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Distribution and abundance of beaked whales (Family Ziphiidae) Off Cape Hatteras, North Carolina, U.S.A.

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ABSTRACT

Beaked whales are vulnerable to the impacts of disturbance from several sources of anthropogenic sound. Here we report the distribution and abundance of beaked whales off Cape Hatteras, North Carolina, U.S.A., an area utilized by the U.S. Navy for training exercises, and of particular interest for seismic geophysical surveys. From May 2011 through November 2015, monthly aerial surveys were conducted at the site. Beaked whales were encountered 74 times (n = 205 individuals) during these surveys. *Ziphius cavirostris*, the most commonly encountered species, was observed in every month of the year. *Mesoplodon* spp. were encountered in ten months of the year. Photographs of adult males with erupted teeth permitted six sightings to be identified conclusively as *M. europaeus*; *M. mirus* was also photographed just outside the study area. Beaked whale surface densities stratified by depth (0.005–0.007/km^2) were among the highest reported in the world for small ziphiids. A quantitative comparison of sightings and stranding records suggests that strandings do not accurately reflect the relative abundance of beaked whale species in this area. We conclude that Cape Hatteras, at the convergence of the Labrador Current and Gulf Stream, is a particularly important year-round habitat for several species of beaked whales.

Key words: beaked whales, Cape Hatteras, *Ziphius cavirostris*, *Mesoplodon europaeus*, *Mesplodon mirus*, densities, strandings.

Beaked whales (Family Ziphiidae) are found in deep water habitats worldwide, including submarine canyons (Hooker and Baird 1999*a, b*; Waring *et al*. 2001; D'Amico *et al*. 2009; Arcangeli *et al*. 2014), around oceanic islands (Baird *et al*. 2006; Tyack *et al*. 2006; Schorr *et al*. 2009, 2014) and the continental slope (Waring *et al*. 2001, Hamazaki 2002, Mullin and Fulling 2003). Beaked whales are

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a phylogenetically diverse family (22 species in six genera currently recognized by the Committee on Taxonomy of the Society for Marine Mammalogy), distributed throughout the world's oceans (reviewed by MacLeod *et al*. 2006), but these remain some of the most poorly understood species of large mammals.

Recently, the extreme deep diving abilities of multiple species of beaked whales have been described through the use of digital archival tags and satellite-linked dive recorders (*e.g*., Baird *et al*. 2006, Tyack *et al*. 2006, Schorr *et al*. 2014). *Ziphius cavirostris*, for example, can dive to 3,000 m and remain submerged for over 2 h (Schorr *et al*. 2014). The deep foraging dive records of both *Z. cavirostris* and *Mesoplodon densirostris* are the longest and deepest of any air-breathing vertebrate (Tyack *et al*. 2006). Their long dive times, short surface durations, and inconspicuous behavior when surfacing, make beaked whales particularly cryptic (Barlow *et al*. 2006, Barlow 2015). In addition, although *Z. cavirostris* is relatively easy to identify at close range, most mesoplodonts are not, and neither group is readily distinguishable from a distance (Davis *et al*. 1998, Waring *et al*. 2001, Mullin and Fulling 2003, Aguilar de Soto *et al*. 2017). Due to these challenges, beaked whales are often managed as complexes of multiple species (*e.g*., Waring *et al*. 2014).

There is a growing need for more precise and specific information on the distribution and abundance of beaked whale species, as they are particularly vulnerable to certain sources of anthropogenic acoustic disturbance (Tyack *et al*. 2011). Mass strandings of beaked whales have occurred in association with naval sonar exercises (reviewed in Cox *et al*. 2006) and possibly seismic survey activities (Taylor *et al*. 2004). Barlow *et al*. (2006) noted that better information on abundance and density is needed to evaluate the risks to, and mitigate potential impacts of, anthropogenic disturbance on beaked whales. Cox *et al*. (2006) suggest that this information is particularly needed in areas where such anthropogenic impacts are known to occur or are planned.

We conducted year-round aerial surveys off Cape Hatteras, North Carolina, from May 2011 through November 2015, as part of an ongoing monitoring project of sites utilized by the U.S. Navy for training and testing activities in the Atlantic. The aim of the surveys was to provide data on all cetaceans, sea turtles, and vessel activity in the survey area. Here we present data on the spatial and temporal patterns of occurrence, density, and abundance of beaked whales in the study site. The waters off Cape Hatteras are used by the U.S. Navy for its Atlantic Fleet Training and Testing activities (http://aftteis.com/Background/Navy-Training-and-Testing/Training-Ranges) and have been included as an area of particular interest in permit applications for commercial seismic surveys (http://www.nmfs.noaa.gov/pr/permits/incidental/oilgas.htm). Stranding records can provide additional information on cetacean species diversity (Pyenson 2011), so we also compared the beaked whale sighting data set from Cape Hatteras with cumulative stranding records for the state of North Carolina.

Methods

Study Area

The study area consists of a 15,765 km^2 straddling the shelf break east of Cape Hatteras, North Carolina (Fig. 1). Twenty-six transect lines were placed perpendicular to the shelf break, ranging from 73.5 km to 81.5 km in length and spaced ~8 km apart. Each transect extended from the continental shelf to abyssal (depth of

