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RESEARCH ARTICLE

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# Habitat utilization by Blainville's beaked whales off Great Abaco, northern Bahamas, in relation to seabed topography

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**Abstract** We investigated habitat utilization in Blainville's beaked whale, *Mesoplodon densirostris*, in the northern Bahamas and, as such, this is the first analysis of fine-scale habitat utilization of any member of the genus *Mesoplodon*. We divided the area into 500×500 m grid squares and each square was assigned a classification for presence or absence of Blainville's beaked whales, along with details of water depth, seabed gradient and seabed aspect. All squares where Blainville's beaked whales occurred had gradients from 68 to 296 m/km and depths from 136 to 1,319 m and most faced northeast compared with 0–526 m/km, 10–3,000 m and all aspects for the whole study area. Generalized additive models and classification trees indicated that, in order of importance, aspect, gradient and depth were related to occurrence of Blainville's beaked whales within the study area. We hypothesize that the relationships between habitat utilization and these topographic variables relates to the effects of interactions between a deepwater current and the seabed topography on preferred prey. Locally, prey animals may be concentrated in areas with a northeast aspect, intermediate gradients and depths between 200 and 1,000 m where the Deep Western Boundary Current is forced towards the surface by the local topography. These are the areas where Blainville's beaked whales preferentially occurred.

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## Introduction

Little is known about the biology of beaked whales (Order Cetacea; Family Ziphiidae), and most of what is currently known has come from the study of stranded animals. In particular, habitat preferences and utilization remain poorly understood. Currently, detailed analysis of habitat utilization has only been published for one species of beaked whale, the northern bottlenose whale (*Hyperoodon ampullatus*) at one location, the Gully, off Nova Scotia (Hooker 1999; Hooker et al. 2002). This lack of information on habitat preference is due to the occurrence of beaked whales in deep oceanic waters combined with problems in identifying beaked whales, particularly females and juveniles of the genus *Mesoplodon*, to species level in the field.

Blainville's beaked whale (*Mesoplodon densirostris*) is the most widely distributed of the 14 species in the genus *Mesoplodon* and occurs in all warm temperate, subtropical and tropical oceanic waters throughout the world, with the exception of the Mediterranean (Mead 1989). In the North Atlantic, this species has been recorded from the eastern coasts of the United States, the Bahamas, several parts of the West Indies, Great Britain, France, Spain, Madeira and the Canaries (Mead 1989; MacLeod 2000). This species, therefore, offers the opportunity of examining geographic differences in the ecology of a *Mesoplodon* species and how such a species interacts with, and adapts to, a variety of environments. Such comparisons will aid in the ecological understanding not just of this species but of the genus *Mesoplodon* as whole. However, despite its widespread occurrence, data on free-ranging Blainville's beaked whales have only been collected at a limited number of locations, such as the Bahamas, the Canaries, Hawaii, the Society Islands and the Cook Islands (Shallenberger 1981; Claridge and Balcomb 1995; Carrillo and Lopez-Jurado 1998; Ritter and Berderlau 1999; Gannier et al. 2000; Hauser, personal communication). In addition, these data have usually been collected during general research programs on all species of cetaceans rather than as part of a dedicated study aimed specifically at Blainville's beaked whales (e.g. Ritter and Berderlau 1999; Gannier et al. 2000).

This study examined the distribution of Blainville's beaked whale east of Great Abaco in the northern Bahamas and related fine-scale habitat utilization to seabed topography. The proximity of deep oceanic waters close to land in this area allowed the use of small boats to locate and follow groups of whales with minimal disturbance. This, in conjunction with the unique morphology of the species (a noticeable arch in the posterior half of the mandible) which allows individuals of all ages and sexes to be identified to species level with relative ease, allowed the first detailed analysis of factors which affect the fine-scale distribution of a member of the genus *Mesoplodon*.

Only by understanding where, and why, a species occurs within the range of potential habitats is it possible to assess and mitigate potential anthropogenic impacts upon that species. Beaked whales are subject to a number of potential anthropogenic impacts. For example, since the mid-1980s there has been increasing evidence that mid-frequency sonars may, under some circumstances, result in mass strandings, and subsequent death, of beaked whales within the vicinity (Simmonds and Lopez-Jurado 1991; Frantzis 1998; Frantzis and Cerbrian 1998: Balcomb and Claridge 2001; Evans et al. 2001). However, mitigation of such impacts has been hampered by a lack of understanding of where free-ranging beaked whales occur and what factors affect their distribution and occurrence within the marine environment.

## Materials and methods

The study area was selected to cover as wide a range of habitat types as possible within an area east of Great Abaco, The Bahamas. The exact location of the study area was chosen based on information from previous research (e.g. Claridge and Balcomb 1995) and the location of passes from inside the local barrier reef to the open ocean which were required to access to study area from the nearest port. The size of the area was limited by distances which could be covered by the research vessels within a single day before returning to port. The study area was approximately 35 km in length and up to 16 km in width, with the southern edge aligned with the 26°20′ N parallel and the western edge aligned with the 77°00′ W meridian, and included areas of coral reefs, shallow shelf-like areas, steeply sloping shelf-edge-like areas, the upper reaches of a marine canyon (Little Abaco Canyon) and deep oceanic areas (Fig. 1). To allow fine-scale habitat preferences to be investigated, the study area was divided into 1,744 grid squares of 500×500 m (Fig. 2).

Regular surveys were conducted between May and August each year between 1998 and 2000 using small (approximately 6 m long) boats, with an eye height of 2–3 m, travelling at a set speed (approximately 12–16 km/h) with two to four observers on board. Surveys were only undertaken in sea states of Beaufort three or less to minimize the likelihood that groups of beaked whales which were present in the study area were not detected. The study area was systematically covered to ensure as many grid squares were surveyed as possible and that coverage throughout the area was as even as possible. The position of the research vessel was automatically recorded every 5 min using a Garmin 40 Global Positioning System (GPS) receiver. When any beaked whales were encountered, their position was recorded and the group was followed until it left the study area, or had not been sighted for up to 30 min, at which point the coverage of grid squares was continued as before. In 1998 and 1999 photo-identification photographs were taken using a Nikon F90x camera fitted with a 100–300 mm zoom lens. Individual animals were identified using patterns of scars and from the shape and nicks on the dorsal fin. On return to shore, the track of the research vessel was downloaded from the GPS to a laptop computer using Garmin PCX5 software version 2.09. A straight-line course and consistent speed allowed the route between these points to be plotted and allowed each grid square visited and utilized by Blainville's beaked whales to be identified.

