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ARTICLE

Using passive acoustic monitoring to document the distribution of beaked whale species in the western North Atlantic Ocean

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Abstract: Little is known about the ecology of many beaked whale species, despite concerns raised by mass strandings linked to certain sources of anthropogenic noise. Here, we used passive acoustic monitoring to examine spatial and temporal patterns in beaked whale occurrence at six locations along the continental slope in the western North Atlantic Ocean. We analyzed 2642 days of recordings collected between 2011 and 2015, and identified echolocation signals from northern bottlenose whales (*Hyperoodon ampullatus*), Cuvier's (*Ziphius cavirostris*), Sowerby's (*Mesoplodon bidens*), Gervais', (*Mesoplodon europaeus*), and Blainville's (*Mesoplodon densirostris*) beaked whales, and one signal type of unknown origin. We recorded multiple species at each site, with detections generally occurring year-round, and observed latitudinal gradients and site-specific variation in relative species occurrence. Notably, we regularly detected Cuvier's beaked whales in a region where they have not been commonly observed, and discovered potential habitat partitioning among Cuvier's and Gervais' beaked whales within their overlapping ranges. This information on the distribution and seasonal occurrence of North Atlantic beaked whale species offers new insight into patterns of habitat use, and provides a year-round baseline from which to assess potential anthropogenic impacts.

Résumé : Les connaissances sur l'écologie de nombreuses espèces de baleines-à-bec sont limitées, et ce, malgré les préoccupations soulevées par les échouages massifs associés à certaines sources de bruit d'origine humaine. Nous avons employé la surveillance acoustique passive pour examiner les motifs spatiaux et temporels de présence de baleines-à-bec en six endroits le long de la pente continentale dans la partie ouest de l'Atlantique Nord. Nous avons analysé 2642 jours d'enregistrements réalisés de 2011 à 2015 et identifié des signaux d'écholocalisation de baleines-à-bec boréale (*Hyperoodon ampullatus*), de Cuvier (*Ziphius cavirostris*), de Sowerby (*Mesoplodon bidens*), de Gervais (*Mesoplodon europaeus*) et de Blainville (*Mesoplodon densirostris*) et un type de signal d'origine inconnue. Nous avons enregistré plus d'une espèce dans tous les sites, des détections étant généralement faites durant toute l'année, et observé des gradients latitudinaux et des variations dans chaque site de la fréquence relative des espèces présentes. Fait à noter, nous avons régulièrement détecté des baleines-à-bec de Cuvier dans une région où elles n'ont pas été fréquemment observées et découvert une possible division de l'habitat entre les baleines-à-bec de Cuvier et de Gervais dans leurs aires de répartition se chevauchant. Ces renseignements sur la répartition et la présence saisonnière des espèces de baleines-à-bec du nord-ouest de l'Atlantique jettent un nouvel éclairage sur les motifs d'utilisation de l'habitat et fournissent une référence à l'échelle annuelle pour l'évaluation d'éventuels impacts d'origine humaine. [Traduit par la Rédaction]

Introduction

Efforts to develop conservation strategies for elusive, rarely observed animals are often impeded by insufficient data and a limited understanding of species' biology and ecology. Beaked whales (family Ziphiidae) comprise one of the most species-rich families within the order Cetacea, with 22 described species (Committee on Taxonomy 2016), yet are among the most poorly understood large mammals on earth. This critical lack of information on the abundance, distribution, habitat preferences, and population structure of beaked whale species around the world is particularly concerning in light of the documented sensitivity of some beaked whales to certain types of anthropogenic noise (Cox et al. 2006; Weilgart 2007).

In recent decades, a number of mass strandings of beaked whales have been linked to human-generated noise, specifically mid-frequency active military sonar (D'Amico et al. 2009; Filadelfo et al. 2009). These events have raised concerns about the acute effects of anthropogenic noise on beaked whales (e.g., Parsons et al. 2008), and prompted substantial research into behavioral responses to various noise stimuli (Tyack et al. 2011; Pirotta et al. 2012; DeRuiter et al. 2013; Moretti et al. 2014). As this work begins to shed light on species-specific responses to acoustic disturbance, there is a fundamental need to improve baseline information on

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the spatiotemporal occurrence of beaked whale species, particularly in regions where potentially harmful noise exposure is likely to occur (Weilgart 2007).

Traditional survey methods based on direct visual observation can be ineffective for assessing the abundance and distribution of rare or elusive species, particularly in remote or inaccessible habitats and across broad geographic regions (Thompson 2004). Among cetaceans, beaked whales present a particular observational challenge. Distributed throughout the world's oceans, they primarily inhabit deep waters along and beyond continental shelf edges, and perform lengthy foraging dives to prey on deepwater squid and fish (Mead 2009). These dives can last more than an hour and exceed 1000 m in depth, with surfacing intervals as short as a few minutes (e.g., Baird et al. 2006; Tyack et al. 2006). Due to their offshore habitat and deep-diving behavior, beaked whales are notoriously difficult to observe from ships and aircraft, and sighting rates are often further constrained by weather and sea state. Barlow (2015) estimated that the probability of sighting beaked whales along a transect line during standard vessel-based surveys declines exponentially with increasing sea state, and may be lower than 0.2 in the conditions most commonly encountered offshore. Even in good survey conditions, the cryptic surface behavior and similar morphology of species, particularly in the genus *Mesoplodon,* make it difficult to identify animals to the species level (MacLeod et al. 2006; Pitman 2009).

In most species, the position of erupted teeth in adult males can be used as an identifying characteristic, but females and younger individuals lack this distinguishing feature. As a result, many beaked whale sightings are reported only to the genus or family level. The scarcity of beaked whale observations with confirmed species identifications has commonly led to the aggregation of data by genus, family, or larger ecological guild to increase statistical power in habitat modeling analyses (Waring et al. 2001; Davis et al. 2002; Ferguson et al. 2006; Roberts et al. 2016) and abundance estimation (Waring et al. 2014). However, there is evidence that beaked whales occupy ecological niches that are distinct from other deep-diving odontocetes, and that individual beaked whale species exhibit fine-scale habitat partitioning within overlapping ranges (Schick et al. 2011).

Understanding the basic ecology and distribution of individual species is an important step toward effectively managing their populations and mitigating the effects of anthropogenic disturbance. Passive acoustic monitoring (PAM) with autonomous, seafloor-mounted recording instruments is uniquely suited to gathering species-specific information on beaked whales over long time scales. Like other odontocetes, beaked whales use echolocation to find prey in the deep ocean environment; studies employing acoustic recording tags on beaked whales have revealed that they consistently produce echolocation clicks while performing deep foraging dives, typically throughout much of the dive duration (e.g., Tyack et al. 2006). Many beaked whale species produce stereotypical echolocation clicks with unique temporal and spectral characteristics, and recent studies have made important progress in describing and attributing these click types to specific species (Baumann-Pickering et al. 2013). These advances, combined with innovations in recording technology that allow the collection of broadband acoustic recordings over long deployment periods, have facilitated the use of PAM to effectively study the spatiotemporal occurrence of beaked whale species (e.g., Baumann-Pickering et al. 2014). PAM systems are not dependent on weather conditions and are a particularly useful method for monitoring remote regions and obtaining year-round data on species presence.

