus in the water column per species, a binomial generalized linear model (GLM) was implemented in R. Due to the relatively fast ship speed, the spatial coverage of the study area by the transect lines, and the short detection range of beaked whale clicks by a towed array (<3.5 km, DeAngelis et al. 2017), it was assumed that the events were independent and not temporally autocorrelated. For this test, the data were truncated to only events where the bathymetry was ≤3000 m, as this is the current maximum reported diving depth measured for beaked whales (Schorr et al. 2014, Shearer et al. 2019) (thus 'in proximity' to the seafloor would have been less probable).

Fig. 2. Daily presence of beaked whale detections across 10 of the 11 HARP sites, shown from north (top) to south (bottom) from 1 July to 31 August 2016. No beaked whales were detected at JA (southernmost site) during the study period. See Table 1 for site abbreviations

3. RESULTS

Between 1 July and 31 August 2016, each of the 11 HARPs individually recorded a total of 1488 h of passive acoustic data. For the shipboard survey data, only those periods in which the echosounders were not active were used for this analysis. Within that data set, the northern shipboard survey recorded a total of 281.85 h, and the southern shipboard survey recorded a total of 428.55 h. Five beaked whale species were present in each data set: goose-beaked, Gervais', True's, Sowerby's, and Blainville's beaked whales; in addition, we also had a sixth Gervais'/True's beaked whale combined category. Although the detector used for the HARP data set was not designed to detect northern bottlenose whale clicks, the detector used for the towed array data sets was configured to detect this species. However, no clicks matching those described as belonging to northern bottlenose whales (Clarke et al. 2019) were detected in the towed array data sets.

3.1. Temporal patterns

Beaked whale species were detected at 10 of the 11 HARP sites (with none at JA; Fig. 2). Of these 10 HARPs (n = 620 cumulative recording days; Table 1), beaked whales were acoustically present on a total of 440 d (71%). At least 2 beaked whale species were detected at 9 sites, and 4 sites had detections of 3 or more species during the recording period. BC had the greatest number of species present (n = 4), WC and BP had the most days with beaked whales present (98%, n = 61 d each), and OC had the fewest days with beaked whales present (21%, n = 13 d). Sites with near-continuous daily Sowerby's beaked whale presence were HZ and WC; goose-beaked whales were present nearly continuously at HZ, WC, and HA; and Gervais' beaked whales were present nearly continuously at GS and BP, and through the beginning of August at HA. True's beaked whales mainly occurred in July through the beginning of August at NC, BC, and WC. Blainville's beaked whales were intermittently present at BS.

Days with only a single species of beaked whale detections present were more common (65% of days combining all sites) than days with multiple species detections (35% of days combining all sites). Species co-occurred at the daily scale at specific HARP sites, with WC and HZ containing the most co-occurrences of beaked whales (N = 40 and 39 d, respectively, Fig. S1 in the Supplement). Out of all beaked whale species, Sowerby's beaked whale was the one that most commonly co-occurred with other species, especially with goose-beaked whale at HZ (Node 8, N = 67 d). Gervais' beaked whale was the least likely to co-occur with other beaked whale species (Node 15, N = 150 d). At 2 sites (BC and WC), goose-beaked, Sowerby's, and True's beaked whales all co-occurred on the daily scale (N = 4 and 10 d, respectively), but sample size was too low to create a separate node. There were no other co-occurrences of 3 or more species besides this combination.

3.2. Spatial patterns

From the towed array data set, a total of 394 beaked whale events were detected from both northern and southern data sets, of which 333 could be localized using PAMGuard's Target Motion Analysis module (84.5%, Table 2). Most detections were of goose-beaked whales (n = 184 events). There were very few detections of Sowerby's beaked whale (n = 8). As it is difficult to distinguish between True's and Gervais' beaked whales acoustically, the environmental covariates of SST, salinity, chlorophyll, and bathymetry were reviewed for potential relationships. Of the 4 covariates, only SST was considered informative in distinguishing between the 2 species (Fig. 3; Figs. S2–S4 in the Supplement). True's beaked whale occurred in water temperatures between 20.8 and 26.4°C, and Gervais' beaked whale between 26.3 and 30.8°C. The Gervais'/True's beaked whale category exhibited a distinct bimodal distribution, with events aligning within each respective classified species' temperature range.