A Geographic Information System (GIS) of the study area was constructed using Environmental Systems Research Institute (ESRI) ArcView 3.2 software. Each grid square was assigned values for three characteristics of topography: Water depth, gradient and aspect of the seabed. For depth, the value for the central point of each cell was obtained by overlaying the grid onto the best available bathymetric chart of the northern Bahamas (Waterproof Charts, Chart 120F) which had been previously been scanned. The central depth value for each cell was interpolated from the relative distance to neighboring depth contours. These depth values were used to calculate the gradient of the seabed between a grid square and the eight surrounding grid squares. In all cases gradient was expressed as the vertical drop in meters per horizontal kilometre. The aspect of the seabed in each grid square was calculated using the ArcView spatial analyst tool and assigned to one of the nine categories: north-facing, northeast-facing, east-facing, southeast-facing, south-facing, southwest-facing, west-facing, northwest-facing or flat for cells which had no gradient.

As the main aim of this study was to investigate habitat utilization in relation to seabed topography, data from all months and years were combined and any seasonal or annual variations in occurrence or habitat utilization were not investigated. Grid squares were then classified into three categories: Presence — grid squares where Blainville's beaked whales were recorded on at least one occasion during an encounter; Absence — grid squares which were surveyed at least once but which Blainville's beaked whales never entered during an encountered; Not Surveyed — grid squares which were not surveyed at any point during the study.

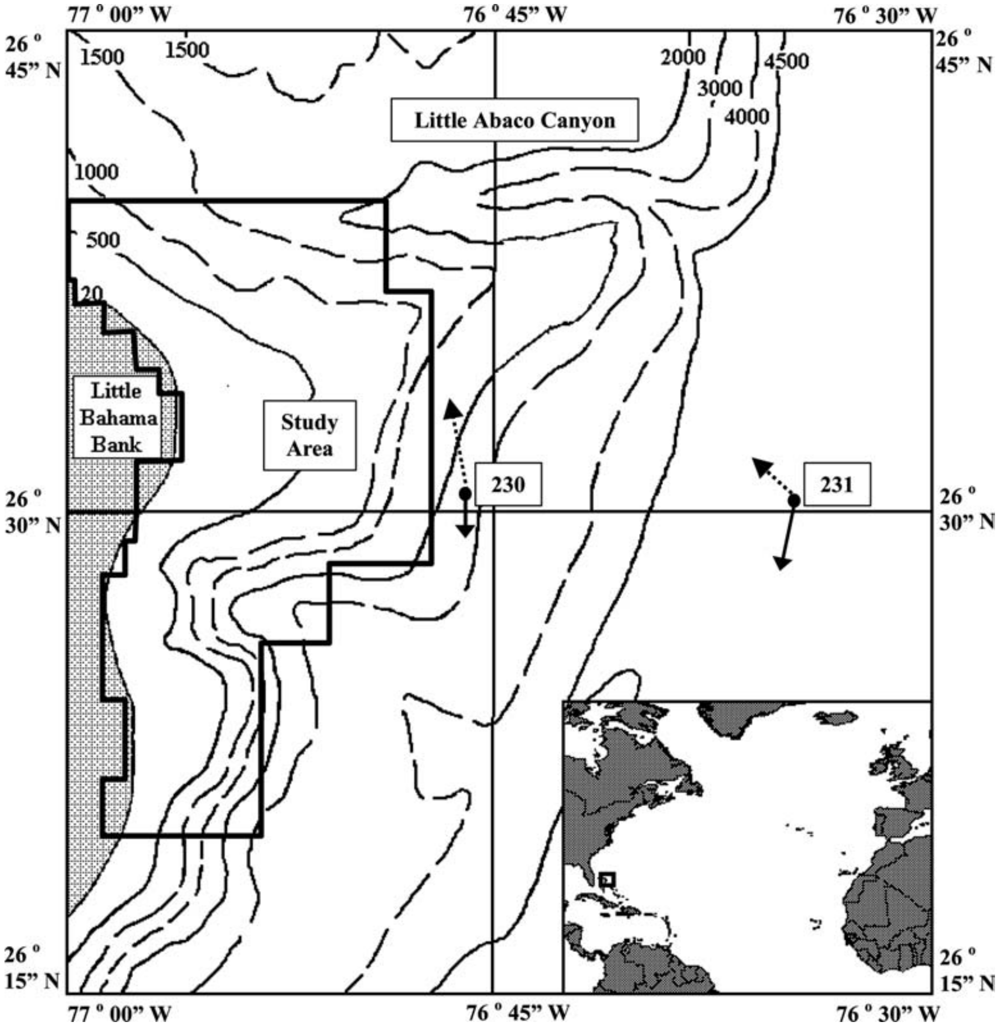



**Fig. 1** The location and extent of the study area, with bathymetry of the surrounding area (adapted from Waterproof Charts, Chart 120F). Depths are in meters. *230* and *231* are the positions of current meters in place between 17 April 1987 and 19 June 1988. *Dashed arrows* indicate direction and relative strength of currents at 400 m depth, *solid arrows* the direction and relative strength of the Deep Water Boundary Current (DWBC) at depths of 1,200 m and deeper (from Lee et al. 1990)

Data were analyzed in three ways. Firstly, in terms of focal follow groups. A focal follow group was defined as any encounter which lasted longer than 10 min. Although some individual animals were resighted, no focal follow groups were found to contain exactly the same identified individuals, therefore each group was treated as an independent encounter. To investigate whether different focal follow groups utilized different grid squares of depths, the depth of each cell utilized during each encounter was tabulated. As the number of cells per focal follow group differed, a Kruskal-Wallis test was used to investigate whether there was a difference between depths of grid cells utilized by the different focal follow groups. A similar analysis of gradient of grid cells by the different focal follow groups was also conducted. In both cases the null hypothesis tested was that there was no difference in the median values of cells utilized by the different focal follow groups.

