FINE-SCALE DISTRIBUTION AND HABITAT SELECTION OF BEAKED WHALES

A thesis presented for the degree of Master of Science in Zoology

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BLAINVILLE'S BEAKED WHALE

MESOPLODON DENSIROSTRIS

DECLARATION OF CANDIDATE

I, Diane E. Claridge, herein declare that I have composed this thesis myself, that I have done the work presented here within, and that all sources of information have been specifically acknowledged.

I further declare that this thesis has not been accepted in any previous application for a degree.

Signed: ______________________

Date: 9 September 2006

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Abstract

Mass strandings coincident with naval operations have demonstrated that beaked whales are particularly vulnerable to anthropogenic noise pollution. Further understanding of their distribution is essential to know how to apply mitigation measures to protect these enigmatic, deep-diving whales. To address this knowledge gap, small vessel surveys were conducted off southern Great Abaco Island in the northern Bahamas from 1997 – 2002, including portions of the Great Bahama Canyon.

Seventeen cetacean species were sighted in 776 groups, including Cuvier's beaked whales (*Ziphius cavirostris*, 18 sightings) and Blainville's beaked whales (*Mesoplodon densirostris*, 111 sightings). Cuvier's beaked whales were found in significantly smaller groups (mean group size = 2.4, SD = 1.2) than Blainville's beaked whales (mean = 4.1, SD = 1.9). Photo-resight rates were higher for Blainville's beaked whales (0.40), and differed by age and sex class, with adult females having the highest mean resight rate. A harem mating system was found from analysis of Blainville's beaked whale association patterns, with some social segregation between adults and sub-adults.

Univariate analyses using line transect data showed Cuvier's beaked whales at a mean depth of 1051 m (SD = 111), and sharing offshore habitat with sperm whales. Blainville's beaked whales were found along the edge of the canyon wall (mean depth = 393 m, SD = 283), and shared this shallower, near-shore environment with *Kogia* species. ANOVA tests showed no significant difference in the habitat described for beaked whales when comparing line transects and opportunistic surveys. Habitat partitioning occurred between adult and sub-adult Blainville's beaked whales, with sub-adults found further offshore and in deeper water (ANOVAs, $p < 0.01$). A dominance hierarchy may be the driving force for adult and sub-adult male Blainville's beaked whale habitat selection.

ACKNOWLEDGEMENTS

I wish to begin by acknowledging and thanking Ken Balcomb for introducing me to field biology and cetacean research. Ken supported me in returning to The Bahamas, my home country, to begin fieldwork on cetaceans, which initiated my interest in beaked whales. Without Ken's influence, this study would not have occurred.

Drs. Kim Parsons and John Durban have provided endless support to me both personally and professionally since I first met them 10 years ago, and with whom I've shared so many of these encounters. Both Kim and John were instrumental in my decision to return to academia; and since, have always been eager to share ideas, review my work, and provide feedback and comments. I thank them also for sharing their home in Cromarty and their love of Scotland when I first came to the UK to begin analysis for this study.

I am especially grateful to Charlotte Dunn for providing me an escape from hurricane Jeanne and a lovely "cupboard" in her flat for me to hide in and complete my writing up. Thanks also for taking me on wonderful walks on the beach to remind me of the world waiting for me outside the "cupboard", and for trying your best to keep me focussed!

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PREFACE

This work begins with a general introduction to beaked whales and the study area. The data chapters (Chapters 2 – 4) are then presented as individual papers. Within these chapters, reference has been made to earlier chapters to avoid repetition as much as possible, particularly in the Methodologies sections. However, some repetition occurred in order for the reader to follow the chapter more easily. The final chapter concludes with a general discussion of the main themes presented throughout.

It should be noted that a beaked whale mass stranding event took place during the study period (March 15^{th}, 2000) as the result of a naval exercise using multiple sonars within the study area. It is unclear how this event affected local populations of beaked whales, although one beaked whale species disappeared from the study area for almost two years.

The section on social organisation of Blainville's beaked whales in Chapter 2 has been presented previously at the 14^{th} Biennial Conference on the Biology of Marine Mammals, Vancouver, Canada (December 2001).

CHAPTER ONE

GENERAL INTRODUCTION

Habitat selection

Animals make habitat selections to satisfy three basic needs: foraging, reproduction, and protection against predation. The relative suitability or goodness of different habitats for these purposes leads, through the evolutionary process, to habitat selection, which then determines a species' distribution (Fretwell 1972). Individuals, and even species, choosing poor habitats will be selected against. The *Ziphiidae* family, or beaked whales, selected the deep ocean environment, which provided an ecological niche that allowed beaked whales to flourish during the middle Miocene (de Muizon 1991). Although the ziphiids have slowly decreased in diversity since having first appeared in the early Miocene (Mead 1989), they still remain one of the largest and most diverse mammalian groups today.

Despite the diversity of the *Ziphiidae*, most beaked whale species share common behavioural characteristics making field observations difficult. They are typically very cryptic, are found in small groups, are not active behaviourally at the surface, have very short surfacing intervals and dive for extraordinarily long periods making them extremely difficult to detect (Barlow 1999). Furthermore, their offshore distribution makes the practicality of field studies challenging. As a result, beaked whales have been described as the rarest large mammal group (Wilson 1992), and their natural history, including their distribution, has primarily been described from stranded specimens

(Mead 1989, Klinowska 1991) and rare, opportunistic sightings at sea (e.g. Shallenberger 1981, Ritter and Brederlau 1999, Hooker and Baird 1999). Recent concern that mass strandings of beaked whales are associated with anthropogenic sounds, such as military sonar (Frantzis 1998, Anon 2001, Balcomb and Claridge 2001, Jepson *et. al* 2003) and seismic airguns (Anon 2003), has resulted in a more immediate need for information on their abundance, density and habitat selection to better mitigate these effects.

Assessing habitat selection

The study of a species' distribution and an understanding of its habitat selection are essential to effectively develop and implement conservation strategies for its protection. Furthermore, knowledge of how a species' distribution relates to its environment, both physical and biological, is paramount to the study of its ecology. Identifying critical or important habitats may be the most effective management tool to protect marine species, and is recognized as such through legislation at both global and national levels (e.g. United Nations Convention on the Law of the Sea; the US Marine Mammal Protection Act). The success of these areas is dependent on the quality of information available, not only for defining boundaries, but also to understand how these areas are utilised by the animals and what factors affect their distribution and abundance (Wilson *et al.* 1997).

For these reasons, extensive research has been conducted to examine the distribution and habitat selection of organisms, but the majority of these efforts have been focussed on more accessible terrestrial species (e.g. McGraw and Bshary 2002, Lemckert 2003, Eide *et al.* 2004). In the marine environment, species distribution is defined in terms of spatially fixed physical features, such as bottom topography, and temporally variable oceanographic features, such as sea surface temperature (Hooker *et al.* 1999) making it more challenging to study. Despite the increased difficulty in studying marine species, numerous studies have examined habitat use and distribution of cetaceans on both large (e.g. Kenney and Winn 1987, Davis *et al.* 1998, Waring *et al.* 2001) and small scales (e.g. Wilson *et al.* 1997, Gowans and Whitehead 1995). However, the difficulty is magnified even more when studying deep-diving, oceanic species, such as beaked whales. Hence our understanding of the distribution and habitat selection of beaked whales is very limited (Mead 1989, Barlow 1999).

Methods used to study distribution of cetaceans have changed dramatically in the last five decades from the relatively limited information from whaling harvest records and recovery of discovery tags, to dedicated vessel and aerial surveys, with some associated mark-recapture studies using photo-identification, and radio and satellite telemetry studies that are employed today. As such, our understanding of cetacean distribution and habitat use may be strongly biased by the methods used to gather distribution data. For example, data collected from whaling ships was limited by the vessel's location, both spatially and temporally, and told more about hunting effort than the actual distribution of whales (Bowen and Siniff, 1999).

Techniques used to analyse survey data have improved substantially also. Geographic Information Systems (GIS) are commonly used today to assess spatial and temporal distribution of cetaceans (e.g. Baumgartner 1997, Hamakazi 2002). Combining GIS tools with statistical analysis using generalised linear models (GLMs) has not only increased our understanding of species' habitat use, but also allowed us to predict areas of preferred habitat (e.g. Davis *et al.* 1998, Waring *et al.* 2001).

Bowen and Siniff (1999) noted five factors that influence the distribution and habitat selection of marine mammals. These were: 1) habitat availability, 2) biology of the species (abundance of predators, prey and competitors), 3) demography (population size, age, sex and reproductive status), 4) species adaptations (morphological, physiological and behavioural) and 5) human effects (e.g. pollution and disturbance). This study explores aspects of the first three of these factors, with the long-term objective of contributing towards effective science-based mitigation, thereby decreasing the impact of human effects.

In this study, the distribution and habitat selection of beaked whales within a large submarine canyon in the northern Bahamas is assessed on a fine-scale. This study contributes to our understanding of beaked whale biology by examining the relationships between species' distribution and their habitat. To understand why beaked whales choose particular habitats, topographic and oceanographic variables were collected. It was not possible to assess abundance of prey directly, but it was hoped that the topographic and oceanographic variables would provide a proxy for prey abundance. Competition and habitat partitioning between beaked whales and other cetacean species inhabiting the study area was also explored, and habitat partitioning between different age classes of the same species was examined for individually recognised whales.

BEAKED WHALES – FAMILY *ZIPHIIDAE*

Phylogeny

Beaked whales are part of the Superfamily Ziphoidea, and their evolutionary relationship with Physeteroidea and Delphinoidea as well as the relationship between ziphiids is unclear (Rice 1998). Muizon (1991) classified the *Ziphiidae* into three subfamilies: the *Hyperoodontinae*, which includes *Hyperoodon* and *Mesoplodon* (including *Indopacetus*); and *Ziphiinae*, which includes *Ziphius, Berardius, Tasmacetus* and four fossil genera; and the *Squaloziphiinae*, which includes *Squaloziphius.*

The *Ziphiidae* family presently comprises six genera and twenty-one recognized species, with two new species being recorded within the last 15 years (Reyes *et al.* 1991, Dalebout *et al.* 2002). Two species are the subject of this thesis: Cuvier's beaked whale, *Ziphius cavirostris* (Cuvier 1823), which is also known as goose-beaked whale; and, Blainville's beaked whale, *Mesoplodon densirostris* (Blainville 1817), which is also known as dense-beaked whale.

General characteristics

Beaked whales have a robust, cigar-like body shape with a small dorsal fin located on the posterior third of the body. They have small, narrow flippers, which are tucked into a shallow depression or pocket on each side of the body as the whale descends on a deep dive (*pers. obs.*), and proportionately large tail flukes, which lack a medial notch. Beaked whales have a high forehead that merges smoothly with the elongated rostrum or beak. They have a pair of grooves in the throat region with the apex of the "v" pointing forward, which allow the throat to expand as they slurp in their prey by suction feeding

(Heyning and Mead 1996). Ross *et al.* (1988) provided a review of beaked whale pigmentation patterns, and describe Cuvier's and Blainville's beaked whales as dark grey dorsally to lighter grey or white ventrally, but the body is often extensively covered with diatoms (*Bacillariophyta*) giving it a yellowish-brown hue (*pers. obs.*). Adult Cuvier's beaked whales have a distinctive white head, which is more prominent in males than females (Heyning 1989). While adult male Blainville's beaked whales have a distinctive ridge along the dorsum, posterior to the blowhole, which appears to be the area targeted during intra-specific fighting, resulting in overlapping, deep-furrowed, linear scars from tooth-rakes of other adult males (*pers. obs.*). Oval scars caused by sea lampreys (*Petromyzon marinus*) and cookie cutter sharks (*Isistius* sp.) often cover the body of beaked whales, which can contribute to natural scarring patterns that help researchers differentiate individual whales.

Beaked whales are considered medium-sized cetaceans ranging in adult size from 3 – 13 m (Mead 2002). The maximum recorded lengths for Cuvier's beaked whale specimens are 6.7 m for males and 7.0 m for females, but no significant sexual dimorphism in size exists (Heyning 1989), although there is a lot of morphological variation throughout their range, which may be indicative of separate stocks (Klinowska 1991). Omura *et al.* (1955) reported mean lengths at sexual maturity for Cuvier's beaked whales of 5.5 m and 5.8 m for males and females, respectively, although this length is suspected to be too long for females (Heyning 1989), while Mead (1984) reported an average size at birth of 2.7 m. The maximum recorded lengths for Blainville's beaked whales was 5.8 m for males, and 4.7 m for females, and size at birth estimated to be less than 2.4 m. (Klinowska 1991).

Beaked whales are characterised internally by reduced dentition and the development of extremely dense rostral elements in males. The reduction in teeth is to the point that there is only a single pair of teeth in the lower jaw of males. Females and immature males have a pair of vestigial teeth that are not considered functional, while the teeth in adult males appear to be primarily used in male-male aggression and may be better described as “tusks” (Heyning 1984, Mead 2002). Stalked barnacles (*Conchoderma auritum*) often grow in large clusters on the erupted teeth enlarging their effective size and increasing the abrasiveness of the tusks. The densely ossified rostral bone may function to reinforce the skull when males fight (Heyning 1984). There are several exceptions to this extreme reduction in dentition: the two species of *Berardius*, which have two pairs of mandibular teeth, and *Tasmacetus,* which has normal odontocete dentition.

Distribution

Cuvier’s beaked whale has a cosmopolitan distribution and is found in all oceans, except in the high polar regions (Heyning 1989) and is the only beaked whale species regularly recorded from the eastern Mediterranean Sea (Politi *et.al.* 1994). The Blainville’s beaked whale has the widest distribution of all *Mesoplodon* species occurring presumably continuously across the world’s tropical and warm temperate waters, with the exception of the eastern Mediterranean Sea (Mead 1989). Beaked whales inhabit deep-water environments, and show a habitat preference for topographically diverse areas such as shelf edges, submarine canyons and seamounts (Whitehead *et al.* 1997, Waring e*t al.* 2001, D’Amico *et al.* 2003). This is probably because these topographic features influence the oceanographic processes that concentrate prey (Hui 1985, Kenney and Winn 1987, Baumgartner 1997). Previous studies in which both Cuvier's beaked whales and Blainville's beaked whales were encountered, found that Cuvier's showed preference for deeper water, with Cuvier's found at depths greater than 1000 m and Blainville's beaked whales in depths of 200 – 1000 m (Baird *et al.* 2004, MacLeod *et al.* 2004).

Life history and behaviour

Life history data for beaked whales is very limited and is based almost entirely on stranded whales or from whale fisheries. Age at sexual maturity is reported at 11 and 9 growth layer groups (GLGs) in the teeth, for Cuvier's beaked whales and Blainville's beaked whales, respectively (IWC 1989, Ross 1984). The maximum recorded layer groups counted in male Cuvier's beaked whales' teeth was 47 GLGs, while a maximum of 30 GLGs were recorded in females (IWC 1989, Ross 1984). Similar data do not exist for Blainville's beaked whales, although a Gervais' beaked whale (*M. europaeus*) had more than 48 GLGs (Mead 1989).

Cuvier's beaked whales and Blainville's beaked whales have been reported in groups of similar size ranging from 1 to 9 whales (Shallenberger 1981, Heyning 1989, Baird *et al.* 2004). The social organisation of both species has only been described by anecdotal observations, with group compositions noted for Blainville's beaked whales consisting of a single adult male with several adult females (e.g. Ritter and Brederlau 1999).

Beaked whale prey species are primarily mesopelagic, or deep-water benthic fish and cephalopods, with cephalopods being the most common prey (Clarke 1986, Heyning 1989). In a review of prey species by MacLeod *et al.*

(2003), Cuvier's beaked whale were found to consume larger prey than *Mesoplodon* species. Recent studies on diving behaviour using time-depth recorder suction cup tags suggest that Blainville's beaked whales may feed at or close to the bottom (Baird *et al.* 2004).

Conservation status

The conservation status of Cuvier's beaked whales and Blainville's beaked whales is largely unknown and both species are listed in the IUCN Red List of Threatened Species as data deficient (DD), which means that appropriate data is lacking on abundance and/or distribution (IUCN 2003). As with almost all cetaceans, both species are also listed under CITES Appendix II, which means they may become threatened unless trade is closely controlled (CITES 2003).

Population trends for beaked whale species are unknown because of the difficulty in obtaining precise estimates of abundance (Read and Wade 2000). The problems include difficulties in developing adequate correction factors to account for their deep-diving behaviour which may negatively bias estimates of abundance, and the difficulty of identifying groups in the field to the species level. Furthermore, even if the species is known, the number of sightings are generally low, so all beaked whales are often grouped together for analysis. Sightings data from shipboard and aerial surveys in the eastern Pacific analysed by Ferguson and Barlow (2001) showed the maximum densities of mesoplodont whales of 6.4 whales per 1000 km^2, and 38 whales per 1000 km^2 for Cuvier's beaked whales.

Cuvier's beaked whales were taken opportunistically in a whaling fishery in Japan, which has largely ceased, although a few were still taken up until the 1980's (Heyning, 1989). While there is no commercial fishery for Blainville's beaked whales, they are occasionally taken in other fisheries, e.g. Japan (Mead 1989) and occasionally both species are taken in a small whale fishery in St. Vincent in Lesser Antilles (IWC, 1989). Beaked whales are also taken incidentally in pelagic driftnet fisheries. Read and Wade (2000) reported that these takes exceed the removal limits set under the US Marine Mammal Protection Act, or the potential biological removal levels, for both species in the western North Atlantic and for mesoplodonts in the North Pacific. Mass strandings of beaked whales coincident with naval operations (Simmonds and Lopez-Juraco 1991, Frantzis 1998), and, more recently, in The Bahamas (Balcomb and Claridge 2001) and the Canary Islands (Jepson *et. al* 2003.) have demonstrated that beaked whales are particularly vulnerable to anthropogenic noise pollution. Further understanding of their distribution is essential to know where and when to apply mitigation measures to protect these rare, deep-diving whales (Anon 2001).

In this study, sightings data for Cuvier's beaked whales were limited, but analyses of this species' distribution and habitat use were included because Cuvier's beaked whales have been the most represented species in these global mass stranding events. Analyses of distribution data collected for other species not found in the Bahamas stranding event, for example dwarf sperm whales (*Kogia simus*), was also included to help further our understanding of this stranding event and its effect on specific species.

Ziphiid occurrence in The Bahamas

Three species of ziphiids are known from stranded specimens to have occurred historically in The Bahamas: Cuvier's beaked whale (Caldwell and

Caldwell, 1974), Blainville's beaked whale (Moore 1958) and Gervais' beaked whale (Balcomb 1981). There is also a record of a True's beaked whale, *M. mirus*, from The Bahamas (Anon, 1981), but this record can not be confirmed because the skull has since been lost.

Some of the first ever sightings at sea of *Mesoplodon* beaked whales were reported off Long and Eleuthera Islands in the central Bahamas (Balcomb, 1981), suggesting that the deepwater basins and canyons of The Bahamas are potential habitat for beaked whales and deserved further study. Fieldwork conducted by Claridge and Balcomb (1993) in the northern and central Bahamas in 1991-1992 confirmed this observation with regular sightings of beaked whales. Field studies have been continued in the northern Bahamas by the Bahamas Marine Mammal Survey (BMMS), and cetacean species recorded by BMMS are summarized in Appendix I.

STUDY AREA

The islands of The Bahamas lie on shallow, carbonate banks that are divided by numerous deepwater channels and basins. The largest of these channels forms the Great Bahama Canyon, which lies between Great Abaco and Eleuthera Islands (Figure 1.1). The Great Bahama Canyon is one of the world's largest submarine canyons stretching more than 270 km in length and 40 km in width, has the highest canyon walls dropping from the bank margin to depths of almost 5 km (Sealey 1994).

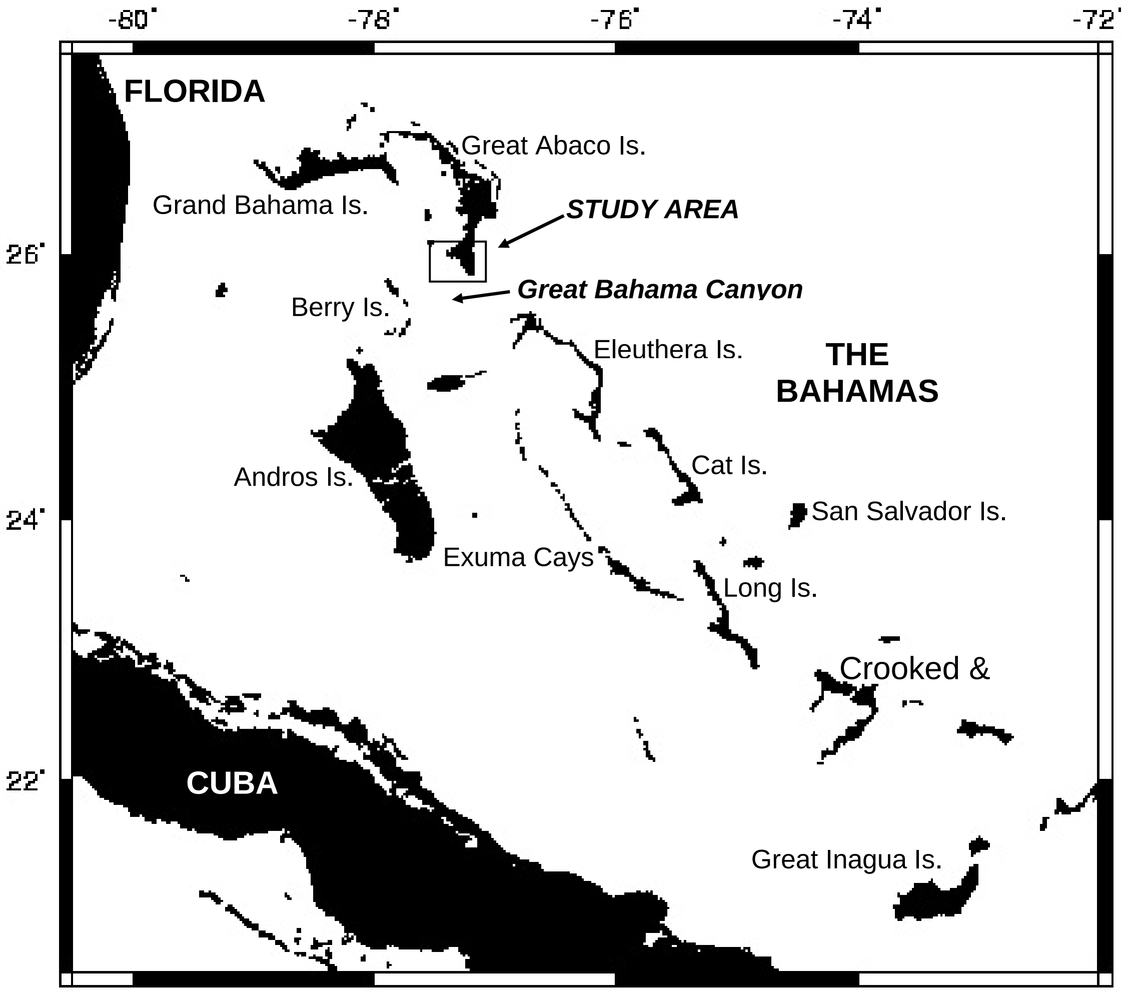


Figure 1.1 The island archipelago of The Bahamas, showing the study area off the southern coast of Great Abaco Island in the northern Bahamas.

The Great Bahama Canyon has two large branches which merge to form the canyon itself (Figure 1.2). The two branches are Northwest Providence Channel between Great Abaco Island and the Berry Islands; and, Northeast Providence Channel which extends southwest towards the Tongue of the Ocean, east of Andros Island. Sediments from the carbonate bank are moved down the walls of the U-shaped trough by turbidity currents which erode the canyon wall, forming numerous gullies, and cut a V-shaped canyon on the trough floor (Sealey 1994).