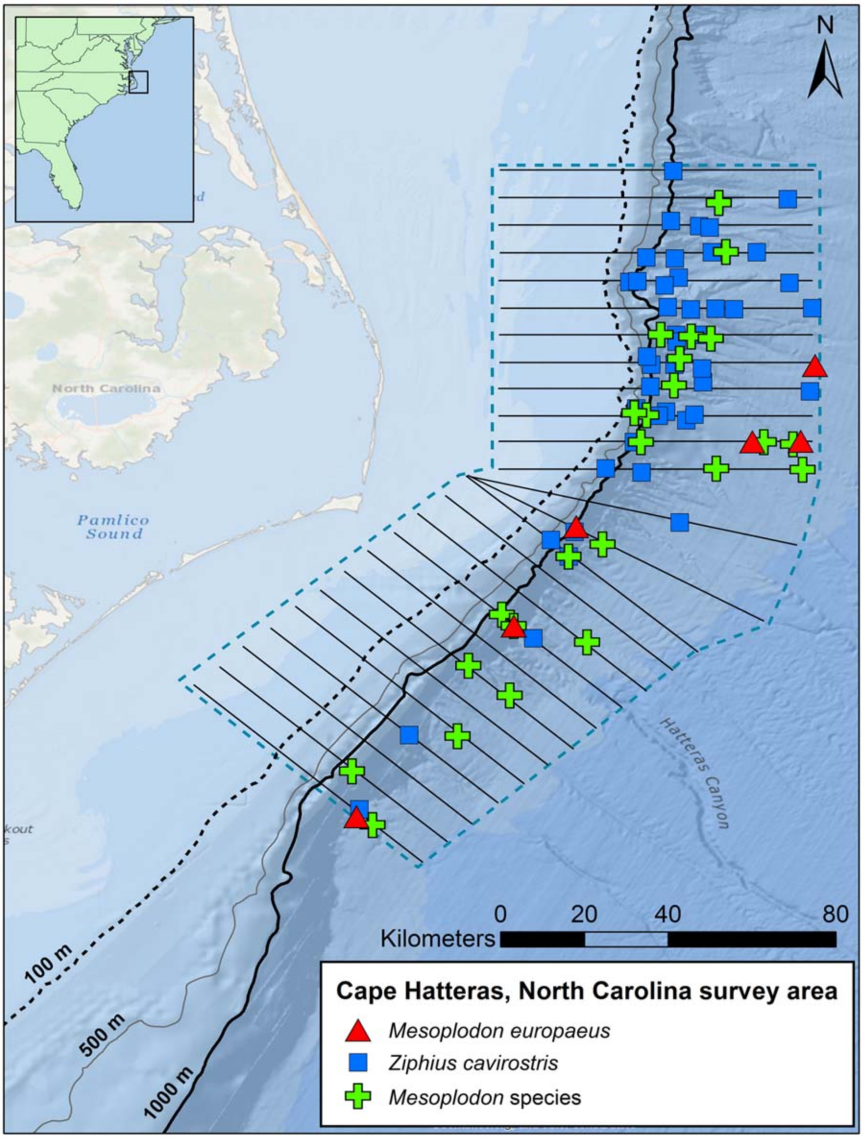

Figure 1. Cape Hatteras, North Carolina survey site, tracklines flown and on-effort beaked whale sightings during the study period. Note beaked whales were encountered almost exclusively in waters 1,000 m or deeper.

approximately 2,500–3,000 m) waters. The oceanography of the study area is dominated by the convergence of two large current systems—the cold, southward flowing Labrador Current and the warm, northbound Gulf Stream current—which meet near Cape Hatteras at 35.2°N, 75.5°W.

The southern limit of the study area is approximately 80 km north of Onslow Bay, North Carolina, a site surveyed by this team from June 2007 to June 2010

Table 1. Monthly aerial survey effort, and beaked whale sightings, at the Cape Hatteras, North Carolina survey site during the study period, May 2001 through December 2015.

Month	Effort (km) 2011	Effort (km) 2012	Effort (km) 2013	Effort (km) 2014	Effort (km) 2015	Total Effort (km) 2011–2015	Total sightings
January	0	1,325	0	0	0	1,325	3
February	0	582	0	583	0	1,165	2
March	0	1,456	149	0	0	1,605	2
April	0	0	0	1,010	0	1,010	2
May	766	1,160	709	407	492	3,534	19
June	964	1,901	0	1,068	549	4,482	9
July	1,031	0	1,755	1,192	142	4,120	9
August	0	701	1,744	1,164	648	4,257	12
September	0	735	0	0	635	1,370	3
October	1,184	0	556	990	0	2,730	2
November	1,030	314	0	0	551	1,895	6
December	0	981	0	573	0	1,554	5
Totals	4,975	9,155	4,913	6,987	3,017	29,047	74

(see Read *et al.* 2014). The Onslow Bay site, originally identified by the U.S. Navy as the preferred site for construction of an Undersea Warfare Training Range (USWTR), was the focus of monthly aerial surveys identical to those utilized in the present study (described below). On three occasions surveys were extended beyond the 1,000 m isobath in Onslow Bay, to search for beaked whales, which were never observed within the core study area. Resulting sighting data of beaked whales from these offshore surveys in Onslow Bay are included in the spatial comparison of sightings and strandings (see below).

Aerial Surveys

Aerial surveys were conducted off Cape Hatteras from May 2011 through November 2015 in a Cessna 337 Skymaster at an altitude of 305 m and a speed of 185 km/h, using methods similar to those outlined in Read *et al.* (2014). Surveys were conducted on days with low sea states and optimal visibility. Although Beaufort Sea States encountered during surveys ranged from 0–5, effort was targeted to low sea states. Annual average Beaufort Sea States were 3.48 (2011), 3.01 (2012), 2.44 (2013), 3.00 (2014), and 2.62 (2015). The goal was to complete a subset of 26 tracklines each month, although weather occasionally prevented this goal from being reached (Table 1). Total distance surveyed ranged from 149 km to 1,901 km per month.

During surveys, two experienced observers (*i.e.*, each with at least 3 yr of small cetacean aerial survey experience), equipped with a GPS unit, data sheet, and binoculars, monitored each side of the plane through a standard (not bubble) window. Each sighting was independent and analyzed with its own covariates. The observers recorded the start and end of transect lines, any changes in environmental variables (*i.e.*, cloud cover, sea state, visibility, and glare), and sightings of marine mammals, sea turtles, and vessels. When a cetacean sighting cue was observed, the observer took a GPS waypoint and measured the vertical sighting angle using fixed marks on the wing struts of the plane. Initial forward angle was also recorded to determine the observation window when animals can be seen at the surface (see availability calculations below). The aircraft then went off-effort, broke from the trackline and closed directly on the sighting, and a sighting waypoint was recorded. Thus, the distance from the trackline sighting cue and the position of the cetacean(s) (*i.e.*, the distance between the two waypoints) could be calculated to provide an independent measure of distance of the sighting from the trackline. The plane circled over the sighting while obtaining photographs to confirm species identity and number of individuals.

During each encounter, the left observer was designated as data recorder and the right observer obtained digital photographs with a Canon 40D or Canon 70D camera and a 100–400 mm image-stabilized lens. The observers rotated between these two positions during each survey. These images were used to confirm species identification (see below), refine estimates of group size and confirm sightings of calves. Each observer independently estimated the minimum and maximum number of animals in each sighting. A best estimate of group size was then established by integrating field observations and subsequent examination of digital images. Once photographs and sighting data were collected, the plane returned to the original cue position from which it had broken from the trackline and resumed survey effort.