Secondly, habitat utilization by individually-identified animals was investigated. For intra-individual comparisons, individuals which were seen in two or more focal follow groups and which used a sufficient number of grid squares (five of more) on each occasion were used. For this analysis, when pairs of individual animals were always seen in the same groups (e.g. mother-calf pairs) only one of the animals was used in this analysis. For inter-individual comparisons, individuals which were seen on two or more focal follows were used. As the number of cells per individual differed, a Kruskal-Wallis (for individuals encountered on three or more encounters) or Mann-Whitney (for individuals encountered only twice) test was used to investigate whether there was a difference between the depth and gradient of grid cells utilized by individuals on different encounters and by different individuals. The null hypothesis tested was that there was no difference in the median values of cells utilized during the different encounters for the same individual (intra-individual comparisons) or between all the individuals seen in two or more focal follow groups (inter-individual comparison).

Finally, overall habitat preferences of Blainville's beaked whales within the study areas were investigate in terms of depth, gradient and aspect. The relationship between whale occurrence and the three habitat variables were analyzed using generalized additive modelling (GAM) techniques (Hastie and Tibshirani 1990). Because the whale data were presence-absence, a GAM

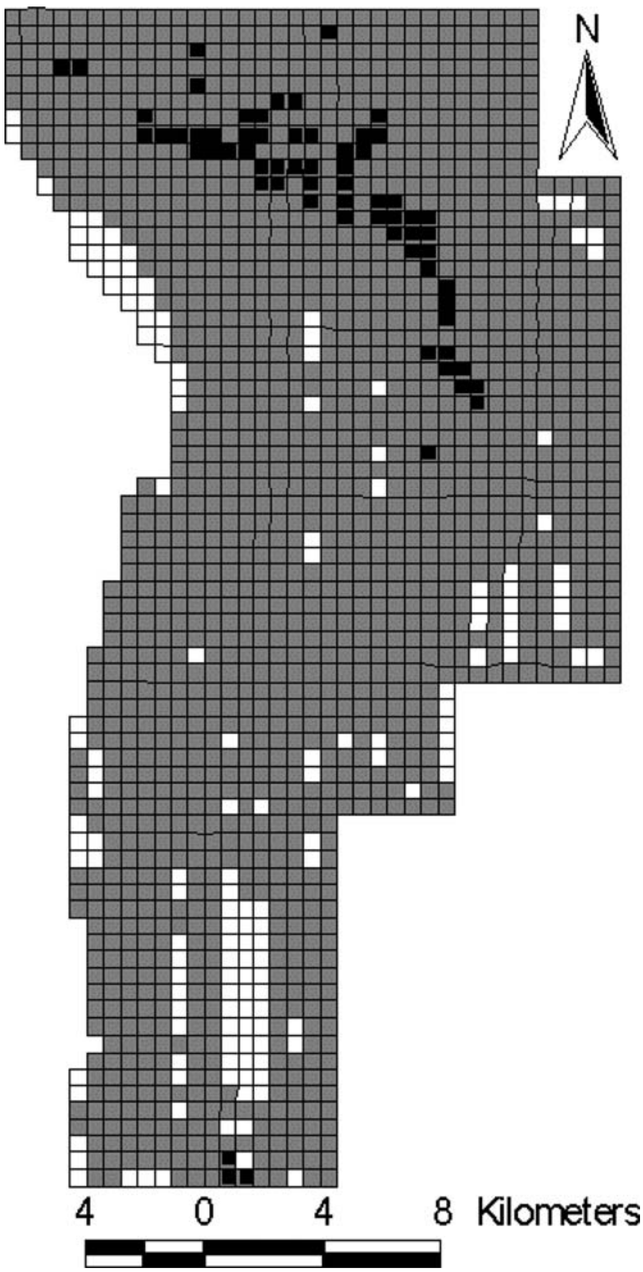



**Fig. 2** Grid squares used for this study ($n = 1{,}744$). Each square is 500×500 m in size. *Black squares* Blainville's beaked whales recorded as present; *grey squares* Blainville's beaked whales recorded as absent, *white squares* not surveyed during the study

with a binomial distribution and logistic link function were used. The model was given by:

$$\text{Log}\left(\frac{\Pr(\text{Whale} = 1|\text{Gradient, Depth, Aspect})}{\Pr(\text{Whale} = 0|\text{Gradient, Depth, Aspect})}\right) = f_1(\text{Gradient}) + f_2(\text{Depth}) + \text{Aspect}$$

The term "Aspect" was modelled as a factor (nominal variable) and $f_1$ and $f_2$ represent smoothing functions. The GAM was fitted using S-Plus software. To better understand the results of the GAM model, classification trees (De'ath and Fabricius 2000) were applied using the rpart function in the R-software package. For both analyses, all presence and absence grid squares were utilized. Although this resulted in multiple grid squares from individual encounters being included and associated problems of correlation in topographic variables between neighboring squares, this approach was used for three reasons. Firstly, although values for topographic variables in neighboring squares will be related, all nine neighbors will not be identical. Therefore, when moving during an encounter, groups still have a choice, although limited, in what habitat to utilize. A group can choose either to remain in exactly the same habitat (i.e. not move from the square they are in) or choose which neighboring cell to enter based on the topographic variables. As a result, all the squares utilized during an encounter will reflect a habitat choice, albeit reduced in scope, of the group and it was assumed that the group would move to neighboring square with the most preferred combination of habitat variables. Secondly, if only independent grid squares were utilized from this dataset it would mean selecting only one grid square from each encounter, greatly reducing the sample size. In addition, it would be inaccurate to assign squares which were utilized in an encounter to any category other than presence. They certainly cannot be assigned to the absence category and probably should not be assigned to the not surveyed category. Therefore, if only one square per encounter were included in this analysis, all other grid squares utilized would have to be discarded from the analysis. This would effectively remove the majority of squares used by, and presumably much of the preferred habitat of, Blainville's beaked whales from the analysis altogether and would make interpreting the results problematic. Thirdly, if it is assumed that any group of whales would have utilized all squares used during an encounter regardless of whether they were being observed and, had each square housed a stationary observer who recorded presence or absence of whales, the same data would have been obtained.