Table 2. Beaked whale detection events (BWEs) detected using the towed array data set. For each species, the table lists the event type as either <2 min or as 2+ min (BWE2), the total number of events in those categories, how the localization information was collected (Localization), and the maximum detection duration for BWE2 events only. Localizations labeled as 'Ship position' represent events that did not have enough clicks for Target Motion Analysis (TMA); for these, the ship's position at the time of the event was used. '2D' denotes events that were localized with TMA, but could not compute a dive depth; '3D' denotes events that were localized with TMA and have a dive depth estimated. –: not applicable

Species	Event type	Total number of events	Localization		Maximum duration (min)
			Ship position	2D (3D)	
Blainville's beaked whale	<2 min	9	6	3	–
	BWE2	35	1	34 (31)	18.37
Goose-beaked whale	<2 min	75	17	58	–
	BWE2	109	8	101 (82)	20.46
Gervais' beaked whale	<2 min	27	10	17	–
	BWE2	46	4	42 (38)	31.89[a]
Sowerby's beaked whale	<2 min	5	–	5	–
	BWE2	3	1	2 (2)	6.73
True's beaked whale	<2 min	19	5	14	–
	BWE2	51	9	42 (35)	15.71
Gervais'/True's beaked whale	<2 min	6	–	6	–
	BWE2	9	–	9 (4)	10.78

[a] One event had 3 individuals grouped together, as it was difficult to attribute all clicks to each of the 3 individuals. The next maximum detection duration for Gervais' beaked whales was 15.41 min

The resulting classification tree using the towed array data set and the environmental covariates of SST, salinity, and chlorophyll contained a total of 10 nodes (Fig. 4). Blainville's beaked whale only occurred in the leftmost 4 nodes (3, 5, 6, and 8), at low chlorophyll levels (≤0.10 mg m^{-3}) and mainly in warm water (>29.8°C). Gervais' beaked whales also occurred at the lowest chlorophyll levels, up to ≤0.14 mg m^{-3} (nodes 3, 5, 6, and 8), and in waters slightly cooler than Blainville's beaked whale. These low chlorophyll levels and warm waters align with what is reported as characteristics of the Gulf Stream (Reul et al. 2014). Sowerby's beaked whales mainly occurred in nodes with bathymetries ≤2010 m (nodes 11, 13, and 14) and around 34.2 ppm. The shelf break front in the western North Atlantic is characterized as having a salinity of 34.5 ppm (Linder & Gawarkiewicz 1998, Fratantoni & Pickart 2007). Thus, most of the Sowerby's beaked whale detections were in the shelf break front on the continental slope. There was some probability of Sowerby's beaked whales occurring in abyssal waters with relatively low SST values (node 18), resulting from a single Sowerby's beaked whale detection in the New England Seamount chain (Fig. 1). True's beaked whales were more common in nodes with deep bathymetries (nodes 17–19), representing abyssal areas (>2010 m), though they were predicted to be on the continental slope if salinities were ≤34.2 ppm or chlorophyll levels were between 0.14 and 0.38 mg m^{-3} (nodes 11 and 13). Goose-beaked whales were represented in each node, but mostly comprised node 13, which consisted of salinities >34.2 ppm, relatively medium