In the western North Atlantic, there are growing concerns about the effects of anthropogenic ocean noise on cetaceans, including noise generated by heavy shipping traffic along the eastern seaboard of the United States and Canada, naval training exercises employing mid- and high-frequency active sonar and explosives, and the exploration and development of offshore energy resources involving the use of seismic airguns. Six beaked whale species in three genera are known to inhabit this region: Cuvier's beaked whale (*Ziphius cavirostris*), the northern bottlenose whale (*Hyperoodon ampullatus*), Sowerby's beaked whale (*Mesoplodon bidens*), Blainville's beaked whale (*Mesoplodon densirostris*), Gervais' beaked whale (*Mesoplodon europaeus*), and True's beaked whale (*Mesoplodon mirus*). The geographic ranges of these species have been described in a preliminary manner, based substantially on stranding records (Macleod 2000; MacLeod et al. 2006), but their distribution and seasonality remain poorly understood, particularly for species in the genus *Mesoplodon*.

In this paper, we use multi-year PAM data to describe spatiotemporal patterns in beaked whale species occurrence along the continental slope in the western North Atlantic. Our objectives are to expand knowledge of the distribution of beaked whale species along the shelf edge and to generate baseline data on year-round species occurrence to inform future monitoring and mitigation efforts in this region.

Methods

Acoustic data collection

We collected high-frequency passive acoustic recordings between August 2011 and May 2015 at six sites in the western North Atlantic Ocean (Table 1; Fig. 1). The study region extended from Florida, USA to Nova Scotia, Canada, with recording sites located at ocean depths ranging from 800 to 1800 m. All sites were situated along the continental slope, with the northernmost site located inside the Gully, a large undersea canyon at the eastern edge of the Scotian Shelf.

At each site, we deployed either a High-frequency Acoustic Recording Package (HARP; Wiggins and Hildebrand 2007) or an Autonomous Multi-channel Acoustic Recorder (AMAR; JASCO Applied Sciences) to collect passive acoustic recordings. Both instruments are autonomous, bottom-mounted, archival systems that include an omni-directional hydrophone suspended approximately 12–55 m above the seafloor, and on-board electronics and hard drives for data storage. Each HARP was equipped with an ITC–1042 (International Transducer Corporation, Santa Barbara, California) sensor with a flat (±2 dB) sensitivity of –200 dB re $V \cdot \mu Pa^{-1}$ from 10 Hz to 100 kHz, connected to a custom built preamplifier board and bandpass filter (Wiggins and Hildebrand 2007). We corrected for the calibrated system response during analysis. Each AMAR was equipped with a GeoSpectrum M8 hydrophone with a nominal frequency response of –164 dB re $V \cdot \mu Pa^{-1}$ from 20 Hz to 170 kHz.

The data included in this paper were collected under the auspices of multiple long-term PAM projects with varying research objectives; as a result, there was variation in the sampling rates and recording schedules used, as well as in the timing and duration of instrument deployments (Table 1). Most of the recordings were collected at sampling rates of 200 kHz and above, providing a recording bandwidth of at least 10 Hz – 100 kHz, sufficient for detecting all known beaked whale signal types, which have peak frequencies between 16 kHz and approximately 70 kHz. The only exception was the first year of recordings from the mid-Gully site (MGL), which were collected at a sampling rate of 128 kHz, adequate for detecting all but one beaked whale signal type, which is higher in frequency (energy mainly between 65–70 kHz). This click type is attributed to Sowerby's beaked whale, and was not included in our analysis of the first year of recordings from MGL. During each HARP deployment, recordings were made either continuously or on a 50% duty cycle, while the AMARs were programmed to record at lower duty cycles due to limitations in data storage capacity (see Table 1 for details on each duty-cycled recording schedule). We analyzed all recording days for which data were available across a full 24 h period, and excluded partial recording days at the start and end of each deployment.

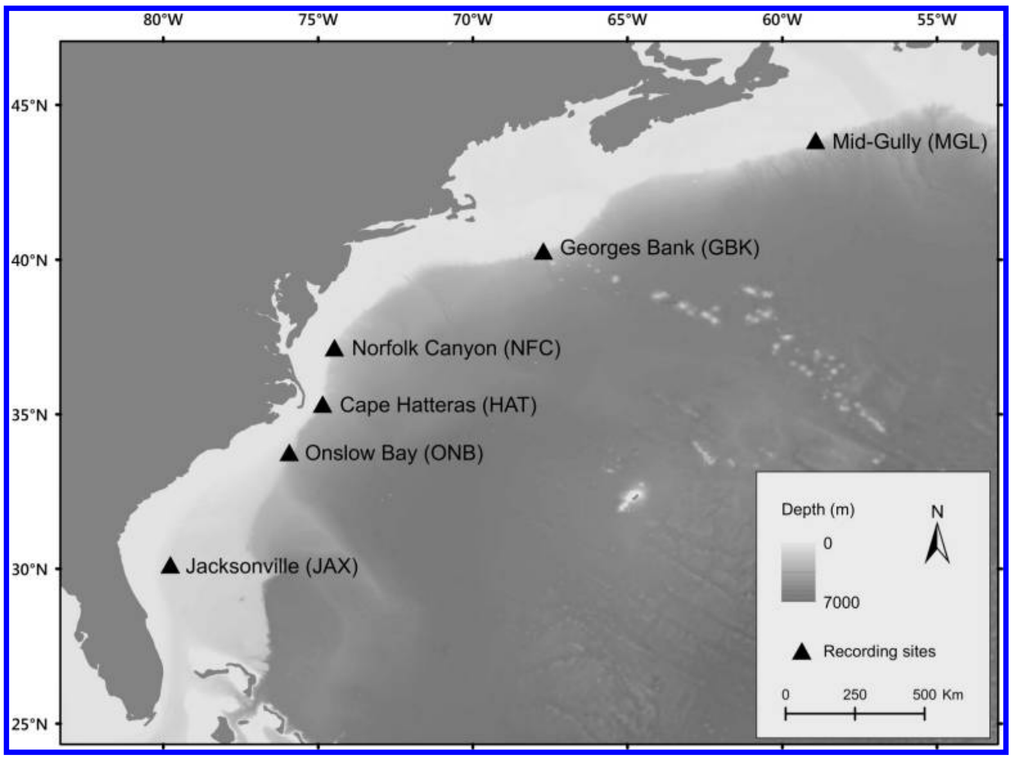
Table 1. Summary of passive acoustic monitoring (PAM) effort along the continental slope in the western North Atlantic between 2011 and 2015.

Site	Location	Instrument type[a]	Depth (m)	Recording dates	No. of recording days	Duty cycle[b] (mm:ss) (%)	Sampling rate (kHz)
Mid-Gully (MGL)	43.87°N, 58.92°W	AMAR	1780	12 Oct. 2012 – 10 Apr. 2013	179	2:00, 15:00 (13%)	128
			1580	8 May 2013 – 25 Sept. 2013	140	2:00, 15:00 (13%)	128
			1525	15 Nov. 2013 – 6 Apr. 2014	141	2:10, 20:00 (11%)	375
			1615	3 May 2014 – 26 Sept. 2014	145	2:10, 20:00 (11%)	375
Georges Bank (GBK)	40.29°N, 67.72°W	AMAR	800	27 Jul. 2014 – 26 May 2015	304	2:40, 30:00 (9%)	250
Norfolk Canyon (NFC)	37.16°N, 74.47°W	HARP	980	20 Jun. 2014 – 4 Apr. 2015	289	Continuous (100%)	200
Cape Hatteras (HAT)	35.34°N, 74.85°W	HARP	950	16 Mar. 2012 – 10 Apr. 2012	26	Continuous (100%)	200
			970	10 Oct. 2012 – 30 Apr. 2013	203	Continuous (100%)	200
			970	30 May 2013 – 14 Mar. 2014	289	Continuous (100%)	200
			850	9 May 2014 – 10 Dec. 2014	216	Continuous (100%)	200
Onslow Bay (ONB)	33.78°N, 75.93°W	HARP	950	19 Aug. 2011 – 30 Nov. 2011	104	5:00, 10:00 (50%)	200
			915	14 Jul. 2012 – 1 Oct. 2012	80	5:00, 10:00 (50%)	200
			850	25 Oct. 2012 – 29 Jun. 2013	248	5:00, 10:00 (50%)	200
Jacksonville (JAX)	30.15°N, 79.77°W	HARP	800	24 Aug. 2014 – 28 May 2015	278	Continuous (100%)	200

[a]Autonomous Multi-channel Acoustic Recorder (AMAR) or High-frequency Acoustic Recording Package (HARP).