However, when interpreting the results of this analysis, possible biases associated with correlation between neighboring grid squares should be considered. In particular, a small number of groups of animals that used a large number of grid squares could bias the results of this analysis towards the habitat used by these groups. To investigate if this was the case, values of each variable for the first cell from each encounter were compared to all other grid squares utilized to see if there was a significant difference between the two. In addition, the GAM was repeated using only the first cell from each encounter and removing all other cells utlized by Blainville's beaked whales from the research to investigate whether this would provide a substantially different view of habitat utilization.

## Results

Between May and August in 1998, 1999 and 2000, 227.4 h of systematic effort were conducted. Eighteen groups of Blainville's beaked whales were encountered and this species was the second most frequently encountered cetacean species after the Atlantic spotted dolphin (*Stenella frontalis*). During these encounters, just over 8.4 h of data on habitat utilization were collected. The overall encounter rate was 0.079 groups per hour of effort, with a relative density of 0.29 individuals per hour. Out of a total of 1,591 cells surveyed during this study, Blainville's beaked whales were only recorded in 66 (Fig. 2). Water depths of grid squares utilized varied from 136 to 1,319 m (mean: 495 m; SD 251 m), while gradient varied from 68 to 296 meters per kilometre (mean: 139 m/km; SD 42 m/km). The majority of cells where Blainville's beaked whales were recorded had a north-east aspect (44/66). The next most commonly utilized cells in terms of aspect were east-facing (13/66), north (6/66), north-west (2/66) and south-east (1/66). No cells with other aspects were utilized.

## Focal follow groups

Fourteen groups were followed for periods longer than 10 min. The Kruskal-Wallis tests found that both the median depth and the median gradient differed significantly between focal follow groups (Depth: $H = 47.34$, $df = 13, P < 0.001$, adjusted for ties; Gradient: $H = 45.25$, $df = 13$, $P < 0.001$, adjusted for ties). Therefore, the null hypotheses were rejected and it was concluded that there is a difference in habitat use, in terms of the median values of the two variables, between the different focal follow groups of Blainville's beaked whales.

## Comparison of habitat utilization by individual animals

In 1998 and 1999 combined, 36 individual animals were identified from photographs. Up to 10 additional individuals were seen but were not identified. The majority of individuals identified (28/36) were encountered only once, with four being encountered twice, one three times and two five times. These latter two consisted of a mother-calf pair which was always encountered together throughout the 3 years of the study.

For intra-individual comparisons, three individuals were seen on two or more focal follows and utilized a sufficient number of grid squares on both occasions to be statistically compared in terms of habitat utilization. The first animal differed in the median depth and gradient of grid squares utilized between four focal follows (Kruskal-Wallis test: Depth, $H = 20.44$, $df = 3$, $P < 0.001$; Gradient, $H = 9.16$, $df = 3$, $P = 0.027$), while the second animal did not (Mann-Whitney: Depth, $W = 29.0$, $P = 0.626$; Gradient, $W = 40.0$, $P = 0.254$). The third animal differed significantly in median depth but not for median gradient between two focal follows (Mann-Whitney: Depth, $W = 18.0$, $P = 0.0085$; Gradient, $W = 31.0$, $P = 0.2979$) (Fig. 3).

For inter-individual comparisons, five animals (treating the mother-calf pair as a single animal) were seen on two or more focal follows. Both median depth and median gradient of grid squares utilized differed significantly between these individuals (Depth: Kruskal-Wallis test, $H = 21.71$, $df = 4$, $P < 0.001$, adjusted for ties; Gradient: Kruskal-Wallis test, $H = 27.48$, $df = 4$, $P < 0.001$, adjusted for ties). Therefore, it was concluded that while some individuals did not differ in the habitat which they utilized on different focal follows (in terms of median values of cells utilized); other individuals did differ in their habitat use between focal follows. It was also concluded that there was a difference, in terms of median values of cells utilized, in habitat used by different individuals.

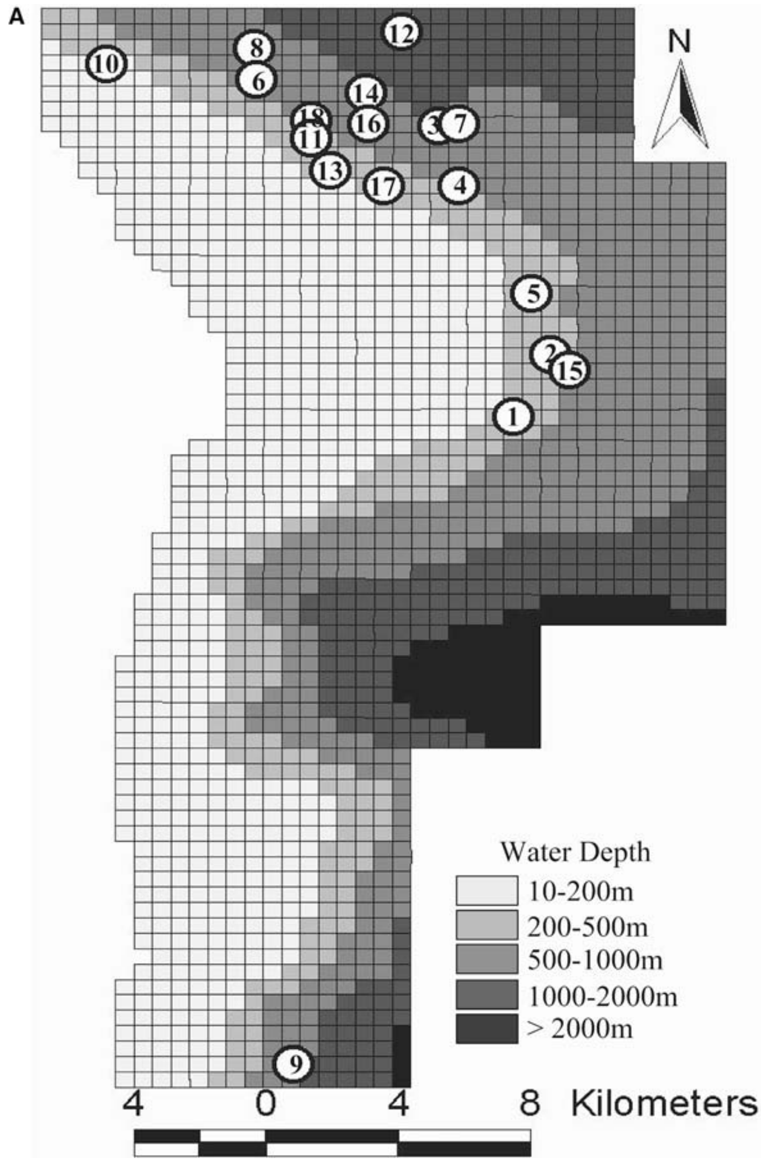
As multiple statistical tests were used to test the differences between individuals followed on different occasions, between different individuals and between focal follow groups, it is possible that type one statistical errors may have accounted for some of identified differences. However, if the Bonferroni correction is used to counter this possibility and the level of significance is adjusted to $P = 0.005$ (0.05/10), only one test, the median gradients between focal follows of the second individual, becomes non-significant. Therefore, the significant variation in habitat utilized between some individuals followed on different occasions, between different individuals and between focal follow groups is likely to be real rather than a statistical artefact.

