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Diversity, relative density and structure of the cetacean community in summer months east of Great Abaco, Bahamas

Colin D. MacLeod*[†∫], Nan Hauser[†] and Hoyt Peckham[†‡]

*Department of Zoology, School of Biological Sciences, University of Aberdeen, Tillydrone Avenue, Aberdeen, AB24 2TZ, UK.
[†]Center for Cetacean Research and Conservation, 800 Mere Point, Brunswick, Maine, USA.
[‡]Present address: Department of Ecology and Evolutionary Biology, University of California Santa Cruz, Santa Cruz, CA, USA.
[∫]Corresponding author, e-mail: c.d.macleod@abdn.ac.uk

Little is known about cetacean communities in the tropical and sub-tropical Atlantic. This paper describes the cetacean community found east of Great Abaco in the northern Bahamas (26.5°N) during summer months between 1998 and 2001. Nine species of cetaceans were recorded, which could be divided into two distinct groupings: firstly, 'permanent' species, which had relative sightings rates between 0.026–0.084 sightings per hour and which were recorded on many occasions in all years and most months; secondly, 'sporadic' species, which had relative sightings rates an order of magnitude lower (0.004–0.008 sightings per hour) and which were recorded on very few occasions. The 'permanent' species were the *Stenella frontalis* (Atlantic spotted dolphin), *Kogia simus* (the dwarf sperm whale), *Mesoplodon densirostris* (Blainville's beaked whale) and *Ziphius cavirostris* (Cuvier's beaked whale). These four species differed significantly in the depth of grid squares utilized ($\chi^2=20.25$, df=9, $P<0.01$) suggesting that these species occupied four separate niches. *Stenella frontalis* dominated the surface feeding niche, while the remaining three deep-diving species segregated into different depth ranges. *Kogia simus* was the dominant species in water depths of less than 200 m, *M. densirostris* in water depths of 200 to 1000 m and *Z. cavirostris* in water depths of greater than 1000 m. The overall relative density (2.533 individuals per hour of effort) and diversity of species in the study area was relatively low and may relate to low levels of local productivity. It is hypothesized that the four 'permanent' species may competitively exclude ecologically similar species, resulting in a reduced number of species and that 'sporadic' species may only enter the study area during times of higher than usual productivity when the 'permanent' species are no longer able to dominate their individual niches.

INTRODUCTION

In comparison to other areas of the world, little is known about cetacean communities in the tropical and sub-tropical waters of the Atlantic. This paper describes the occurrence, distribution and relative density of cetaceans in an area of deep, oceanic waters east of the island of Great Abaco in the northern Bahamas. Data were collected as part of a study examining the habitat preferences and other aspects of the biology of Blainville's beaked whales (*Mesoplodon densirostris* de Blainville, 1817—MacLeod & Claridge, 1999; Hauser & MacLeod, 2002). However, the methodologies used for this study also allowed for the investigation of the structure of the cetacean community in the local area. This cetacean community is of interest for two main reasons. Firstly, this community contains a number of poorly known oceanic species, such as *M. densirostris*, *Kogia simus* Owen, 1866 (dwarf sperm whales) and *Ziphius cavirostris* G. Cuvier, 1823 (Cuvier's beaked whales—Mead, 1989; Heyning, 1989; Caldwell & Caldwell, 1989; Reeves & Leatherwood, 1994). Secondly, it is situated in a province of the world's oceans which is typified by relatively low levels of primary production (Longhurst, 1998). Therefore, possible relationships between cetacean communities and levels of local primary production can be investigated by comparing this region with other more productive regions.