[b]Duty cycle is calculated as the duration of the recording period (first value) divided by the cycle period (second value) in minutes and seconds and is additionally summarized by the percent recording time, shown in parentheses.

Fig. 1. Locations of passive acoustic recording sites along the continental slope in the western North Atlantic Ocean. Bathymetry data source: General Bathymetric Chart of the Oceans (GEBCO 2008).



Detection and classification of beaked whale signals

To detect and classify beaked whale echolocation signals, we used a multi-step approach based on the methods described in Baumann-Pickering et al. (2013). We performed all signal processing using the custom software program Triton (Wiggins and Hildebrand 2007) and custom-written MATLAB (Mathworks, Inc., Natick, Massachusetts) routines. First, we applied an automated detection algorithm to identify and extract individual echolocation clicks within each data set (see Soldevilla et al. 2008; Roch et al. 2015). Next, we applied a band-pass filter to each extracted signal, calculated spectra using 2.56 ms of Hann-windowed data centered on the click, and measured signal parameters including: peak and center frequencies, bandwidth, duration, signal-to-noise ratio, and inter-click-interval (ICI) between consecutive detections (Baumann-Pickering et al. 2013). To separate beaked whale clicks from other odontocete clicks, we applied a set of criteria based on spectral and temporal characteristics. Compared with echolocation clicks produced by other odontocetes, beaked whale echolocation clicks produced during the search phase of foraging dives are typically characterized by longer durations, consistent ICIs, and a frequency upsweep (Baumann-Pickering et al. 2013). We considered detected clicks to be potential beaked whale signals if they exhibited peak and center frequencies above thresholds of at least 32 and 25 kHz, respectively, durations of at least 0.355 ms, and frequency upsweeps with a sweep rate of at least 23 kHz·ms^{-1} (as in Baumann-Pickering et al. 2016). We then applied a set of duration-based criteria, requiring the waveform envelope of each click to increase over the first 0.1 ms and to remain above a 50% energy threshold for a duration of at least 0.1 ms for the click to be considered a potential beaked whale click. Detection criteria were applied in a consistent manner across all data sets, except for the peak and center frequency thresholds, which we reduced to 23 kHz during analysis of MGL recordings to ensure optimal detection of northern bottlenose whale clicks, which are lower in frequency than the other beaked whale signals recorded. While there are few existing records of northern bottlenose whales south of the Scotian Shelf (Wimmer and Whitehead 2004), we acknowledge that the frequency thresholds we initially applied may have resulted in the omission of northern bottlenose whale clicks by the detection system at the other recording sites, and we address this possibility in our discussion of the results.

For data sets comprised of continuous recordings, we grouped all potential beaked whale clicks into detection events based on the timing of their occurrence, defining a detection event as all potential beaked whale clicks separated by a gap of no more than 5 min between consecutive detections. In the case of duty-cycled recordings, we defined a detection event as all potential beaked whale clicks occurring within a single data file corresponding to the 2–5 min "on" period of the recording cycle. For each detection event, an experienced analyst (author JES) reviewed summary figures displaying histograms of peak frequency and ICI, a concatenated spectrogram of all clicks in the event, and a plot of mean click spectra overlaid on spectral templates of known beaked whale echolocation signal types (as per Baumann-Pickering et al. 2013). After examining these figures and browsing waveforms and spectrograms of individual clicks, the analyst assigned one or more species classifications to each detection event, or marked the event as a false detection. All detection events that did not have clear, unambiguous characteristics of beaked whale clicks were marked as false detections likely produced by other odontocetes, and these detections were excluded from the analysis. Among the remaining detection events, most consisted of clicks produced by a single beaked whale species; however, overlapping detections of multiple beaked whale species also occurred and were identified as such.

This multistep detection process has been extensively evaluated in previous studies and the rate of missed detections estimated to be approximately 5% (Baumann-Pickering et al. 2016). We spot-checked the detection results for each of our data sets by visually examining long term spectral averages (LTSAs; Wiggins and Hildebrand 2007) and spectrograms. We noted a few instances where the automated detection process failed to detect visible beaked whale clicks in the presence of strong background noise; however, beaked whale clicks that were not initially apparent during visual examination of LTSAs were also detected by the automated system, notably when they occurred amid intense bouts of echolocation from other odontocetes, a common occurrence at some of our recording sites. We were therefore not able to precisely characterize detector performance, but we considered the automated detection method comparable to or slightly better than manual analysis of LTSAs for estimating hourly and daily presence of beaked whale clicks, based on substantive qualitative comparisons of our detection results with LTSAs and spectrograms. Since the final step of this process involved manual review and classification of each detected event, we were able to largely eliminate false detections of non-beaked whale clicks. Classification decisions were made by an experienced analyst (author JES), and detections of unidentified or poorly known click types were reviewed by additional co-authors (SBP, HMM, DMC). We took a conservative approach to this analysis, excluding all detection events that could not be confidently identified to the level of species or recognized signal type, and our results should therefore be considered a minimum estimate of the presence of each beaked whale species or signal type at each recording site.

Analysis of spatial and temporal patterns

To examine spatial patterns in beaked whale acoustic presence across recording sites, we binned the manually classified beaked whale click events into daily presence or absence of each species. We compared species occurrence across sites by expressing the number of days each species was detected at each site as a percent of the number of recording days available. In addition, we compared the relative occurrence of species within each site by determining the percent of total daily beaked whale detections at each site attributed to each species. We performed these comparisons at the level of daily presence rather than on finer temporal scales to reduce potential bias in detection rates that may result from comparing data collected using different duty-cycled recording schedules. A detailed analysis of the effects of using duty-cycled recording schedules to detect different beaked whale species was performed by Stanistreet et al. (2016) using similar data sets, and we discuss these potential biases in our results.