## Habitat preferences of Blainville's beaked whales east of Great Abaco

The estimated smoothing curves (using 4 *df*) and nominal variable from the GAM are shown in Fig. 4a. This analysis suggests a non-linear relationship between whale occurrence and gradient and between whale occurrence and depth. There was no overdispersion. A backwards selection using the Akaike Information Criteria (AIC) indicated that no terms should be dropped from the model (Table 1). The classification tree indicates that the first split between the 1,591 squares in relation to whale occurrence is based on aspect (Fig. 5). However, due to the small number of positive sightings, tree pruning using cross-validation is not positive, and therefore the tree should be interpreted with common sense. Pre-pruning is possible and was applied (De'Ath and Fabricus 2000).

The left-hand branch groups samples with aspects of east, north, south, southeast, southwest and squares with no gradient (flat). Of the 1,591 grid squares surveyed, 1,118 were classified into this branch of the classification tree and for these squares, all beaked whale occurrences (20 grid squares) were at gradients greater than or equal to 86.1 m/km. The right-hand branch at this first split grouped squares with aspects of northeast and northwest and contained 473 squares. Of these the vast majority (463) were of northeast aspect. Gradient represented the next split in this right-hand branch, with all but one grid square where Blainville's beaked whales

**Fig. 3a** The locations of grid squares where each group was first encountered. **b** The tacks followed by each group that used more than one grid square during the encounter. For encounter 10, the animals were lost during the encounter but were resighted within 30 min and the encounter was continued. However, it was uncertain which cells were used during the period they were not observed. In all cases, squares represent individual 500×500 m grid square and shading represents central depth



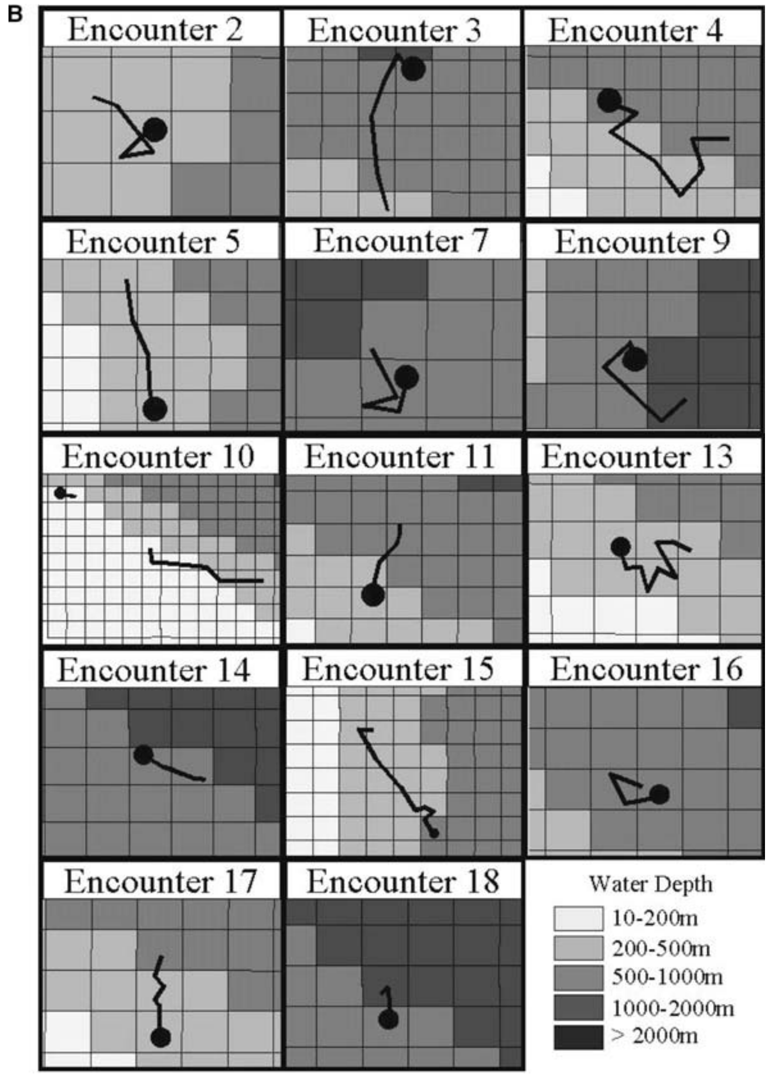

occurred having a gradient greater than or equal to 83.0 m/km. The next split occurred at water depth of 605 m, with the majority of presence squares being grouped at shallower depths. A visualization of the right-hand branch of the first split on the classification tree indicates in grid squares with aspects of northeast and northwest, the majority of squares where Blainville's beaked whales were recorded as present (31/46) had gradients between 82.96 and 177.8 m/km and depths between 249 and 605 m (Fig. 6). The probability of Blainville's beaked whales being recorded as present in grid squares within this classification was 41.9%.