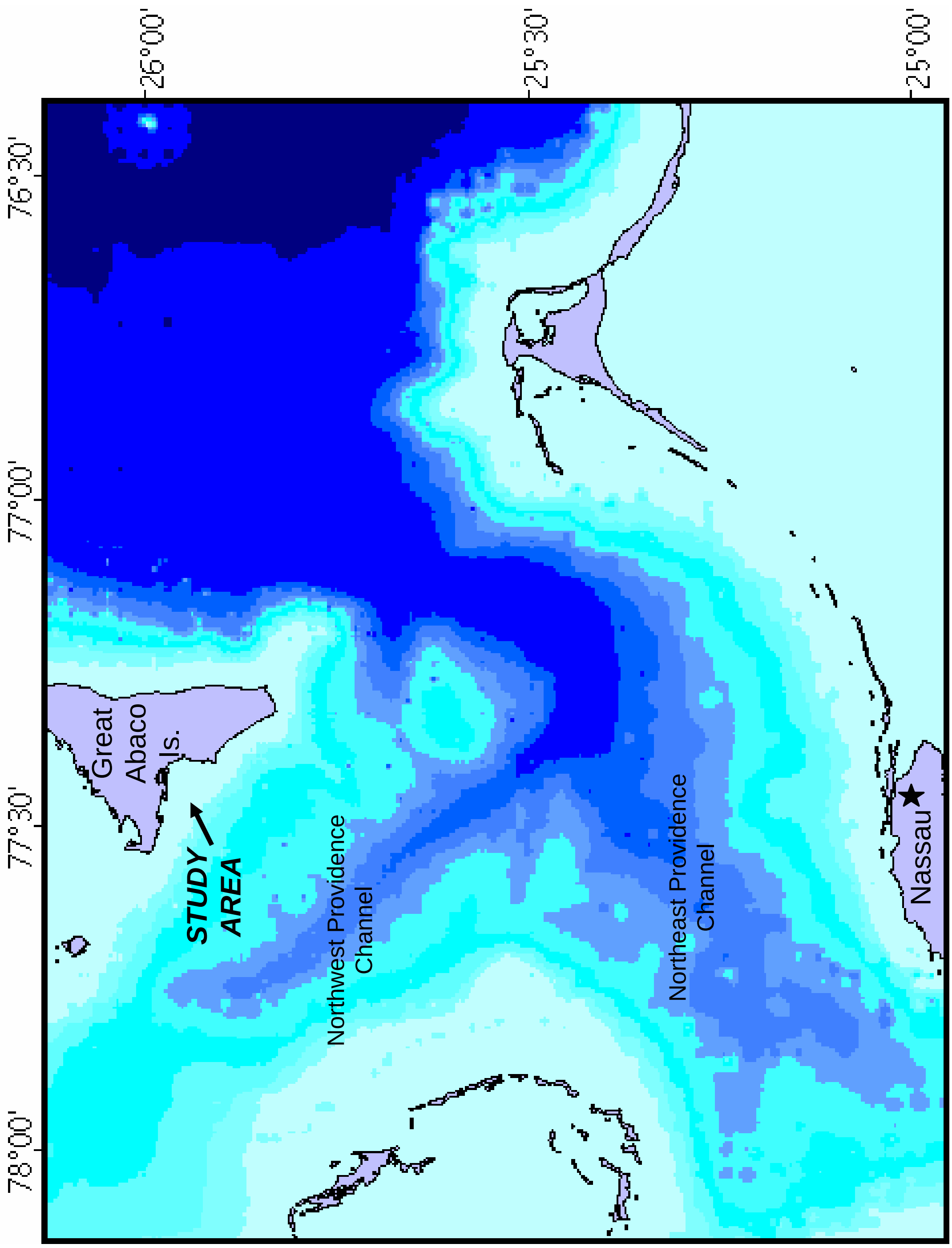


Figure 1.2 The Great Bahama canyon, showing the two branches into Northwest Providence Channel and Northeast Providence Channel, and the study area.

The study area is located off the southern end of Great Abaco Island, which includes the northern margin of Northwest Providence Channel branch of the canyon. There is asymmetry to the slope on either side of Northwest Providence Channel, with the northern margin having a narrow and steep slope averaging 6 – 20°, which gets steeper towards the southeast, whereas the slope along the southern margin is broad and gentle, averaging only 1 - 3° (Mullins 1978). Mullins *et al.* (1979) characterised the bottom topography and sediment types in the study area and found rugged bottom topography with numerous v-shaped submarine eroded canyons and gullies, and coarse bank-derived coralgal sands that cascade down the nearly vertical marginal escarpment by grain fall or rock fall.

Northwest Providence Channel is one of seven main passages between the Atlantic Ocean and the Caribbean Sea (Johns *et al.* 2002). On average New Providence Channel contributes about 1.2 Sv to the Florida Current transport (Leeman *et al.* 1995). This westward flow is influenced by the warm Antilles current and the cold Deep Western Boundary Current, both on the eastern side of The Bahamas. Satellite data shows that productivity levels range in chlorophyll *a* concentrations from 0.05 to 7.0 mg/m^3 (Figure 1.3), and are higher on the bank platforms than in the deep-water basins and channels throughout The Bahamas. In Northwest Providence Channel, the highest levels are along the bank margins. There is seasonal variation in chlorophyll *a* levels on the bank platforms with the highest levels in summer when the sea surface temperature on the banks exceeds 30° C.

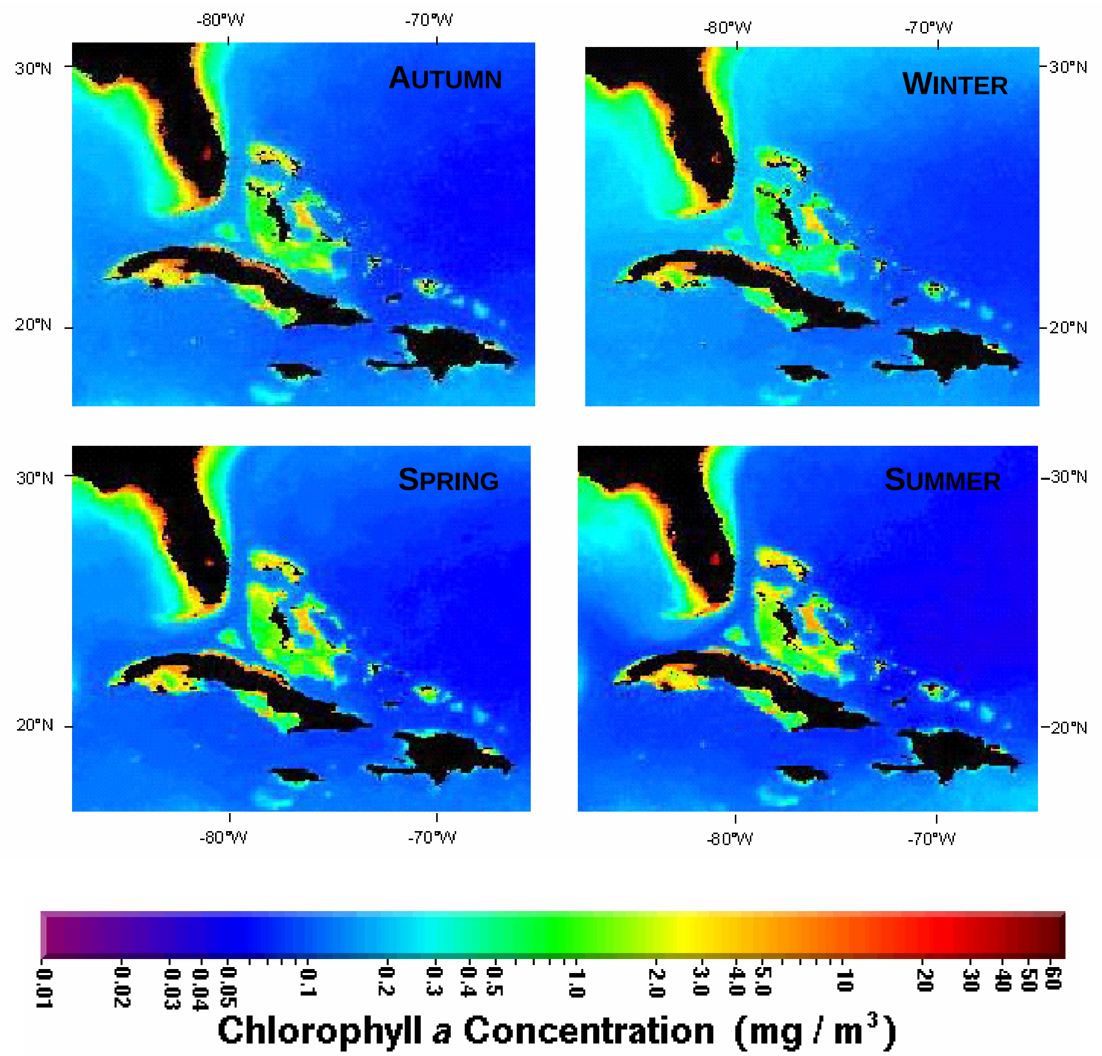


Figure 1.3 Seasonal changes in chlorophyll *a* concentrations in The Bahamas, showing highest levels in the summer months on the shallow carbonate banks. (Composite data from SeaWiFS.)

STUDY OBJECTIVES

This study represents the first effort to characterise beaked whale habitat use based on small-scale systematic and randomised surveys designed specifically for assessing habitat selection in these species.

This involved five specific objectives:

1) To describe the occurrence and occupancy patterns of beaked whales in the study area.

2) To determine the habitat selection of beaked whales relative to fixed physical and variable oceanographic features.
3) To describe beaked whale habitat selection relative to the distribution of other cetacean species sighted in the study area.
4) To compare species' distribution as determined from random and non-random surveys.
5) To examine the social organisation of Blainville's beaked whales in order to determine whether all age classes are occupying the same habitats.

CHAPTER TWO

OCCURRENCE, OCCUPANCY PATTERNS AND SOCIAL ORGANISATION OF BEAKED WHALES

INTRODUCTION

In this chapter I describe the occurrence of beaked whales in the Great Bahama Canyon as determined from vessel surveys conducted along the southwestern coast of Great Abaco Island, northern Bahamas from 1997 – 2002. Photo-identification techniques were employed to assess occupancy patterns of individual whales which were photo-identified and later re-sighted and to make inference about individual site fidelity. When all members of a group in an encounter were photo-identified, I examined the relationships between different age classes to describe their social structure.

Specific objectives addressed in this chapter include:

1) To summarize survey effort from opportunistic and line transect surveys and compare the effectiveness of these two survey methods.

2) To analyse sightings data from vessel surveys to describe species occurrence, including temporal occurrence and group sizes in the Great Bahama Canyon.

3) To analyse photo-identification data to determine occupancy patterns and assess site fidelity of individual beaked whales.

4) To assign different age classes to individual whales photo-identified more than once to examine Blainville's beaked whale social organisation.

METHODOLOGIES

FIELD WORK

Field studies were based on two different survey types: opportunistic surveys and line transect surveys, each with differing goals. During opportunistic surveys, the aim was to maximise the chance of encountering marine mammals to obtain photo-identification data for the statistical assessment of abundance, population structuring and individual life history studies. While line transect surveys were specifically designed to provide random area coverage to yield appropriate data for assessing species' distribution and habitat use (see Chapter 4).

Opportunistic surveys

Opportunistic vessel surveys were conducted off the southern end of Great Abaco Island in the northern Bahamas (25° 55.0'N, 77° 20.0'W) over a six-year study period, 1997 – 2002. Surveys were initiated from two different land bases during the study: from Cross Harbour, 1997 – 1999; and from Sandy Point, 2000 – 2002 (Figure 2.1). Surveys were conducted throughout the year, depending on the weather conditions, and more frequently in the summer months. Vessels used for surveys ranged in length from 5 – 10 m, and were powered by either single or twin outboard engines from 100 Hp to 200 Hp. During opportunistic surveys, the vessel conducted a non-random search for cetaceans and frequently returned to supposed "hot spots", or areas that yielded a high probability of cetacean encounters during previous surveys. After travelling to these "hotspots", the vessel would often remain in the same area for up to an hour with the intention of encountering animals that may surface at the end of a long dive. Opportunistic surveys were conducted in sea state conditions that ranged from Beaufort 0 to 5.

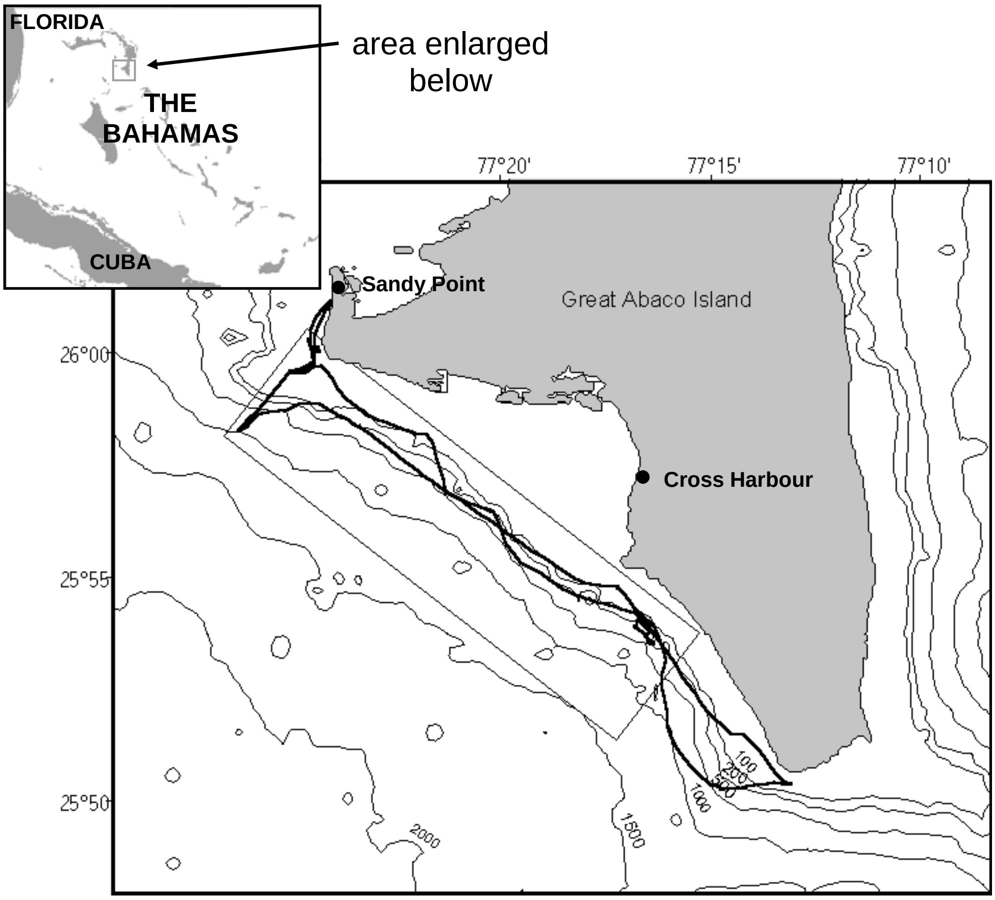


Figure 2.1 Opportunistic vessel surveys were conducted around the southern end of Great Abaco Island in the northern Bahamas, but were primarily run along the canyon wall off the southwestern coast. The route shown in this figure illustrates the non-random opportunistic survey conducted on 5 July 2001. The rectangle shown is the line transect grid. Isobaths are shown in metres.

Line transect surveys

Cetacean sightings and environmental data were also collected during standardised line transect surveys conducted over a three year period, 2000 –

2002, off the southwest coast of Great Abaco Island. Small boats (< 7 m) were used to run randomly selected line transects using an equal angle (70°) zigzag pattern within a 3 X 11 nm (5.6 km X 20.4 km) grid overlaid along the coastal escarpment as shown in Figure 2.2. The grid size was chosen to encompass the maximum area that could be surveyed in a single daily trip, on a repeatable basis, and was therefore limited by the duration of good weather windows, and the daily range of the small boats available. The equal angle zigzag design was chosen because the transect grid was rectangular and the design axis was parallel to one side of the rectangle, producing even coverage of the survey area (Thomas *et al.*, 2002).

Transect lines were pre-determined by randomly selecting the starting position and the initial direction from that position for each transect using a random number generator. To determine the start point, the 3 nm southeast end of the transect grid was divided into 30 equal intervals, and a random number between 0 and 30 was generated. The resulting number was measured as the distance from the southeast corner of the rectangle to the begin position of the transect. A second random number between 0 and 1 was generated to determine whether to run the first leg of the transect in a north-northeast (0 – 0.5) direction or south-southwest (> 0.5 – 1). For example, in the transect shown in Figure 2.2, random numbers generated were 18 and 0.2 resulting in the transect beginning at 1.8 nm from the southeast corner of the rectangular grid with the first leg heading 010°. Depending on the starting position, each transect consisted of 7 or 8 zigzag lines, or “legs”, within the rectangular grid. When all legs were added together to form a single transect, the total distance of each transect was approximately 19.5 nm (36 km).

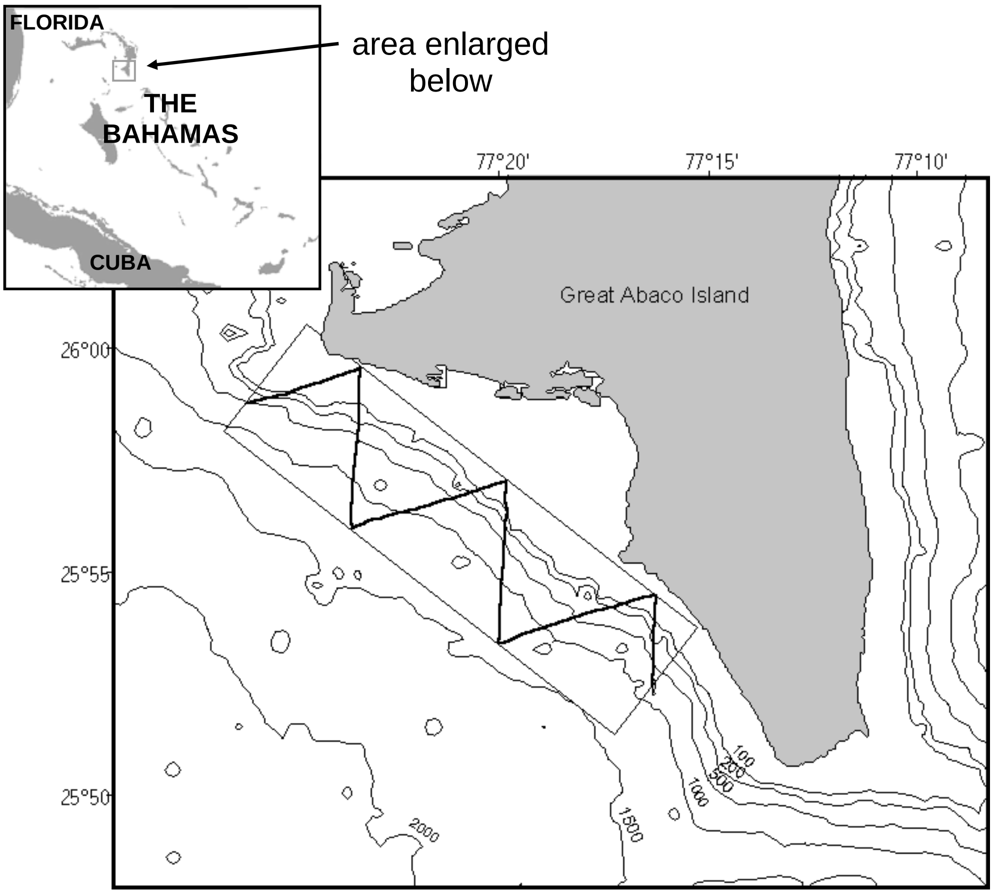


Figure 2.2 Line transects were run using an equal-angle zigzag pattern within a rectangular grid along the southwest coast of Great Abaco Island as shown by the survey run on 25 August 2002. Isobaths are shown in metres.

To optimise sighting conditions, line transect surveys were only run during calm conditions, when the sea state was less than Beaufort 3. However, if the sea state increased to a Beaufort 3 during the last leg of a transect, it was completed. Because transects were only attempted in good weather, they were run more frequently during the summer months, but also throughout the year when possible. Transects were run at a speed of approximately 15 knots, and each survey took about 1 hour and 20 minutes to complete. Observers searched for cetaceans without binoculars, with one observer scanning 180° on either side of the vessel, standing at a height of 2 – 2.5 m above sea level. The number of observers ranged throughout the study period, but at least one experienced observer was always aboard the survey vessel. Not more than one transect was conducted per day.

When marine mammals were sighted, the vessel left the transect line to close in on the group, and a GPS waypoint was recorded at the break position on the transect line, before closing. At the end of the encounter, the vessel returned directly to the break position and completed the transect. If the same group was re-sighted when the transect was resumed, the vessel would again break transect, but remained with the group only long enough to confirm the same group size and individuals, when possible.

Field data collection

A summary of the data that were recorded whilst in the field is given in Table 2.1. Whilst some of the data were recorded for contribution to other on-going studies, variables analysed during this study included time, position, average speed, depth, sea surface temperature and Beaufort sea state. For opportunistic surveys, survey conditions were recorded at the start of the survey and at regular intervals (typically 30 minutes). During line transect surveys, survey conditions were recorded at the beginning and end of each transect leg (approximately every 12 minutes) or, if the transect line was broken, at the time the transect was resumed. Depth and sea surface temperature data were collected using a Garmin Fishfinder with a hull-mounted sensor, which was limited to recording depths less than 200 m. For both survey types, a Garmin GPS 48 was used to record the vessel's position every minute and the track line was later downloaded for analysis.

Table 2.1 Data collected and frequency of collection during vessel surveys and cetacean encounters during the study. Variables included in analyses in this study are marked with an asterix (*).

Data collected	*Opportunistic surveys*	*Line transect surveys*	*Cetacean encounters*
Time *	X	X	X
GPS position *	X	X	X
Heading		X	
Average speed (kts) *		X	
Depth (m) *	X	X	X
Bottom substrate (if visible)	X	X	X
Sea surface temperature (°C) *	X	X	X
Tide state		X	X
Beaufort sea state *	X	X	X
% cloud cover	X	X	X
Sun glare		X	
Number of boats			X
Behaviour state			X
Frequency collected	every 30 min	end of leg	every 15 min

Cetacean encounters

Cetaceans were identified to the lowest taxonomic level possible, but this was dependent on the sea state, the observer's experience and animals' behaviour. At the beginning of the encounter, data were collected on the location, species, group size and composition, and direction of travel (if any). Additional data that were gathered every 15 minutes throughout the encounter are shown in Table 2.1.

To document individually recognisable marine mammals, identification photographs were taken using high-speed black and white film to obtain high quality photographs of the head, dorsal fin and side of each beaked whale, and of the body part that provided the most individually identifiable characteristics (either the tail flukes or dorsal fin) for all other species. During encounters, as many individuals within a group were photographed as possible. Individual identifications were made visually by comparing photographed individuals between encounters with an existing photo-identification catalogue for that species. In this way, subsequent sightings of the same group(s) of animals on a single transect could be removed from some analyses. Group size was determined by the number of individuals visually identified by experienced observers and later confirmed by the photographs.

All fieldwork was conducted under The Bahamas Marine Mammal Survey (BMMS) research permit issued annually by The Bahamas Department of Fisheries (permit # MAF/FIS/12[A]). Protocols developed by BMMS regarding vessel approaches and interactions with marine mammals were followed (see Appendix II).

PHOTO-IDENTIFICATION ANALYSIS

Photographic data collected during encounters with Blainville's beaked whales and Cuvier's beaked whales from 1997 – 2001 was analysed for two purposes. Rates of photographic resightings were used to examine species-specific occupancy patterns within the study area and to describe the social organisation of Blainville's beaked whales and examine the differences in habitat use between different age and sex classes (in Chapter 4).

The black and white identification film taken during each encounter was push-processed to 1600 ASA to increase contrast and help reveal patterns of natural markings on each photographed animal. The photographic negatives were visually examined over a light table using a magnifying eyepiece to distinguish between the different individuals photographed. Individual beaked whales were identified using the pattern of nicks in the dorsal fin, distinctive dorsal fin profiles and unique scarring patterns, including intra-specific linear scars and oval scars caused by cookie cutter sharks on both right and left sides. Identifications were assigned a quality grade (Q) ranging from 0 to 3 (3 being the highest quality photograph) based on the image size, focus, lighting, angle, and exposure of the photograph. IDs based on only high quality images (Q > 1) were used in subsequent analyses. From high quality photographs, photo-resightings of individual whales can be readily made, even when some degree of mark change has occurred, as shown in Figure 2.3.

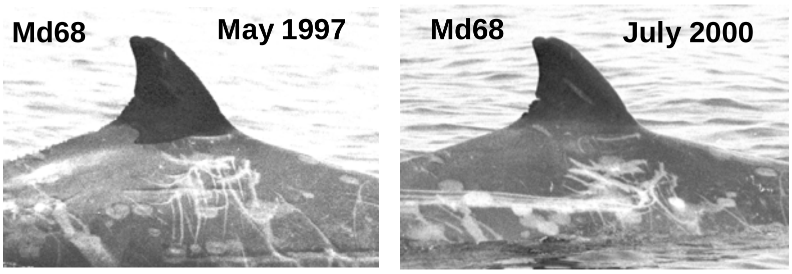


Figure 2.3 Photo-identification photographs of Blainville's beaked whale Md68 demonstrate that beaked whales can be reliably re-identified from high quality photographs of the natural markings on the body, despite some mark changes from 1997 – 2000.

To examine the distribution of different age classes, high quality photographs of the head and thoracic region of Blainville's beaked whales were examined and individuals were separated into different age classes. Sexual dimorphism has been described for Blainville's beaked whales and Cuvier's beaked whales by both Mead (1989, 2002) and Heyning (1989). Five different age and sex classes were used: 1) adult males, 2) adult females, 3) sub-adult males, 4) unknown immature animals and 5) juveniles or calves. The characteristics which distinguish the different age and sex classes are shown in Figure 2.4.

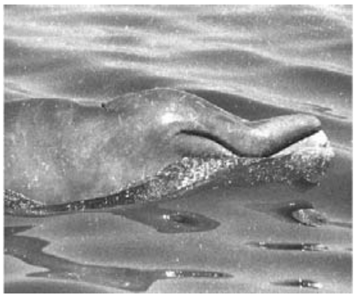
Adult male

- Teeth erupted above gum-line
- Extremely stepped mandible
- Extensive intra-specific scarring on head and dorsum
- Ridge on dorsum behind blowhole
- Adult size

Sub-adult male

- Teeth not erupted
- Extremely stepped mandible
- Light intra-specific scarring on head and dorsum
- Adult size

Adult female



- Stepped mandible
- Numerous cookie cutter shark scars (*Isistius* sp.) as described by Walker & Hanson (1999) for older adult female *M. stejnegeri*
- Seen with a calf at least two times
- Adult size

Unknown immature

- Slightly stepped mandible
- None or minimal intra-specific and *Isistius* sp. scarring
- Lighter pigmentation
- Size smaller than above classes

Calf / juvenile

- Travelling in echelon position or alongside an adult
- May be seen nursing
- Small size

Figure 2.4 Sexual dimorphism in Blainville's beaked whales makes it possible to readily distinguish five different age and sex classes from high quality photographs of the head and thoracic region.