Species Identification

Beaked whale species identification was confirmed in the laboratory after review of digital photographs gathered during each sighting, using methods described in Read *et al*. (2014). Only photographs of extremely high quality that captured detailed physical features of an individual were utilized for species identification. Physical features diagnostic of *Ziphius cavirostris* are well-described and distinctive (Jefferson *et al*. 2008). *Mesoplodon* species, in contrast, are more difficult to discriminate. The placement of the mandibular teeth, which erupt only in adult males, can be used to identify species (Moore 1966, Mead 1989). Thus, mesoplodonts were only identified to species after an adult male, with visible erupted teeth, had been photographed. The physical characteristics of the adult male, and all other individuals within the same sighting, were used to identify past and current sightings to species, even if an adult male was not present in these sightings.

During the course of this study, *Mesoplodon europaeus* was consistently identified using this method. On 16 September 2015, a *M. mirus* adult male was also identified. This latter sighting occurred 25 km north of the study area, and is not included in any of the quantitative analyses presented herein, but photographic data from this sighting are presented here, given the extremely rare occurrence and identification of this species at sea (Aguilar de Soto *et al*. 2017). Sightings of mesoplodonts that lacked sufficient detail to diagnose to species, due, for example, to environmental conditions or image quality, were termed "unidentified *Mesoplodon*."

All sightings were plotted using ArcGIS Version 10.1 (ESRI). For temporal analysis, monthly sightings were plotted using Excel 2010 (Microsoft).

Abundance and Density Estimates of Beaked Whales in the Cape Hatteras Survey Area

The survey data were used to generate density estimates for all beaked whales combined, and for *Z. cavirostris* alone, using *Distance* sampling methods (Buckland *et al*. 2001) and then these estimates were adjusted to take into account the fact that not all individuals were available at the surface. The densities were then used to obtain abundance estimates over both the entire survey area and a subset of the area greater than 1,000 m depth as this was thought to be the preferred habitat of the taxa under consideration (Waring *et al.* 2001, Tyack *et al.* 2006).

Estimation of detection probabilities—In conventional line transect sampling, the probability of detection depends only on the perpendicular distance of the sighting to the transect line (y) and at zero perpendicular distance the probability of detection is assumed to be one (denoted by $g[0] = 1$). Both a hazard-rate ($1 - \exp[-y/\sigma]^{-b}$) and a half-normal ($\exp[-y^2/2\sigma^2]$) form were considered as suitable forms for the detection functions (σ is the scale parameter). Thus, the probability of detection becomes a multivariate function, $g(y,v)$, representing the probability of detection at perpendicular distance y and covariates $\mathbf{v}$ ($\mathbf{v} = v_1,\ldots,v_Q$ where Q is the number of covariates). The scale term, σ, has the form:

$$\sigma_k = \exp\left(\beta_0 + \sum_{q=1}^{Q}(\beta_q v_{kq})\right)$$

and β_0 and β_q ($q = 1,\ldots,Q$) are parameters to be estimated. With this formulation, it is assumed that the covariates affect the rate at which detection probability decreases as a function of distance, but not the shape of the detection function. The covariates considered for inclusion into the detection function were Beaufort sea state, group size, cloud cover, visibility, glare (all continuous), and species (factor). A forward, stepwise selection procedure was used to decide which covariates to include in the model, with a minimum Akaike's Information Criterion (AIC) inclusion criterion. All model selection was performed using a set of customized functions (mrds v.2.1.14, Laake *et al.* 2014) in R (R Development Core Team 2002). This facilitated estimation of variance within R (see below).

Estimation of density surfaces—The "count model" of Hedley *et al.* (2004) was implemented to model the trend in spatial distribution of the different species. The response variable for this model is the estimated number of individuals in a small segment i of trackline, $\hat{N}_i$, calculated using an estimator similar to the Horvitz-Thompson estimator (Horvitz and Thompson 1952), as follows:

$$\hat{N}_i = \sum_{j=1}^{n_i} \frac{s_{ij}}{\int_0^w \hat{g}(y, v_{ij})\pi(y)dy}, \qquad i = 1, K, \ldots, T,$$

where for segment i, $\int_0^w \hat{g}(y, v_{ij})\pi(y)dy$ is the estimated probability of detection of the jth detected group, n_i is the number of detected groups in the segment and s_{ij} is the size of the jth group. The total number of effort segments is denoted by T. By assumption, $\pi(y)$ the probability density function of actual (not necessarily observed) perpendicular distances is uniform up to the truncation distance; this is satisfied by locating transects randomly or with a random start point.

The above detection probability assumes detection on the trackline ($g[0]$) is one, *i.e.*, all surface animals on the trackline are seen. However when estimated from a similar aerial survey protocol to that used here, Forney *et al.* (1995) found $g(0)$

corrected for perception bias was actually 0.95 so this figure was used to modify the $\hat{N}_i$.

Note, all animals must be at the surface to be seen, so to estimate the total population, a further estimate of surface abundance needs to be estimated. To obtain an estimate of the total population of beaked whales, the proportion of animals available at the surface has to be considered. An index of availability at the surface for each sighting was made by considering the reported proportion of time the animals spend at the surface. The probability of an individual being available at the surface was given by

$$P(\text{Avail}) = \frac{E[s]}{(E[s]+E[d])} + E[d] \times \frac{1-e^{-\frac{t}{E[d]}}}{(E[s]+E[d])}$$

after Laake *et al.* (1997), where s = surface time, d = dive time and t = window of time during which an animal is within the visual range of an observer. The time period that the animal was within the visual range of the observer was taken to be the quotient of 973.4 m and the plane speed. This distance was in turn based upon the mean perpendicular distance for sightings of medium sized whales (*i.e.*, beaked whales and pilot whales) of 421.5 m. This latter distance being the "height" of a right angle triangle (treating the hypotenuse as the base) horizontal from the plane encompassing the viewing angle of the observers (60° forward and 30° aft). Sensitivity to the assumed length of this "window of opportunity" was tested by considering a number of different window of opportunity lengths. A range from 833 m to 2 km, changed the estimated densities by only a few thousandths of an animal per kilometer^2.