The number of grid squares utilized during an encounter varied from 1 to 11 (Fig. 3). Therefore, some encounters contributed more to the total number of grid squares and so habitat used, than others. However, when the first square used during each encounter ($n=18$) were compared to all other squares ($n=48$), there were no significant differences in habitat usage in relation to the three topographic variables (Table 2). This indicates that no one encounter was biasing the results of the analysis based on all cells used. Similarly, when the GAM analysis was rerun using the first cell for each encounter, rather than all cells, there was still a significant relationship with all three variables (Depth: $P=0.01$, Aspect: $P=0.02$; Gradient: $P<0.001$; Fig. 4b). This suggests that while there is the possibility of autocorrelation between successive cells used in a single encounter, using multiple cells from each encounter rather than restricting the analysis to the first cell did not alter the identified relationship between the distribution of Blainville's beaked whale and the three variables.

## Discussion

Sightings of Blainville's beaked whales did not occur randomly throughout all oceanic waters east of Great

**Fig. 3b** (Contd.)




Abaco in the Bahamas during this study. Water depths of grid cells where the whales were recorded ranged from 136 to 1,319 m, in comparison to a range of 10 to over 3,000 m for the study area as a whole, while gradients ranged from 68 to 296 m/km in comparison to 0 to 526 m/km for the whole study area. The GAM indicates that the aspect of seabed, its gradient and the depth of the water are all important in determining the occurrence of Blainville's beaked whales within the study area. The classification tree suggested that, as it defines the first split, aspect is the most important of these variables, followed by gradient (the defining variable for the second split in each branch) and depth. Most grid squares where Blainville's beaked whales were recorded as present were grouped as squares with northeast and northwest aspects. However, the vast majority of grid squares within these two classes were the former rather than the latter, suggesting a northeast-facing aspect is the most important topographic factor related to the occurrence of Blainville's beaked whales in the study area. Within areas with these aspects, Blainville's beaked whales preferentially utilized squares with gradients between 83.0 and 177.8 m/km and depths between 249.5 and 605 m. In the study area, grid squares with these values for the three topographic variables are concentrated over the southern side of the upper reaches of Little Abaco Canyon, where most encounters occurred. Different individual and groups of Blainville's beaked whales varied in the way they used the study area. However, there were within relatively narrow ranges in comparison to the study area as a whole and there were no major differences between the results of the general habitat usage analysis and that of different individuals and groups.

Determining why the occurrence of Blainville's beaked whales in the waters around Great Abaco is closely linked to specific types of seabed topography around Little Abaco Canyon will require further research. Even in the best studied marine mammal species, determining the fundamental reasons behind the linkage between habitat variables and distribution can be problematic and often requires extensive datasets. It may be that this topographic feature for some reason increases local primary productivity, which in turn leads