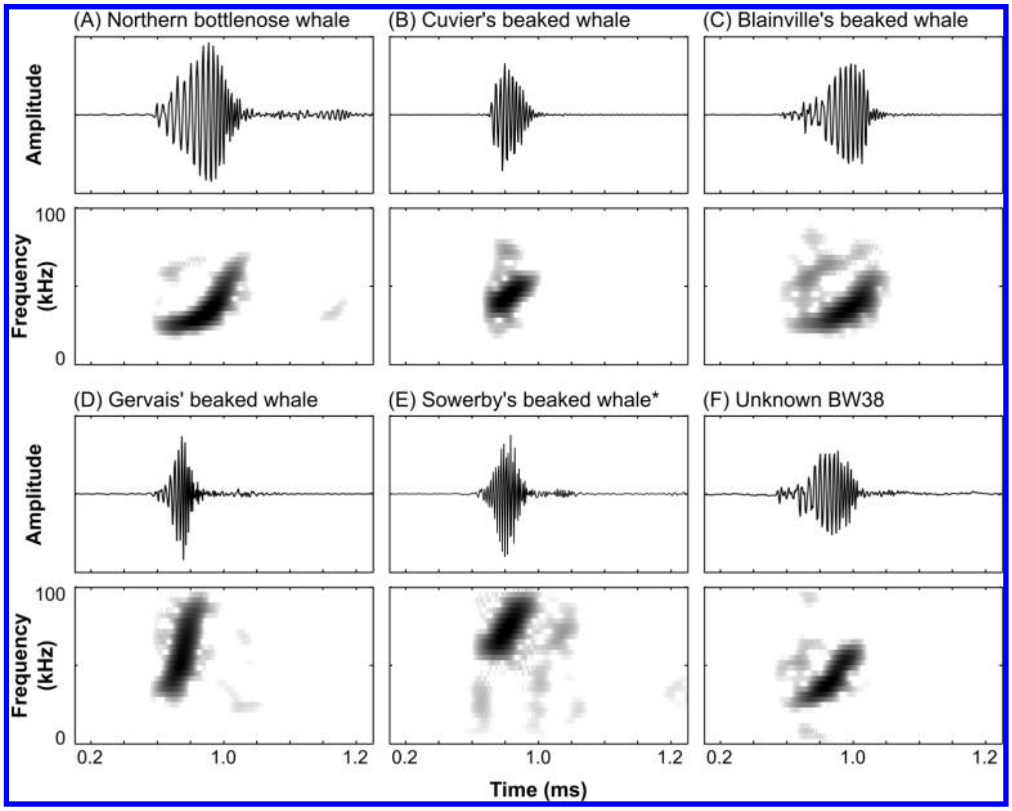
To examine temporal patterns across months and years within each recording site, we binned detections of each beaked whale species into hourly presence and calculated the percent of hours per week with detections. For duty-cycled data, hourly presence was determined based on the recording periods that occurred within each hour of the day. For weeks of the year with more than 1 year of data available, we also calculated the mean percent of hours with detections, averaged across all monitoring years, and plotted the weekly mean along with the minimum and maximum values to illustrate the range of interannual variation. To examine temporal patterns on diel time scales, we plotted counts of species presence for each hour of the day, pooled across all recording days at each site. To compare hourly presence between day and night light regimes, we divided each calendar day into night and day diel periods based on local sunrise and sunset times. We calculated the proportion of hours within each diel period with detections of each species, to account for variation in the length of diel periods across different latitudes and seasons, and used a non-parametric Mann–Whitney *U* test to test for differences in beaked whale presence during day and night. We performed this test for each species at each site, as well as for each species pooled across all sites with detections. We also examined plots of the percent of diel period hours per week with detections to identify any seasonal changes in diel behavior that were not apparent when data were pooled across all recording days.

Results

Beaked whale echolocation signals

We identified six different beaked whale click types within the recordings (Fig. 2). Four of these were consistent with signals produced by northern bottlenose whales (Fig. 2A) (Wahlberg et al. 2011), Cuvier's beaked whales (Fig. 2B) (Zimmer et al. 2005), Blainville's beaked whales (Fig. 2C) (Johnson et al. 2004), and Gervais' beaked whales (Fig. 2D) (Gillespie et al. 2009). The remaining two click types did not closely match any beaked whale signals previously described in the literature. However, we posit that one of these unknown click types is produced by Sowerby's beaked whales (Fig. 2E), based on similarities in frequency content and ICI to a small sample of high-frequency clicks recorded in a visually-confirmed encounter with Sowerby's beaked whales by Cholewiak et al. (2013). This presumed species identification is further supported by the geographic occurrence of the click type, which matches the described range of the species (MacLeod et al. 2006; Waring et al. 2015). In particular, these clicks were frequently detected in the Gully, where Sowerby's beaked whales and north-

Fig. 2. Example waveforms (upper panels) and spectrograms (lower panels) of each beaked whale click type recorded in this study. Spectrograms were calculated using a Hann window, 60 pt fast Fourier transform, and 98% overlap. Sowerby's beaked whale (panel E) clicks are labeled as such based on a posited species identification of this click type.



ern bottlenose whales are the only ziphiid species known to occur regularly (Whitehead 2013). We thus refer to this click type as Sowerby's beaked whale throughout this paper. The second unidentified click type had a similar spectral shape to clicks produced by Blainville's beaked whales, but was higher in frequency, with a peak frequency around 38 kHz (Fig. 2F). These click events were also differentiated from typical Blainville's beaked whale clicks by shorter click durations and slightly longer ICIs. We refer to this click type as "BW38" and the species remains unknown.

Spatial patterns

We analyzed 2642 days of recordings, and detected beaked whale signals at all six recording sites. Two to four different click types were present at each site, and we observed considerable variation in relative species occurrence across the study region. Figure 3 shows the daily presence of each species at each site as a percentage of the number of recording days; Fig. 4 shows the daily presence of each species as a percentage of all beaked whale detection days at each site.

The highest levels of beaked whale presence occurred at MGL, even though the recordings at this site were collected at relatively low duty cycles (see Table 1 for details). Two beaked whale species were nearly always present at this location: northern bottlenose whales, detected on all 605 recording days, and Sowerby's beaked whales, detected on 95% of the 286 days with high-frequency data. Data for the remaining 319 days at MGL were collected at a sampling rate of 128 kHz, providing insufficient recording bandwidth to reliably detect the higher-frequency Sowerby's beaked whale clicks. Cuvier's beaked whales were present less frequently at MGL, and were detected on 26% of the 605 recording days, although their daily presence may be underestimated as a result of the duty-cycled recordings, which are likely to have greater effects on the assessment of daily presence of rarely detected species (Stanistreet et al. 2016).

The Georges Bank (GBK) and Norfolk Canyon (NFC) sites were characterized by lower overall beaked whale presence, with no species detected across a majority of recording days. At GBK, Sowerby's and Cuvier's beaked whales were detected on 15% and 13% percent of the 304 recording days, respectively, and Gervais' beaked whales were detected only once. Based on analyses by Stanistreet et al. (2016), it is likely that these results significantly underestimate daily presence, particularly of the *Mesoplodon* species, since data at this site were collected using a low duty cycle (less than 10% recording time; see Table 1). At NFC, recordings were made continuously, and Sowerby's, Cuvier's, and Gervais' beaked whales were detected on 36%, 20%, and 15% of the 289 recording days, respectively.

In contrast, beaked whale detections at both the Cape Hatteras (HAT) and Onslow Bay (ONB) sites were dominated by a single species present on nearly all recording days. At HAT, Cuvier's beaked whales were detected on 96% of the 734 recording days, with Gervais' beaked whales detected on 35% of days, Blainville's beaked whales on 1% of days, and a single detection of Sowerby's beaked whales (0.14% of days). At ONB, Gervais' beaked whales were detected on 97% of the 432 recording days, together with infrequent detections of Cuvier's (6% of days) and Blainville's (5% of days) beaked whales and the unknown BW38 click type (1.4% of days). Recordings at ONB employed a 50% duty cycle (5 min of recording time per 10 min cycle period), and beaked whale daily presence may therefore be slightly underestimated. However, this duty cycle is unlikely to have significantly reduced the daily detection rates of either Gervais' or Cuvier's beaked whales at this site, since Gervais' clicks were commonly present throughout multiple hours of the days, and Cuvier's clicks are usually detected for more than

Fig. 3. Percentage of total recording days (*n*) at each site with detections of each beaked whale species. Recording sites are shown from north (top) to south (bottom): Mid-Gully (MGL), Georges Bank (GBK), Norfolk Canyon (NFC), Cape Hatteras (HAT), Onslow Bay (ONB), and Jacksonville (JAX). [Colour online.]