MATERIALS AND METHODS

A study area was constructed to cover as wide a range of habitat variables as possible east of Great Abaco, the Bahamas. The exact location of the study area was based on information from previous research in the area (e.g. Claridge & Balcomb, 1995) and the location of passes from the shallow waters of Little Baham Bank (where the research vessels were kept at night) through the reef system which fringes the bank to the open ocean, where the study was conducted. The size of the area was limited by distances which could be covered by the research vessels within a single day and the area was approximately 35 km in length and up to 16 km in width. The southern limit was aligned with 26°20′N latitude and the western limit was aligned with 77°00′W longitude (Figure 1). This study area was divided into 500×500 m grid squares. Grid squares which were inside the barrier reef system were excluded from the study area, leaving a total of 1744

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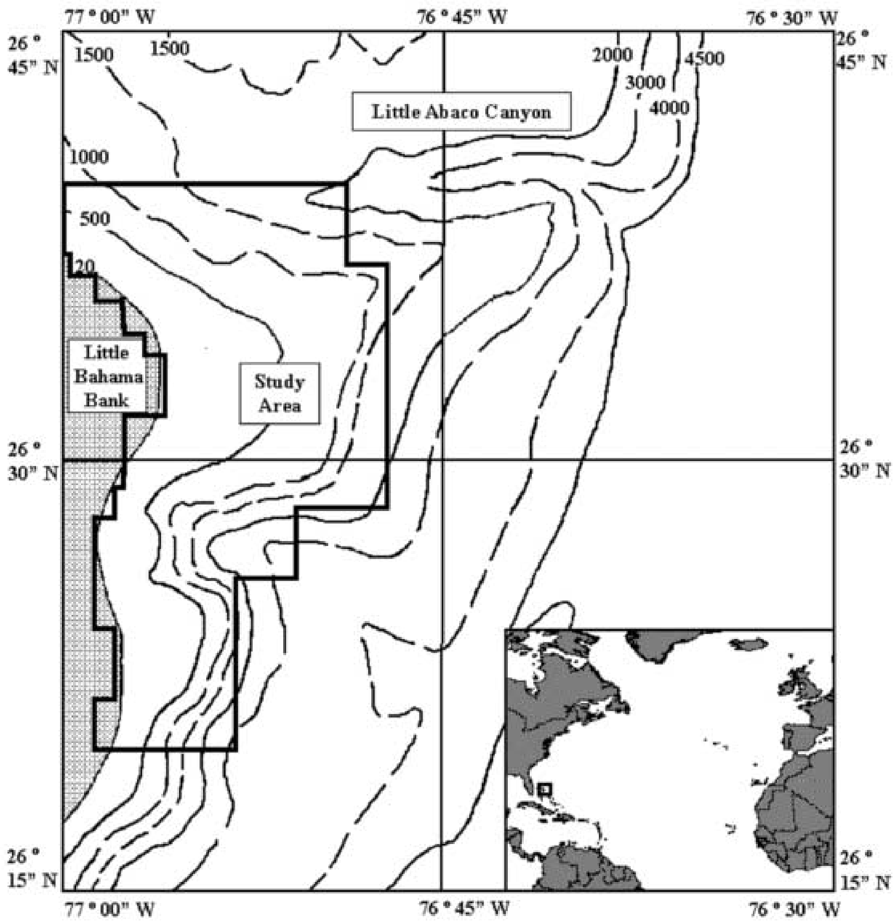

Figure 1. The location and extent of the study area, with bathymetry of the surrounding area (adapted from Waterproof Charts Inc., Chart 120F). Depths are in metres.

grid squares. The research was conducted between May and August each year between 1998 and 2000 and in May of 2001. The research vessels used for this study were small (around six m) fibreglass boats, with an eye height of between about two and three m. Handheld Global Positioning System (GPS) receivers were used to record the position of animals sighted and the tracks of the research vessels while in the study area.

Effort within the study area was divided into two types. The first type was systematic surveys which involved a single research vessel at a set speed (12–16 km h^{-1}) with two to four observers on board. Systematic surveys were only undertaken in sea states of Beaufort three or less to ensure that few or no cetaceans present at the surface were missed within a 500 m wide swathe (250 m on either side of the vessel). However, any cetaceans not at the surface were likely to be missed. While this bias will have relatively little impact on observations of surface-dwelling cetaceans, it is likely to lead to an under-recording of deep and long diving species, such as beaked whales and *Kogia* species. It was attempted to cover as many grid squares as possible, and specifically to visit grid squares and areas which had not previously been surveyed wherever possible. The position of the research vessel was automatically recorded every five min. The species and group size were recorded for each encounter, as well as additional information on behaviour and ecology. When any cetaceans were sighted they were followed until they 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. On return to shore, the track of the research vessel was downloaded from the GPS to a computer and the length of time spent in each grid square was calculated, as well as the number of groups, individuals and length of time spent with animals in each grid square. The relative sightings rate and relative density of cetaceans were calculated from the systematically collected data as follows: the relative sighting rate was calculated by dividing the total number of sightings for a taxonomic group by the total number of hours of systematic effort, while the relative density was estimated by summing the best estimate of the number of individuals for each sighting of a taxon and then dividing the total by the total number of hours of systematic effort. Time was used as the unit of effort rather than distance, a more traditional measure of effort, due to the problems of accurately controlling the speed of the research boats used for these surveys, and therefore it was not possible to obtain consistent coverage in terms of distance sampled.