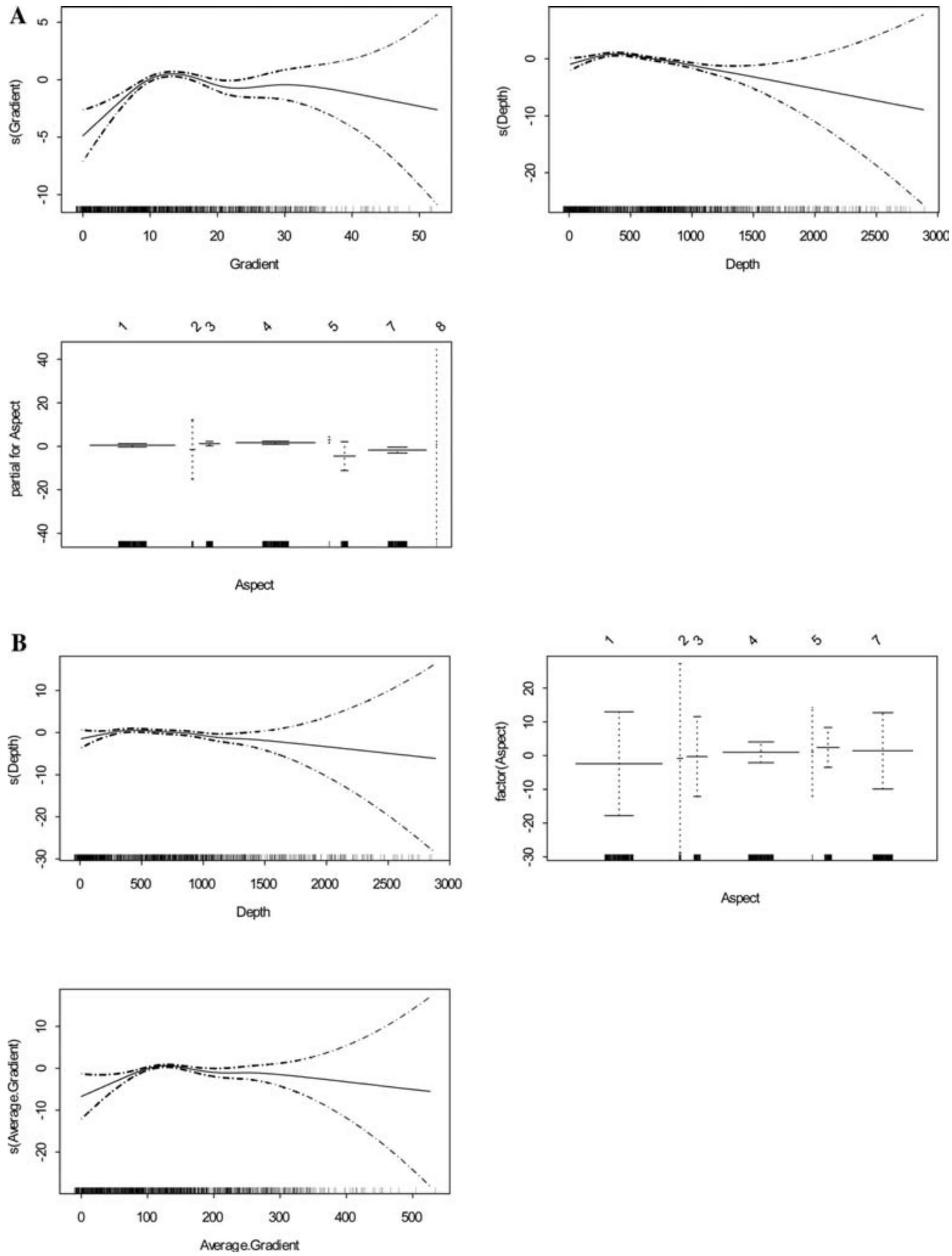



**Fig. 4a** Estimated smoothing curves (using 4 *df*) and nominal variable for GAM of occurrence of Blainville's beaked whale east of Great Abaco in relation to topographic variables using all cells utilized. In the top two panels, the *solid line* indicates the smoothing curve, while the *dotted lines* represent the 95% point-wise confidence bands. **b** A repeat of this analysis restricted to the first cell of each encounter

to higher secondary production and a local increased availability of prey. This may be particularly important in the waters around Abaco, which lies in an oceanic province with generally very low levels of primary productivity (under 6 mg m$^{-2}$, Longhurst 1998) and any local hotspots in production may attract all elements of the local food web from primary consumers to apex predators.

**Table 1** The results of backwards selection using Akaike Information Criteria (AIC) of GAMs using different permutations of variables

| GAM model | AIC |
|---|---|
| Full model | 403 |
| Depth and aspect | 421 |
| Gradient and aspect | 435 |
| Gradient and depth | 436 |

However, other cetacean species were not similarly concentrated in the same areas as Blainville's beaked whales (MacLeod et al. 2004), suggesting that there are additional factors involved. This may include habitat segregation between other species that occupy a similar ecological guild. For example, MacLeod et al. (2004) found that each of the three main deep-diving cetacean species recorded in the study area differed in the depths where they were primarily recorded. Cuvier's beaked

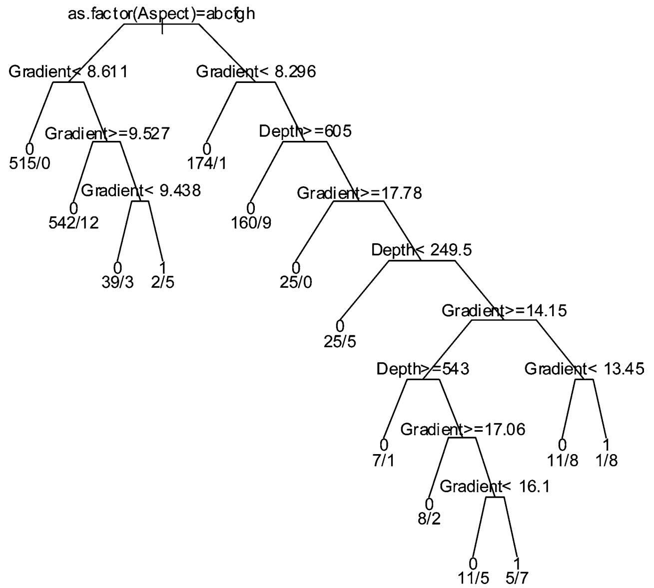



**Fig. 5** The classification tree of the occurrence of Blainville's beaked whale east of Great Abaco based on three variables. For aspect: *a* east, *b* flat, *c* north, *d* northeast, *e* northwest, *f* south, *g* southeast, *h* southwest. In each case, the statement used to split the grid squares is given above the branching point and the *left-hand branch* indicates squares for which the statement is true. The upper number at the end of a terminal branch indicates whether beaked whales are likely to occur within that classification, with *1* indicating predicted presence and *0* predicted absence. The lower numbers indicate the total number of grid squares classified (*left*) and the number where Blainville's beaked whales were recorded as present (*right*)

whales (*Ziphius cavirostris*) were primarily found in deeper waters than Blainville's beaked whales and the dwarf sperm whale (*Kogia simus*) in shallower waters. However, while this would explain the preferences for a specific range of depths, this would not necessarily explain why Blainville's beaked whales were not recorded evenly through all waters of their preferred depth and instead were clumped in the area over Little Abaco Canyon.

For many marine species, the distribution of available prey is important in determining their spatial and temporal distribution (e.g. MacLeod et al. 2004), and it may be that the relationship between Blainville's beaked whale habitat usage and seabed topography is related to the local distribution of their preferred prey. In particular, we hypothesize that there may be some aspect of the Little Abaco Canyon that results in the concentration of the prey of Blainville's beaked whales within this area.

The Little Abaco Canyon penetrates approximately 35 km westward into the main escarpment between the shallower slope areas around Little Bahama Bank and the abyssal areas of the Western Atlantic Basin (Fig. 1). The southern side of the upper reaches of this canyon forms a relatively shallow (between 100 and 2,000 m) area with a slight to moderate slope. The structure of oceanic currents east of Abaco can be summarized as follows: Surface waters are influenced by a permanent anticyclonic gyre which re-circulates water from the Gulf Stream. Near the study area in the upper 400 m there is a northward movement. Deeper waters (below 1,000 m) are influenced by southward movements of the Deep Western Boundary Current (DWBC—Lee at al. 1990). In the study area, the DWBC will meet the shallower southern side of the Little Abaco Canyon below 1,000 m. As a result, it will be deflected up the slope and over the southern side of the canyon (which is as shallow as 100 m in places) before continuing southward. Therefore, on the south side of Little Abaco Canyon, the DWBC will be flowing up the slope towards the surface between depths of approximately 1,000 and 100 m. Therefore, Blainville's beaked whale primarily utilizes areas where the local topography causes the DWBC to be pushed towards the surface.