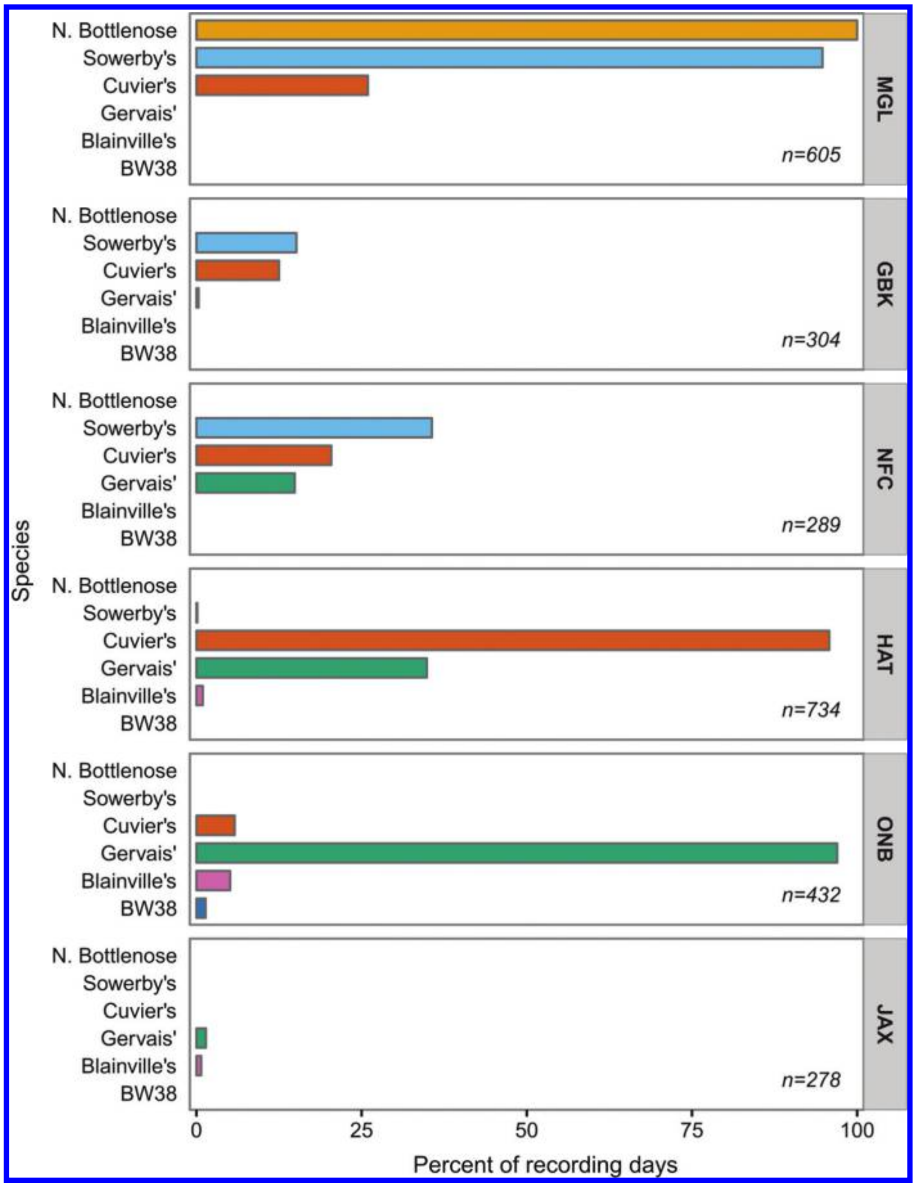


Fig. 4. Percentage of total beaked whale detection days (*n*) at each site attributed to each species. Recording sites are shown from north (top) to south (bottom): Mid-Gully (MGL), Georges Bank (GBK), Norfolk Canyon (NFC), Cape Hatteras (HAT), Onslow Bay (ONB), and Jacksonville (JAX). At MGL, the relative percentages shown are based only on detection days with a sufficient sample rate to detect all beaked whale click types. [Colour online.]

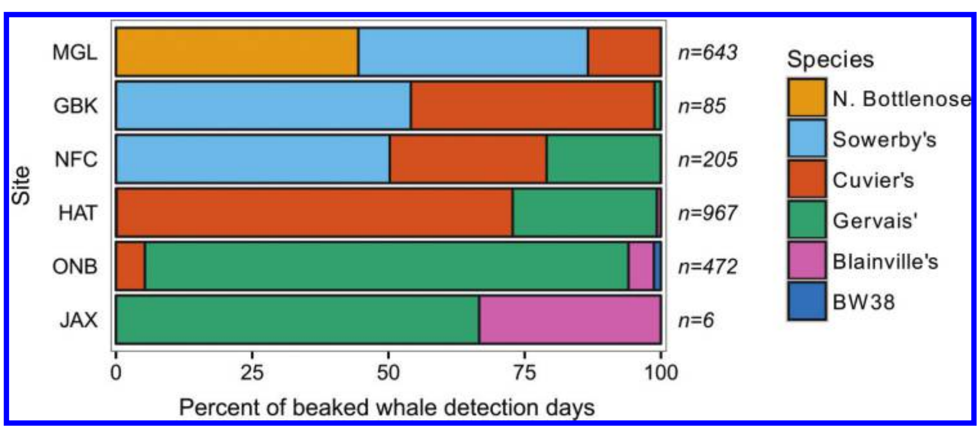
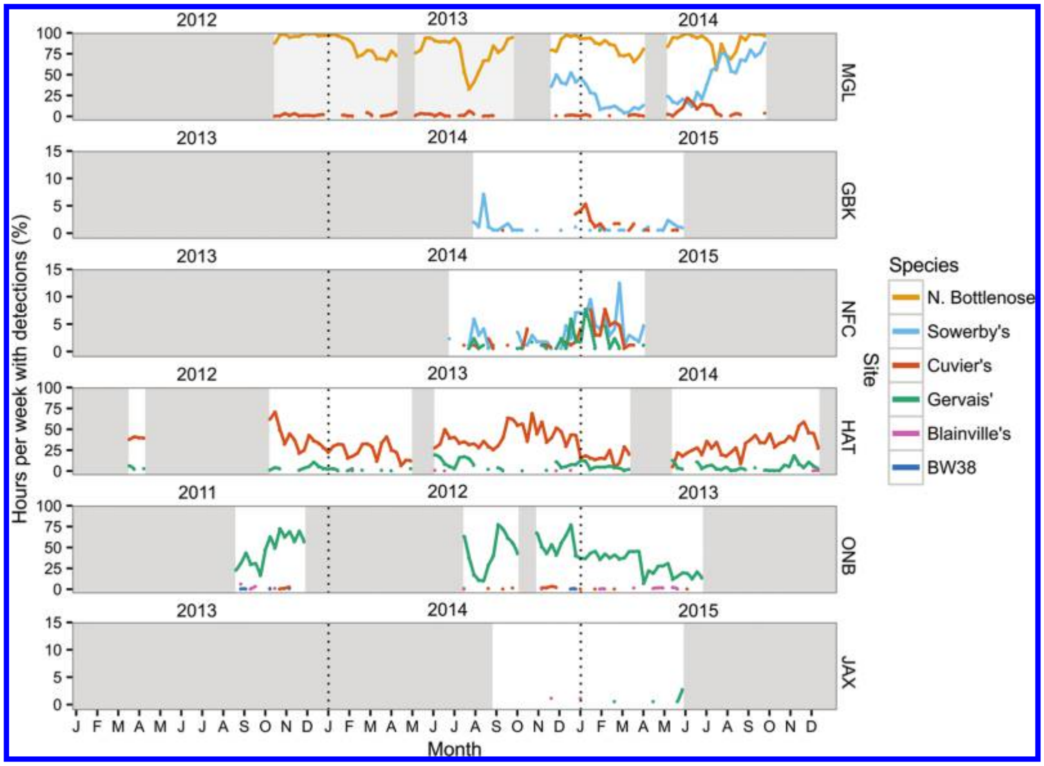


Fig. 5. Percentage of hours per week with beaked whale detections at each recording site across all monitoring periods. Note that *y*-axis scales differ. Zero values are not plotted to distinguish between absence and low levels of presence. Years are indicated above each panel and separated by dotted lines. Dark gray shading indicates periods with no recording effort, light gray shading (top panel) indicates periods with data collected at a sampling rate insufficient for detecting Sowerby's beaked whale clicks. [Colour online.]