DATA PROCESSING

Line transects

Vessel tracks from line transect surveys were downloaded from the GPS and saved as text files, and all “off effort” portions of the tracks were deleted. Off effort portions of track lines included: vessel tracks before a transect survey began and after the survey was finished, tracks generated whenever the vessel left the transect line, and tracks generated during cetacean encounters. Each transect line was then imported as a set of points to a GIS project as separate event themes using the software package ESRI ArcView GIS 3.2 (ESRI Inc.). Each transect line was generated by joining all the points within a transect using an ArcView extension “Animal Movement” which converts points to polylines, and the length of each transect line was calculated (Hooge *et al.*, 1999).

Sighting data

In this study, a “sighting” refers to each group of animals sighted, and therefore, a sighting may represent one or more animals. Sightings during transects which were not completed, and those of unknown species were only included in the analysis of group size. “Sighting rate” was defined as the number of sightings per kilometre of track line surveyed. This was used to compare sighting rates between opportunistic and line transect surveys conducted during this study and to compare to other studies (e.g. Waring *et al.* 2001).

ANALYTICAL METHODS

Statistical analyses

Statistical analyses were performed using standard tests available in S Plus 2000 Professional Release 2 (MathSoft, Inc.) and Microsoft Excel 97 SR-1 (Microsoft, Inc.). Correlation co-efficients were calculated to look at the relationship between the distance surveyed and the number of sightings, and between the variation in effort and sightings temporally. One-way ANOVA tests were used to compare sighting rates between opportunistic and line transect surveys and to compare group size between beaked whale species.

Photo-resighting rates were defined as the number of individuals seen more than once divided by the total number of individuals identified during the study period (not including same day resightings). These analyses were done on a subset of the photographic data (1997 – 1999).

To assess differences in habitat use of Blainville's beaked whale age classes (Chapter 4), it was first necessary to test if different association patterns between age classes exists. A Simple Ratio Index (Cairns and Schwager 1987) was applied to the Blainville's beaked whale photographic dataset to determine pair-wise association indices between individuals that were photographed more than once from 1997 – 2001. Association indices ranged between 0, for two individuals that were never photographed together, to 1 for two individuals that were always photographed in the same group. The programme SocProg written for MATLAB was then used to generate a dendrogram using the average linkage clustering method (Whitehead 1999, Whitehead and Dufault 1999).

RESULTS

FIELDWORK

Opportunistic surveys

Opportunistic surveys accounted for the majority of the field effort, with almost 37,000 km surveyed off the southern coast of Great Abaco Island from 1997 to 2002. These non-random surveys covered the study area more broadly, extending offshore into the Great Bahama Canyon and around to the east side of Abaco Island, but the majority of effort was concentrated along the canyon wall off the southwestern coast of Abaco.

Opportunistic surveys were conducted in sea states ranging from Beaufort 0 to 5, resulting in relatively low sighting rates (the number of sightings per kilometre surveyed), as shown in Table 2.2. Effort varied substantially between years with a three-fold difference in the distance covered during 1998 and 2000. The number of sightings was correlated to the distance surveyed (r = 0.75), but this did not represent a consistent pattern during all years. For example, the distance surveyed during 2000 represented 29% of the total distance surveyed in all six years combined, but had one of the lowest sighting rates.

Table 2.2 Summary of opportunistic vessel surveys conducted during 1997-2002.

Year	*No. surveys*	*No. sightings*	*Distance (km)*	*Sighting rate (sightings/km)*
1997	88	55	4780	0.012
1998	60	71	3220	0.022
1999	86	120	6010	0.020
2000	158	160	10540	0.015
2001	158	131	6520	0.020
2002	112	157	5870	0.027
Overall	662	694	36940	0.019

Line transect surveys

Between 2000 and 2002, sixty-two line transect surveys were conducted in the waters off the southwest coast of Great Abaco Island. Of these, 58 transects were completed (Table 2.3). Uncompleted transects (n = 4) were used only in the analysis of group size. The total distance covered for all completed transects over the three-year study period was 2,270 km, but one year (2000) represented only 20% of the total.

As with opportunistic surveys, there was a positive correlation between the distance surveyed and the number of sightings (r = 0.77). The sighting rate during line transect surveys was significantly higher than during opportunistic vessel surveys (one-way ANOVA: p = 0.0049).

Table 2.3 Summary of line transect surveys, 2000-2002. The number of uncompleted transects and sightings during uncompleted transects are shown in parentheses. The distance and sighting rate for each year were calculated for completed transects only.

Months/Year	*No. transects*	*No. sightings*	*Distance (km)*	*Sighting rate (sightings/km)*
May – December 2000	12 (2)	22 (2)	460	0.048
January – October 2001	25 (1)	28 (1)	980	0.029
January – September 2002	21 (1)	32	830	0.039
Overall	58 (4)	82 (3)	2270	0.036

Line transect surveys were run during all months of the year, although the plot in Figure 2.5 shows a slightly bimodal distribution in survey effort temporally, with an increase in the number of transects during “winter” and “summer” months, and fewer transects during the shoulder (spring and fall) seasons. This partly reflects increased funding available for surveys during these times of year, but the peak in effort during summer months also results from more favourable weather conditions. The temporal variation in the number of sightings during transects was a strongly correlated with the variation in effort (*r* = 0.95).

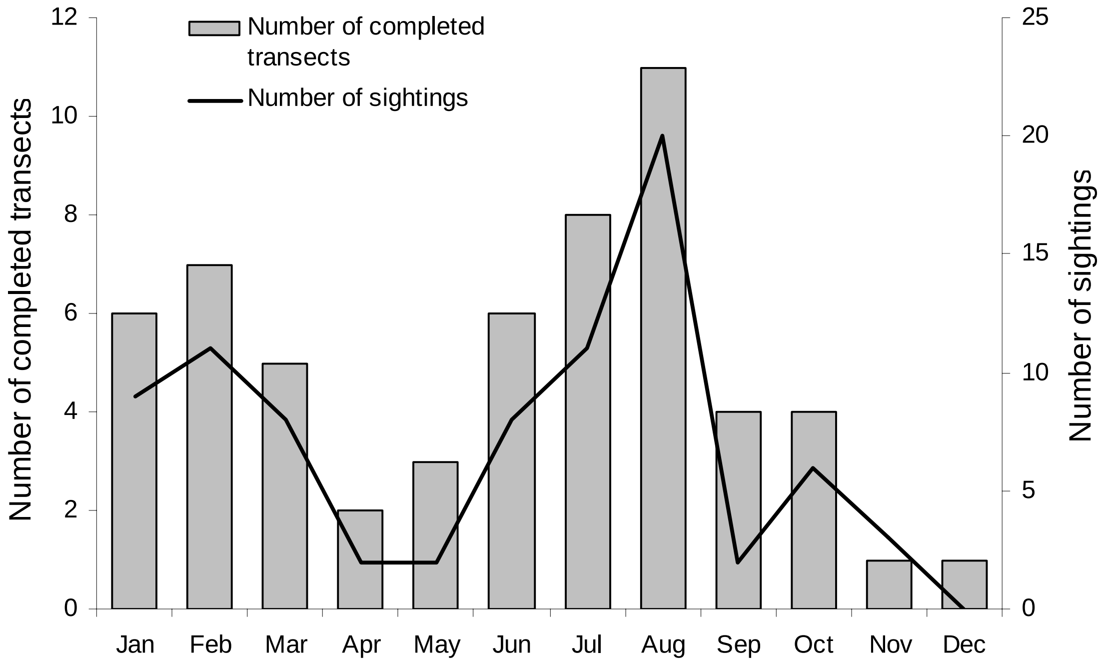


Figure 2.5 Seasonal variation in survey effort, showing an increase in the number of completed line transect surveys conducted during winter and summer months (bars) and the number of sightings (line).

The combined vessel tracks for all completed line transects run during the study period are shown in Figure 2.6. The map shows how extensively the survey area was covered, but also shows that the survey area only included the waters along the edge of the canyon wall.

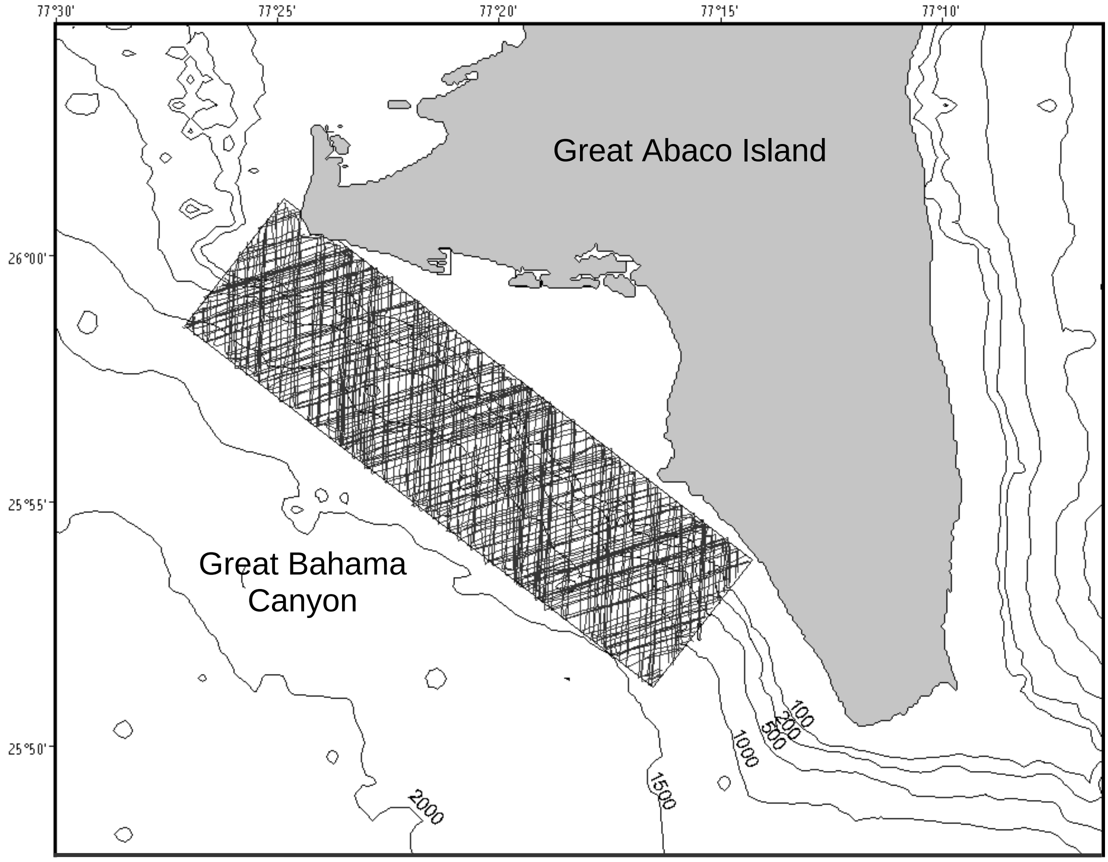


Figure 2.6 Combined tracks for all completed line transects off the southwest coast of Great Abaco Island during the study period, 2000-2002. Isobaths are shown in metres.

CETACEAN SIGHTINGS

Seven hundred and seventy-six cetacean groups were sighted during opportunistic and line transect vessel surveys conducted off the southern end of Great Abaco Island during the study period (1997 – 2002). The majority of sightings (89%) occurred during opportunistic vessel surveys spanning the entire study period, resulting in 694 opportunistic sightings; while 85 sightings occurred during line transect surveys conducted during 2000 – 2002, although 3 of these were sighted on uncompleted transects. A total of 6,713 individuals of 17 different species were sighted (Table 2.4). These included members of 5 cetacean families from both Sub-orders, *Odontoceti* and *Mysticeti*, although odontocetes represented 99.7% of all groups sighted during the study.

Table 2.4 Cetacean species recorded on all vessel surveys, 1997-2002. *n* represents the number of sightings for each species.

Common name	*Scientific name*	*n*
Blainville's beaked whale	*Mesoplodon densirostris*	111
Cuvier's beaked whale	*Ziphius cavirostris*	18
Sperm whale	*Physeter macrocephalus*	55
Dwarf sperm whale	*Kogia sima*	133
Pygmy sperm whale	*Kogia breviceps*	8
Killer whale	*Orcinus orca*	1
Pygmy killer whale	*Feresa attenuata*	1
Melon-headed whale	*Peponocephala electra*	2
Short-finned pilot whale	*Globicephala macrorhynchus*	5
Risso's dolphin	*Grampus griseus*	2
Fraser's dolphin	*Lagenodelphis hosei*	2
Rough-toothed dolphin	*Steno bredanensis*	1
Striped dolphin	*Stenella coeruleoalba*	1
Pan-tropical spotted dolphin	*Stenella attenuata*	9
Atlantic spotted dolphin	*Stenella frontalis*	68
Atl. bottlenose dolphin (oceanic)	*Tursiops truncatus*	8
Atl. bottlenose dolphin (coastal)	*Tursiops truncatus*	334
Minke whale	*Balaenoptera acutorostrata*	2
Unknown species		15
	Total	776

Coastal bottlenose dolphins were the most frequently sighted cetaceans, representing 43.7% of all sightings. To explore the relative frequency of occurrence of oceanic species, coastal bottlenose dolphin sightings were removed from the dataset, resulting in a subset of 431 sightings of oceanic species. This subset of the data shows that dwarf sperm whales and Blainville's beaked whales were the most frequently encountered species, representing 30.9% and 25.8%, respectively, of all oceanic sightings.

Variation in temporal occurrence of beaked whales

During the six-year study period, there was a change in the temporal occurrence of beaked whales in the study area as shown in Figure 2.7.

Sighting rates (number of sightings per kilometre surveyed) were calculated each year and compared between species. The sighting rate for Blainville's beaked whales increased until 1999 and then fluctuated between 2000 and 2002. Cuvier's beaked whale sighting rates declined between 1998 and 2001, with no sightings for a 20-month period (May 2000 – February 2002). During this same time period, there was an increase in the sighting rate for sperm whales in the study area.

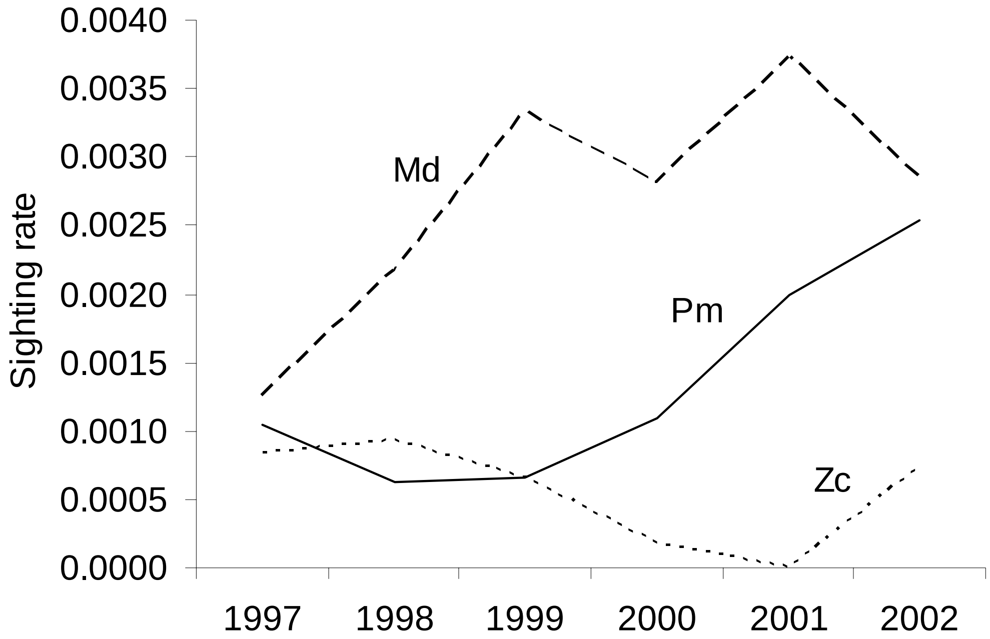


Figure 2.7 The change in temporal occurrence of ziphiids and sperm whales during the study period. Md = Blainville's beaked whale, Pm = sperm whale and Zc = Cuvier's beaked whale. Sighting rate is the number of sightings per distance surveyed (sightings/km).

Group size

Group size varied between cetacean species, ranging from sightings of solitary minke whales to encounters with an estimated 500 melon-headed whales. Group size summary statistics for each species sighted are presented in Table 2.5, and includes data from both opportunistic and line transect surveys during the study.

Group sizes differed significantly between the two ziphiid species sighted during the study period (one-way ANOVA: $p < 0.001$). Blainville's beaked whales were found in slightly larger groups with a mean group size of 4.07 whales (n = 111, median = 4.00, SD = 1.93), and a range of 1 to 11 whales. Mean group size for Cuvier's beaked whales was 2.44 whales (n = 18, median = 2.00, SD = 1.12), and ranged from 1 to 5 whales.

Table 2.5 Summary statistics for cetacean group sizes. *n* represents the number of sightings for each species.

Species	*Mean*	*Median*	*Mode*	*SD*	*Min*	*Max*	*n*
Blainville's beaked whale	4.1	4.0	2	1.9	1	11	111
Cuvier's beaked whale	2.4	2.0	2	1.2	1	5	18
Sperm whale	5.8	5.0	8	4.0	1	19	55
Dwarf sperm whale	3.0	2.0	1	2.4	1	15	133
Pygmy sperm whale	1.4	1.0	1	0.5	1	2	8
Killer whale	7.0	7.0	-	-	-	-	1
Pygmy killer whale	30.0	30.0	-	-	-	-	1
Melon-headed whale	310.0	310.0	-	268.7	120	500	2
Short-finned pilot whale	5.8	4.0	3	4.7	3	14	5
Risso's dolphin	13.5	13.5	-	9.2	7	20	2
Fraser's dolphin	95.0	95.0	-	77.8	40	150	2
Rough-toothed dolphin	13.0	13.0	-	-	-	-	1
Striped dolphin	75.0	75.0	-	-	-	-	1
Pan-tropical spotted dolphin	11.6	7.0	2	12.0	2	30	9
Atlantic spotted dolphin	10.0	8.5	6	7.3	1	30	68
Atl. bottlenose dolphin (oceanic)	11.3	3.0	15	16.8	1	50	8
Atl. bottlenose dolphin (coastal)	10.7	9.0	2	7.7	1	32	334
Minke whale	1.0	1.0	1	-	-	-	2

Photo-resightings

During the line transect surveys, if several groups of whales were seen on the same or adjacent transect legs, photographs were analysed to determine if these groups contained the same individuals. This occurred four times during the study. Photographic analysis confirmed that the survey vessel had sighted the same group of whales on three different occasions during a single line transect, including groups of pygmy sperm whales, sperm whales and Blainville's beaked whales. However, on one occasion the photo-analysis showed that a second group of Cuvier's beaked whales sighted on adjacent transect legs contained different individuals. Resightings of the same groups during a single transect were not counted twice.

Photographic data from opportunistic surveys made between 1997 and 1999 were also analysed to determine the rate at which individual whales were resighted in the study area. Re-sightings of individuals from seven species were recorded, including Blainville's beaked whales and Cuvier's beaked whales. These included both intra- and inter-annual resightings.

Photo-resighting rates for beaked whales varied by species, suggesting a difference in occupancy patterns in the study area. The overall resighting rate for Blainville's beaked whales was 0.40, while Cuvier's beaked whales had a much lower resight rate of only 0.06 during this three-year period. There was also a notable difference in the photo-resightings of different age and sex classes of Blainville's beaked whales. Adult whales were resighted much more frequently than sub-adult animals, with resighting rates of 0.42 and 0.08, respectively. Additionally, adult females had a much higher resighting rate of 0.75, compared to adult males, with a low resighting rate of 0.09. However, one adult male (Md75) was sighted 18 times in the study area compared to the mean number of sightings of 3.5 times for all adult males (n = 13, median = 1, mode = 1, SD = 5.3).

Examining age class separation in Blainville's beaked whales

Photographic data from 76 groups of Blainville's beaked whales sighted from 1997 – 2001 was used to examine their social organization. Seventy-three different individual whales were identified from high quality photographs and, despite mark changes in some individuals during the study period, twenty-seven individuals were readily recognized and photographed repeatedly. The majority of whales (67%) were only seen in one year, but two individuals were seen in all five years (Figure 2.8). This included one adult female (Md76) and one adult male (Md75). The whales that were seen in more than one year included 14 adults (71% females), and only 1 sub-adult animal.

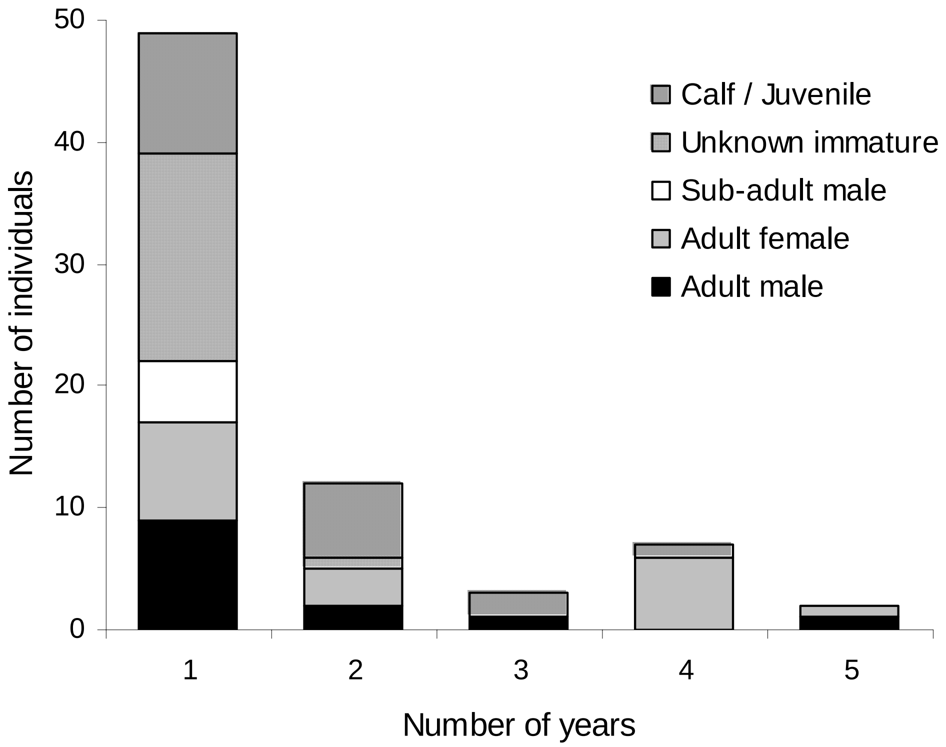


Figure 2.8 Plot showing the number of years that individual Blainville's beaked whales from the five different age classes were identified.

The simple-ratio index of association was calculated for all individually recognized Blainville's beaked whales that were photographed more than once (n = 27). The overall mean association index was 0.04 (SD = 0.19), with the highest degree of association, excluding mother/calf pairs, between adult females (mean association index = 0.10, SD = 0.25). In contrast, adult males were never observed associating with each other, but were photographed primarily in groups with adult females as shown in the association cluster plot in Figure 2.9. The cluster plot also shows that the two sub-adult whales (a sub-adult male and an unknown immature) that were seen more than once had no association with the adults.