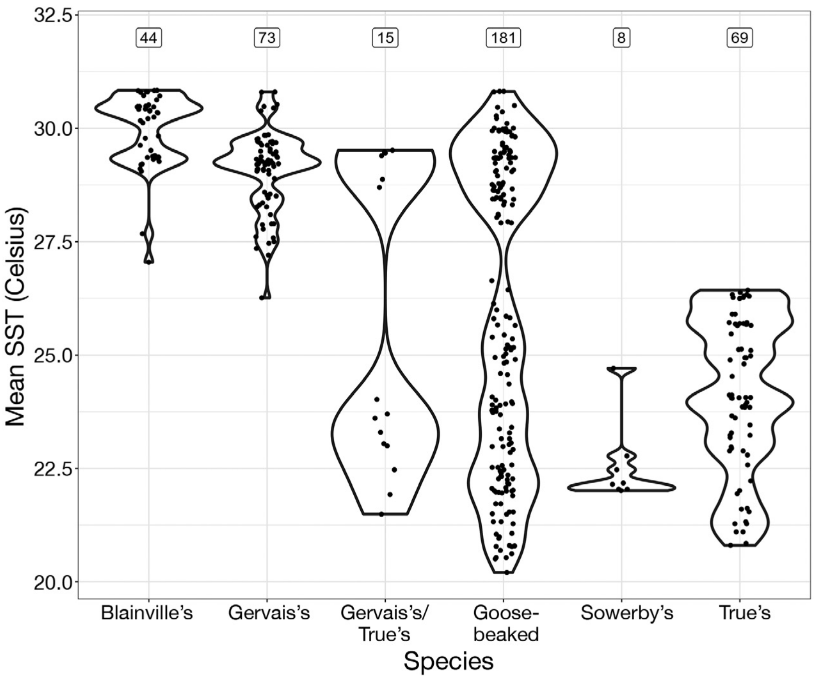

Fig. 3. Mean sea surface temperature (SST) values extracted from the jplMURSST41 data set at the location of towed array beaked whale events by species. Numbers at the top are the sample sizes for each beaked whale species

levels of chlorophyll (0.14–0.38 mg m^{-3}), and indicative of the continental slope (bathymetry ≤2010 m).

3.3. Dive depth patterns

Out of the 230 localized 'BWE2' events, 192 (83.5%) yielded dive depth estimates. For goose-beaked, True's, Gervais', and Blainville's beaked whales, there were over 30 events each in which dive depths could be calculated, while Sowerby's beaked whales had only 2 events (Table 2). The longest event duration was a 31.89 min detection of Gervais' beaked whale, but this event had multiple animals diving in close proximity to one another, so it was difficult to separate the bearings. As not all clicks recorded contained a multipath, the duration of the dive based on multipath clicks in most instances was shorter than the duration of the original event (see Appendix, Fig. A1). Regardless of the measured dive durations (which are likely to be underestimates of the full dive duration; see Appendix), all 192 'BWE2' events were used to examine the depth category across species (Fig. 5).

The weighted mean depths for Blainville's, Gervais', and True's beaked whales were between 870 and 960 m (Fig. 5). Weighted mean dive depths for Gervais' and True's beaked whales were 872 ± 321 and 939 ± 416 m, respectively, representing the first published dive information for these 2 species. The weighted mean depth was shallower for Sowerby's beaked whales (590 ± 93 m), but this is more likely a byproduct of the shorter detection range of Sowerby's beaked whales and the survey speed than a biological result. Goose-beaked whales had the deepest weighted mean depth (1116 ± 412 m). Truncating the data to bathymetries ≤3000 m

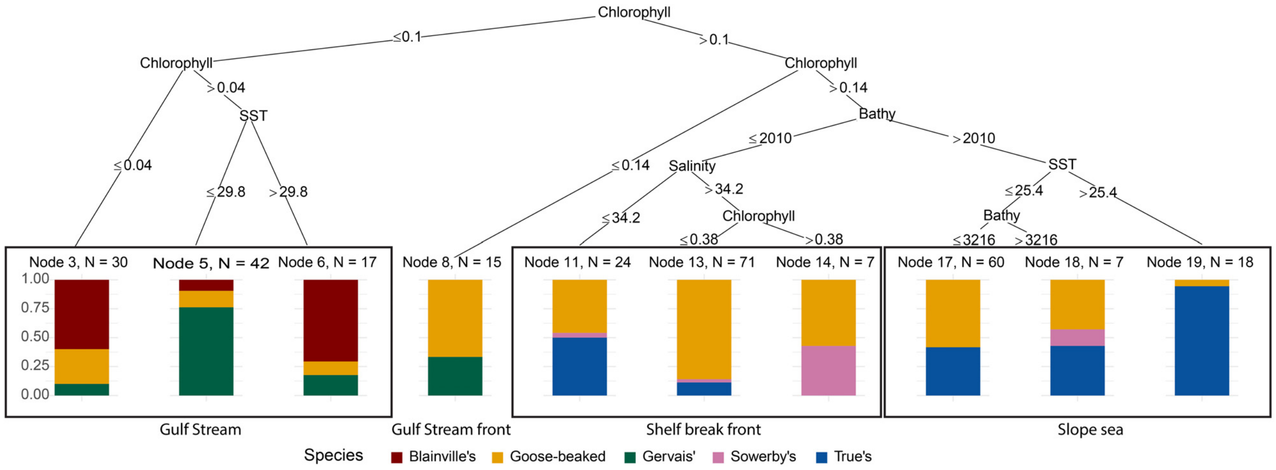

Fig. 4. Classification tree of the proportion of beaked whale species detection events from the towed hydrophone arrays with covariates bathymetry (Bathy), sea surface temperature (SST), salinity, and chlorophyll. Each node is labeled at the top left of each bar followed by the total number of beaked whale events (N) in that node. Beaked whale species are represented by colors