The second type of effort consisted of non-systematic surveys, which were specifically aimed at locating cetaceans for the collection of behavioural and ecological data. Non-systematic surveys were undertaken by up to two research vessels at any one time and were assisted by a spotting plane in June 1999 and May 2001. Data on cetaceans sighted during these surveys were combined with

Table 1. *Number of groups and individuals sighted per hour of effort during systematic surveys east of Great Abaco, the Bahamas for all cetaceans and by taxonomic groupings. Total effort was 227.412 h over 65 d. Actual number of groups and animals sighted is in parentheses.*

Taxonomic grouping	No. groups sighted per hour	No. animals sighted per hour
Cetacea	0.312 (71)	2.480 (564)
Ziphiidae	0.128 (29)	0.365 (83)
Mesoplodon densirostris	0.079 (18)	0.290 (66)
Ziphius cavirostris	0.026 (6)	0.035 (8)
Kogiidae	0.048 (11)	0.185 (42)
Kogia simus	0.044 (10)	0.180 (41)
Delphinidae	0.097 (22)	1.895 (431)
Grampus griseus	0.004 (1)	0.088 (20)
Globicephala macrorhynchus	0.004 (1)	0.035 (8)
Stenella frontalis	0.084 (19)	1.332 (303)
Tursiops truncatus	0.008 (2)	0.440 (100)

sightings data from the systematic surveys to examine the occurrence and comparative distributions of cetaceans within the study area. These sightings were entered into a Geographic Information System (GIS) and the occurrence of cetaceans within each grid square was plotted by taxonomic groupings. Data on water depth and seabed gradient of each grid square were interpolated from a topographic map of the study area and were added to the GIS. A mean depth and gradient were calculated from all separate grid squares utilized during each encounter. The occurrence of different species in relation to depth and gradient were examined and compared between species. As not all sightings had associated effort data, these comparisons only looked at relative differences between species occurrence in different categories of depth and gradient. Although this resulted in a bias in terms of preferential coverage of any particular variable category, this bias was equal for all species. Chi-squared tests were used to test whether the mean depth and gradient for encounters differed between species. The expected values were calculated on the assumption that, if there were no differences between species, each would have the same proportion of encounters per variable category in relation to the total number of encounters per that species.

Figure 2. Distribution of systematic survey effort within each grid cell within the study area. White-cells not surveyed; light grey, <0.1 hours of survey effort per grid cell; intermediate grey, 0.1–0.5 hours of effort; dark grey, 0.5–1 hour of effort; black, >1.0 hours of effort.

RESULTS

Over the four year period, nine species of cetaceans were recorded in the study area (Table 1). In general, there was a concentration of encounters and grid squares utilized by cetaceans at the northern end of the study area, although this is almost certainly due to a bias in effort in this area (Figure 2). In addition, most of the grid squares utilized were over shelf-edge and shelf-slope-like areas, particularly around the upper reaches of a marine canyon (the Little Abaco Canyon) and around a shallow shelf-like area known locally as 'Shallow Bar'.