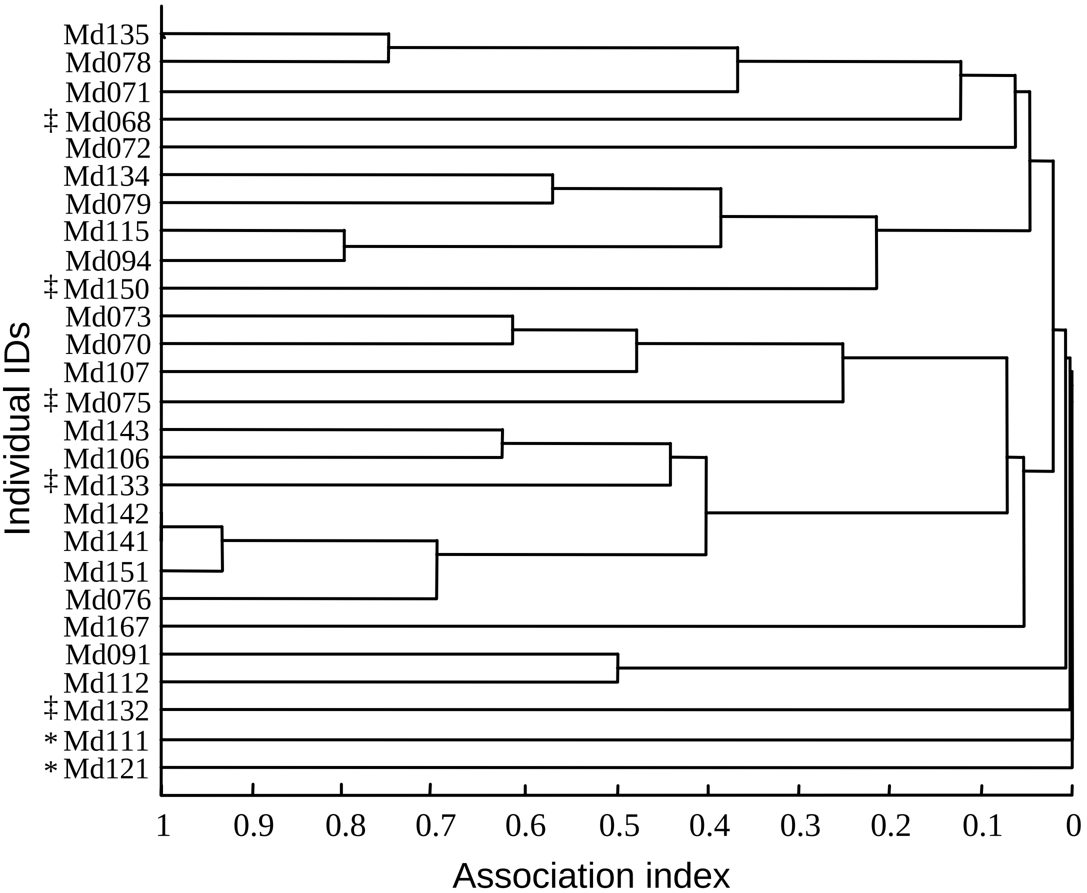


Figure 2.9 Association cluster plot shows the amount of time that whales of different age and sex classes were photographed together in a group, where 0 = never seen together and 1 = always together. Adult males are designated with "‡" next to the ID number (n = 5) and sub-adult whales with "*" (n = 2). Other whales shown include 9 adult females and 11 calves/juveniles.

DISCUSSION

For this chapter, my analyses focused on certain aspects of the beaked whale dataset. This included beaked whale occurrence in the study area, residency patterns and social organisation to help provide background information towards key biological themes presented in subsequent chapters and the final discussion.

Occurrence of beaked whales

During the study period, beaked whales were one of the most commonly sighted cetacean groups, resulting in 129 sightings (Table 2.4) and almost 80 hours of observations of beaked whales. However, the majority of the beaked whale data (86%) was collected during encounters with Blainville's beaked whales.

Variation in the temporal occurrence of beaked whales was found during the study (Figure 2.7). The decline in the sighting rate of Cuvier's beaked whales was following the mass stranding event, which occurred in March 2000 (Anon 2001, Balcomb and Claridge 2001), with no sightings of this species in the study area for 20 months despite increased effort in 2000 and 2001 (Tables 2.2 and 2.3). The sighting rate for Blainville's beaked whales initially declined following the stranding event and then increased in 2001. It is difficult to determine whether these temporal changes in sighting rates were related to the stranding event because opportunistic sightings were included in the calculation of sighting rates, which was not corrected for effort.

Group sizes found for both beaked whale species during this study are similar to those reported previously for Blainville's beaked whales in Hawai'i (Shallenberger 1981, Baird *et al.* 2004) and for Cuvier's beaked whales in the eastern tropical Pacific (Heyning 1989), the Ligurian Sea (D.Amico *et al.* 2003) and Hawai'i (Baird *et al.* 2004). Baird *et al.* (2004) also described Blainville's beaked whales in Hawai'i in slightly larger groups than Cuvier's beaked whales, although this finding was based on small sample sizes (3 and 8 groups respectively). Despite much larger sample sizes analysed in this study, the mean group size for Blainville's beaked whales were still significantly larger ($p < 0.001$) than for Cuvier's beaked whales (Table 2.5).

Occupancy patterns of beaked whales

Little is known about the occupancy (or residency) patterns of beaked whales, although repeated sightings of individual whales have been reported previously for Blainville's beaked whales (Claridge and Balcomb 1995, Durban *et al.* 2001) and Cuvier's beaked whales (Pulcini 1996).

Durban *et al.* (2001) looked at occupancy patterns of Blainville's beaked whales using the same dataset as this study, and found that adult females were more resident to the study area, while adult males moved in and out of the area more frequently. The substantially higher resighting rate of adults of both genders compared to sub-adult animals (of both genders) found during this study (0.42 versus 0.08), suggests that differences in occupancy patterns were not only between genders, but also exist between age classes, with sub-adult whales also moving in and out of the area more frequently than adults. Furthermore, the unusually high number of sightings of one adult male (Md75), which was seen during all five years of the study, suggests that occupancy patterns within the study area is not the same for all adult males.

Limited photo-identification data of Cuvier's beaked whales collected during this study made it difficult to assess occupancy patterns based on photo-resightings for this species, as there were only two animals resighted, including an adult female and a sub-adult. It should be noted though that the sub-adult whale was resighted because it stranded alive (and was rescued) during the mass stranding event in March 2000 (see Balcomb and Claridge 2001 for a description of this stranding event).

Social organisation of Blainville's beaked whales

Within the study area, Blainville's beaked whales exhibited a relatively fluid system of social organisation in which associations within and among age/sex classes are best described by a harem mating system. The highest association, excluding mother/calf pairs, was found between adult females. In contrast, adult males were never observed associating with each other, but were photographed primarily in groups with adult females. Although two adult males were never observed in the same group, based on the extent of intra-specific scarring, aggressive interactions between adult males do occur, but these are apparently brief. The cluster plot (Figure 2.9) showed that the two sub-adult whales that were seen more than once during the study had no association with the adults, suggesting some degree of separation socially between the two age classes.

This harem mating system does not occur only during a particular breeding season, as the same type of group composition was observed year-round. Nor does this structure appear to be unique to this population or even this species. Ritter and Brederlau (1999) described field observations of Blainville's beaked whales in which only a single adult male was found in mixed sex groups, and the same group composition was observed for Cuvier's beaked whales during this study. It is interesting to note, however, that there are several reports of other *Mesoplodon* species observed in groups that consist of more than one mature male. Gaskin (1971) described a group of strap-toothed whales, *M. layardii,* consisting of three animals which included two adult males, and Hooker and Baird (1999) observed a group of three Sowerby's beaked whales, *M. bidens*, which appeared to all be adult males. Lien *et al.* (1990) suggested all male groups of Sowerby's beaked whales based on the group composition of a mass stranding in Newfoundland in which the three whales examined were all mature males.

There is only one other study of a ziphiid population in which similar association analysis has been possible: northern bottlenose whales (*Hyperoodon ampullatus*) in the Gully, which appears to have a different mating strategy to that of Blainville's beaked whales in The Bahamas. Gowans (1999) reported that some male northern bottlenose whales were actually "best buddies", suggesting a mating strategy consisting of male dyads that has been described in Atlantic bottlenose dolphins (e.g. Parsons *et al.* 2001).

CHAPTER THREE

DETERMINING SURVEY EFFORT FROM LINE TRANSECT SURVEYS

INTRODUCTION

In this chapter I employ a unique methodology to assess survey effort during line transect surveys. This technique was developed to address the particular challenges of surveying visually for beaked whales. This was further driven by concern about the effect of varying sighting conditions and the use of a small vessel with a corresponding low viewing platform, resulting in variation in survey effort throughout the study period.

It was necessary to determine survey effort to calculate sightings per unit effort (SPUE) for each species within the study area to make inferences about their distribution and habitat selection (in Chapter 4).

The specific objectives of this chapter are:

1) To determine the perpendicular distance from the track line to sightings.
2) To examine what factors or survey conditions affect the observers' ability to sight animals.
3) To calculate buffer widths for each transect line which reflect the varying survey conditions.
4) To accurately determine the area surveyed during each line transect survey.

METHODOLOGIES

FIELD WORK

Line transect surveys

Standardised line transect surveys were conducted over a three year period, 2000 – 2002, off the southwest coast of Great Abaco Island to collect cetacean sightings data. Small boats (< 7 m) were used to run randomly selected line transects using an equal angle (70°) zigzag pattern within a 3 X 11 nm (5.6 km X 20.4 km) grid overlaid along the coastal escarpment as shown in Figure 3.1.

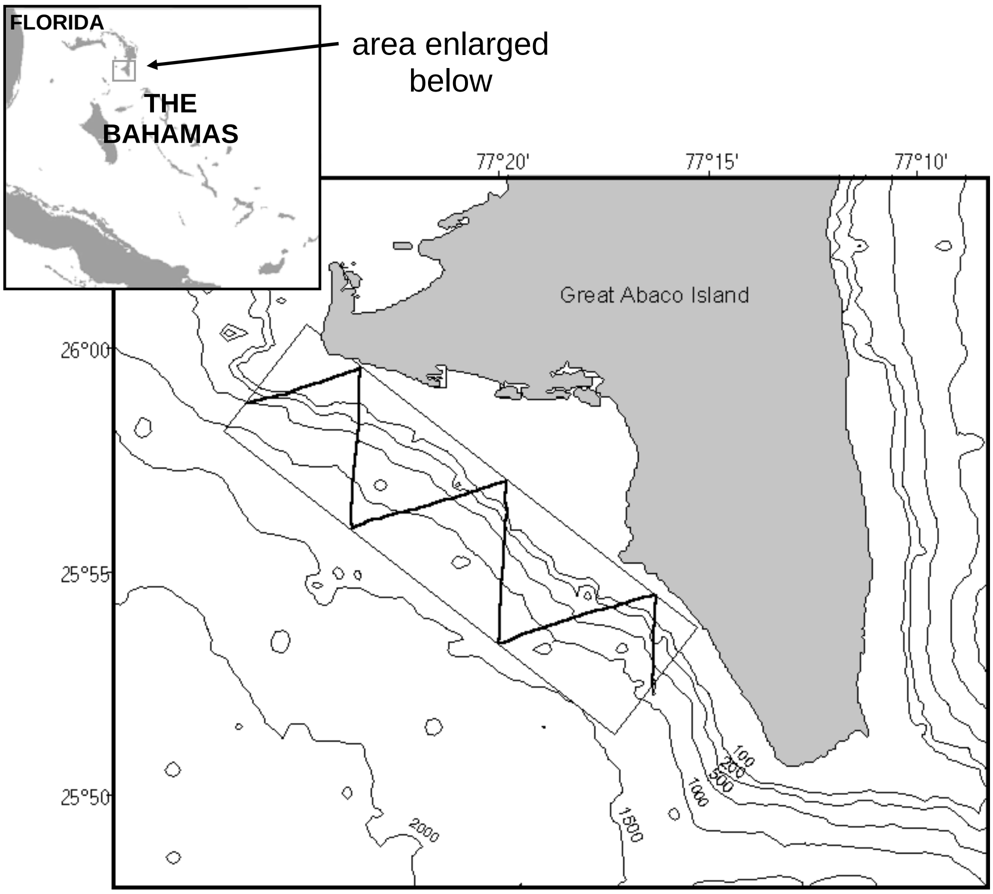


Figure 3.1 Line transects were run using an equal-angle zigzag pattern within a rectangular grid along the southwest coast of Great Abaco Island. Isobaths are shown in metres.

To optimise sighting conditions, line transect surveys were only run during calm conditions, when the sea state was less than Beaufort 3. However, if the sea state increased to a Beaufort 3 during the last leg of a transect, it was completed. Transects were run at a speed of approximately 15 knots, and each survey took about 1 hour and 20 minutes to complete. Observers searched for cetaceans without binoculars, with one observer scanning 180° on either side of the vessel, standing at a height of 2 – 2.5 m above sea level. Not more than one transect was conducted per day.

When marine mammals were sighted, the vessel left the transect line to close in on the group, and a GPS waypoint was recorded at the break position on the transect line, before closing. At the end of the encounter, the vessel returned directly to the break position and completed the transect. If the same group was re-sighted when the transect was resumed, the vessel would again break transect, but remained with the group only long enough to confirm the same group size and individuals, when possible. (For a full description of the transect design and protocols for data collection during cetacean sightings, refer to the Methodologies section in Chapter 2.)

DATA PROCESSING

Line transects

Vessel tracks from the transect surveys were downloaded from the GPS and saved as text files, and all “off effort” portions of the tracks were deleted. Off effort track lines included: all vessel locations before a transect survey began and after the survey was finished, tracks generated whenever the vessel left the transect line, and tracks generated during cetacean encounters. Each transect line was then imported as a separate event theme using the GIS software ESRI ArcView GIS 3.2 (ESRI Inc.). The ArcView extension "Animal Movement" was used to convert each point theme to a polyline (Hooge *et al.*, 1999).

Sighting data

Cetacean sightings data were organized by species, and imported into ArcView as themes with the associated metadata, and converted to shape files for each species. The sightings shape files were used to calculate the perpendicular distance from the break point of the transect line to the sighting location. Sightings during transects which were not completed, and those of unknown species were only included when calculating the distance from the transect line to sightings.

In this chapter, "sighting rate" is defined as the number of sightings per leg of a line transect survey. This was used to examine the relationship between sea state and sighting rates.

Calculating the distance from the transect line to sightings

To determine survey effort, it was necessary to apply a buffer width to the transect lines to measure the actual area on either side of the line that was searched. Applying a buffer width or an effective strip width to transect lines is used in distance sampling to estimate cetacean abundance and is determined by how far from the transect line observers are able to sight animals (Buckland *et al.* 1993).

The perpendicular distance from the transect line at the time of the sighting, or break point, to each sighting location was calculated using the ArcView extension "Identify features within a distance". However, if a group was sighted in front of the vessel, the transect was not broken at the time of the sighting, but waited until the group was closer. In these circumstances, the distances are an under representation of the actual distances at which groups were sighted.

Calculating survey effort during line transect surveys

To calculate survey effort, the study area was divided into 1 km^2 grid cells, termed "effort grids", using the ArcView script "Create a rectangular grid of polygon shapes based on the extent of selected theme". Many of the grid cells were located beyond the transect grid encompassing the actual area of survey effort, resulting in 311 grid cells as shown in Figure 3.2.

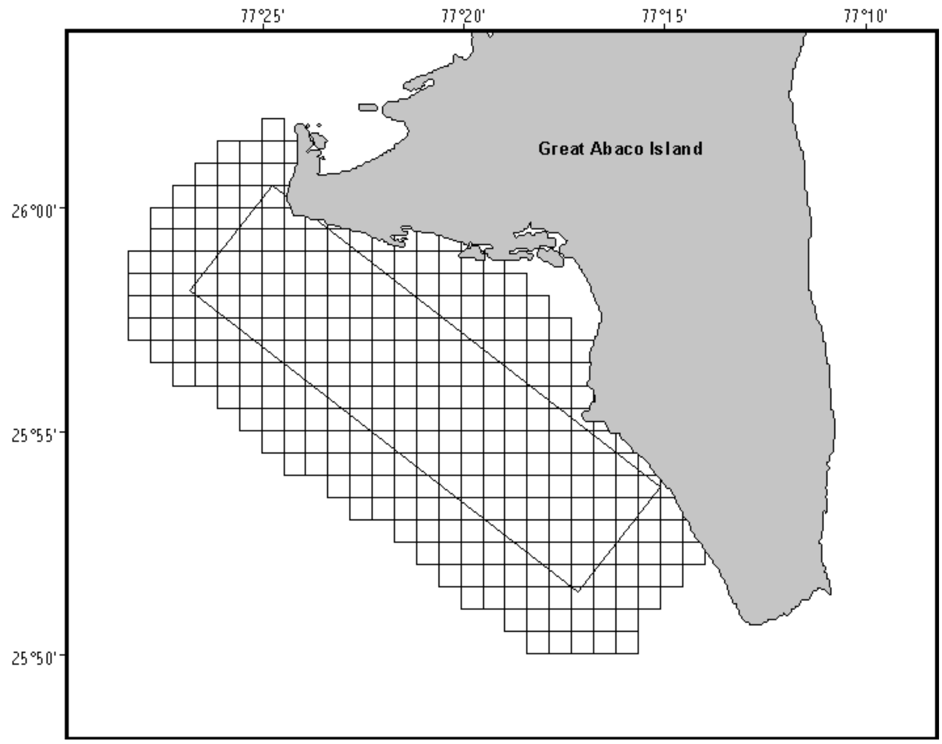


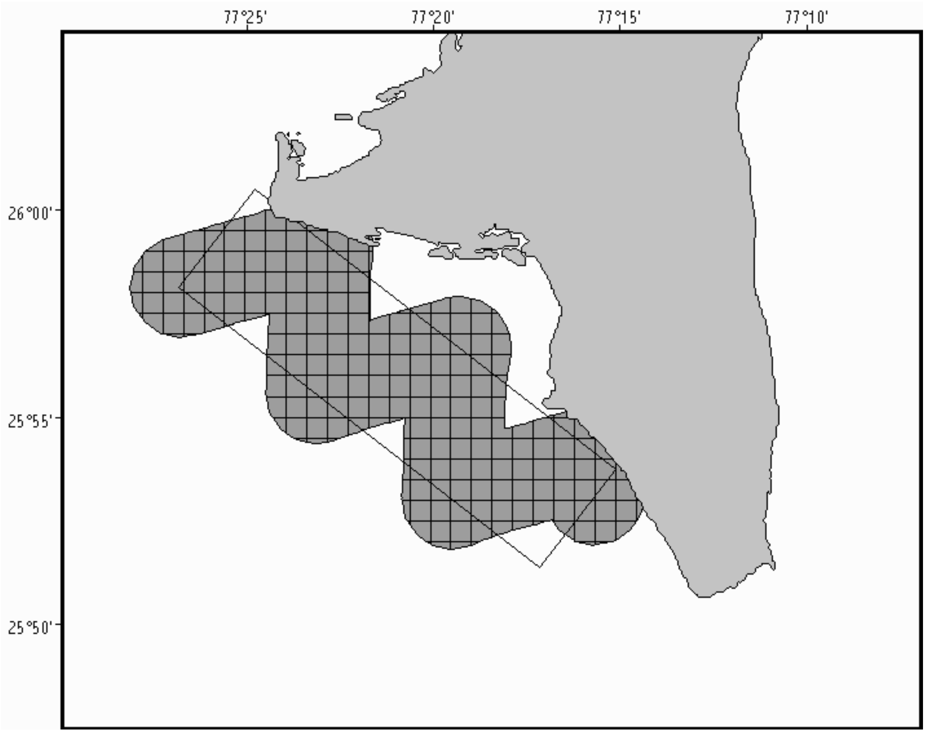
Figure 3.2 Map of the study area shows the 1 km^2 "effort grids" extending beyond the rectangular transect grid.

Effort was measured for each 1 km^2 grid cell within the survey area because the surveys were randomised and effort was not equal throughout all grid cells. Survey effort during line transects was determined by the amount of area covered by observers during transects. As the sea state changed during a transect, the range at which observers could see animals changed, thus changing the amount of area covered or survey effort.

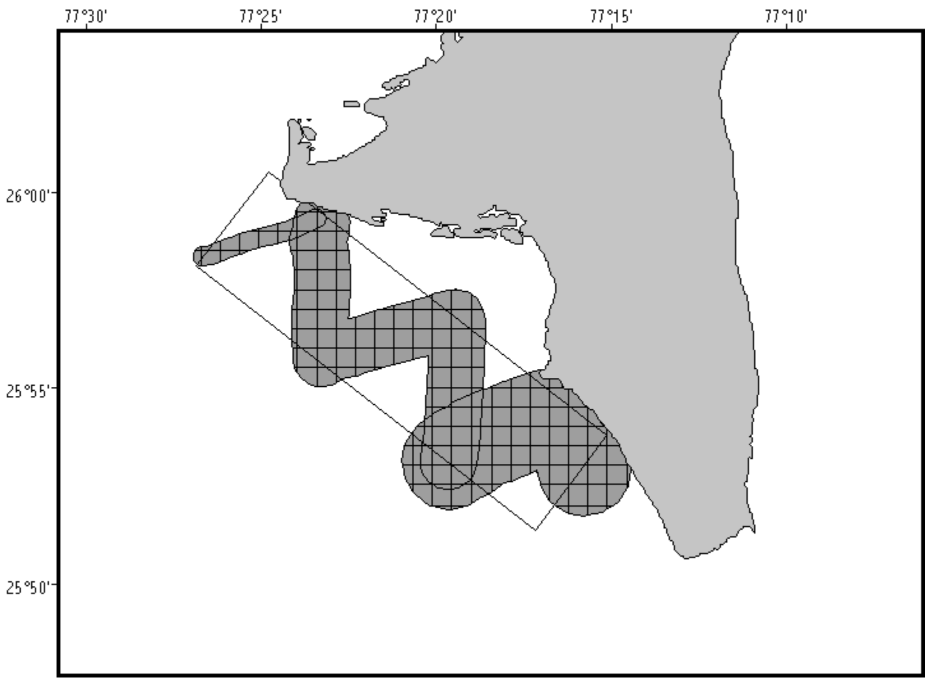
To account for this variation in survey effort, transect lines were partitioned into legs by the average sea state conditions during each leg, and then each leg was assigned a buffer width, which reflected those conditions. To do this, the table attributes for each transect theme were queried for the begin time of each leg when the sea state changed, and all legs of the transect with equal sea states were converted to new shape files using ArcView. The Create Buffers function was then used to add the specified distance for that leg (or legs) of the transect to assign a buffer width based on the particular sea state. If the sea state changed multiple times during a single transect, this resulted in multiple buffered legs, each saved as separate buffered themes.

Several functions in the ArcView extension “XTools” were used to manage the buffered themes and calculate the area covered by each transect. The buffered sections of themes for the entire transect were joined using the Union Polygon Theme function, which eliminated the overlap of buffers that would have occurred if each buffered section remained separate. Using the Erase Features function, portions of the Great Abaco Island coastline that overlapped the buffered transect were then removed. The remaining polygon theme consisted solely of the area that was surveyed during the transect. The buffered transect theme was joined with the theme containing the 1 km^2 effort grids by using the Intersect Themes function. Finally, the amount of area covered within each effort grid cell for the buffered transect was calculated using the Calculate Area function.

Figure 3.3 shows an example of the buffer widths for two different transects run in different sea state conditions. In lower sea states, the buffer is wider and much more area is covered by visual observers during the transect (a), but when conditions vary throughout a transect (b), this methodology accounts for the change in observers' viewing conditions and calculates survey effort accordingly.



(a) Beaufort 0 – 1 sea state conditions throughout a line transect survey.



(b) Sea state changing from Beaufort 0 – 1 to Beaufort 3 during a line transect survey.

Figure 3.3 Buffer widths for transects run in varying sea state conditions. The small polygons within the buffered transect are the result of intersecting the transect and effort grid themes using ArcView. The area of each polygon is then calculated describing the survey's effort in km^2.

ANALYTICAL METHODS

Statistical analyses

Statistical analyses were performed using standard tests available in S Plus 2000 Professional Release 2 (MathSoft, Inc.) and Microsoft Excel 97 SR-1 (Microsoft, Inc.), and were complemented by exploratory graphics to validate model assumptions.

Variation in the distribution of the perpendicular distance from the transect line to sightings was tested for uniformity using a one-sample Kolmogorov-Smirnov Goodness of Fit test, while the significance of any differences between mean distances for datasets including and excluding outlying data points was tested using a Wilcoxon rank-sum test.

Several factors were analysed to determine their effect on the observers' ability to sight animals and how these influenced the buffer width. These factors included the effects of sea state (both on the distance to sightings and on sighting rates), animal size, and the group size. Sea state condition was averaged from the beginning to the end of each transect leg, and sighting rates (defined here as the number of sightings per transect leg) were calculated for each sea state. Both perpendicular distances to sightings and sighting rates were plotted against sea state and correlation tests were performed.

To look at the effects of animal size on sighting distances, species were divided into groups according to their body length, and plotted by increasing size, and the relationship between size and sighting distances was tested for correlation. Wilcoxon rank-sum tests were used to test if group size affected the distance to sightings and to test if beaked whale group sizes differed from other species.

When determining buffer widths, Wilcoxon rank-sum tests were performed to test for a difference in the perpendicular distance to beaked whale sightings compared to all other species. Finally, the Kolmogorov-Smirnov Goodness of Fit test was applied to the survey effort data to test the null hypothesis that effort was evenly distributed throughout the survey area.

RESULTS

FIELD WORK

Line transect surveys

Between 2000 and 2002, sixty-two line transect surveys were conducted in the waters off the southwest coast of Great Abaco Island. Of these, 58 transects were completed (Table 3.1). Uncompleted transects (n = 4) were used only in the analysis of group size and the distance to sightings from the transect line. The total distance covered for all completed transects over the three-year study period was 2,270 km, but one year (2000) represented only 20% of the total.

Table 3.1 Summary of line transect surveys, 2000-2002. The number of uncompleted transects and sightings during uncompleted transects are shown in parentheses. The distance and sighting rate for each year were calculated for completed transects only.

Months/Year	*No. transects*	*No. sightings*	*Distance (km)*	*Sighting rate (sightings/km)*
May – December 2000	12 (2)	22 (2)	460	0.048
January – October 2001	25 (1)	28 (1)	980	0.029
January – September 2002	21 (1)	32	830	0.039
Overall	58 (4)	82 (3)	2270	0.036

FACTORS AFFECTING SURVEY EFFORT

Variability in survey conditions

Ideally, all surveys would be conducted under equivalent conditions. Realistically, this is not possible; and as expected, there was variability in the conditions encountered both between and during line transect surveys (Table 3.2). For example, as a result of deteriorating weather conditions during transects, 7 transects were aborted when sea state increased to greater than Beaufort 3.