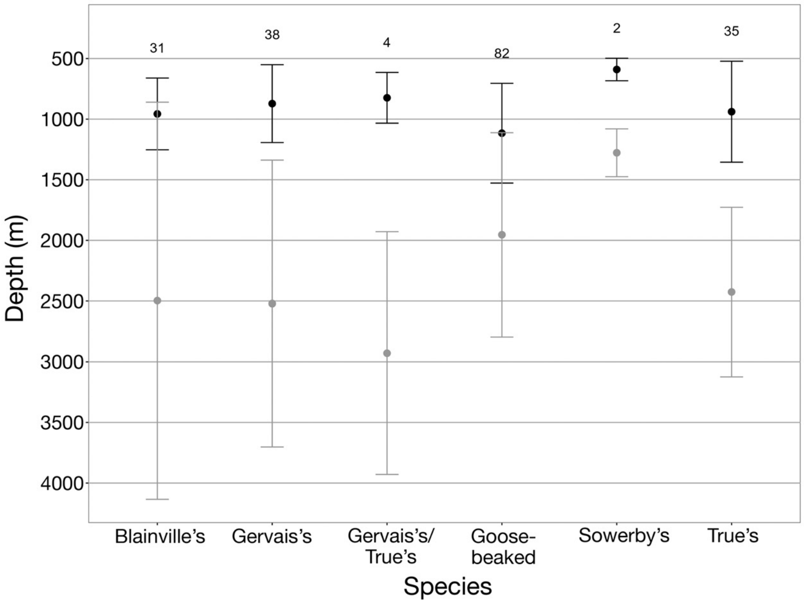

Fig. 5. Species weighted mean click depths with weighted standard deviations shown in black, and the mean and standard deviation of the seafloor per each species event shown in gray. The number of events used per species is shown at the top

excluded 4 goose-beaked whale events from the 'Seafloor' category, and did not exclude any *Mesoplodon* events (Table 3). Only Gervais', True's, and goose-beaked whales were used in the binomial GLM test, as they had large enough sample sizes and data in both 'in proximity to the seafloor' and 'water column' categories. Results from the binomial GLM comparison between species indicated significant differences (z = 5.114, $p < 0.0001$) only for goose-beaked whale. There was no significant difference in the number of events in proximity to the seafloor versus the water column for Gervais' (z = 0.848, p = 0.396) or True's (z = −0.192, p = 0.847) beaked whales.

Table 3. Number of beaked whale detection events from the towed array where the 90th percentile click depth was estimated to be in the same 400 m bin as the seafloor ('In proximity to seafloor') or in a different 400 m bin ('Water column'). The data set was subdivided into events located in ≤3000 m water depth, in which there is the physiological possibility of diving in proximity to the seafloor, versus those events located in >3000 m (and thus less likely to be in proximity to the seafloor). Only the samples listed as bottom depth ≤3000 m were included in the binomial generalized linear model (*), and species that had a significant difference ($p < 0.05$) are labeled with **

Species	Bottom depth ≤3000 m		Bottom depth >3000 m	
	Water column	In proximity to seafloor	Water column	In proximity to seafloor
Goose-beaked whale**	11	59	8	4
Blainville's beaked whale	0	16	15	0
Gervais' beaked whale*	9	13	16	0
Sowerby's beaked whale	0	2	0	0
True's beaked whale*	14	13	8	0

4. DISCUSSION

Two different passive acoustic platforms (stationary bottom-mounted recorders and towed hydrophone arrays) were used to examine the temporal, spatial, and depth distributions of beaked whale species during July and August 2016 in the western North Atlantic Ocean. The bottom-mounted data set showed that, while ephemeral, beaked whales are commonly present at the daily scale (71% of recording days) along the shelf break. For a given site, no more than 3 species were present on a given day, and most days contained only 1 or 2 species. Spatially using the towed array data set, certain species were more likely to be found on the continental slope (e.g. Sowerby's beaked whale) while others were more commonly detected in the abyssal plain (e.g. True's beaked whale). Lastly, beaked whale species exhibited differences in the depths at which they forage, with some found to dive more often in proximity to the seafloor in water depths ≤3000 m (goose-beaked whales), and others less so (True's and Gervais' beaked whales).