Given individual availability above, group availability (Group avail) was calculated as follows

$$P(\text{Group avail}) = 1-(1-P[\text{Avail}])^k$$

where the right hand side represents the probability that at least one member of the group is at the surface during their diving behavior. k is a parameter which took different values dependent on what assumptions are made about the synchronicity of the individuals in the pod. If animals are perfectly synchronous the animals surface as one, so $k = 1$. If the animals surface independently of each other, then k is the corrected pod size. These two conditions, and one that assumed half the animals surfaced such that the effective number of independent surfacing "units" was half the estimated pod size, were used here. If pods come up in synchrony their availability at the surface is low leading to an increased estimate of abundance. Beaked whale dive and surface times were not available from Cape Hatteras, North Carolina, so comparable data were taken from *Mesoplodon densirostris* tagged in the Canaries (2003–2010) by the University of La Laguna and the Sea Mammal Research Unit, University of St. Andrews (see Acknowledgments). Dive and surface times for *Ziphius* were taken from DeRuiter *et al.* (2013*a*), available from DeRuiter *et al.* (2013*b*, see also Tyack *et al.* 2006 as the primary source of some of the data). Because the diving behaviors of mesoplodonts encountered at Cape Hatteras are not known, and because *Ziphius* dive behaviors in this region may be different from those in other geographic regions and habitats, we acknowledge that this approach provides only an estimate of group availability. These estimates will be improved in the future by using dive data for, and by understanding dive synchrony of, local ziphiids.

Having obtained the estimated number of individuals in each segment, the density in segment i, $\hat{D}_i$, was estimated from $\hat{N}_i/a_i$ where a_i is the area of segment i. Segment area was calculated as the length of the segment multiplied by twice the truncation distance, which was decided when modeling the detection function (see Results). The realized effort was divided into distinct segments based on when the plane had gone on or off search effort and whether there was a change in environmental characteristics (not currently of relevance to beaked whales but of relevance to other species encountered during these surveys). A target segment length of 10 km was chosen as an appropriate compromise between maximizing the ratio of nonzero to zero segments, maintaining environmental resolution and giving some measure of spatial independence, although some segments were much smaller if there had been a break in effort or change in environmental conditions. Due to the different segment areas, segment area was included as a weight (a term with a known regression coefficient) in the subsequent model. Analyzing the data in this way allowed subsets of the survey area to be readily created based on environmental covariates.

Prediction—The selected models were used to predict density of beaked whales using a uniform 2 min resolution prediction grid. Abundance was estimated by numerically integrating under this predicted density surface. As a uniform density is assumed this is equivalent to a design based estimate of density. The estimation was implemented this way because of the requirement to estimate other species' abundances from the survey. Two areas were considered, the first including the entire surface area and a more restricted subarea where depth was greater than 1,000 m (see above).

Estimation of uncertainty—Variance was estimated by repeating (1,000 times) the entire abundance estimation process on samples drawn from the data to obtain a distribution of abundance estimates, *i.e.*, a nonparametric bootstrap. Samples of dive times and surface times were also redrawn for the availability estimate. Samples were obtained by sampling transects (and associated sightings), at random and with replacement, such that the selected effort reflected the effort in the original sample. Confidence intervals were obtained from this resampling-derived distribution using the 2.5% and 97.5% percentiles to obtain the lower and upper limits of the 95% confidence interval.

Strandings

Beaked whale strandings are relatively rare events in North Carolina (Byrd *et al.* 2014). To increase the sample size for comparison to sightings during the current study, all beaked whale strandings from January 1993 through December 2015 ($n = 47$) were included. Most of these strandings were thoroughly investigated with voucher skeletal material collected to confirm species identification and many were accessioned into the U.S. National Museum of Natural History or the North Carolina Natural Science Museum. The data utilized here included species identification (when known), date, and location of each beaked whale stranding. All strandings were plotted using ArcGIS version 10.1 (ESRI). For temporal analysis, monthly strandings were plotted using Excel 2010 (Microsoft).

Results

Species Identification

Two species of beaked whales were photographically confirmed during surveys: *Ziphius cavirostris* and *Mesoplodon europaeus*. We also describe a *M. mirus* photographed outside the Cape Hatteras survey area.

Z. cavirostris displayed distinctive features characteristic of the species (Fig. 2), including a relatively robust body shape, a short beak, and a head that tended to be lighter in color than the body. Body coloration varied among individuals, ranging from pale to dark gray, and rusty to caramel brown. The dorsal fin was typically falcate, and larger individuals displayed heavier, linear scarring over the dorsal thorax.

The presence of *M. europaeus* was confirmed from a sighting of an adult male on 18 July 2013 (Fig. 3). This individual displayed erupted mandibular teeth at a position less than halfway along the rostrum's length from the tip. This tooth placement confirmed its identity as *M. europaeus* (Moore 1966, Mead 1989 and Smithsonian Institution's Beaked Whale Identification Guide http://vertebrates.si.edu/mammals/beaked_whales/pages/main_menu.htm). The coloration patterns of other individuals in this sighting were used as diagnostic features to identify this species in other sightings (assuming that this was a monospecific group), including three sightings made on 9 June 2012, 28 May 2013, and 16 July 2013, before this adult male was identified (Fig. 4). An additional sighting of a single adult male with erupted teeth was recorded on 14 May 2014 (Fig. 4). Dorsolateral color patterns were used to identify a pair of beaked whales (not associated with an adult male) observed on 11 June 2014 as *M. europaeus*.

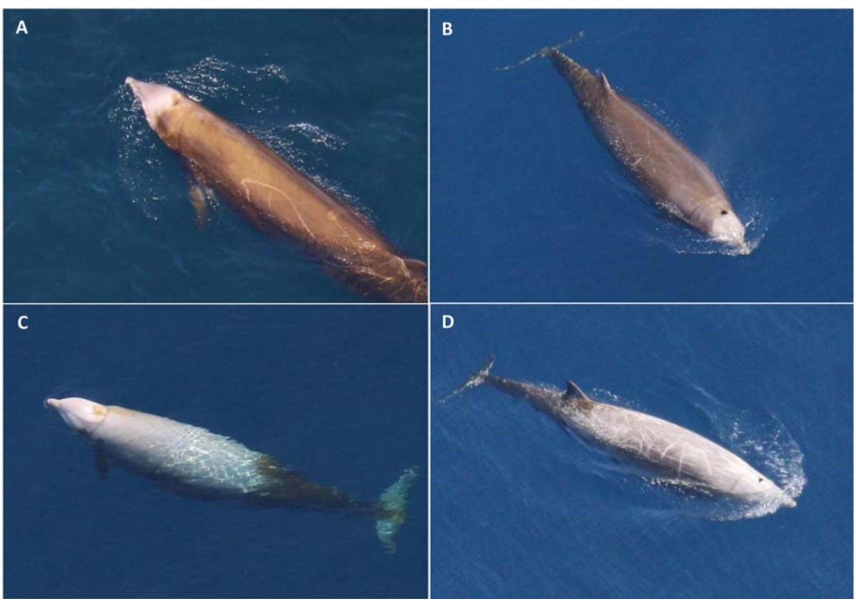

Figure 2. Four *Ziphius cavirostris* individuals encountered in the Cape Hatteras, North Carolina survey site during the study period. A–D display gradation of scarring patterns observed in this species at the survey site.