Table 3.2 Summary statistics show the variability in operational and environmental conditions during line transects.

Variable	*Mean*	*Median*	*Mode*	*S.D.*	*Min*	*Max*
Vessel speed (knots)	14.66	15.00	15.00	1.22	10.00	19.00
Time to complete (days)	1.53	1	1	2.04	1	12
No. observers	4.46	3	2	3.07	1	10
Beaufort sea state	1.17	1	1	0.86	0	3.5

Non-environmental, or operational, conditions were more easily standardised. Vessel operators were able to maintain an average speed of 15 knots. While the intention was always to complete a transect on the day it was started, it sometimes took 2-3 days and, for one transect, as many as 12 days to complete due to poor weather. The number of observers on board also varied considerably with as many as 10 observers on 10 of the transects. There was always at least one experienced observer, and these additional observers often included persons with no previous field experience.

Environmental, or weather, conditions also varied during transects, affecting the observers' ability to find animals. These included the amount of cloud cover, amount and intensity of sun glare, and variation in sea state. Cloud cover changes were considered to have a minimal effect on viewing conditions, and transects were conducted in low sun glare conditions as much as possible. Since animal abundance was not estimated from line transects in this study, the effects of variability in cloud cover and sun glare were not examined in this analysis.

However, it was clear in the field that an increase in sea state had a significant impact on sightings, especially because observers were working from a low platform of only 2 – 2.5 m above sea level. Although the majority of transects were completed in fair to good sea states (mean, median and mode = 1), the average sea state on transect legs ranged from Beaufort 0 to 3.5. To assess the actual survey effort and determine the buffer width for transects, the effect of sea state on sightings was explored further.

Distance from transect line to sightings

To measure the buffer width of the transect lines, it was necessary to determine how far from the transect line the observers were able to sight animals. The results of measured distances to sightings are summarized in Table 3.3.

Table 3.3 Summary statistics for perpendicular distances from the transect line, or break point, to the sighting location for each species.

			Distance (km)		
Species	*N*	*Min.*	*Max.*	*Mean*	*S.D.*
Blainville's beaked whale	16	0.00	4.88	1.09	1.13
Unknown *Mesoplodon* spp.	1	0.74	0.74	0.74	0.00
Cuvier's beaked whale	3	0.75	2.40	1.54	0.78
Sperm whale	7	0.16	2.32	1.33	0.75
Dwarf sperm whale	33	0.00	1.87	0.58	0.48
Pygmy sperm whale	2	0.24	0.38	0.31	0.10
Short-finned pilot whale	1	2.23	2.23	2.23	0.00
Risso's dolphin	1	4.69	4.69	4.69	0.00
Pan-tropical spotted dolphin	2	0.74	0.89	0.81	0.12
Atlantic spotted dolphin	7	0.45	1.32	0.85	0.32
Atl. bottlenose dolphin	9	0.01	1.51	0.55	0.53
Unknown sm. cetacean	3	0.82	0.92	0.89	0.06
All sightings	85	0.00	4.88	0.87	0.82

The distance from the transect line to animals sighted was generally less than 1 km, with an overall mean distance of only 0.87 km (n = 85, median = 0.75 km, S.D. = 0.82), but the range in sighting distances was large due to two outlying data points (Figure 3.4). These included a group of Blainville's beaked whales sighted at 4.88 km from the transect line, and a group of Risso's dolphins sighted at 4.69 km. When the distance data were divided into two datasets, one with and one without the outlying points, neither datasets were distributed uniformly (with outliers: n = 85, KS = 0.1644, p < 0.001; without outliers: n = 83, KS = 0.1027, p = 0.0304). There was also no significant difference between the two dataset means (Wilcoxon rank sum test, Z = 0.2617, p = 0.7935). Further analysis of the factors contributing to the outlying data points was conducted to determine whether or not to exclude them from the dataset when choosing the buffer width.

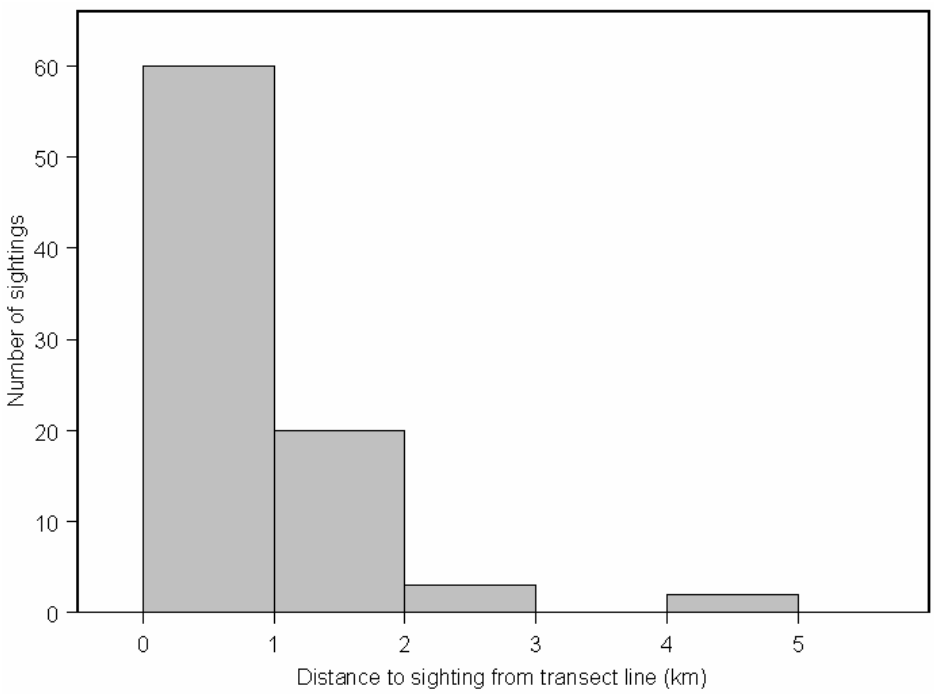


Figure 3.4 Frequency histogram plot of the distance from the transect line to sightings showing the outlying data.

Effect of sea state on distance to sightings

The effect of sea state on the distance at which animals were sighted during line transect surveys was found to be less than expected based on field experience. The distance to sightings and sea state were not correlated (r = -0.12), as shown in Figure 3.5. The negative correlation, although still weak, became slightly stronger once the two outlying data points were removed from the dataset (no outliers: r = -0.29).

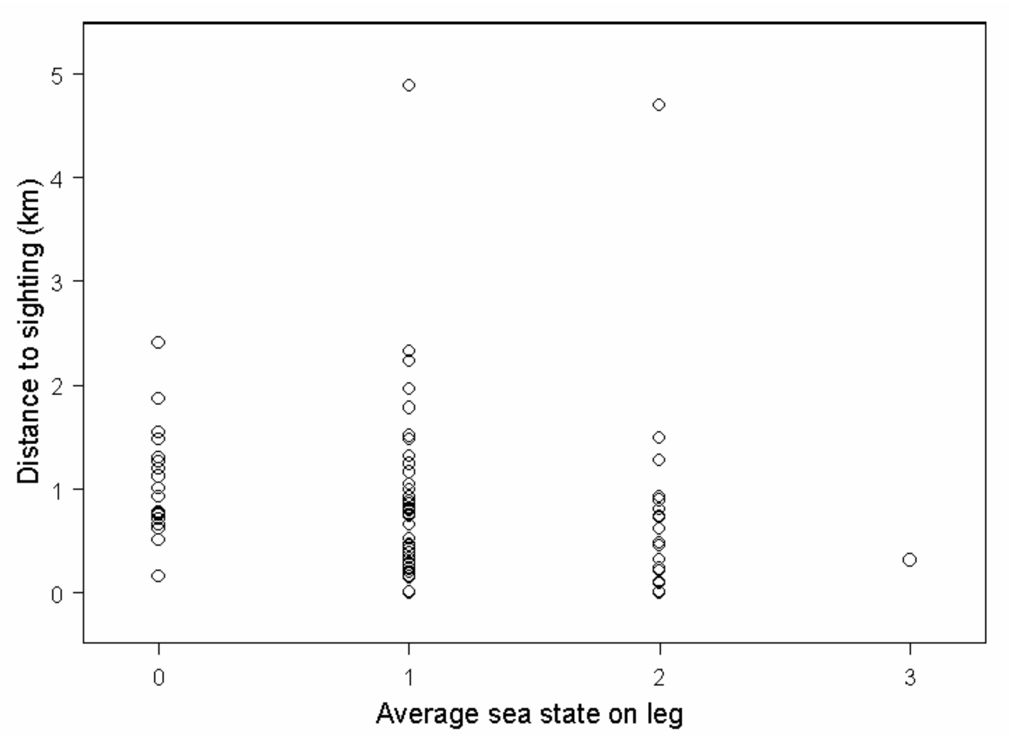


Figure 3.5 Scatter plot of the distance from the transect line to each sighting in the average Beaufort sea state conditions on each transect leg. Data are presented for all sightings data, including the two outlying data points.

Other factors affecting distance to sightings

Other factors were investigated to determine their influence on the distance at which cetaceans were sighted, to help explain the outlying data points. These included the size of the animals and the group size. Figure 3.6 shows how species were categorized based on body length into six groups and plotted by increasing size. Animal size was weakly correlated to the distance to sightings (*r* = 0.27). However, since both Blainville's beaked whales and Risso's dolphins are classified here as medium-sized animals, these findings do not explain why the two data-points became outliers.

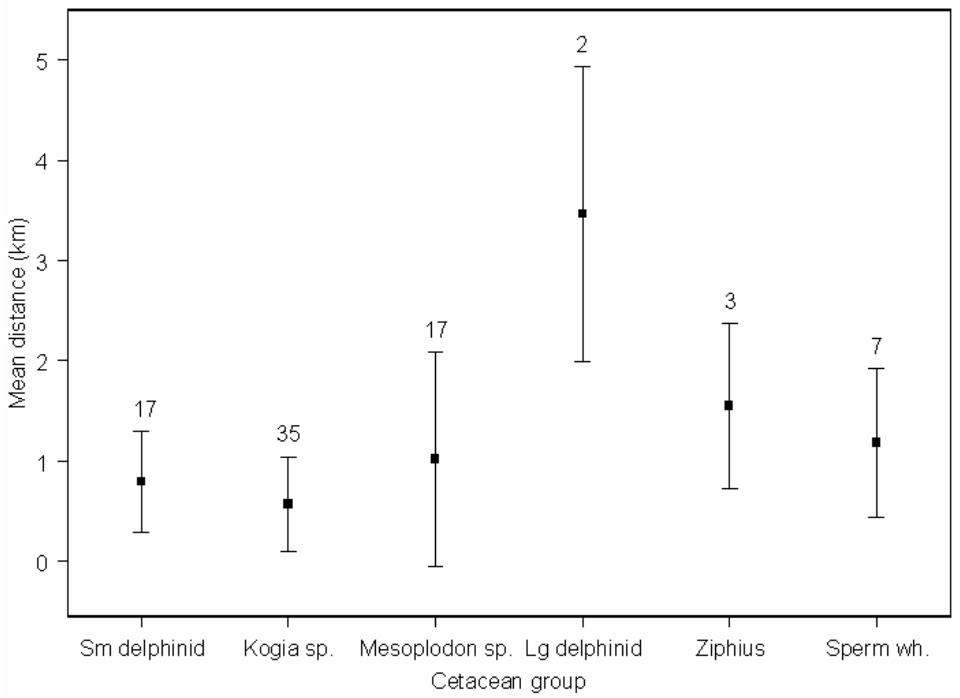


Figure 3.6 Scatter plot with error bars of the mean perpendicular distance from the transect line to sightings for different cetacean groups ordered by increasing size of animals. The number of sightings for each group is given above the error bar. Error bars show standard deviations.

Group size was found to have a significant influence on the distance at which the groups were sighted from the transect line (Wilcoxon rank sum test, $Z = 9.3964$, $p < 0.001$). However, there was no significant difference between beaked whale group sizes and other species (Wilcoxon rank sum test, $Z = 0.3860$, $p = 0.6995$).

Since the Risso's dolphin sighting was one of the larger groups encountered during the study, these findings help to explain why this group was sighted at 4.69 km. Moreover, the sea state conditions at this sighting location were Beaufort 0, further adding to the distance at which the group was seen resulting in this outlying data point.

Field observations showed that the behaviour of the group affected the sighting distance as well, illustrated by a group of breaching Blainville's beaked whales that was sighted at 4.88 km away from the transect line, resulting in the second outlying data point. However, this was the only time that beaked whales were seen breaching during the entire study, suggesting this is an uncommon behaviour for beaked whales in the area.

Effect of sea state on sighting rate

Analysis of the effect of sea state on sighting rates showed that the number of sightings during transects was strongly correlated negatively to sea state conditions (r = -1.0), as illustrated in the plot in Figure 3.7. As the average sea state on a transect leg increased, the number of sightings on the leg decreased. The strong correlation indicated the need to consider sea state conditions when determining the buffer width.

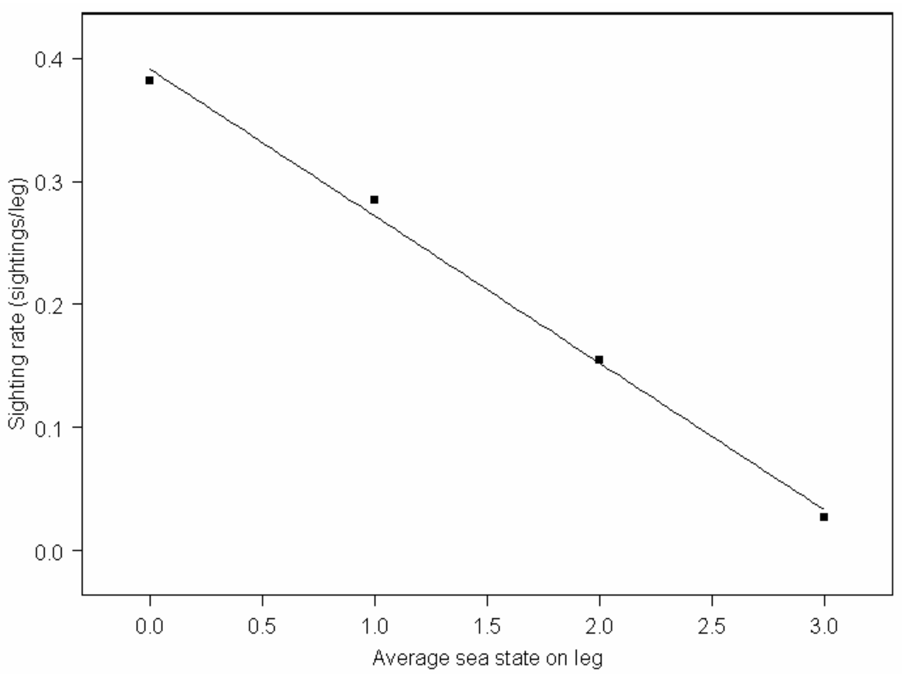


Figure 3.7 Plot shows the negative relationship between the number of sightings on a transect leg and average sea state conditions (Beaufort scale) on the leg.

CALCULATING SURVEY EFFORT

Determining buffer widths

Analysis of the factors that affected sightings indicated that an increase in sea state had the most significant effect; so buffer widths were determined by the distance to sightings in the four different sea states (Beaufort 0 – 3). The frequency histogram plot in Figure 3.4 was reproduced as a stacked bar plot (Figure 3.8), in which distances were categorized in bins to the nearest 0.5 km and the number of sightings in each sea state was included in the plot. The data was then truncated at 2.5 km to remove the outlying data points as recommended by Buckland *et al.* (1993).

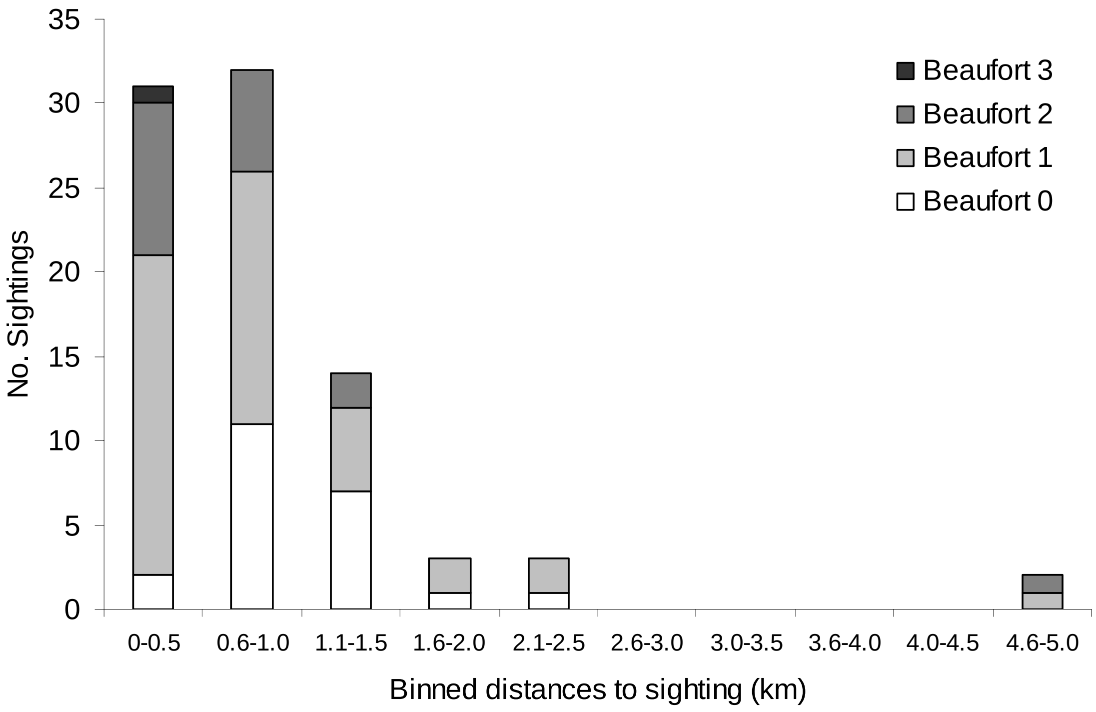


Figure 3.8 The number of sightings and binned perpendicular distances to sightings in varying sea states.

Instead of using a single buffer width for all transect lines completed during the study period, the appropriate buffer width was conditional on the sea state conditions averaged over each individual leg. This method of choosing buffer widths provided an accurate representation of the conditions in which surveys were conducted, ensuring that the estimation of survey effort was not over-estimated if sea states were higher than the overall average, or under-estimated if sea states were lower than average.

To do this, the data was truncated again but this time for each sea state separately (Table 3.4). The truncation points were also the maximum distance to sightings in each sea state which allowed inclusion of all sightings without over-estimating the survey effort.

Table 3.4 Buffer widths were chosen based on truncating data for each Beaufort sea state. Maximum sighting distances show the large decline with increasing sea states.

Beaufort sea state	Buffer width chosen (km)	Max. distance to sighting (km)	Species sighted at max. distance
0	2.50	2.40	Cuvier's beaked whale
1	2.50	2.32	Sperm whale
2	1.50	1.49	Cuvier's beaked whale
3	0.50	0.31	Dwarf sperm whale

The final analysis conducted when determining the survey effort was to compare the sighting data for beaked whales to other species to test if the buffer width chosen biased comparative analyses of habitat use (see Chapter 4) between these groups by over- or under-estimating effort for other species. Mean distance to sightings of beaked whales was not significantly different from other species (Wilcoxon rank sum test, $Z = 1.6541$, $p = 0.0981$), which suggests that the effective strip widths chosen should not bias the survey effort for beaked whales.

Measuring survey effort

Survey effort was determined by calculating the area that was covered within each grid cell by the buffer width for each transect run. Total effort was calculated by totalling the area covered for all transects in each grid cell during the study period. Survey effort was not uniformly distributed across all grid cells (Kolmogorov-Smirnov Goodness of Fit test; $n = 311$, $KS = 0.0963$, $p < 0.001$), with total effort within each grid cell ranging substantially from 0.0002 to 58.1521 km^2, with a mean of 29.27 ($n = 311$, median = 30.67, SD = 19.01). The variability in effort shown in the frequency histogram plot in Figure 3.9, demonstrates that the majority of grid cells had the least amount of effort.

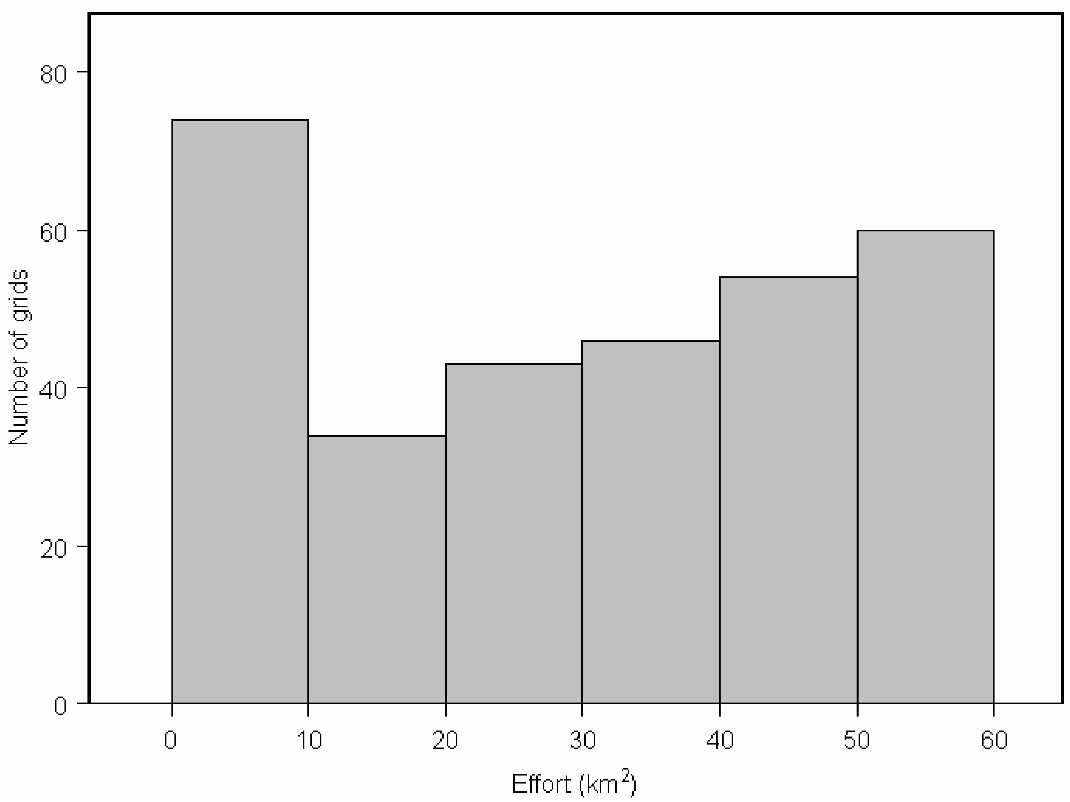


Figure 3.9 Frequency histogram plot for effort in all grid cells throughout the survey area.

Despite the fact that only completed transects were included in the analysis, there was not equal effort throughout the survey area. The disparity in survey effort (Figure 3.10) was only partly due to the fact that the varying sea state conditions were considered when calculating effort. Most of the survey effort is shown as being concentrated in the centre of the transect grid because the overlap between buffered transect legs at the end of each leg was eliminated (not added together). However, effort was more heavily weighted in the northern part of the survey area due to lower sea state conditions found more consistently in this area.

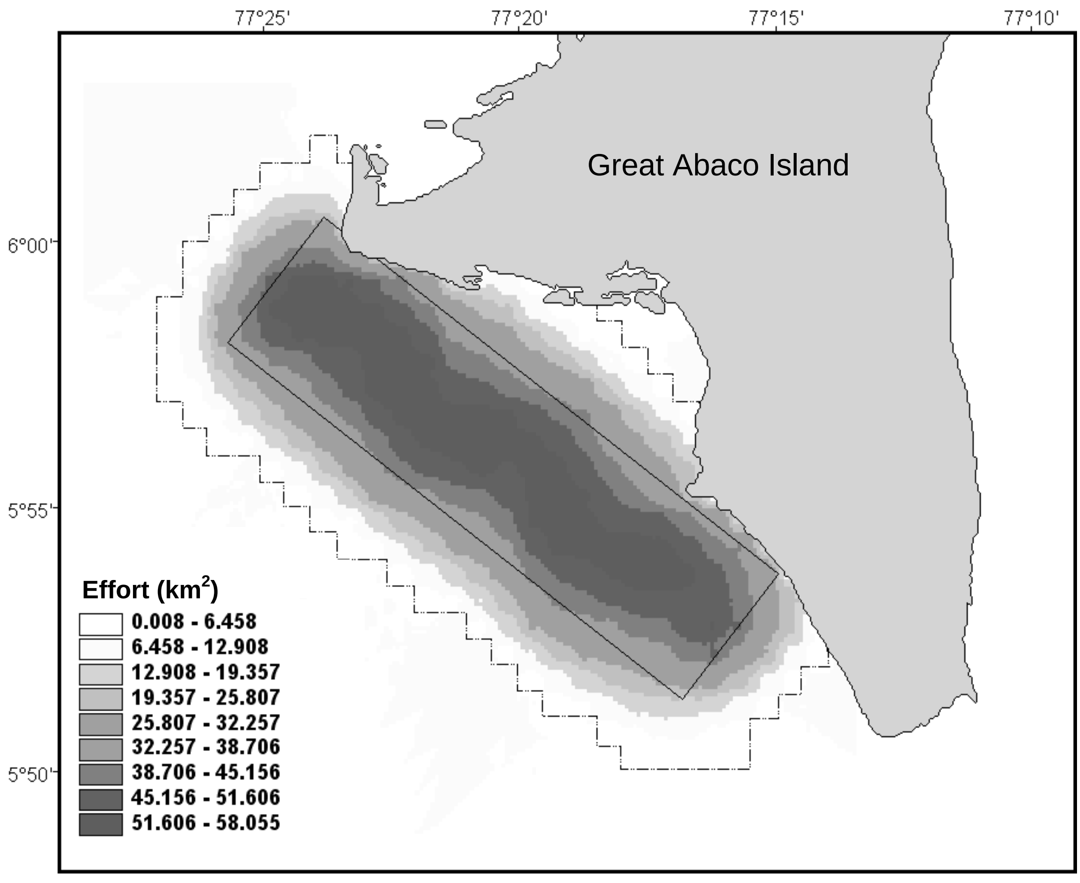


Figure 3.10 Total survey effort mapped using Arcview Spatial Analyst to interpolate effort data. Effort is measured by the amount of area within a grid covered during each transect and totalled over the study period in each grid. Units of effort are the amount of area surveyed in km^2. The dashed line shows the outer boundary of the effort grids and the solid line shows the transect grid.