This study is unique in that it combines passive acoustic data from stationary bottom-mounted recorders and mobile towed hydrophone arrays to understand beaked whale ecology and distribution. Fregosi et al. (2020) utilized a mixture of mobile and stationary PAM platforms to cross-compare the detectability of beaked whales, but they could not address broader ecological concepts due to the short timeframe of the study (2 wk) and asynchronous deployments of the different platforms. In the US waters of the western North Atlantic, various bottom-mounted PAM studies have examined the distribution of beaked whales, but those efforts were focused along the 1000 m bathymetric contour (Stanistreet et al. 2017, Cohen et al. 2022, Kowarski et al. 2023). Here, we show that concentrating effort along this contour may bias our understanding of species distribution in the western North Atlantic. For example, from the towed array data set, True's beaked whales were predominantly found in abyssal waters (>2000 m depth, Fig. 4) and Blainville's beaked whales exhibited regional differences in bathymetric depths (e.g. present between 2000 and 4000 m depth at BP and GS but 1000 and 2000 m depth at BS and JA; Fig. 1A). Additionally, the HARP at OC was deployed at 450 m water depth as opposed to along the 1000 m contour. This most likely explains the low number of days present, as well as the paucity of beaked whale species detected (21% of days, Fig. 2). The HARP at JA was also at a shallower water depth of 736 m and located further inshore than the other southern HARP sites and resulted in no beaked whale detections during our study period. Recorder placement, therefore, is key in assessing the distribution of beaked whales (Cohen et al. 2022, Li et al. 2023), as their detectability is considered short range (~3.5 km, Hildebrand et al. 2015) and varies between species due to their differing frequency ranges and diving behavior (e.g. Visser et al. 2022). For example, Sowerby's beaked whales have a much higher-frequency click and undergo shorter dives (with a shorter vocal phase) than Blainville's beaked whales, resulting in 16% of the detection area of Blainville's beaked whales (Visser et al. 2022). This reduction in detection area could explain why there were fewer minutes for Sowerby's beaked whales on the HARPs than for the lower-frequency, longer foraging-dive species such as goose-beaked and Blainville's beaked whales. Using a larger time granularity, such as the daily scale that was also used here and in other studies (e.g. Stanistreet et al. 2017), can account for those differences. Future studies looking to assess beaked whale distribution via fixed bottom-mounted recorders should consider varied deep-water locations not focused on a single depth contour, and larger time granularities. In addition, more research is needed to quantify the detection ranges for each beaked whale species.

By combining the temporal and spatial acoustic platforms, we can assess the contemporaneous habitat use by these 5 species and assess the manner in which they differ in their habitat use in 3 dimensions over a large spatial scale. The goose-beaked whale is known as a cosmopolitan species, which was also seen in our study as having a presence from Georges Bank down to the Blake Plateau (Fig. 1A), and in all bodies of water (Fig. 4). Goose-beaked whales have been found to have a different trophic niche from the *Mesoplodon* species, primarily consuming cephalopods as opposed to meso- and bathypelagic fish (MacLeod et al. 2003, Santos et al. 2007). This trophic partitioning may be reflected in the depths at which goose-beaked whales forage. In this study, goose-beaked whales were more likely to forage in proximity to the seafloor than the *Mesoplodon* species. Some of the cephalopod prey species of goose-beaked whales are known to sit motionless or drift along the seafloor (Vecchione et al. 2001, MacLeod et al. 2003), which supports this finding. Goose-beaked whales co-occurred on the daily scale on the HARPs with all *Mesoplodon* species except Blainville's beaked whales. Based on their environmental preferences, goose-beaked and Blainville's beaked whales have the potential to overlap in the Gulf Stream (Fig. 4). This seemed to be rare during our study period, as from the towed array data, these 2 species overlapped in time only once and were located ~5 km apart (Fig. 1A). Goose-beaked and Blainville's beaked whales have been found to spatially partition themselves so that there is little overlap in their occurrence in the Bahamas and Hawaii (MacLeod et al. 2004, Claridge 2006, Baird 2019), which also seems to be the case in our study area along the US east coast. Perhaps including other covariates such as prey field indices could explain the spatial relationship between goose-beaked and Blainville's beaked whales; however, combining active and passive acoustic studies is challenging, as the beaked whales in our study area are sensitive to shipboard scientific echosounders (Cholewiak et al. 2017).