The relative sightings rate and relative density per unit effort of cetaceans could only be calculated for data collected during systematic surveys undertaken in the study area, and therefore were not available for all species (for example, *Peponocephala electra* Gray, 1846 (the melon-headed whale) and *Physeter macrocephalus* Linnaeus, 1758—sperm whales). The overall relative sightings rate of cetaceans per hour of effort was relatively low. Only 0.312 groups of cetaceans and 2.533 individuals were encountered per hour of systematic effort (Table 1). The beaked whales were the most frequently encountered family (0.128 groups per hour), with Delphinidae being the second most frequently encountered (0.101 groups per hour). Frequently encountered species were *Stenella frontalis* Cuvier, 1829 (Atlantic spotted dolphin—0.084 groups per hour), *M. densirostris* (0.079 groups per hour) and *K. simus* (0.044 groups per hour). In terms of families, the Delphinidae had the highest estimated relative density in terms of number of animals (1.948 individuals

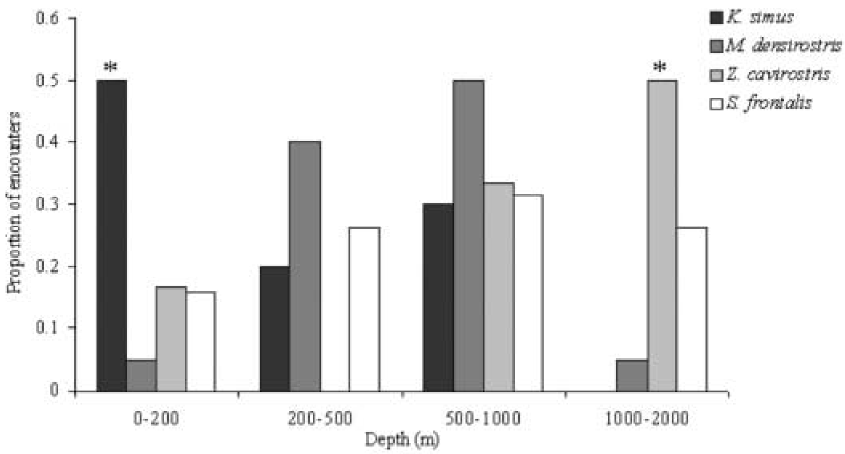

Figure 3. Proportion of encounters with mean depth of grid squares utilized in different depth categories for four most commonly encountered species in summer months between 1998 and 2001 east of Great Abaco, the Bahamas. The number of encounters in each depth range differs significantly from expected (χ^2=20.25, df=9, $P<0.01$). Asterisk indicates individual values that were significantly different from expected at $P<0.05$.

per hour), followed by the beaked whales (0.365 individuals per hour) and the Kogiidae (0.185 individuals per hour). The species with the highest estimated relative density per hour were *S. frontalis* (1.332 individuals), *Tursiops truncatus* Montague, 1821 (bottlenose dolphins—0.440 individuals), *M. densirostris* (0.290 individuals) and *K. simus* (0.190 individuals). At an estimated average speed of 14 km h^{-1}, these relative densities per unit effort ranged from approximately 0.095 individuals per km for *S. frontalis* to approximately 0.014 individuals per km for *K. simus*.

Only four of these species, *K. simus*, *M. densirostris*, *Z. cavirostris* and *S. frontalis*, were recorded more than three times and comparisons of depth and gradient of grid squares used by these species were made. *Kogia simus* were recorded in grid squares with depths ranging from 94 to 883 m (mean: 247 m, SD=206 m). However, 17 out of 24 of these grid squares had depths of less than 200 m. *Mesoplodon densirostris* were recorded in grid squares with depths ranging from 136 to 1319 m (mean: 488 m, SD=255 m). Fifty-nine of the 69 grid squares where *M. densirostris* were recorded had depths between 200 and 1000 m. *Ziphius cavirostris* were recorded in grid squares with depths ranging from 188 to 1710 m (mean: 1153 m, SD=548 m). Seven of the ten grid squares where *Z. cavirostris* were recorded had depths of greater than 1000 m. *Stenella frontalis* were recorded in grid squares with depths ranging from ten to 2191 m (mean: 544 m, SD=531 m) with 109 of the 130 grid squares where *S. frontalis* were recorded having depths of less than 1000 m. There was a highly significant difference between frequency of occurrence of encounters in different depth categories between these four species (χ^2=20.25, df=9, $P<0.01$—Figure 3). *Kogia simus* had significantly more mean depths in the 0–200 m category (χ^2=5.57, df=1, $P<0.05$), while *Z. cavirostris* had significantly more mean depths in the 1000–2000 m category (χ^2=4.15, df=1, $P<0.05$). *Mesoplodon densirostris* had more mean depths in the 200–500 m and 500–1000 m depth categories than expected and less in the other two depth categories, however this difference was not significant. The observed values for *S. frontalis* were all close to the expected values, and did not differ significantly.