DISCUSSION

It was necessary to determine survey effort during the study period to calculate sightings per unit effort (SPUE) for each species which is presented in Chapter 4. SPUE values allow an assessment of habitat selection where higher SPUE values are indicative of areas most often utilised and are useful to develop policies for resource assessments (e.g. US Navy Marine Resource Assessment for the Puerto Rico/St. Croix Operating Area (2002)).

However, SPUE values should be regarded cautiously when referring to beaked whales. Field studies of beaked whales are particularly challenging, primarily due to problems with visually detecting them at sea. The reasons for the difficulty in sighting beaked whales include their deep diving behaviour, their behavioural response to approaching vessels and their lack of surface behaviours (Barlow 1999).

Beaked whales dive for extended periods of time. Maximum dives of up to 70 minutes in duration have been recorded for northern bottlenose whales and 87 minutes for Cuvier's beaked whales using suction-cup attached time-depth recorder/VHF radio tags (Hooker and Baird 1999, Baird *et al.* 2004). Although there is some question as to the reliability of these data, similar dive times have been noted from surface observations of Blainville's beaked whales in The Bahamas (BMMS, unpublished data). In between these deep foraging dives, beaked whales generally spend only 2-3 minutes at the surface (Barlow 1999), so the amount of time available for visual detection is minimal.

Beaked whales are also known to be shy, evasive whales. Often as a vessel approaches, the whales show avoidance by diving (Heyning 1989), making it extremely difficult to identify the group to the species level (Barlow

1999). The fact that small vessels were used during this study, as opposed to large, expensive survey ships, and that distance sampling was not one of the objectives, the survey vessel was able to spend more time with each group of whales. If the whales dove as the vessel approached, the vessel could better justify remaining in the area and often waited for the whales to resurface, allowing opportunity for photo-identification and confirmation of the species. Cuvier's beaked whales were more likely to show avoidance behaviour, while Blainville's beaked whales often approached the vessel closely. Shallenberger (1981) described similar close encounters with Blainville's beaked whales in Hawai'i. This implies a difference in "catchability" of these two species in the study area.

A disadvantage of surveying from a smaller vessel, however, is the lower height of the observers, which was only 2 – 2.5 m above sea level during this study. Beaked whales seldom display surface active behaviours, further adding to the problem of detection, especially from a low platform. They are very inconspicuous when they are at the surface; they rarely breach (breaching was seen once during this study) or perform other percussive surface behaviours that create a splash.

It is for these reasons that the sea state conditions during surveys are so strongly correlated with the sighting rate ($r = -1.0$, in this study). Sighting rates were significantly higher during line transect surveys than during opportunistic vessel surveys ($p < 0.05$, Chapter 2) because line transects were conducted only in sea states less than Beaufort 3. But even in these relatively ideal conditions (compared to average ocean conditions), the maximum perpendicular distance to sightings from the transect line was more than 2 km less between Beaufort 3 to Beaufort 0 conditions, while distances in Beaufort 0 and 1 conditions were almost equal (Table 3.4).

To increase the chances of findings these cryptic species, visual surveys for small and medium sized beaked whales should only be conducted in Beaufort 0 – 1 conditions, even from large survey ships. As this is generally not practical, the number of sightings of beaked whales during surveys is always relatively low compared to other species of similar size (Barlow 1999) which compromises some analyses such as abundance estimates and SPUE values.

Survey effort appeared to be concentrated in the centre of the transect grid and was reported to be low near the outer perimeter of the transect grids (Figure 3.10). However, transects lines extensively covered the entire transect grid (see Figure 2.6 in Chapter 2), so survey effort should be relatively equal, given the same sea state conditions throughout the grid. This disparity is because when buffer widths were applied, buffers from adjacent legs were not overlapped at the bounce points (at the end of each leg). To assess the significance of this bias, effort would need to be recalculated with overlapping buffers and the SPUE values corrected accordingly. An alternative method would be to use transect length as the effort measure and include sea state (as well as animal size, and group size) as additional explanatory variables.

CHAPTER FOUR

DISTRIBUTION AND HABITAT USE OF BEAKED WHALES OFF GREAT ABACO ISLAND

INTRODUCTION

In this chapter I examine the distribution and habitat use of beaked whales off Great Abaco Island. To characterise habitat selection, univariate analyses using line transect data were done for both fixed physical variables (depth, slope and distance from land) and surface environmental variables (sea surface temperature). Habitat use is compared between beaked whale species and other cetaceans sighted, as well as between different age classes.

Specific objectives in this chapter include:

1) To generate spatial distribution plots for beaked whales and other species using sightings data from line transect surveys.
2) To calculate sightings per unit effort (SPUE) values for each species.
3) To test if group size affected habitat selection in beaked whales.
4) To examine habitat selection of beaked whales relative to both fixed physical and surface environmental variables.
5) To compare beaked whale distribution relative to other species.
6) To compare results derived from line transect and opportunistic data.
7) To compare habitat use of different age classes of Blainville's beaked whales.

METHODOLOGIES

FIELD WORK

Line transect surveys were run off the southwestern coast of Great Abaco Island from 2000 – 2002 as shown in Figure 4.1, covering 2,270 km with 82 cetacean sightings (Table 2.3)

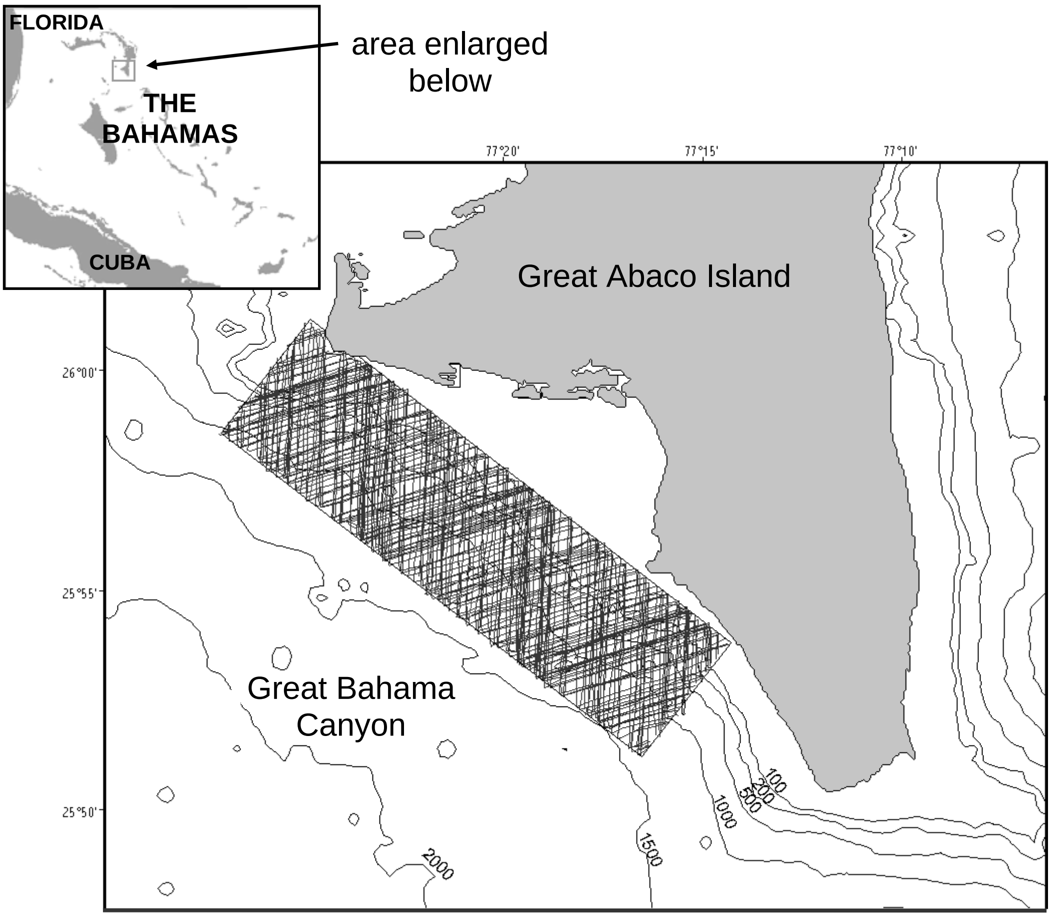


Figure 4.1 Combined tracks for all completed line transects off the southwest coast of Great Abaco Island from 2000-2002. Isobaths are shown in metres.

Sightings data were also derived from opportunistic vessel surveys in the same area from 1997 – 2002, totalling 36,940 km and 694 sightings (Table 2.2). When possible, only the transect data were used for analyses because effort has been stratified by sea state for these surveys as described in

Chapter 3. However, opportunistic sightings data were combined with transect data when it was necessary to increase the sample size to perform statistical analyses and for a comparison to be made between the two survey types. (The field methodologies employed during this study are described in detail in the Methodologies section of Chapter 2.)

DATA PROCESSING

Line transect and sightings data were processed using ESRI ArcView GIS 3.2 (ESRI Inc.). For a detailed description of how this processing was done, as well as how survey effort was calculated, refer to the Methodologies section of Chapter 3.

Photographic data

Photographic data collected during encounters with Blainville's beaked whales from 1997 – 2001 was analysed to examine the differences in habitat use between different age and sex classes. Based on characteristics distinguishing different age and sex classes (see Figure 2.4, Chapter 2), individuals were separated into five age classes: 1) adult males, 2) adult females, 3) sub-adult males, 4) unknown immature animals and 5) juveniles or calves. In the comparative habitat analysis, "adults" refer to both adult males and females, while "sub-adults" include individuals from the sub-adult male and unknown immature age classes (not juveniles and calves). Sightings data was plotted for adults and subadults and the habitat characteristic of each age class was explored.

During line transect surveys, if several groups of whales were seen on the same or adjacent transect legs, photographs were analysed (as described in

Chapter 2) to determine if these groups contained the same individuals. This occurred four times during the study. Photographic analysis confirmed that the survey vessel had sighted the same group of whales on three different occasions during a single line transect, including groups of pygmy sperm whales, sperm whales and Blainville's beaked whales. However, on one occasion the photo-analysis showed that a second group of Cuvier's beaked whales sighted on an adjacent transect leg contained different individuals. Resightings of the same groups during a single transect were not included in the habitat selection analysis.

Environmental variables

Environmental variables used in this study consisted of fixed physical parameters (depth, slope and distance from land) and surface environmental data (sea surface temperature). Variables used in the analysis were derived from remote sensing data and data collected in the field. Bathymetry data were taken from 4 different sources because each provided additional information. These included: US Naval Oceanographic Office (NAVOCEANO) Digital Bathymetry Database Variable Resolution (DBDB-V) data, Sandwell & Smith satellite altimetry and ship depth soundings data (see Smith and Sandwell, 1997 for details), British Oceanographic Data Centre's General Bathymetric Chart of the Oceans (GEBCO) data, and BMMS soundings data collected by the survey vessel in the field. Both the DBDB-V and Sandwell & Smith datasets included remote sensing data at 0.5 and 2 minute resolution, respectively. The BMMS dataset was limited by the 200 m maximum depth limit of the sounder.

These four datasets were combined into one text file and imported into ArcView as an event theme and the surface was then interpolated using ArcView Spatial Analyst at a cell size of 500 m to generate classified bathymetry for the study area. The interpolation method used was the Inverse Distance Weighting (IDW), which assumes each point has a local influence that diminishes with distance. Although the resolution of the resulting bathymetry data was good, the accuracy of some of the data was questionable. In some locations, particularly along the edge of the canyon wall, the vessel's depth sounder was unable to detect the bottom, signifying the depth was greater than 200 m, while the bathymetries generated from the GIS mapping showed the depth to be less than 200 m. Since statistical analyses would not be possible if sightings at these locations were removed from the dataset (making sample sizes even smaller), the combined bathymetry data was used despite this uncertainty because it was the only information available.

Slope was obtained by using the "Derive Slope" function in ArcView Spatial Analyst. Slope is defined as the maximum rate of change in depth from each cell to its neighbours. All views were projected using the Mercator projection, which consists of straight, equally spaced meridians and parallels that intersect at right angles. This scale is true at the equator but distortion increases closer to the poles. However, the study area (26º N) was deemed to be located close enough to the equator for the amount of distortion to be considered negligible.

To describe the different habitat types, the study area was divided into 1 km^2 grid cells, resulting in 311 grids as shown in Figure 3.2 (Chapter 3). Each grid cell was assigned mean depth and slope values, which were generated by using the "Summarize zones of analysis" function in ArcView Spatial Analyst and then exported as text files for statistical analysis. To calculate the distance from each grid cell to land, the latitude and longitude of the centre point of each grid was determined using the CTD function in ArcView. These centre points were converted to a new point theme, and the distance to land from each grid's centre was then calculated using the Animal Movement extension and exported as a text file for analysis.

The environmental variables for each of the three fixed physical parameters (depth, slope and distance from land) were also generated for each sighting location to examine each species' habitat selection relative to the habitat available in the study area, and for interspecies habitat comparisons. For these comparisons, parameters at the sighting location were used instead of the mean value in the grid cell where the sighting occurred. Track lines run during opportunistic surveys were not processed (in the same way as transect lines), so this was the only way to include sightings during opportunistic surveys in some analysis to increase sample size. Additionally, surface environmental data (sea surface temperature) were measured at sighting locations for interspecies comparisons.

Remote sensing data for variable environmental data was limited, making it impossible to assess beaked whale habitat preferences relative to frontal zones. The finest resolution available for SeaWiFS data on chlorophyll *a* concentrations was 6 km^2, which was not on the same scale as the rest of the data used. Furthermore, the SeaWiFS data were patchy spatially and temporally in the study area. The resolution of the data available for sea surface temperature data was better, but the coverage was limited by cloud cover, especially in summer months. For these reasons, these data could not be included in this study.

ANALYTICAL METHODS

Statistical analyses

Statistical analyses were performed using standard tests available in S Plus 2000 Professional Release 2 (MathSoft, Inc.) and Microsoft Excel 97 SR-1 (Microsoft, Inc.), and were complemented by exploratory graphics to validate model assumptions.

Sightings per unit effort (SPUE) values were calculated for each grid cell for all species found within the study area during line transect surveys. This represents the number of groups sighted per area surveyed within each grid cell (sightings/km^2). To display the SPUE values visually, the legend editor was used in ArcView to generate SPUE maps for each species or taxonomic group.

Habitat selection in beaked whales was analysed using sightings data gathered during line transect surveys. Regression analyses were used to test if habitat affected beaked whale group sizes. To examine the relationships between species' distribution and environmental variables, environmental data were summarized for each sighting location and for the effort grids and presented graphically. Statistical analyses were performed using ANOVAs for univariate comparison of the distribution of each cetacean species or group relative to the effort grids, and for interspecies comparisons of environmental variables at each sighting location to test the null hypothesis that each species or taxonomic group had similar distribution.

To examine the distribution of beaked whales relative to other species, two sample *t*-tests were used to compare each variable between species seen during line transect surveys. The same analyses were done for the sightings data from opportunistic surveys for beaked whales and sperm whales. Only beaked whales and sperm whales were included in these analyses (as opposed to all species) to explore sharing and partitioning of habitats between these three species. Univariate ANOVA tests were performed to compare the two survey techniques and to test the null hypothesis that dense-beaked whales of different age classes select the same habitat.

RESULTS

FIELD WORK

The combined vessel tracks for all completed line transects run during the study period are shown in Figure 4.1. Only completed transects were used in the analysis of habitat selection to avoid a bias in the coverage of the transect grid at one end or the other. The map shows how extensively the survey area was covered, but also shows that the survey area only included the waters along the edge of the canyon wall. This bias in survey design must be considered when describing species' distribution and habitat use relative to the entire canyon system.

SPATIAL DISTRIBUTION

There were marked differences in the spatial distribution of the different cetacean species sighted within the survey area. Areas of high use were evident for some species, while others appeared to be more evenly distributed. To visualise these differences, spatial distribution maps were made from sightings during line transect surveys conducted from 2000 – 2002.

The spatial distribution of beaked whales and sperm whales is shown on the plot in Figure 4.2a. Blainville's beaked whale's distribution appears spatially as two loose clusters of sightings, but were primarily concentrated along the canyon wall, in water depths not exceeding 1000 m. Cuvier's beaked whales were found further offshore, near or beyond the 1000 m isobath. Sperm whale sightings were concentrated around the 1000 m isobath, but appeared evenly distributed throughout the offshore waters of the survey area.

Both *Kogia* species were shown on the same distribution plot (Figure 4.2b). Dwarf sperm whales appeared to be evenly distributed throughout the transect grid, but in depths less than 1500 m, and primarily along the canyon wall. There were only two sightings of pygmy sperm whales and both groups were sighted along the canyon wall.

Sightings of all the delphinids found during line transect surveys are shown in the spatial distribution plot in Figure 4.2c. They appeared sparsely distributed across the entire length of the survey area, with the exception of Atlantic bottlenose dolphins which were found only at the north end of the survey area clustered on the edge of the carbonate bank. Both *Stenella* species sighted were grouped because of the small sample size and were found throughout the survey area in both coastal and pelagic waters. Risso's dolphins and short-finned pilot whales (large delphinids) were sighted near the outer boundary of the survey area despite low levels on effort in those regions.

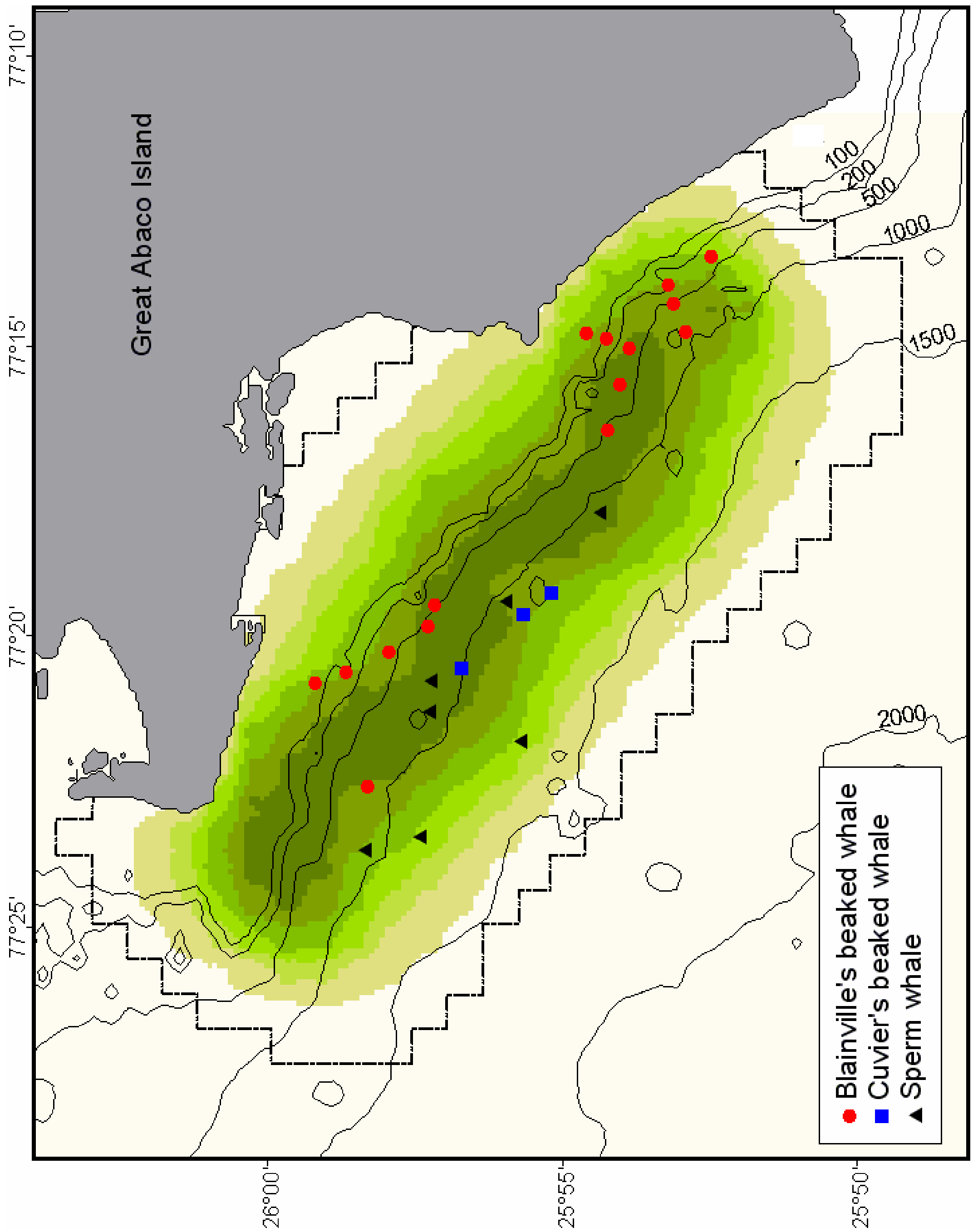


Figure 4.2a Spatial distribution of beaked whales and sperm whales relative to survey effort (shown by the green shading where the darker colour implies more effort). The dashed line shows the outer boundary of the effort grid. Isobaths are in metres.

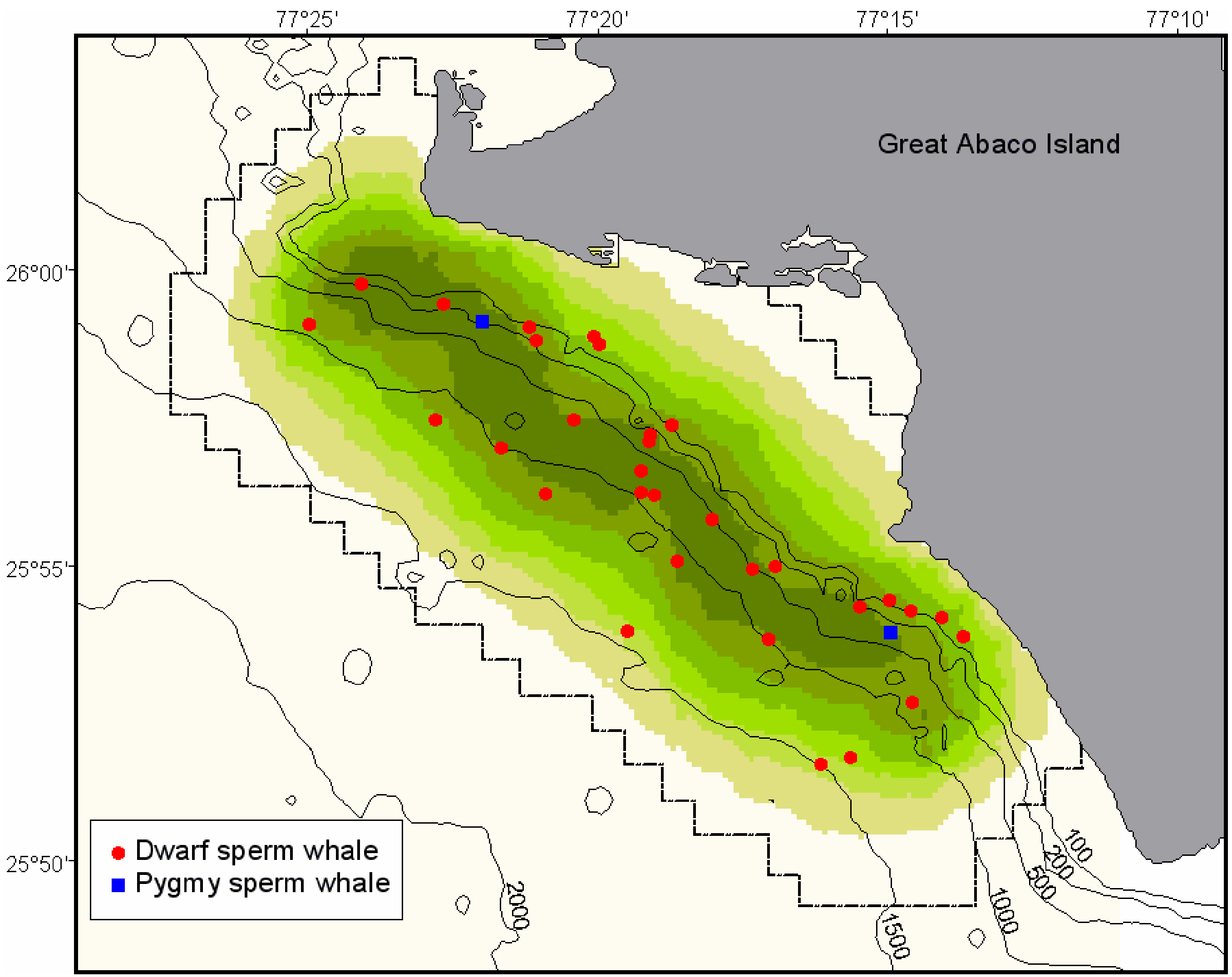


Figure 4.2b Spatial distribution of *Kogia* species relative to survey effort (shown by the green shading where the darker colour implies more effort). The dashed line shows the outer boundary of the effort grid. Isobaths are in metres.