5 min at a time (Stanistreet et al. 2016). Finally, we found the lowest overall beaked whale presence at the Jacksonville (JAX) recording site, where Gervais' and Blainville's beaked whales were detected on only four (1.4%) and two (0.7%) of the 278 recording days, respectively.

We observed substantial overlap among species' ranges, as well as apparent latitudinal gradients in the relative occurrence of some species across the study region (Figs. 3 and 4). Northern bottlenose whales and Sowerby's beaked whales exhibited the most boreal distributions, with detections of northern bottlenose whales occurring only at MGL, and detections of Sowerby's beaked whales extending from MGL as far south as NFC, with a single detection at HAT. Cuvier's and Gervais' beaked whales occupied the broadest latitudinal ranges within the study region, with Cuvier's beaked whales exhibiting a more northerly distribution (MGL to ONB) and Gervais' a more southerly distribution (GBK to JAX). The ranges of these two species overlapped substantially, and both species occurred at four of the six recording sites, but they exhibited strongly contrasting levels of occurrence at HAT and ONB off North Carolina (Figs. 3 and 4). Blainville's beaked whales appeared to be restricted to the southern portion of the study region (HAT to JAX), and were not commonly detected at any recording site. Finally, the unknown BW38 click type was detected only at ONB.

Seasonal and diel patterns

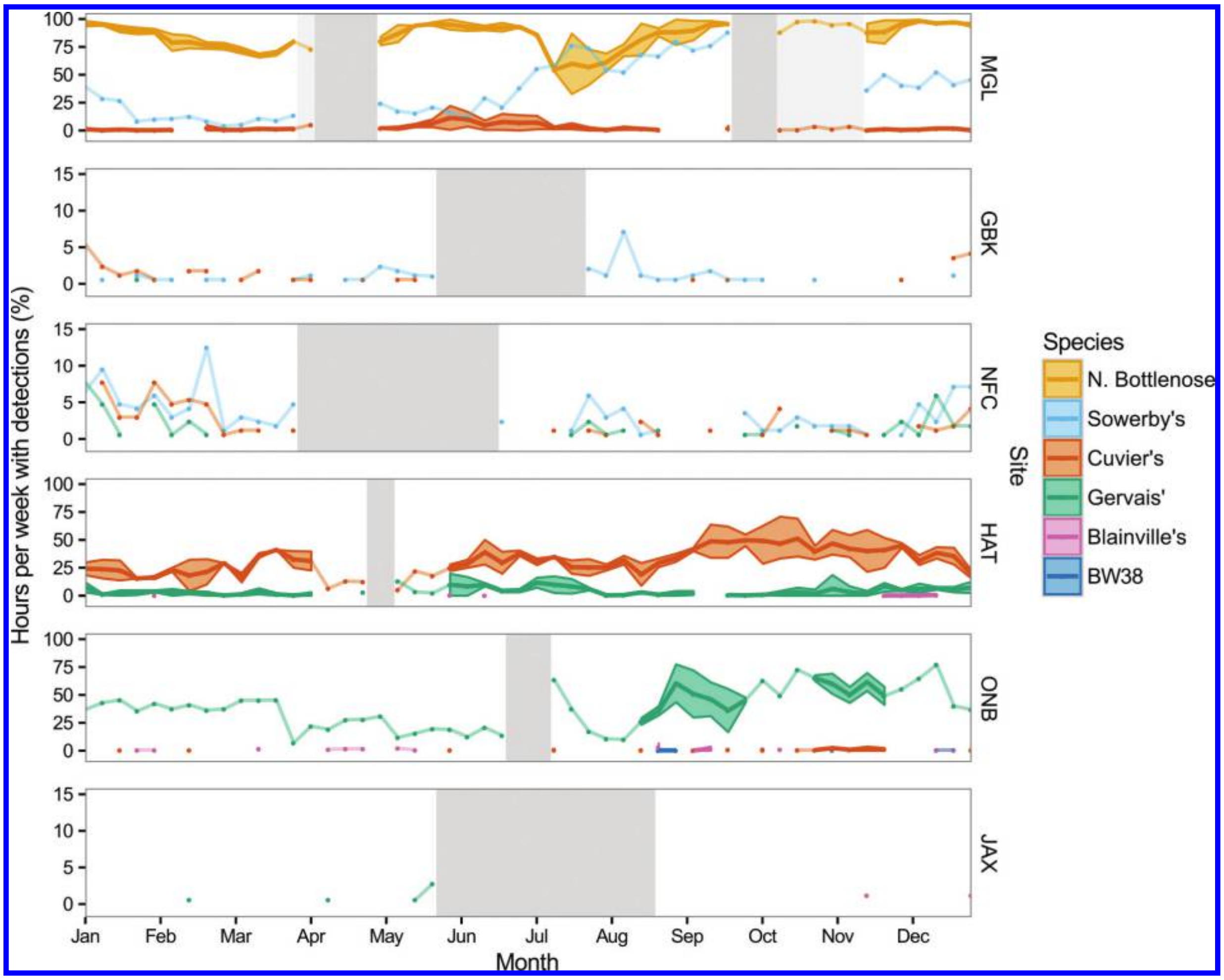
Data were available across multiple years at MGL, HAT, and ONB, with some gaps in monitoring coverage between successive recorder deployments. At each of the remaining sites, data were available from a single deployment spanning approximately 10 months. None of the species recorded exhibited strong evidence of seasonality, and relative species occurrence within each site was generally consistent over time (i.e., the species with the highest weekly occurrence typically remained highest throughout the recording periods) (Fig. 5).

The only seasonal pattern that we observed consistently across multiple years occurred at MGL, where there was a brief decrease in northern bottlenose whale detections during July in both consecutive monitoring years (Figs. 5 and 6). In 2014, when high-frequency recordings were available, we observed an increase in Sowerby's beaked whale detections starting in June and continuing through August. Cuvier's beaked whales were detected at low levels throughout the year.

Data at GBK, NFC, and JAX consisted of only a single year of monitoring, which limited our ability to draw inferences regarding temporal patterns on seasonal scales. On average, Sowerby's, Cuvier's, and Gervais' beaked whales were each detected in less than 1% of hours per week at GBK and less than 3% of hours per week at NFC. At JAX, there were sporadic detections of Gervais' beaked whales only in February, April, and May, and Blainville's beaked whales only in November and December. In Figs. 5 and 6 we use a reduced *y*-axis scale to show the temporal occurrence of beaked whales at these three sites. Again, it is important to note that the GBK recordings were collected at a low duty cycle, thus hourly presence is likely significantly underestimated.