Blainville's beaked whales were detected in waters with low chlorophyll levels and high SSTs (Fig. 4), which translates to the Gulf Stream and possibly extends to the Sargasso Sea, which lies on the trailing edge of the Gulf Stream. Detections of Blainville's beaked whales occurred in deeper waters than those of goose-beaked whales (Fig. 1A), which is opposite to the spatial partitioning of these 2 species in the Bahamas and Hawaii. This could potentially be due to the presence of Gervais' beaked whale also preferring Gulf Stream waters, hence the need for more complex habitat partitioning. Both Blainville's and Gervais' beaked whales had infrequent instances of co-occurrence. It is unclear from our study what drives this segregation, and it would be of interest to examine its causes through future work.

Gervais' beaked whale detections aligned very well with the general track of the Gulf Stream (Figs. 1B & 4). Our study is limited to surveying within US waters; thus, it is possible that their range could extend further northeast within the Gulf Stream. This study presents the first published dive information of both Gervais' and True's beaked whales. Both species dove to similar depths and had similar vocal phase durations. Our method is limited by the vessel speeds used for cetacean abundance surveys; however, with slower vessel speeds it becomes possible to capture more of the foraging dives of beaked whales with towed hydrophone arrays (see DeAngelis et al. 2023). With more of the dive being detected, finer-scale trophic level questions can be addressed, such as the amount of time spent targeting the different prey layers, or the foraging method used (via measured swim speed). Tagging beaked whales remains a challenge, thus the ability to complement tag data with passive acoustic arrays will greatly enhance our knowledge of beaked whale foraging strategies and behavior.

True's beaked whales were predominantly found in the abyssal waters of the slope sea, but also occurred within the shelf break front (Fig. 4). True's beaked whales co-occurred with both goose-beaked and Sowerby's beaked whales. A diet study by Hernandez-Milian et al. (2017) categorized True's beaked whales as 'generalist' foragers due to the prey diversity found in the stomach contents. Being a generalist forager would lend itself well to co-exist with other deep-diving species, especially ones more specialized such as goose-beaked whales that target cephalopods off the seafloor, and Sowerby's beaked whales that target meso- and bathypelagic fish species (MacLeod et al. 2003, Wenzel et al. 2013). The areas in which these 3 co-occurred simultaneously in this study (BC, WC) lay within the shelf break front. Frontal zones are important areas that support a wide diversity of marine organisms due to the increase in advection and primary production (Jahn & Backus 1976, Olson & Backus 1985). This suggests that the Mid-Atlantic represents a highly productive and important ecosystem that can support multiple deep-sea predators, which may warrant more management protection.

5. CONCLUSION

PAM is an invaluable tool for collecting data on beaked whales that can complement data obtained through traditional methods (e.g. visual surveys, strandings), and provide new information on species distributions and habitat use due to the capability of discriminating detections to species and the capacity to record over long periods of time. Here, we demonstrated how different passive acoustic data sources can be used to examine the complexities of habitat segregation across 5 beaked whale species, providing additional details on their ecology and behavior, which is critical in understanding the management and conservation needs of this family.

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Appendix. Amount of beaked whale vocal phase analyzed

Beaked whales echolocate while undergoing deep foraging dives, but not all clicks received by the towed array will contain a viable multipath arrival to be used to estimate a whale's depth. Depending on many factors such as vessel speed, array depth, bathymetry, and properties of the thermocline, not all of the vocal phase will be captured by a towed array. This creates an inherent bias when using this method to understand diving behavior if the whole vocal phase is not captured. For 4 of the 6 North Atlantic beaked whale species, the average vocal phase is known from tagged individuals (goose-beaked = 33 min, Tyack et al. 2006; Blainville's = 25 min, Aguilar de Soto et al. 2020; Sowerby's = 18 min, Visser et al. 2022; True's = 18 min, D. Cholewiak unpublished data). Here, we show how much of the detected beaked whale event is used (Fig. A1a), as well as how beaked whale event durations compare to known vocal phase durations from tagged animals (Fig. A1b).