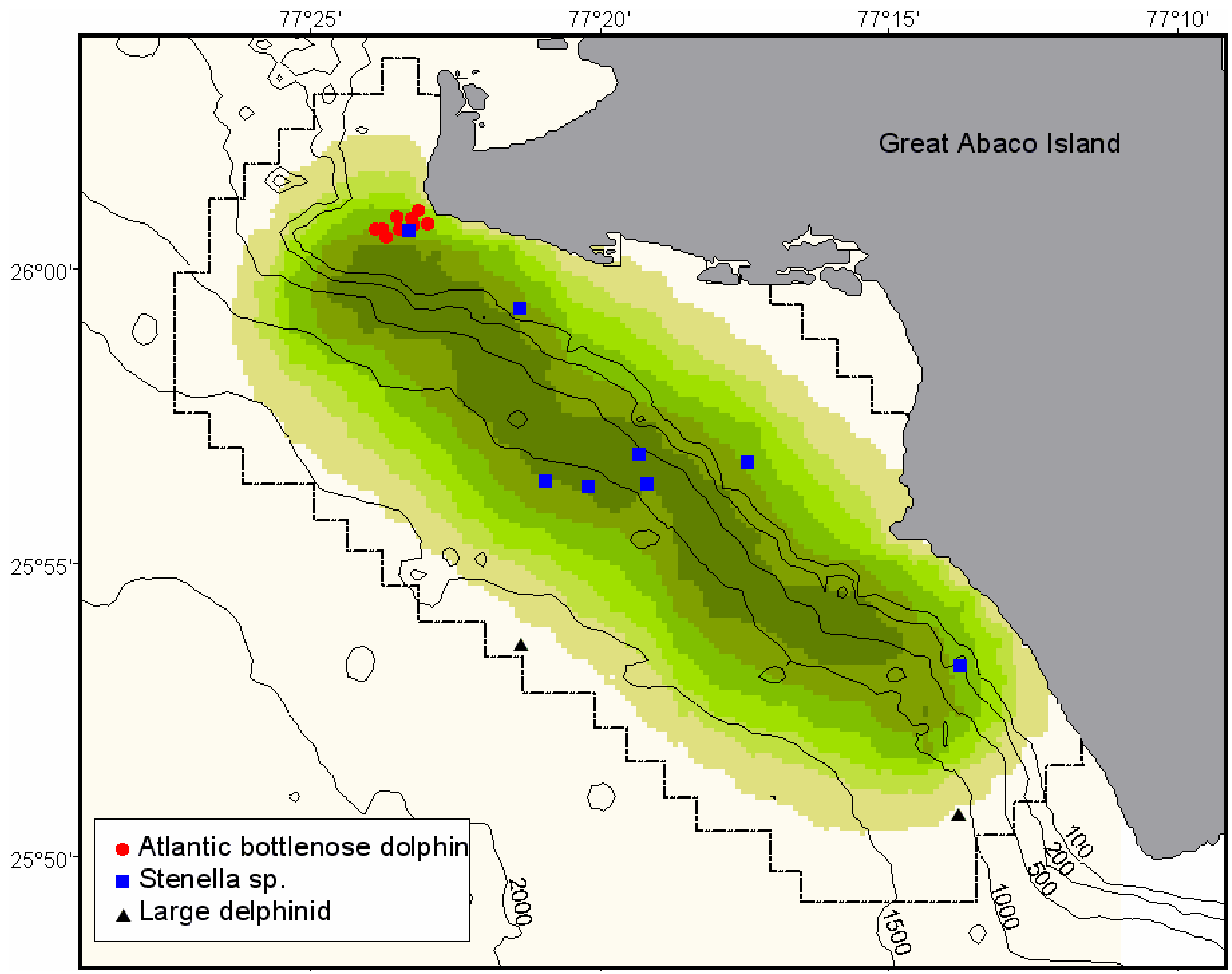


Figure 4.2c Spatial distribution of delphinids relative to survey effort (shown by the green shading where the darker colour implies more effort). The dashed line shows the outer boundary of the effort grid. Isobaths are in metres.

SIGHTINGS PER UNIT EFFORT (SPUE)

Sightings per unit effort (SPUE) values were calculated for each species found during line transect surveys. SPUE is determined by the number of groups sighted per area surveyed within each grid cell (sightings/km^2). Both *Kogia* species were grouped and all oceanic dolphins were combined into one group, due to the small number of sightings of some of these species.

SPUE values ranged by species or cetacean group from 0 to 1.49 with a mean of 0.0017 (median = 0.0008, SD = 0.0021). Beaked whale SPUE values ranged from 0 to 0.02 with a mean of 0.0009 (median = 0, SD = 0.0043). SPUE values were not uniform throughout the survey area for any species or cetacean group sighted during the study, as illustrated in the maps in Figure 4.3.

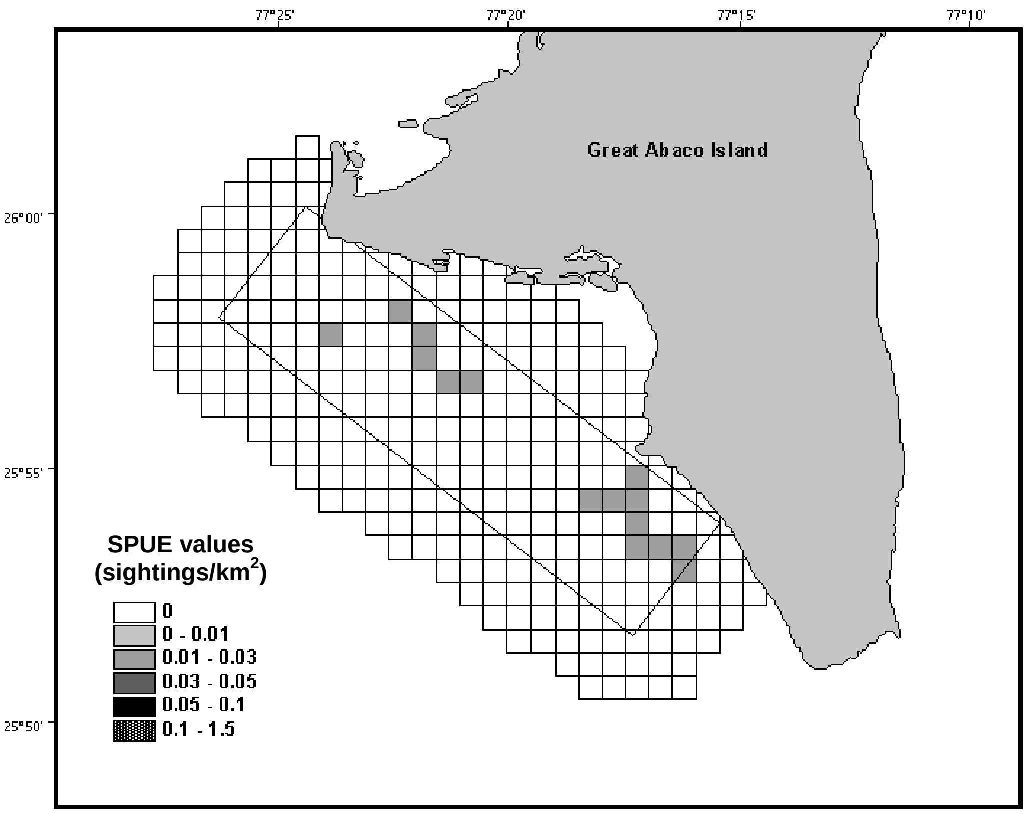


Figure 4.3a Blainville's beaked whale sightings per unit effort throughout the survey area.

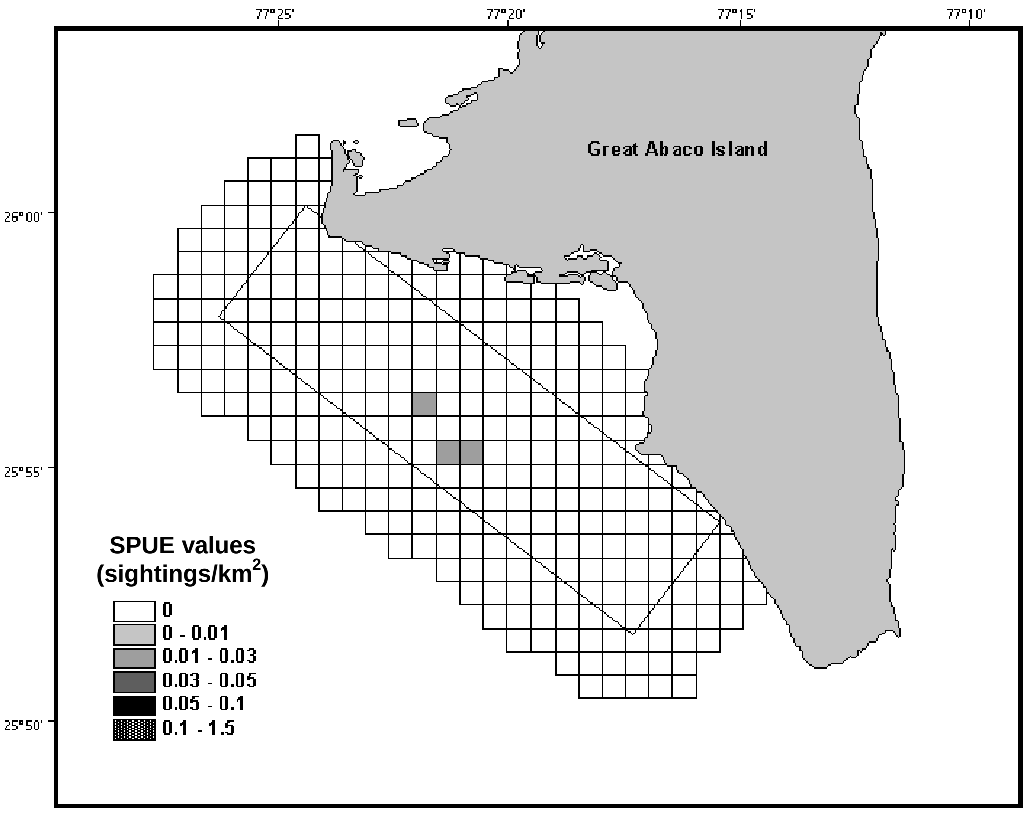


Figure 4.3b Cuvier's beaked whale sightings per unit effort throughout the survey area.

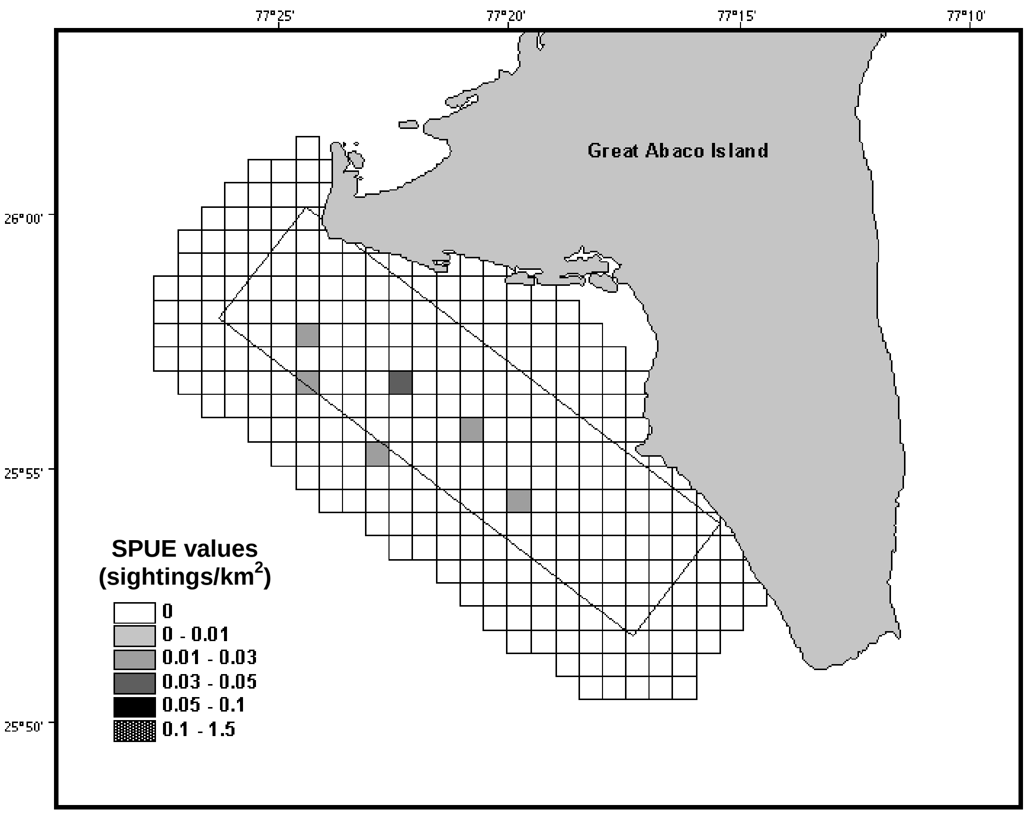


Figure 4.3c Sperm whale sightings per unit effort throughout the survey area.

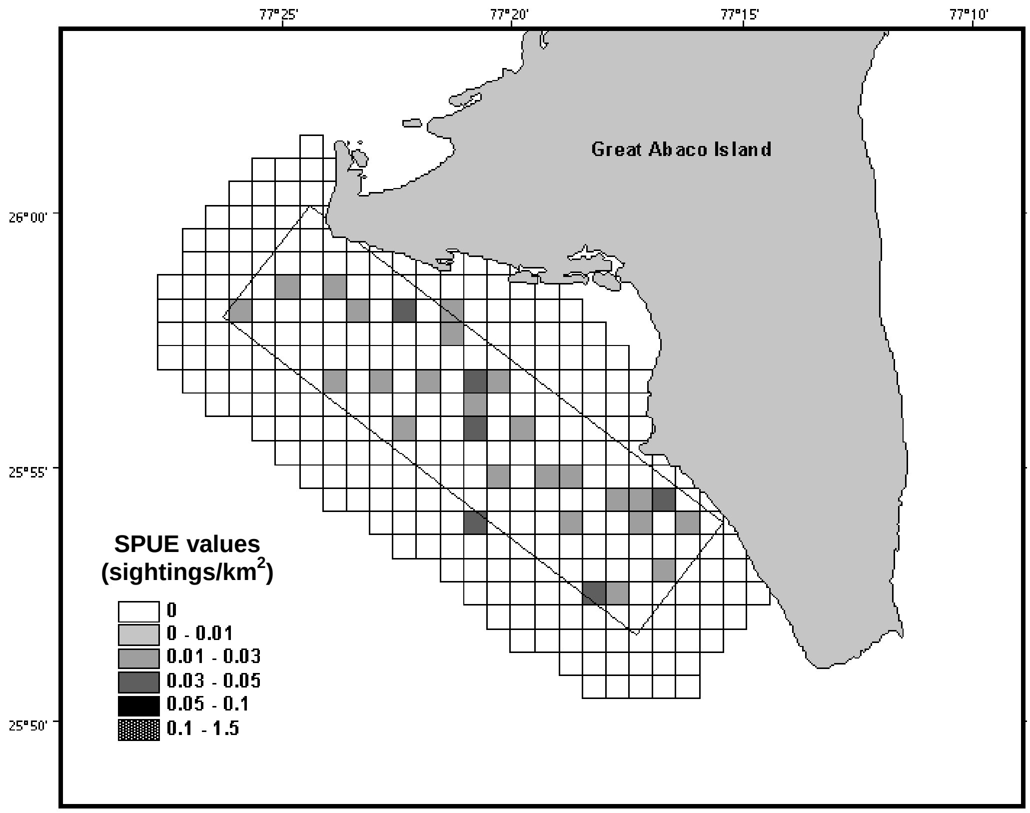


Figure 4.3d *Kogia* sightings per unit effort throughout the survey area.

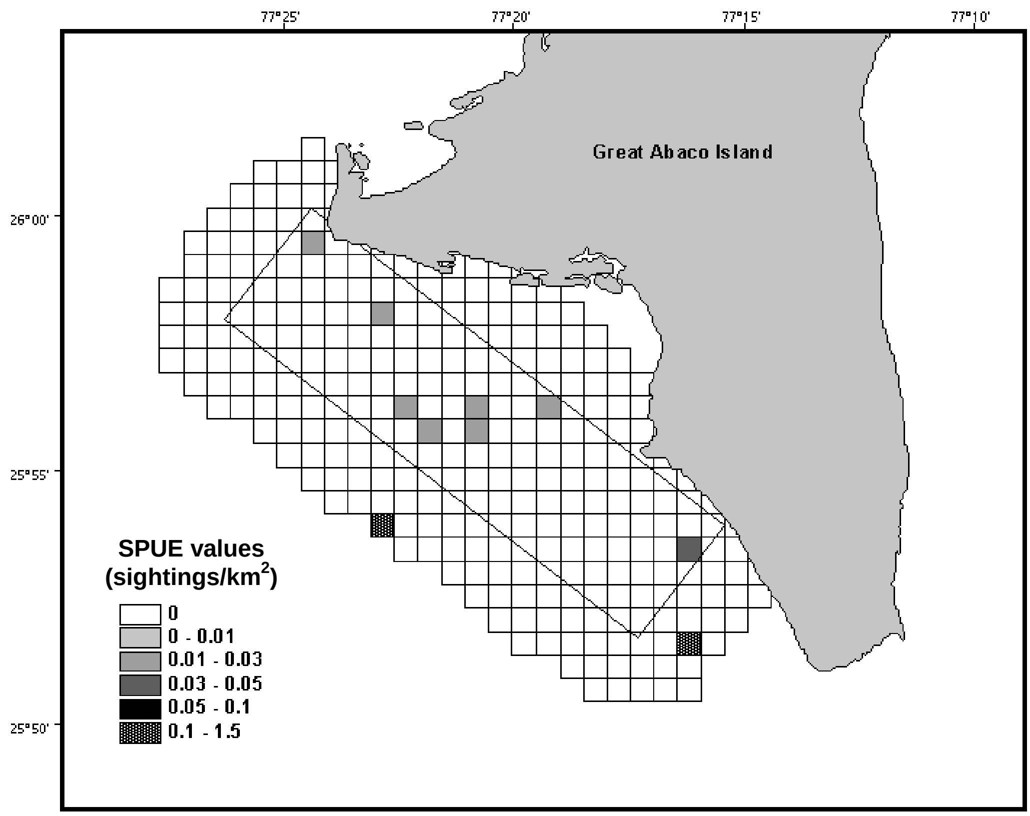


Figure 4.3e Oceanic delphinid sightings per unit effort throughout the survey area.

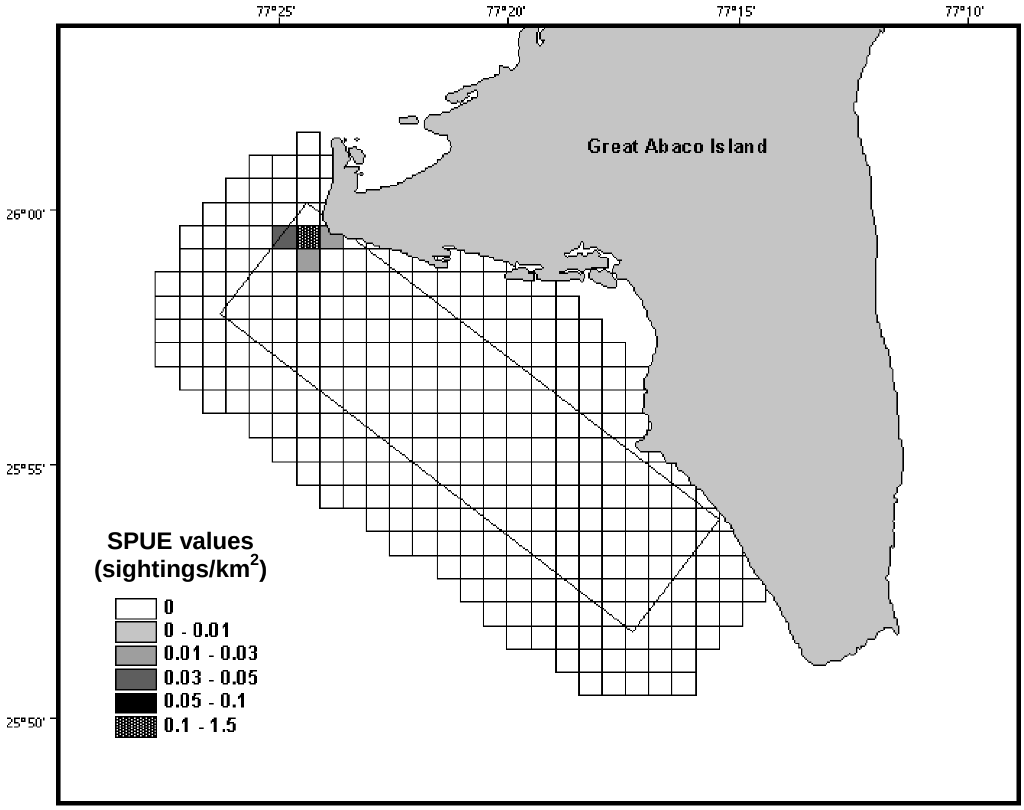


Figure 4.3f Atlantic bottlenose dolphins (coastal ecotype) sightings per unit effort throughout the survey area.

HABITAT SELECTION OF BEAKED WHALES

To explore the habitat selection of beaked whales, fixed physical and surface environmental data were gathered a) at each sighting during line transect surveys and b) in each effort grid, either by direct field observation or by using GIS mapping tools to interpolate depth. These data are summarized for each environmental variable for all species sighted during line transect surveys in Table 4.1. Both *Kogia* species were grouped, and all oceanic dolphins were combined into one group, due to the small number of sightings of some of these species.

Statistical analyses of the datasets were conducted in two ways: analysis was performed for univariate comparison of species' distribution in relation to the environmental variables within the effort grids, and interspecies comparisons were made of the environmental variables at the sighting location.

Table 4.1 Mean and standard deviation (in parentheses) for environmental variables for each cetacean species or group sighted during line transect surveys.

Cetacean species or group	*Depth (m)*	*Slope (°)*	Distance from land *(km)*	*SST (°C)*	*n*
Blainville's beaked wh.	392.8 (282.7)	17.8 (10.7)	3.0 (1.1)	28.3 (1.9)	15
Cuvier's beaked whale	1051.4 (111.0)	12.2 (3.1)	6.9 (0.9)	24.1 (0.6)	3
Sperm whale	1041.8 (171.1)	13.0 (8.8)	5.9 (1.2)	24.6 (0.5)	7
Kogia species	572.2 (489.1)	11.0 (9.6)	4.1 (1.9)	26.5 (3.2)	33
Oceanic delphinids	636.4 (574.9)	8.2 (9.1)	4.7 (3.0)	29.4 (2.3)	11
Atl. bottlenose dolphin	6.4 (3.6)	0.2 (0.6)	1.1 (0.5)	26.0 (2.6)	9
Effort grids	728.9 (738.1)	8.3 (6.4)	4.7 (3.0)	NA	311

Does beaked whale group size affect habitat selection?

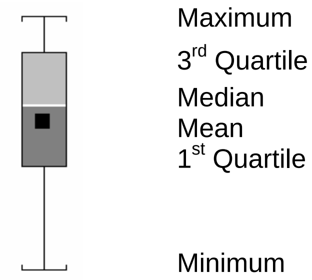
Since sighting locations referred to each group sighted and not the number of individuals present, the analysis conducted thus far has not considered whether or not smaller groups are utilising different habitats than larger groups. To test if habitat selection was affected by beaked whale group size regression analyses were performed and are summarised in Table 4.2. There were no significant relationships found between either Blainville's beaked whale or Cuvier's beaked whale group size and any of the environmental variables for sightings during line transect surveys.

Table 4.2 Summary statistics for regression analyses to test if habitat affected group size of beaked whales.