Figure 3. A series of photographs of an adult male *Mesoplodon europaeus* during a single surfacing event on 18 July 2013 in the Cape Hatteras, North Carolina survey site, where A is at the surface and the best image, B is just diving and C is just surfacing. All display the erupted mandibular teeth at a position less than halfway along the rostrum's length from the tip, which confirms species identification.

The coloration patterns of the larger *M. europaeus* individuals associated with the adult male photographed on 18 July 2013 were distinctive (Fig. 4). Each individual displayed a relatively broad, dark gray stripe along its mid-dorsal surface. The stripe began behind the blowhole and extended to the dorsal fin. Multiple, thin dark gray stripes projected laterally from the broad dorsal stripe; these thin, transverse, "tiger stripes" terminated above the mid-lateral line. These pigmentation patterns are consistent with lateral photographs of *M. europaeus*, taken from vessels, presented in Jefferson *et al*. (2008) and the illustration presented in Aguilar de Soto *et al*. (2017). The two adult male *M. europaeus* did not share the distinctive dorsal pigmentation pattern. The male photographed on 18 July 2013 displayed a relatively uniform gray dorsum, bearing a number of lightly pigmented linear scars (Fig. 3). The dorsal surface of the male photographed on 14 May 2014 was irregularly pigmented, with a large pale-scarred area extending across the cranial third of the dorsum (Fig. 4). These scarred areas are believed to result from agonistic interactions among males that occurs in many beaked whale species (Mead 1989). In all individuals of this species, a subcircular, lightly pigmented patch was present dorsal and rostral to the eye, which appeared darkly pigmented.

On 16 September 2015, an adult male *M. mirus* (Fig. 5), with erupted teeth, was photographed with another closely associated individual. In this species the teeth erupt at the distal-most tip of the mandibles, similar to those in *Z. cavirostris*, but

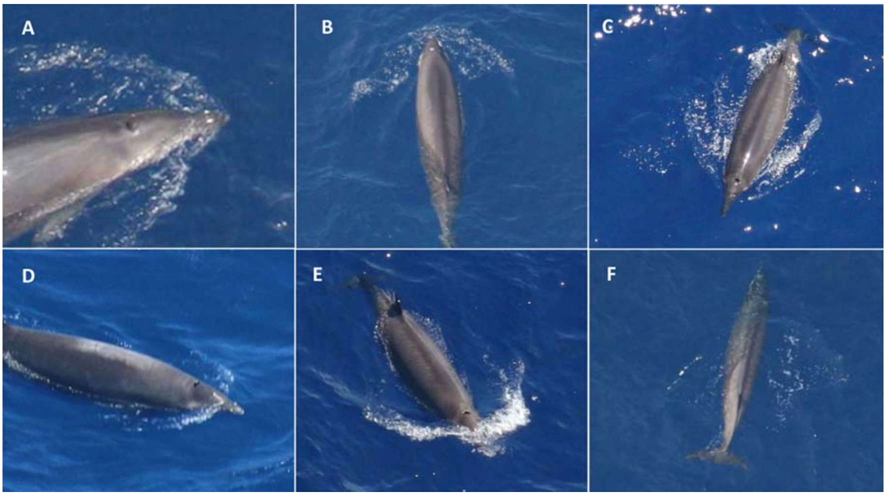

Figure 4. Six *Mesoplodon europaeus* individuals encountered in the Cape Hatteras, North Carolina survey site during the study period. A. Adult male photographed on 18 July 2013 (see Fig. 3). B. Individual associated with adult male (A) during the 18 July 2013 sighting. C. Individual sighted on 28 May 2013. D. Adult male (note tooth position) sighted on 14 May 2014. E. Individual sighted on 16 July 2013. F. Individual sighted on 11 July 2014.

the overall coloration and body proportions of the whale confirmed that it was a mesplodont. The body shape of the male *M. mirus* was more laterally compressed, and the rostrum more elongated than those of *M. europaeus*. Caudal to the blowhole, the dorsal midline appeared to be relatively sharp, almost keel-like, and was lighter

Figure 5. An adult male *Mesoplodon mirus* encountered with another individual on 16 September 2015, at a position 25 km north of the Cape Hatteras, North Carolina survey site during the study period. Tooth placement at the tip on the mandibles confirms species identification.

Table 2. Beaked whale sightings, by species, at the Cape Hatteras, North Carolina survey site during the study period.

Species	No. of sightings	No. of individuals	Mean group size	Range group size
Z. cavirostris	44	128	2.9	1–8
M. europaeus	6	16	2.6	1–5
Mesoplodon spp.	24	61	2.5	1–6

gray in coloration relative to the dorsal flank. A few lightly pigmented linear scars were present across the dorsum. The area surrounding the blowhole was more lightly pigmented relative to other dorsal body surfaces, consistent with the description of the lateral head by Aguilar de Soto *et al.* (2017), based upon photographs taken during vessel surveys. Otherwise the body was relatively uniformly gray in color in both individuals photographed (as is also illustrated by Aguilar de Soto *et al.* 2017), suggesting that identification of females and young of this species could remain challenging at sea.

Sightings During Aerial Surveys

Z. cavirostris was the most commonly sighted species of beaked whale, representing 60% of all sightings (Fig. 1, Table 2). *M. europaeus* contributed 8% and unidentified mesoplodonts made up the remaining 32% of beaked whale sightings. *Z. cavirostris* were sighted in every month of the year, while *M. europaeus* was observed only in May, June, and July (Fig. 6a). Unidentified mesoplodonts were observed in all months of the year except September and October.

Most beaked whale sightings (64 of 74) occurred at or beyond the 1,000 m isobath (Fig. 1). Most sightings (37 of 44) of *Z. cavirostris* occurred at or north of Cape Hatteras Point, while *M. europaeus* and unidentified mesoplodonts were distributed more evenly across the study area.