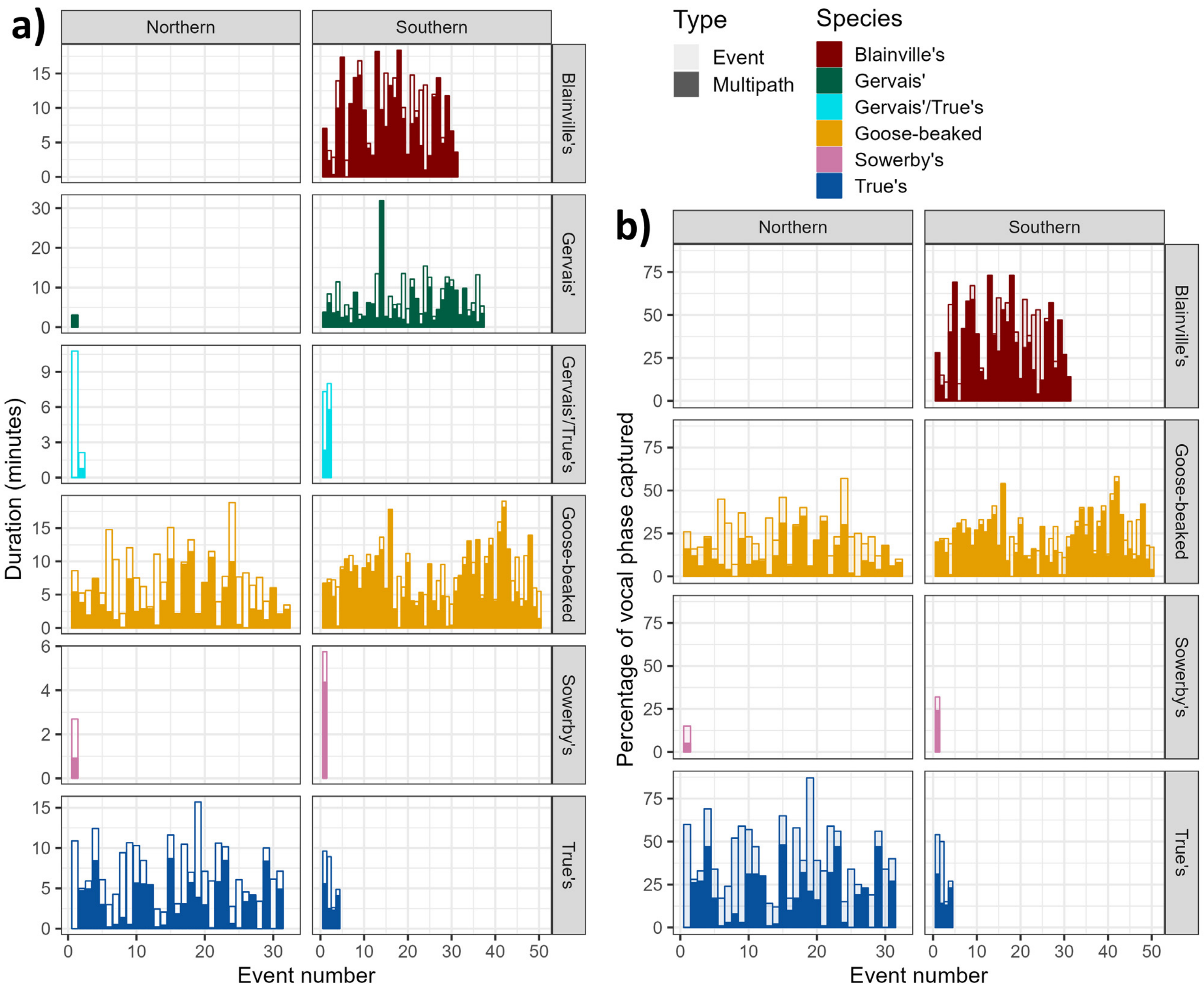

Fig. A1. (a) Duration of events detected by the towed array (unfilled bars) compared to the duration of the same event based on the clicks in which multipaths were present (filled bars). (b) Percentage of the vocal phase captured by the towed array both at the event (unfilled bars) and multipath (filled bars) level. The data are subdivided based on the survey (northern/southern)

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