Nesis (1993) suggested that certain types of cephalopod (including many of those recorded from beaked whale stomachs) may become accidentally associated with seamounts and other steeply sloping oceanic areas

**Fig. 6** A visualization of the right-hand branch of the classification tree after the first split. All squares in this branch have aspects of northeast or northwest. Each box represents a terminal branch of the classification tree, with its associated range of gradients and depths and the number of grid squares where Blainville's beaked whales were recorded as present which fall within this classification. The majority of grid squares with these aspects where beaked whales were recorded (31 of 46) had gradients between 82.96 and 177.8 m/km and depths between 249 and 605 m (*shaded area*). The probability of Blainville's beaked whales being recorded as present in grid squares within this classification was 41.9%

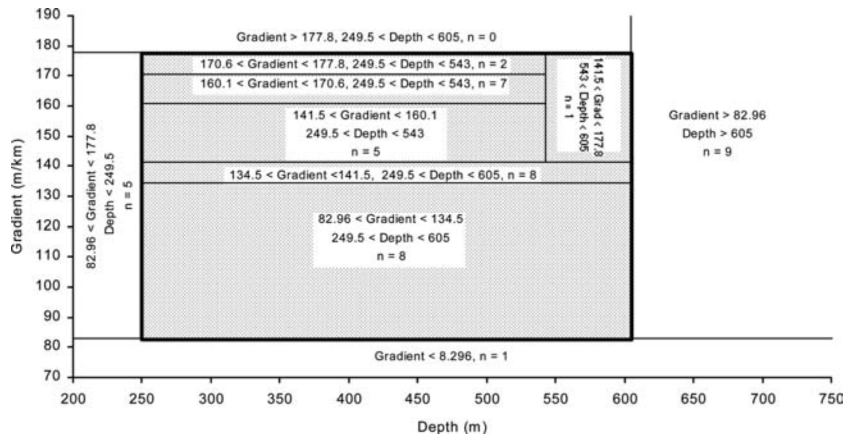


**Table 2** A comparison of first cells used during all encounters ($n=18$) and all other cells utilized ($n=48$). For depth and gradient, main value indicates the median value and the full range is given in parentheses. For aspect, the proportion of cells in each aspect category is given

| Variable | First cells ($n=18$) | All other cells ($n=48$) | Comparison of datasets |
|---|---|---|---|
| Depth (m) | 510<br>(163–1319) | 409.5<br>(136–1105) | Mann-Whitney: $W=729.5$, $P=0.07$ |
| Gradient (m/km) | 134.4<br>(86.6–251.1) | 138.4<br>(68.0–296.2) | Mann-Whitney: $W=570.0$, $P=0.65$ |
| Aspect | North-east 55%; east 22%; others 22% | North-east 71%; east 19%; others 10% | Chi square = 1.88<br>$df=2$<br>$P=0.39$ |

when they are passively carried onto slope areas by oceanic currents. As a result, such species can become concentrated in the near-bottom layer and so form an important resource of predators (Nesis 1993). The concentrating effects of currents on prey will be affected by the gradient. In areas with steeper gradients animals may disperse down the slope rather than accumulating (Nesis 1993). In contrast, at the most gentle gradients, prey may either be spread over a relatively larger area or upwelling of the deep water current may not be sufficiently strong to cause prey animals to be carried onto the slope area. Therefore, habitat utilization by Blainville's beaked whales east of Great Abaco may be primarily driven by the way in which the local deepwater current interacts with the seabed topography to produce accumulations of preferred prey. However, further research will be required to test this hypothesis. In particular, concomitant recordings of the speed and direction of currents throughout the water column and of beaked whale distribution in the study area would be beneficial.

Comparisons between the results of this study and those on Blainville's beaked whales from other parts of the world, and with other *Mesoplodon* species, are limited by a lack of suitable published data. However, some comparisons can be made. Around other groups of oceanic islands, Blainville's beaked whales have been seen in similar habitats to those recorded in this study. For example, from 100 to 850 m off the Island of La Gomera in the Canaries (Ritter and Brederlau 1999); between 700 and 1,000 m in Hawaii (Shallenberger 1981; Mead 1989); close to oceanic islands in the Society Islands (Gannier 2000).

Few data are available for other *Mesoplodon* species. Stejneger's beaked whale (*Mesoplodon stejnegeri*) have been sighted in water depth between 730 and 1,560 m. Loughlin et al. 1982); Sowerby's beaked whales (*Mesoplodon bidens*) between 550 and 1,500 m in the north-west Atlantic (Hooker and Baird 1999); *Mesoplodon* species in water depths between 700 to over 1,800 off the west coast of Scotland (Weir 2000); *Mesoplodon* species in water depths between 680 and 1,933 m and gradients between 4 and 26 m per 1.1 km in the Gulf of Mexico (Davis et al. 1998).

In comparison to what is known about Blainville's beaked whales, other *Mesoplodon* species have been found in deeper waters and, in the Gulf of Mexico, in areas with lesser gradients. These differences may reflect interspecific differences in habitat preferences between *Mesoplodon* species, with Blainville's beaked whale occurring in shallower waters than other *Mesoplodon* species. However, the sightings of Blainville's beaked whale discussed above, including those in the Bahamas, all come from around oceanic islands, while the sightings of other *Mesoplodon* species all come from continental shelf edge/slope areas. Therefore, differences may reflect differences in habitat utilization by *Mesoplodon* species between oceanic islands and shelf edge/slope areas rather than interspecific differences. Such potential differences should be taken into account when transferring inferences between different areas, particularly with regards to mitigation of potential anthropogenic impacts.

In summary, the distribution of Blainville's beaked whale east of Great Abaco, the Bahamas, is closely related to the topography of the seabed. The exact reasons for this link remain unclear, however, it may relate to interactions between local deep-water currents and the seabed topography. However, further research is required to test this proposed relationship. In addition, further research is required to examine how applicable the results of this study are to Blainville's beaked whales in other areas, particularly shelf edge/slope areas rather than around oceanic islands, and what generalizations can be made regarding habitat utilization by other *Mesoplodon* species.

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