At HAT, beaked whale presence was fairly consistent throughout the year, characterized by detections of Cuvier's beaked whales in a mean of 33% (±14%) of hours per week, and detections of Gervais' beaked whales in a mean of 3.8% (±4.6%) of hours per week. No clear seasonal patterns were apparent in the mean detection rates per week of the year (Fig. 6). At ONB, the mean detection rate of Gervais' beaked whales was 41% (±19%) of hours per week, and appeared to be slightly higher during the months of September to March and lower from April to August, though for most time periods we lacked replicate years of monitoring at this

Fig. 6. Mean percentage of hours per week of the year with beaked whale detections, averaged across all years with data. Thin studded lines indicate weekly detection rates during time periods with one year of data; bold lines indicate mean values during time periods with 2–3 years of data, and shaded ribbons show the range of values from minimum to maximum across years. Note that *y*-axis scales differ. Zero values are not plotted to distinguish between absence and low levels of presence. Dark gray shading indicates periods with no recording effort, light gray shading (top panel) indicates periods with data collected at a sampling rate insufficient for detecting Sowerby's beaked whale clicks. [Colour online.]



site (Fig. 6). Sporadic detections of Cuvier's, Blainville's, and BW38 signals also occurred throughout the year.

For most species and sites, we detected similar rates of hourly presence across day and night diel periods, and did not observe distinct diel patterning (see online Supplementary material, Figs. S1 and S2[1]). Significantly higher daytime presence occurred only for Sowerby's beaked whales at GBK (Mann–Whitney *U* test, $W = 1669.5$, $p = 3.12 \times 10^{-4}$) and Gervais' beaked whales at HAT (Mann–Whitney *U* test, $W = 37\,812$, $p = 0.039$). However, sample sizes were limited, especially in the former case, and more data are needed to assess the biological significance of these patterns. At MGL, northern bottlenose whales exhibited significantly higher nighttime presence (Mann–Whitney *U* test, $W = 152\,230$, $p = 2.46 \times 10^{-7}$), and this result appeared to be driven mainly by seasonal differences in day and night detection rates occurring from February through April in both consecutive years of monitoring, with no discernible diel patterning throughout the rest of the year (Fig. S3[1]).

Discussion

The results of our study provide a new perspective on the occurrence and distribution of beaked whale species along the western North Atlantic shelf break. Despite their oft-cited status as "rare and elusive" species, beaked whales were acoustically detected regularly throughout most of the study region, suggesting that low sighting rates in traditional visual surveys reflect inherent difficulties in observing beaked whales at sea rather than their rarity of occurrence within the region. In fact, beaked whales were a common component of the acoustic record at most of the sites we sampled.

We recorded clicks produced by four of the six beaked whale species known to inhabit the North Atlantic, as well as a click type likely produced by Sowerby's beaked whales. This posited species identification remains to be conclusively confirmed with additional field recordings or animal-borne acoustic tags, but represents an important new finding, since this click type was regularly recorded at several sites and may provide new insight into the occurrence of Sowerby's beaked whales.

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2016-0503.

The only North Atlantic beaked whale species apparently absent from the recordings was True's beaked whale (*Mesoplodon mirus*), an enigmatic species known primarily from stranded specimens. In the western North Atlantic, True's beaked whales have stranded between Newfoundland and Florida (Macleod 2000; Pitman 2009), and historically there have been few documented sightings at sea. During shipboard surveys conducted by the Northeast Fisheries Science Center in the summer of 2016 (Northeast Fisheries Science Center, unpublished data), several potential groups of True's beaked whales were identified at sea and concurrent acoustic recordings were collected during these encounters. However, quantitative analyses have not yet been conducted, and at present there are no available descriptions of True's beaked whale echolocation signals. We recorded one unidentified beaked whale click type at ONB, referred to as BW38, but there is currently no evidence linking this signal type to True's beaked whales, and more recordings are needed before we can reasonably speculate on which species produces the BW38 click type.

Our results revealed considerable spatial variation in beaked whale species' presence among recording sites. These patterns are largely consistent with prior knowledge of the latitudinal ranges of beaked whale species (MacLeod et al. 2006), but also offer new insights into species-specific habitat use which merit further examination. The low but consistent acoustic presence of Cuvier's beaked whales in the Gully was surprising, as this species has rarely been encountered along the Scotian Shelf despite several decades of survey efforts (Whitehead 2013). MacLeod et al. (2003) hypothesized that Cuvier's beaked whales and northern bottlenose whales compete for similar prey and therefore do not occur sympatrically; in contrast, our results indicate that there is some degree of geographic overlap among these two species. The Gully is critical habitat for a small, highly resident population of northern bottlenose whales known to occupy the canyon and surrounding areas year-round (Fisheries and Oceans Canada 2016), and became a federal marine protected area (MPA) in 2004 (DFO 2004). Whitehead (2013) documented a significant increase in the abundance of Sowerby's beaked whales in the Gully between 1998 and 2011, which he suggested might have been related to changes in the ecology of the Scotian Shelf ecosystem (Frank et al. 2011), or to the reduction in human activities in the Gully region after MPA protections were implemented, including a decrease in anthropogenic noise. It is possible that the presence of Cuvier's beaked whales in the Gully during the 2012–2014 monitoring period represents a similar, recent trend toward increasing use of this habitat by a species that was not historically present. A confirmed sighting of Cuvier's beaked whales during the summer of 2015 represents the first known visual record of this species inside the Gully (H. Whitehead, unpublished data).

We report northern bottlenose whale detections only at MGL, but acknowledge the possibility that northern bottlenose whales were present and not detected at our other recording sites, since the detection criteria were not adjusted to optimally detect the lower-frequency clicks of this species in all data sets. However, northern bottlenose whales have very rarely been sighted south of the Scotian Shelf, with the southernmost sighting occurring east of New Jersey during the 1980s (Reeves et al. 1993; Wimmer and Whitehead 2004). The geographic range of this species is better known than many of the other Atlantic beaked whale species, since they are easier to observe and identify at sea due to their larger size and tendency to approach vessels (Barlow et al. 2006). It is highly unlikely that northern bottlenose whales occur at any recording site south of GBK, where the low duty cycle limited our ability to record rare events regardless of the click detection parameters used. Nevertheless, we note that our description of the occurrence of this species within our study region may be incomplete and recommend that future recordings collected off the northeastern US be analyzed for northern bottlenose whale clicks.

To the south along the US east coast, we observed remarkably different levels of presence of Cuvier's and Gervais' beaked whales at HAT and ONB, located just 200 km apart at similar depths along the continental slope. This pattern remained consistent across multiple years of monitoring. The degree to which this apparent habitat partitioning may relate to foraging preferences and the distributions of prey resources is uncertain, as the diets of both species are poorly known (MacLeod et al. 2003). HAT is considered an important biogeographic boundary due to the convergence of distinct water masses, which may affect the assemblages of demersal squid and fish species present north and south of this boundary (e.g., Briggs and Bowen 2012; Pappalardo et al. 2015). Further data on the diets of individual beaked whale species, as well as the ecology of their prey, could help shed light on the patterns observed. For now, we simply note that there is clear spatial patterning in the use of slope habitats at similar depth strata by co-occurring beaked whale species.