The tendency for beaked whale sightings to occur at or beyond the 1,000 m isobath was also observed in Onslow Bay (Fig. 7). All sightings at this site were of unidentified mesoplodonts, suggesting that the pattern of species distribution observed in the Cape Hatteras survey area may continue southward. This result should be viewed with caution, however, as it is based upon only 3 d of surveys that extended beyond the Onslow Bay core study area.

Beaked Whale Abundance and Density Estimates in the Cape Hatteras Study Area

To produce a robust detection function with a low uncertainty, sightings of all medium sized whales (ziphiids, pilot whales, kogiids, and *Pseudorca*) were considered. A total of 175 groups were considered within a truncation distance of 900 m, 62 of which were of ziphiids (23 of *Mesoplodon* spp., 1 *M. mirus*, 5 *M. europaeus*, and 33 *Ziphius cavirostris*). The final selected model consisted of distance only (Fig. 8), which gave a mean probability of detection of 0.652 (SE: 0.091) with truncation distance of 900 m.

The surface density of all beaked whales, uncorrected for availability bias, was estimated as 0.005 (95% CI 0.003–0.008) whales/km^2 over the entire Cape Hatteras survey area, leading to an abundance estimate of 80 (50–130) animals in

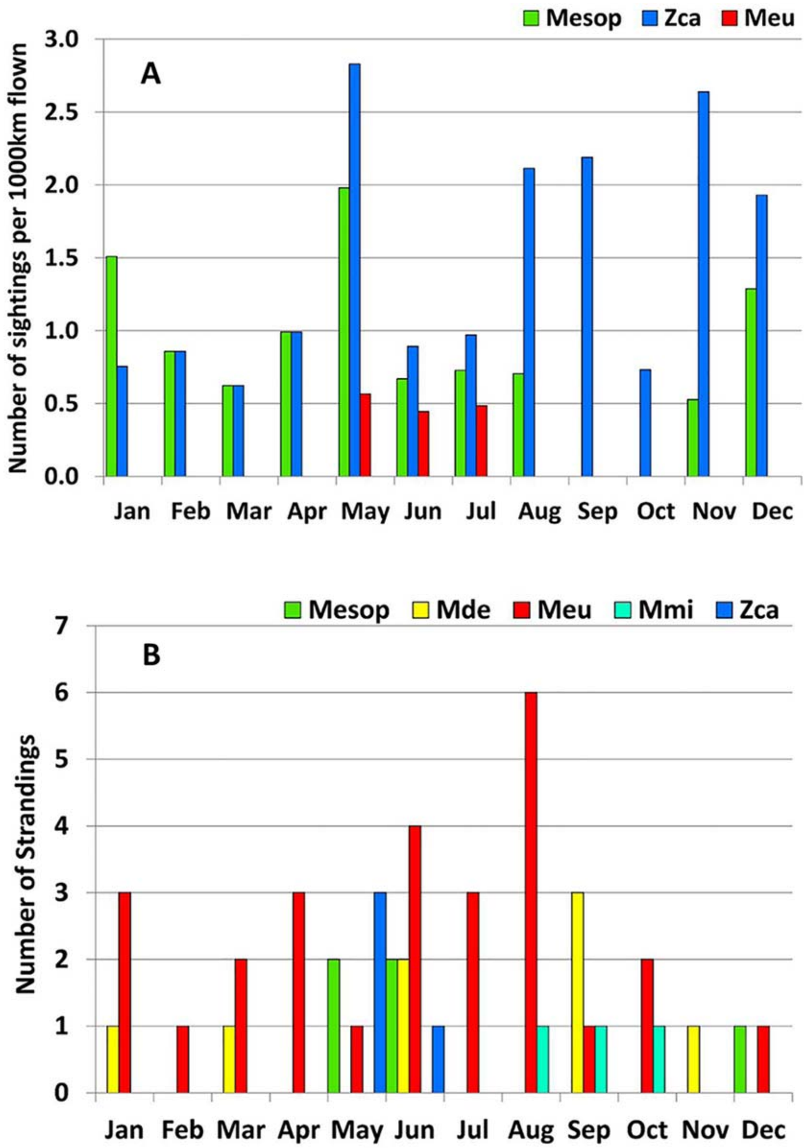

Figure 6. Beaked whale sightings and strandings. A. Cumulative monthly on-effort sightings of beaked whales, per 1,000 km of trackline flown, in the Cape Hatteras, North Carolina survey site during the study period (May 2011 through November 2015). B. Cumulative monthly strandings of beaked whales in North Carolina from January1993 through December 2015.

total (Table 3). When the subarea deeper than 1,000 m is considered, the mean density is 0.007 (95% CI 0.005–0.011) whales/km^2, for a total of abundance of 60 (40–100) whales. Density estimates that corrected for animal availability at the surface, yielded values that were 2.4–5.6 times higher than estimates for surface only