In terms of gradient, *K. simus* were recorded in grid squares with gradients of between 6.8 and 27.0% (mean: 11.8%, SD=5.8%) with most grid squares (13 out of 24) having a gradient of less than 10%. *Mesoplodon densirostris* were recorded in grid squares with gradients of 9.0 to 45.8% (mean: 20.5%, SD=7.2%) with most grid squares (60 out of 69) having gradients of between 10 and 30%. *Ziphius cavirostris* were recorded in grid squares of between 10.2 and 35.8% (mean: 21.7%, SD=7.1%), with most grid squares (6 out of 10) having gradients of 20 to 30%. *Stenella frontalis* were recorded in grid squares with gradients between 0 and 58.8% (mean: 19.8%, SD=13.28%), with most grid squares (111 out of 130) having gradients of less than 30%. For four gradient categories (0–10%, 10–20%, 20–30%, >30%), there was no significant difference between the frequency of occurrence of the mean gradient of grid squares utilized during each encounter in different gradient categories between these four species (χ^2=12.62, df=9, $P>0.05$ —Figure 4).

Peponocephala electra were encountered three times. These encounters all occurred on the same day and in close proximity to each other, and probably all represent individuals from one group as one encounter contained around 100 individuals, while the other two contained three and five individuals. The mean depth of grid squares utilized by *P. electra* during these three encounters were 512, 549 and 646 m, while the mean gradients were 19.9%, 21.1% and 17.8%. *Grampus griseus* G. Cuvier, 1812 (Risso's dolphins) were encountered on two occasions, once in grid squares with a mean depth and gradient of 241 m and 20.8% and once on grid squares with mean depth and gradients of 770 m and 21.2%. *Tursiops truncatus* were encountered on two occasions and each sighting was of a distinct morphological type which could be easily separated by eye in this study area. The first occasion consisted of a group of approximately 100 animals with relatively large body sizes, proportionately smaller fins and relatively shorter beaks (type A), while the second occasion consisted of a group of 12 animals with relatively smaller body size, proportionately larger flippers and relatively longer beaks (type B). Type B animals were similar to *T. truncatus* which were regularly encountered in the shallow waters of Little Bahama Bank while transiting to and from the study area, and were recorded just offshore of the barrier reef in a water depth of approximately 10 m and a zero gradient. In contrast, type A *T. truncatus* were recorded well beyond the barrier reef in grid squares with a mean depth of 366 m and a mean gradient of 20.1%. These two morphologically distinct *T. truncatus* may represent an 'offshore' (type A) and an 'inshore' (type B) ecotype as has been recorded in other parts of the world (e.g. north-west Atlantic—Hersh & Duffield, 1990). *Globicephala macrorhynchus* Gray, 1846 (short-finned pilot whales) were recorded on one occasion in grid squares with a mean depth of 962 m and a mean gradient of 29.7%. *Physeter macrocephalus* were also recorded on one occasion in grid squares with a mean depth of 730 m and a mean gradient of 13.9%.

DISCUSSION

The cetacean community in the study area east of Great Abaco can be summarized as follows. The overall relative density of cetaceans in the study area was relatively low and only nine species of cetaceans were recorded. Four species were regularly sighted in the study area. These are *Stenella frontalis*, *Mesoplodon densirostris*, *Kogia simus* and *Ziphius cavirostris*. The remaining five species were only recorded occasionally in the study area on an irregular basis in summer months. All of these five species are oceanic odontocete species, with the exception of a single group of type B *Tursiops truncatus* which probably came from a local population which occurs in the neighbouring inshore waters of Little Bahama Bank. It is hypothesized that these groupings of species into regularly sighted and occasionally sighted represent two separate components of the local cetacean community: (1) a group of 'permanent' species which form the core of the summer cetacean community in the study area east of Great Abaco; and (2) a group of 'sporadic' species which are only intermittently part of this summer cetacean community. In terms of relative sightings rate, the 'sporadic' were an order of magnitude lower than the 'permanent' species ('permanent' species: 0.026–0.084; 'sporadic' species: 0.004–0.008), despite the fact that three of the 'permanent' species (*K. simus*, *M. densirosrostis* and *Z. cavirostris*) as deep-diving species would normally be considered difficult to detect during sightings surveys in comparison to the 'sporadic' species. This suggests that this classification is biologically meaningful and not simply an arbitrary division along a continuum of relative sightings rates.