The dearth of beaked whale detections at JAX is likely related to the bathymetry of the continental margin off the southeastern US. The area beyond the continental shelf is characterized by the Blake Plateau, a relatively flat region of intermediate depth (500–1000 m) that extends 375 km offshore before steeply dropping off to the deep ocean basin. Beaked whales are often associated with complex topography, including steep shelf edges and canyons (Waring et al. 2001; MacLeod and Zuur 2005), and we hypothesize that higher beaked whale presence likely occurs along the outer edge of the Blake Plateau, where oceanographic and bathymetric characteristics are more similar to continental slope environments further north. The Blake Plateau extends almost to the edge of the US Exclusive Economic Zone and little survey effort has been conducted near the outer edge, but habitat modeling performed by Roberts et al. (2016) also predicted higher beaked whale abundance along this outer slope than along the continental shelf break further inshore.

Previously, most data on beaked whale occurrence in the western North Atlantic has come from shipboard and aerial surveys conducted primarily during the spring and summer months, when weather conditions are most favorable for survey effort. In many areas there is little to no information on species occurrence during other times of year (Waring et al. 2014). In the present study, we did not find strong seasonal variation in beaked whale occurrence at most recording sites, and species were generally present at similar levels year-round, which we believe is an important finding given the difficulty of conducting visual surveys outside of the spring and summer months. Temporal coverage was limited to a single year or included substantial gaps at several of our monitoring sites, and data from additional years may be necessary to reveal subtler seasonal or interannual trends. However, results from large-scale PAM in the North Pacific demonstrated a similar lack of temporal patterning in the detection of beaked whale acoustic signals (Baumann-Pickering et al. 2014), and coordinated seasonal movements have not been documented in any beaked whale species. Studies utilizing photographic identification or animal-borne satellite telemetry tags have revealed a high degree of site fidelity within some beaked whale populations, including Cuvier's and Blainville's beaked whales in Hawai'i (McSweeney et al. 2007; Schorr et al. 2010), Blainville's beaked whales in the Bahamas (Claridge 2013), and northern bottlenose whales in Nova Scotia (Hooker et al. 2002; Wimmer and Whitehead 2004). Preliminary results from ongoing research off HAT, North Carolina have suggested a similar pattern for Cuvier's beaked whales at this site, with satellite-tagged individuals remaining within a small core area along the continental slope for weeks or months at a time (Baird et al. 2016). The consistent year-round acoustic presence we documented provides further evidence that Cuvier's beaked whales are highly resident at this location.

The absence of clear diel patterning in the hourly acoustic presence of beaked whale echolocation signals at most recording sites suggests that the species recorded generally perform foraging dives throughout the day and night in these areas. Diel pattern analyses were based only on hourly acoustic presence within day and night diel periods, and do not provide a detailed comparison of relative foraging effort across all hours of the day, which would require analysis at a finer temporal scale or the use of a different metric, such as click rates. Previous studies examining the diving behavior of Cuvier's and Blainville's beaked whales found that individuals of these species performed deep foraging dives at similar rates during night and day (Baird et al. 2008; Schorr et al. 2014). Little is known about the foraging behavior or diving patterns of Gervais' and Sowerby's beaked whales. Moors (2012) found evidence of higher nighttime click rates and seasonal variation in the diel behavior of northern bottlenose whales, similar to our results for this species, but it is unknown whether these patterns are driven by prey availability, predator avoidance, social behavior, or some combination of factors.

There are several sources of uncertainty that are important to consider when interpreting the results of this study. Firstly, the range over which beaked whale clicks are detected may vary between recording sites due to differences in hydrophone depth and instrument sensitivity. In general, detection ranges for beaked whale clicks are expected to be fairly small due to the rapid attenuation of high frequency sound (Zimmer et al. 2008; Küsel et al. 2011). Hildebrand et al. (2015) estimated that beaked whale clicks are detected with certainty only within a few hundred meters of a bottom-mounted HARP, with a maximum detection range of no more than 3.5 km for on-axis clicks directed at the hydrophone. While these ranges were found to be invariant across monitoring sites, our study included a broader range of depths and two instrument types with different sensitivities, which may result in greater variation in site-specific detection ranges.

Secondly, the effects of species-specific behavior on detection rates of beaked whales on bottom-mounted recorders are largely unknown. Quantitative estimates of the probability of detecting each species at each recording site would require detailed information on the acoustic behavior of each species during foraging dives, including source levels and directionality of clicks as well as rates of click production and patterns of movement during dives (see Hildebrand et al. 2015). For most beaked whale species this information does not exist, or is available only from a small number of individuals sampled at specific locations. We caution that our results should only be interpreted as the amount of time one or more individuals of a species were present and acoustically active at a site, and do not necessarily provide an indication of relative abundance, since we do not know the number of individuals present.

Lastly, we classified beaked whale clicks based on existing information on click types and acoustic behavior. Prior studies have shown that many beaked whale species produce a stereotyped echolocation signal type that is stable across geographic regions (Baumann-Pickering et al. 2014). However, we acknowledge that scientific understanding of the acoustic behavior of most beaked whale species is far from complete, particularly for True's, Sowerby's, and Gervais' beaked whales in the Atlantic Ocean. Collecting additional data on the acoustic behavior of these species may allow further insight to be gained from PAM data in the future.

While there are many remaining gaps in our scientific knowledge of beaked whale ecology, PAM is a useful method for obtaining species-specific presence data, and can be a valuable tool for identifying important beaked whale habitats. Although PAM methods do not allow detection of silent animals, numerous studies have shown that echolocation is a consistent feature of deep foraging dives performed by Cuvier's (Johnson et al. 2004; Tyack et al. 2006) and Blainville's (Johnson et al. 2004, 2006, Madsen et al. 2005, 2013; Tyack et al. 2006; Arranz et al. 2011) beaked whales, and it is reasonable to assume that echolocation is an essential aspect of foraging for all beaked whale species. Acoustic detections on bottom-mounted recorders can therefore be considered a proxy for foraging activity, providing insight into species' ecology. We suggest that, in addition to MGL, which is known critical habitat for beaked whales, HAT and ONB should also be considered important beaked whale habitats, with at least one species present in these areas on more than 95% of days throughout the year. By contrast, JAX appears to be an area infrequently visited by foraging beaked whales, which is an important result due to the potential for future acoustic disturbance at this site. Installation of a new Undersea Warfare Training Range by the US Navy is currently underway just inshore of the recording site, and the collection of baseline data on species occurrence before this range becomes operational is critical to assess potential effects of increased human activity and sonar use in this region. While these effects may extend beyond the range over which beaked whale clicks were detected on the HARP, our results provide an initial baseline for this site and support previous research suggesting that the inner continental slope and Blake Plateau region may not provide quality foraging habitat for beaked whales (Roberts et al. 2016).

In summary, our study revealed the year-round presence of multiple beaked whale species along the western North Atlantic continental slope, including nearly continuous beaked whale presence at three of the six monitoring sites. These results provide insight into variations in the relative occurrence of beaked whale species, and help advance our limited understanding of the distribution of species in the genus *Mesoplodon*. We observed distinct differences in habitat use among species throughout the study region, and we reiterate the importance of improving species-specific information on the ecology, distribution, and habitat preferences of beaked whales, particularly when considering the potential effects of anthropogenic noise. Assessment of population-level effects of anthropogenic disturbance is challenging for any cetacean species, and particularly problematic for beaked whales, due to the low encounter rates during visual surveys (Taylor et al. 2007). We did not attempt to estimate species' abundance, although methods are being developed to use PAM data for that purpose (Marques et al. 2009; Hildebrand et al. 2015). Instead, we demonstrate the utility of PAM to estimate baseline levels of occurrence of beaked whale species across broad spatial scales and at high temporal resolutions, facilitating the detection of changes in distributions and habitat use over time. Critically, and unlike the results of many visual surveys, our results are species-specific, improving the information available to managers for assessing and mitigating potential threats to these species.

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