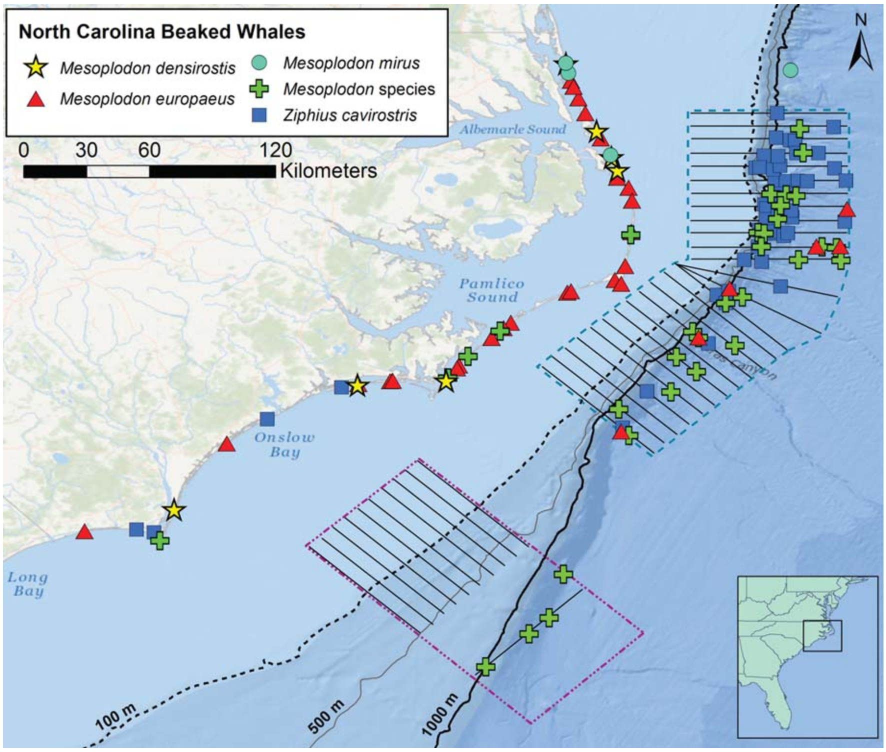

Figure 7. Geographic positions of beaked whale sightings and strandings. Sightings include those during the study period at the Cape Hatteras, North Carolina survey site and those off the shelf break in Onslow Bay from June 2007 to June 2010. Strandings data include all beaked whales that have been documented in North Carolina from January 1993 through December 2015.

animals, depending upon the assumptions of surfacing synchronicity (Table 3). Density and abundance estimates for *Z. cavirostris*, the most commonly sighted beaked whale species, are also presented in Table 3.

Beaked Whale Strandings in North Carolina

Between January 1993 and December 2015, 47 beaked whale strandings were recovered in North Carolina (Fig. 7, Table 4). The latitudinal pattern and species composition of strandings differed from that of sightings. *Z. cavirostris* contributed only 9% of all beaked whale strandings, and these events occurred at or south of the southern-most sightings of this species. No *Z. cavirostris* stranded in North Carolina from June 2000 to December 2015. *M. europaeus* comprised 57% of all beaked whale strandings, and their distribution stretched both north and south of the range of confirmed sightings of this species. Half of all *M. densirostris* and all *M. mirus* strandings have occurred along a small portion of the northern Outer Banks of North Carolina. One species in the stranding record, *M. densirostris*, has not been detected during aerial surveys off the North Carolina coast.

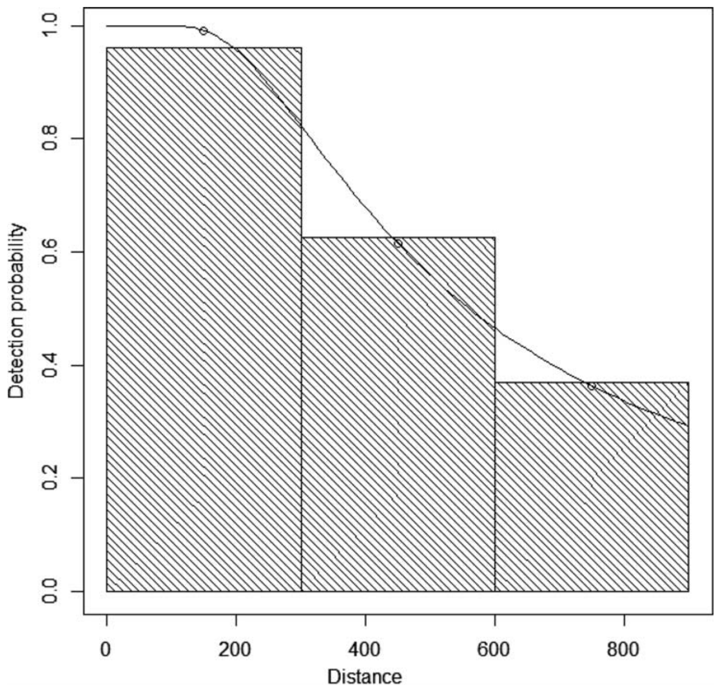

Figure 8. Probability of detection with distance (different levels shown by circles) for beaked whales (assuming detection on the trackline = 0.95). Solid line: mean fit against distance. Note: There is a strip width that cannot be observed directly under that plane. Thus, the actual left truncation distance is 149 m.

Beaked whales have stranded in all months of the year in North Carolina (Fig. 6b). For all beaked whale species combined, strandings did not vary significantly by month ($\chi^2 = 16.6$, df = 11, $P = 0.12$), but did by marine season (*i.e.*, January through March = winter, *etc.*; $\chi^2 = 8.2$, df = 3, $P = 0.041$), with disproportionately more strandings in spring.

Discussion

Beaked whales are present year-round off Cape Hatteras, North Carolina. *Ziphius cavirostris* was encountered in every month of the year, and mesoplodont whales were encountered in 10 out of 12 mo. Of the six species of beaked whales known to occur in the Northwest Atlantic, four—*Z. cavirostris*, *Mesoplodon densirostris*, *M. mirus*, and *M. europaeus*—occur off Cape Hatteras (MacLeod 2000, MacLeod *et al.* 2006). Two of these species were photographically documented within the survey area and a third was encountered just a few kilometers to the north (Fig. 2–5). To our knowledge, this is the first aerial survey to successfully discriminate mesoplodonts to species, a task that can be difficult even with a stranded specimen in hand. The ability to identify these species was entirely dependent upon clear photographic records of adult males with erupted mandibular teeth. The consistent sightings of *M. europaeus* in the study area also permitted description of species-specific pigmentation patterns that allowed confirmation of females and juveniles

Table 3. Density estimates (±95% CI) for all beaked whales (top panel) and for *Ziphius cavirostris* only (bottom panel) at the Cape Hatteras, North Carolina survey site during the study period, for both the entire survey area and the subarea consisting of locations with depth greater than 1000m. Note that differences in density estimates, corrected for availability bias, vary dependent upon surfacing synchronicity.

	Whole site		1,000 m+ depth	
	Estimated density animals/km^2	Estimated numbers	Estimated density animals/km^2	Estimated numbers
All beaked whales				
Surface only	0.005 (0.003–0.008)	80 (50–130)	0.007 (0.005–0.011)	60 (40–100)
Whales surface individually	0.012 (0.008–0.019)	190 (130–300)	0.019 (0.012–0.030)	170 (110–260)
Whales surface such that half the pod comes up individually	0.022 (0.015–0.033)	350 (240–520)	0.034 (0.022–0.054)	300 (190–480)
Whales surface as one group	0.028 (0.018–0.045)	420 (280–710)	0.042 (0.026–0.066)	370 (230–580)
Ziphius cavirostris				
Surface only	0.003 (0.002–0.005)	50 (30–80)	0.004 (0.002–0.007)	40 (20–60)
Whales surface individually	0.006 (0.003–0.011)	90 (50–170)	0.008 (0.004–0.015)	70 (40–130)
Whales surface such that half the pod comes up individually	0.009 (0.005–0.018)	140 (80–280)	0.013 (0.008–0.026)	110 (70–230)
Whales surface as one group	0.012 (0.007–0.024)	190 (110–380)	0.017 (0.008–0.034)	150 (70–300)

Table 4. Beaked whale strandings, by species, recovered in North Carolina from January 1993 through December 2015.