In summer months, the study area east of Great Abaco has a relatively low diversity of cetacean species (nine species, only four of which are regularly encountered), when compared to the cetacean community found around another oceanic island at a similar latitude in the North Atlantic. La Gomera in the Canaries lies at a latitude of approximately 28°N in the eastern Atlantic (compared to 26.5°N for this study area), where 21 species of cetaceans have been recorded, including six species of baleen whale, three species of beaked whale and ten species of delphinids (Ritter, 2001). Six of these species are seen year round and may be considered 'permanent' members of the cetacean community. Ritter (2001) suggested that the high diversity of species occurring off La Gomera relates to the upwelling areas around the Canaries and the resulting increased levels of production. The Eastern (Canary) Coastal Province has a chlorophyll-*a* profile for which monthly averages can remain over 20 mg m^{-2} throughout the year and can reach over 60 mg m^{-2} in some months. In comparison, the oceanic province in which the Bahamian study area is located (North Atlantic Tropical Gyral Province), the monthly average is much lower and can remain under 6 mg m^{-2} throughout the year (Longhurst, 1998). The waters of the study area itself are characterized by extremely clear oceanic waters indicating low standing stocks of phytoplankton. Such low levels of primary production may have a knock-on effect in reducing local production throughout the food webs and, in turn, this may explain the low abundance of cetaceans. However, how this relates to local cetacean diversity is less clear.

One possibility is that low levels of production may lead to increased levels of competition for the limited available resources. This may have led to the 'permanent' species partitioning the study area into a number of distinct niches. The first partition is between surface feeding species and deep-diving species. Within the study area, *S. frontalis* was the only 'permanent' species observed foraging in surface waters. For example, during this study *S. frontalis* was frequently observed chasing and catching flying fish. In contrast, the remaining three species are all thought to be deep divers which forage at depth (Caldwell & Caldwell, 1989; Mead, 1989). Of the three deep-diving species, each occupies a distinct depth range, which may represent a further partitioning of local resources. *Kogia simus* is the dominant deep-diving species in waters less than 200 m, *M. densirostris* is the dominant deep diving species in waters between 200 and 1000 m and *Z. cavirostris* is the dominant species in water depths between 1000 and 2000 m. These four 'permanent' species may then competitively exclude other ecologically similar species which occur in the sub-tropical waters of the Atlantic from the local area. For example *S. frontalis* may competitively exclude other near-surface feeding delphinids from the study area, such as *Stenella attenuata* Gray, 1846 (pan-tropical spotted dolphin) or other *Stenella* species. *Stenella attenuata* has been recorded at other locations around Abaco (C.D.M., personal observation). Similarly *K. simus* may exclude the ecologically similar and sympatric *Kogia breviceps* de Blainville, 1838 (pygmy sperm whale—Caldwell & Caldwell, 1989), *M. densirostris* may exclude the apparently ecologically similar and sympatric *Mesoplodon europeaus* Gervais, 1855 (Gervais' beaked whale—Mead, 1989; MacLeod, 2000) and *Z. cavirostris* may exclude other beaked whales or deep-diving cetaceans. Other cetacean species may occasionally enter the study area for short periods of time, but do not remain in the area for long periods of time. It is hypothesized that 'sporadic' members of the cetacean community may enter the study area during periods of higher local production, driven by variations in local oceanographic conditions, when a single species cannot dominate a specific niche due to an increased availability of prey at such times. However, further research is required to test this hypothesis and to investigate whether it may also apply to other cetacean communities. In particular, a comparative study of the diversity and species composition of cetacean communities around a number of tropical/sub-tropical oceanic islands with different levels of local productivity and a comparison of species diversity in relation to variations in local productivity at a number of locations would allow a detailed investigation of the hypotheses presented here.

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