Species	No. of strandings	Inclusive dates	No. of males	No. of females
Z. cavirostris	4	May 1996–Jun 2000	0	4
M. europaeus	27	Jul 1993–Jan 2015	11	16
M. densirostis	8	Sep 2001–Jun 2012	3	5
M. mirus	3	Oct 2003–Sep 2012	1	2
Mesoplodon spp.	5	Jun 1993–May 2015	1	3

of this species. The opportunity to obtain such photographs is rare, but these results demonstrate that it is possible to identify mesoplodonts to species during aerial surveys.

The overall density of all beaked whales at the Cape Hatteras study site was remarkable (Table 3), with surface density estimates of 0.005/km^2 for the entire survey area, and 0.007/km^2 for the deep subarea. These values, which are not corrected for availability bias, are higher than most g(0) corrected values, excluding those for *Berardius bairdii*, presented by Barlow *et al*. (2006) in their comprehensive review of beaked whale densities from around the globe (see their Table 2). The perception and availability corrected density values of 0.019–0.042/km^2 in the deep subarea (Table 3) are higher than for any beaked whale species, except *Berardius*, reported by Barlow *et al*. (2006).

Cape Hatteras, at the convergence of the Labrador Current and Gulf Stream, is a region of high biological productivity (Schaff *et al*. 1992). The continental slope and deep shelf waters at this site experience extremely high rates of carbon flux and sedimentation (reviewed in Cahoon *et al*. 1994), host dense assemblages of benthic macrofauna (Schaff *et al*. 1992, Blake and Hilbig 1994), and represent a transition and transport zone for larval fishes from the Mid-Atlantic and South Atlantic Bights (Grothues and Cowan 1999, Grothues *et al*. 2002). The results of this study demonstrate that these waters also host extremely high densities of multiple species of beaked whales.

Barlow *et al*. (2006) identified both sea state and observer experience as critical factors in the ability to detect smaller beaked whales. In the present study, surveys were conducted in good sighting conditions by two highly trained observers, each with multiple years of experience. Barlow *et al*. (2006) also noted that many previous beaked whale abundance estimates included shallow shelf and slope waters, where beaked whales were unlikely to occur. Beaked whale density estimates should be generated from slope or deep waters, *i.e.*, known beaked whale habitat. The present study accomplished this goal, and as would be predicted, estimates of beaked whale densities are comparatively very high. The present surveys also occurred year-round and across multiple years. Multiyear and/or multiseason focused survey efforts to assess the presence of beaked whales are rare (Balcomb and Claridge 2001, MacLeod and Zuur 2005, Soto 2006, Claridge 2013, Arcangeli *et al*. 2014, Cañadas and Vazquez 2014), and there are few other comparable data sets generated from focused, multiyear, year-round survey efforts.

Pyenson (2011) compared stranding and sighting records at eight locations across the globe and discovered that stranding records provided "high fidelity" records of the species richness and relative abundance of living cetacean assemblages documented through surveys. He also determined that species richness was almost always higher in the stranding record than in the survey record. In some regards, the results presented here support these conclusions. Beaked whales stranded in all months of the year in North Carolina, reflecting the results of the aerial surveys described here. More beaked whale species were recovered as stranded specimens in North Carolina than observed during aerial surveys, with one species, *Mesoplodon densirostris*, found only in the stranding record.

The relative abundance of species differed dramatically across the stranded and sighted data sets. The most commonly sighted species, *Z. cavirostris* (60% of all beaked whale sightings) was rare in the stranded sample (8% of all stranding). Likewise, *M. europaeus* comprised only 8% of all sightings (although this species is also likely to be included in the *Mesoplodon* spp. sightings), but was the most common stranded beaked whale species in North Carolina (57% of all strandings). *Z. cavirostris* and *M. europaeus* both occur off Cape Hatteras, but during the study period no *Z. cavirostris* stranded in this region. The reasons for the differences in the stranding and sighting records are currently unknown, are likely to be complex, but may be important to inform mitigation strategies under MMPA authorizations issued by the National Oceanographic and Atmospheric Administration (NOAA) for U.S. Navy Atlantic Fleet Training and Testing (AFTT) activities, as well as for seismic exploration. Under the Stranding Response Plan in the current MMPA authorization for AFTT (http://www.nmfs.noaa.gov/pr/pdfs/permits/aftt_stranding_response.pdf), if an "uncommon stranding event," which includes the stranding of a single beaked whale, occurs locally during a major training exercise, the Navy may be required to alter their activities. The lack of *Z. cavirostris* strandings in the Cape Hatteras region suggests that this mitigation strategy may not be as effective for this species at this site since they appear to be less likely to strand regardless of the cause.

Effective management and conservation of cetaceans requires knowledge of their abundance and distribution in areas where they are vulnerable to anthropogenic activities (Hammond *et al.* 2013). The waters off Cape Hatteras are an important year-round habitat for several beaked whale species. These results complement those of Roberts *et al.* (2016), who identified this area as a hotspot of cetacean biodiversity, and one with high beaked whale abundance. This site is also currently utilized by the U.S. Navy for its training and testing activities and has been included in the areas of interest for large-scale commercial seismic surveys. Beaked whale species appear to be particularly vulnerable to certain types of anthropogenic disturbance (Barlow *et al.* 2006, Cox *et al.* 2006, Tyack *et al.* 2011). Therefore, building on the recommendations of Cox *et al.* (2006) and Barlow *et al.* (2006), future research efforts in this area should be aimed at enhancing our understanding of beaked whale: (1) population structure through photo-ID, genetic sampling and telemetry; (2) diving behavior and ecology, using archival tags and satellite-linked dive recorders; (3) anatomy and physiology, through the detailed investigation of strandings; and (4) behavioral responses to anthropogenic sounds, through controlled exposure experiments. Such studies are required to fully understand and mitigate anthropogenic impacts on multiple species in this important beaked whale habitat.

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