Species	*Variable*	R^2	*F stat*	*df*	*p value*
Blainville's beaked whale	depth slope distance SST	0.0257 0.2731 0.1643 0.1108	0.3426 4.5080 2.5550 0.9971	13 12 13 8	0.5683 0.0552 0.1340 0.3473
Cuvier's beaked whale	depth slope distance SST	0.1712 0.6582 0.1623 0.8710	0.2065 1.9250 0.1937 6.7500	1 1 1 1	0.7285 0.3976 0.7360 0.2339

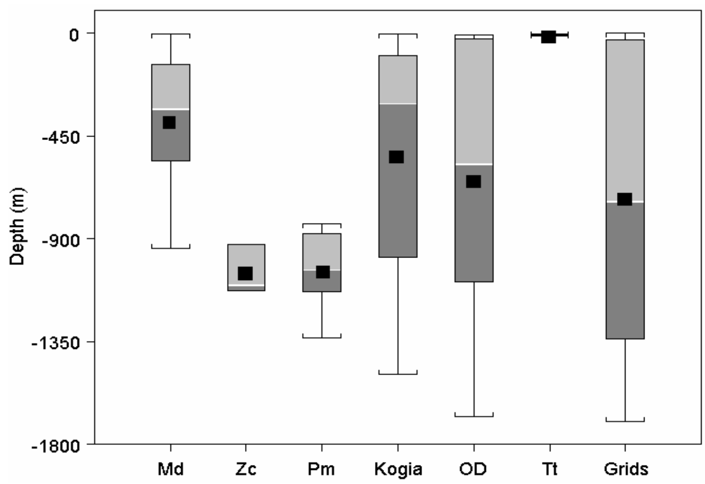
Habitat selection relative to environmental variables

To examine the relationship between each species' distribution and environmental variables, box plots were generated (Figure 4.4) to help visualise the relationships summarized in Table 4.1. These plots show the summary statistics of the environmental variables at the location of each cetacean species or group sighted during line transect surveys and for all effort grids in the survey area. The box plots clearly show variability both between species, and between each species and the effort grids for depth, slope, distance from land, and sea surface temperature.

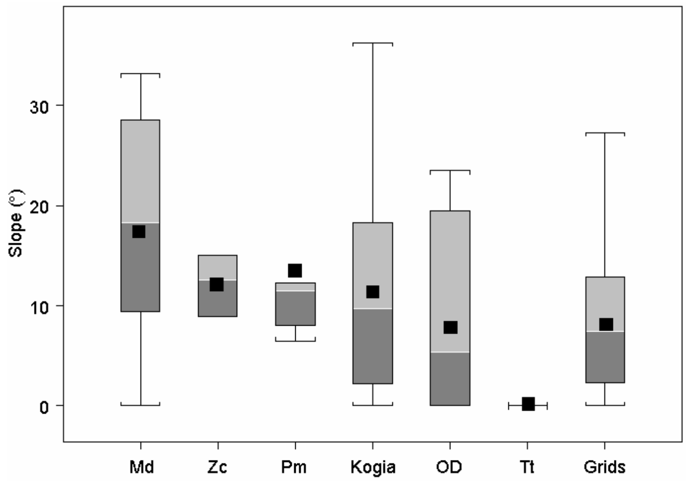


Md = Blainville's beaked whale
Zc = Cuvier's beaked whale
Pm = sperm whale
Kogia = dwarf & pygmy sperm whale
OD = oceanic dolphin
Tt = Atlantic bottlenose dolphin
Grids = effort grids

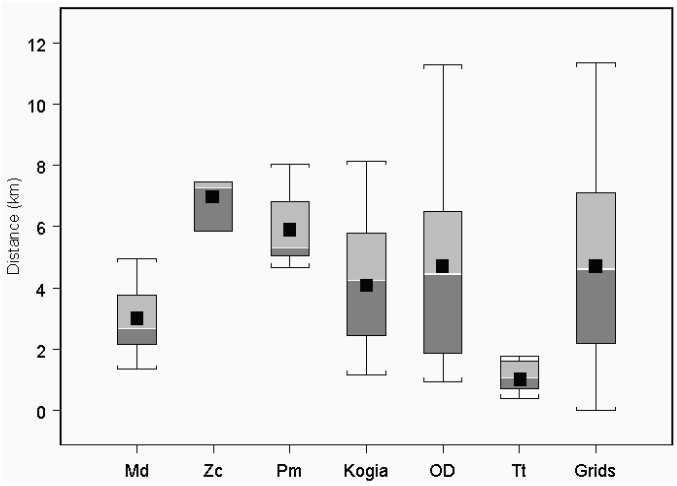
DEPTH



SLOPE



DISTANCE FROM LAND



SEA SURFACE TEMPERATURE

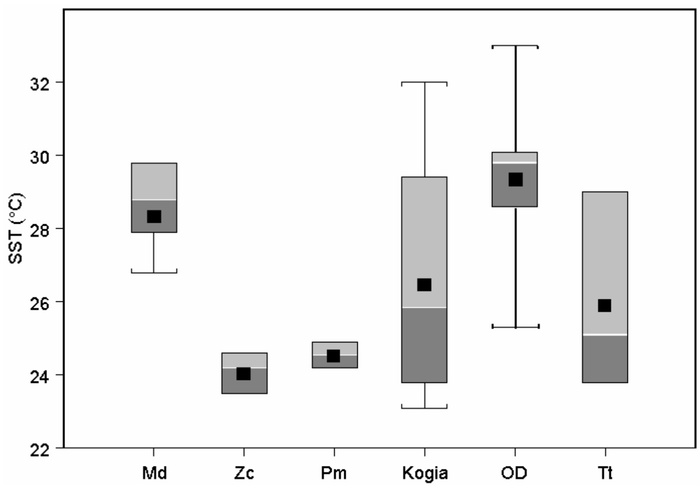


Figure 4.4 Summary statistics of environmental variables for each cetacean species or group sighted during line transect surveys and the effort grids. All variables were derived from GIS mapping, with the exception of sea surface temperature which were actual measurements taken at the sighting location.

To examine the relative importance of the relationships between each species' distribution and environmental variables, univariate ANOVA tests were performed for each cetacean species or group (Table 4.3). These analyses compared the environmental variables at each sighting location during line transect surveys with the values for all grid cells from the study area. Depth, slope and distance to land significantly influenced the distribution of Blainville's beaked whales and bottlenose dolphins (Blainville's beaked whales: $p < 0.05$ for depth and distance and $p < 0.01$ for slope; bottlenose dolphins: $p < 0.01$ for depth, slope and distance), while slope also influenced the distribution of *Kogia* species ($p < 0.05$). None of the variables had a significant effect on the distribution of Cuvier's beaked whales, sperm whales or oceanic dolphins ($p > 0.05$ for all variables).

Table 4.3 Results of univariate ANOVA tests (*p* values) for each cetacean species or group relative to the effort grids. Sightings data are from line transect surveys.

Cetacean species or group	*Depth*	*Slope*	*Distance from land*
Blainville's beaked whale	0.038*	1.3×10^{-7}**	0.026*
Cuvier's beaked whale	0.370	0.298	0.208
Sperm whale	0.185	0.055	0.287
Kogia species	0.162	0.028*	0.268
Oceanic delphinids	0.627	0.967	0.949
Atl. bottlenose dolphin	0.001**	1.9×10^{-4}**	2.5×10^{-4}**

* $p < 0.05$
** $p < 0.01$

Beaked whale distribution relative to other species

To compare differences between the distribution of beaked whales and other species relative to each environmental variable, two-sample *t*-tests were applied (Table 4.4). Bottlenose dolphins did not share the same habitat as either beaked whale species ($p < 0.001$), representing different habitat selection, coastal versus oceanic. Cuvier's beaked whales and sperm whales shared the same habitat ($p > 0.05$, for all variables), but did not select the same habitat as Blainville's beaked whales ($p < 0.01$, for depth and distance from land), although slope was similar ($p > 0.05$) for all three species. Slope and distance from land differed significantly between Blainville's beaked whales and *Kogia* sp. ($p < 0.05$), while depth was similar ($p > 0.05$). The distance of the sighting from land was the only variable that differed between Cuvier's beaked whales and *Kogia* sp. ($p < 0.05$). The oceanic dolphins utilised similar habitat as Cuvier's beaked whales but not Blainville's beaked whales (slope, $p < 0.05$).

Table 4.4 Two sample *t*- test results from line transect surveys for each variable showing relationships between the habitat selection of Blainville's beaked whales (Md), Cuvier's beaked whales (Zc) and all other cetacean species or groups. Values shown are *p* values.

Interspecies comparison	*Depth*	*Slope*	*Distance from land*
Md – Zc	0.0013**	0.3814	0.0000**
Md – Pm	0.0000**	0.3194	0.0000**
Md – Kogia	0.1939	0.0339*	0.0367*
Md – OD	0.1658	0.0247*	0.0597
Md – Tt	0.0005**	0.0001**	0.0001**
Zc – Pm	0.9317	0.8721	0.2493
Zc – Kogia	0.1037	0.8411	0.0191*
Zc – OD	0.2497	0.4855	0.2423
Zc – Tt	0.0000**	0.0000**	0.0000**

* $p < 0.05$
** $p < 0.01$

COMPARING LINE TRANSECT AND OPPORTUNISTIC SURVEYS

Assessing habitat selection from opportunistic surveys

Similar analyses were performed for fixed physical and surface environmental data collected during opportunistic surveys at sighting locations of beaked whales and sperm whales. These data are summarized for each environmental variable and species in Table 4.5. Sperm whales were included in this analysis because interspecies comparisons made using transect survey data showed that sperm whales and Cuvier's beaked whales share habitat (Table 4.4), but these results may have been misleading based on the small samples sizes during line transect surveys for sperm whales (n = 7) and Cuvier's beaked whales (n = 3). Larger sample sizes were obtained during opportunistic surveys (n = 48 and 15, respectively), so it was valuable to run the same analyses again to compare habitat selection between these three species.

Table 4.5 Mean and standard deviation (in parentheses) for all environmental variables for beaked whales and sperm whales sighted during opportunistic surveys. For SST, n = 42 for Blainville's beaked whales, n = 5 for Cuvier's beaked whales and n = 21 for sperm whales.

Cetacean species	*Depth (m)*	*Slope (°)*	*Distance from land (km)*	*SST (°C)*	*n*
Blainville's beaked wh.	583.2 (456.2)	15.2 (10.0)	4.0 (2.3)	26.3 (2.3)	96
Cuvier's beaked whale	1319.2 (432.8)	10.1 (6.7)	7.5 (2.9)	25.7 (2.0)	15
Sperm whale	962.6 (331.3)	13.8 (6.8)	5.6 (1.8)	26.4 (2.2)	48

Although the mean values of each variable for each species differed from the line transect survey results (see Table 4.1), the relative differences between each species are the same for all variables, except sea surface temperature (Figure 4.5). Cuvier's beaked whales were found in greater depths and distance from land than sperm whales, which in turn were in greater depths and distance from land than Blainville's beaked whales. Conversely, Blainville's beaked whales were found in areas with greater slope than sperm whales, which were in areas with greater slope than Cuvier's beaked whales.

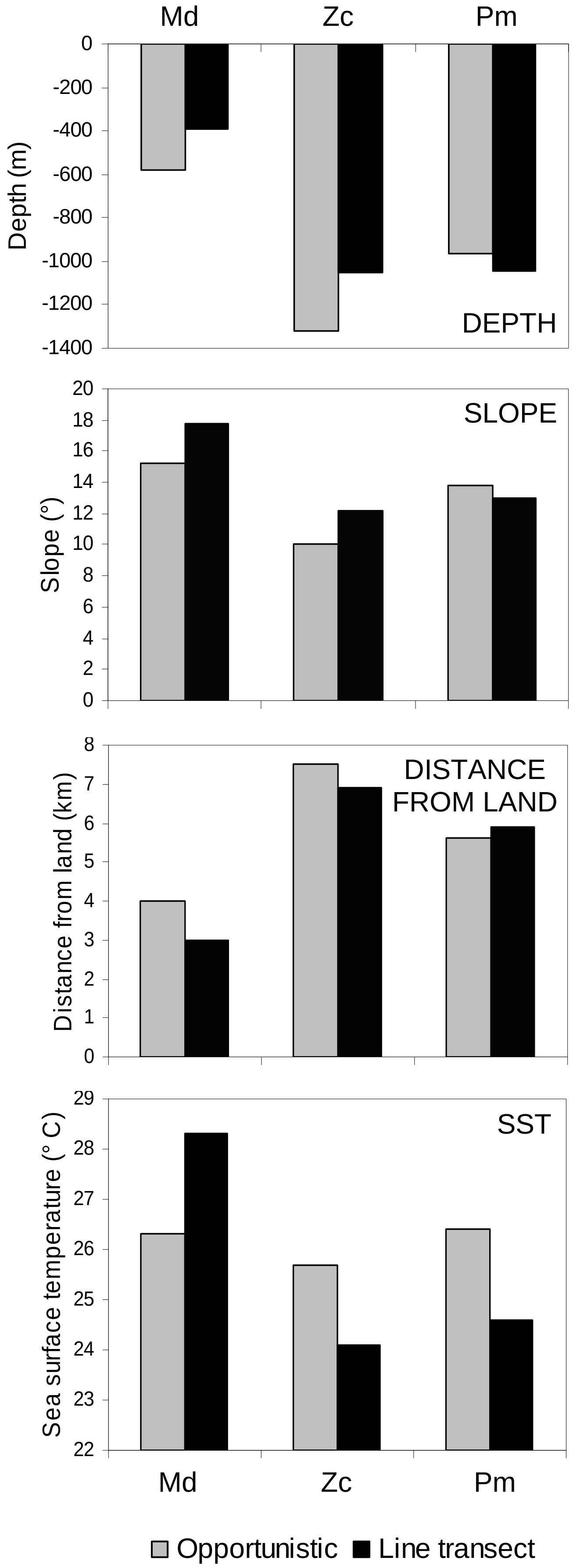


Figure 4.5 Comparisons in the mean values of each environmental variables at sighting locations for Blainville's beaked whales (Md), Cuvier's beaked whales (Zc), and sperm whales (Pm) for opportunistic and line transect surveys.

Environmental data from sightings during opportunistic surveys were analysed to compare differences in habitat selection between the two species of beaked whales and sperm whales. Two sample *t*-tests were used to compare variation between each species for the fixed physical variables for sightings during opportunistic surveys (Table 4.6).

Depth and distance from land were again the most important variables in distinguishing differences in habitat selection between the three species. These differences were highly significant for all interspecies comparisons for these two variables ($p < 0.001$), except for the depth comparison between Cuvier's beaked whales and sperm whales ($p < 0.01$). However, the slope at sighting locations was not a significant variable between any of the interspecies comparisons ($p > 0.05$). In contrast to the results found during line transect surveys (see Table 4.4), Cuvier's beaked whales and sperm whales did not appear to share the same habitat.

Table 4.6 Two sample *t*-test results from opportunistic survey data for each variable showing relationships between the habitat selection of Blainville's beaked whales (Md), Cuvier's beaked whales (Zc) and sperm whales (Pm). Values shown are *p* values.

Interspecies comparison	*Depth*	*Slope*	*Distance from land*
Md – Zc	0.0000**	0.0591	0.0000**
Md – Pm	0.0000**	0.3858	0.0000**
Zc – Pm	0.0031**	0.0717	0.0005**

* $p < 0.05$
** $p < 0.01$

Comparing results from opportunistic and line transect surveys

Similarities were found in the mean values for the environmental variables associated with the sighting locations of beaked whales and sperm whales, irrespective of whether the sighting was on or off transect (see Figure 4.5). Analyses were performed to test if the larger sample of opportunistic surveys produced statistically valid results describing habitat selection in beaked whales when compared to the less frequent line transect surveys. Univariate ANOVA tests compared fixed physical variables from beaked whale sighting locations both on and off transect lines. There were no significant differences found for any of the variables (Table 4.7), suggesting that opportunistic surveys can provide a valuable description of general habitat selection in these cetaceans.

Table 4.7 Results of univariate ANOVA tests for fixed physical variables from beaked whale sighting locations on and off transect.

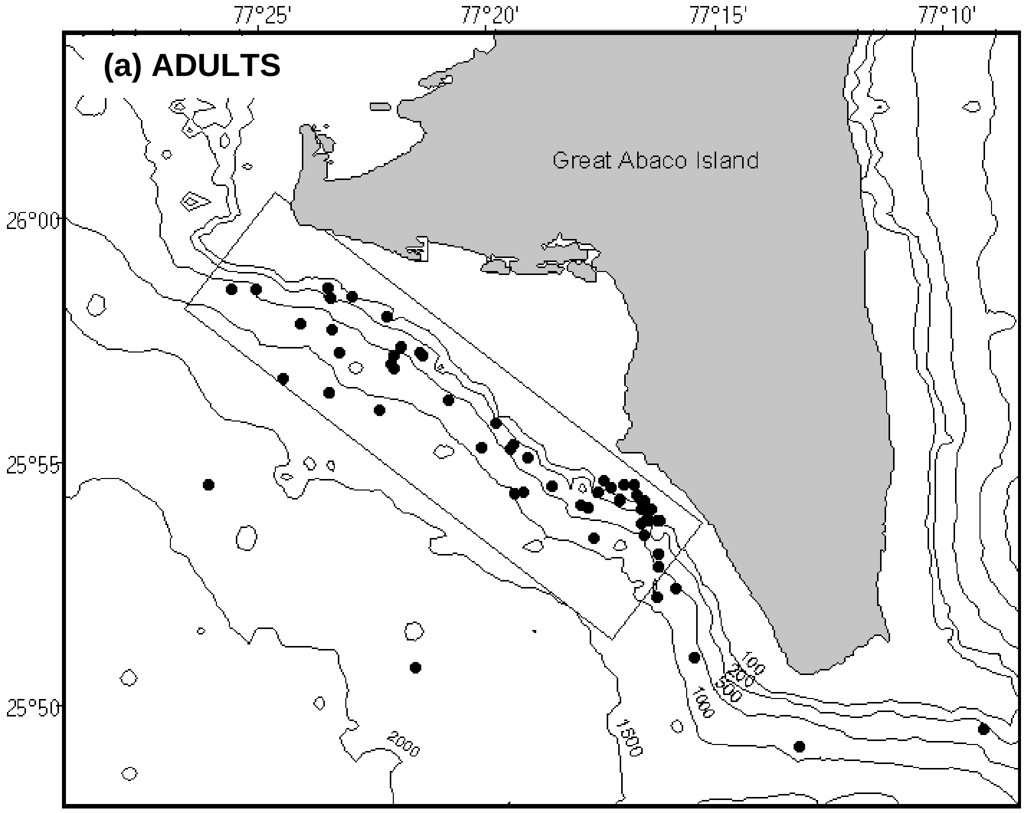
	Blainville's beaked whales		Cuvier's beaked whales	
Variable	*F*	*p value*	*F*	*p value*
Depth	2.45	0.1202	1.08	0.3135
Slope	0.85	0.3587	0.25	0.6259
Distance from land	3.02	0.0852	0.12	0.7307

Blainville's beaked whales: df = 110, F critical = 3.93
Cuvier's beaked whales: df = 17, F critical = 4.49

HABITAT USE OF DIFFERENT AGE CLASSES

Blainville's beaked whales were separated into two age classes: adults and sub-adults based on analysis of photographic data from sightings during opportunistic and line transect surveys from 1997 – 2001. The sub-adult age-class excluded juveniles and calves that were not seen independently of adults (see Figure 2.4 in Chapter 2 for age-class characteristics). These analyses resulted in the identification of 60 groups which included adults and 16 groups which included sub-adults, and there were 5 occasions in which the two age classes were found in the same group. Analysis of photographic data showed that adult and sub-adult Blainville's beaked whales rarely associate (Chapter 2).

The spatial distribution of each age class within the study area was plotted to compare habitat use of these two different classes (Figure 4.6). The distribution maps suggest that the two age classes differ in their choice of habitat. Adult Blainville's beaked whales were found primarily along the canyon wall in depths of less than 1000 m. In contrast, the distribution of sightings of sub-adult Blainville's beaked whales suggests that they occur further offshore, in deeper waters.



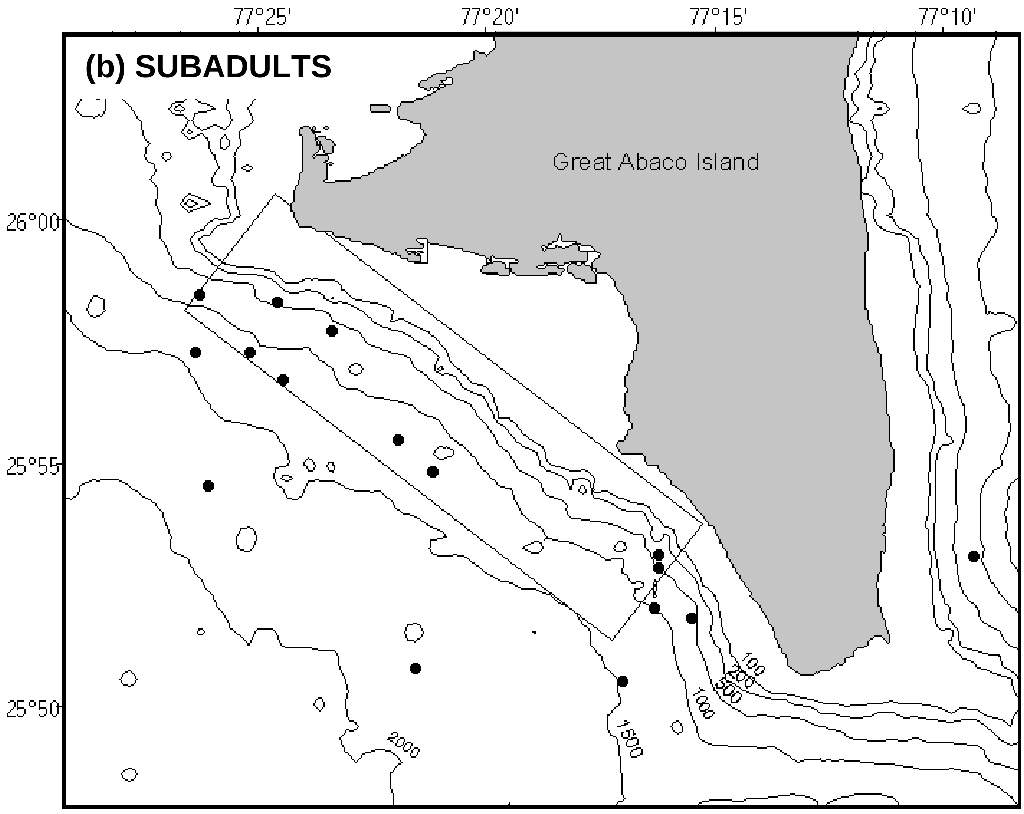


Figure 4.6 Spatial distribution of Blainville's beaked whales separated by age classes: (a) groups which include adults and (b) groups which include subadults. Sightings data are from both opportunistic and line transect surveys conducted from 1997 – 2001.

Environmental data collected at sighting locations for groups with adults and groups with subadults were analysed to test if the differences in spatial distribution reflected differences in habitat selection. Univariate ANOVA tests compared differences in habitat selection between the two age classes, and the results are shown in Table 4.8. Adult and sub-adult Blainville's beaked whales did not appear to occupy the same habitat. There was a highly significant difference in the mean water depths in which the two age classes were sighted, with sub-adult whales found in deeper water ($p < 0.001$). Sub-adults were also found significantly further offshore ($p < 0.05$), but there was no apparent difference in the mean slope at locations where adults and sub-adults were sighted ($p > 0.05$).

Table 4.8 Results of univariate ANOVA tests for fixed physical variables for adult and sub-adult Blainville's beaked whales sighted during surveys from 1997 - 2001.

Variable	*F*	*p value*
Depth	19.62	3.21×10^{-5}**
Slope	1.06	0.3057
Distance from land	5.39	0.0230*

df = 75, *F* critical = 3.97
* $p < 0.05$
** $p < 0.01$

DISCUSSION

Within the study area, the physical environment significantly influenced the distribution of Blainville's beaked whales, and the factor that correlated best with their distribution was slope, or depth gradient. On the other hand, Cuvier's beaked whales were not strongly influenced by any of the fixed physical features analysed relative to the habitat surveyed. Interspecies comparisons showed a highly significant difference in the physical environment that beaked whale species selected, with Cuvier's beaked whales found in deeper water and further from land. However, there were discrepancies noted in the bathymetry data which may have implications on the results, especially due to the fine-scale nature of this study. Hence the results should be interpreted with caution.

In other studies where both these species were present, Cuvier's beaked whales were found in deeper waters than Blainville's beaked whales (Baird *et al.* 2004, MacLeod *et al.* 2004). Beaked whales are generally noted as being distributed offshore (e.g. Mead 1989, Heyning 1989), but a difference in the distance from land for sightings of these two species has not been described previously. This finding may have been possible because the area surveyed was along the coastal escarpment where depth increased with distance from land and these two variables were highly correlated.

It should be noted that the survey was biased in its design because the survey area only included the canyon wall, and not more of the entire canyon system, limiting the variability and types of habitat available. However, since SPUE values for Blainville's beaked whales were highest in the middle of the survey area (and not on the southwest edge of the effort grids), this suggests that the survey design did adequately cover habitat for this species, allowing for reliable analysis of their habitat use.

To overcome the problem of small sample sizes for beaked whales sighted during this study, opportunistic sightings data was included in some of the analyses. Opportunistic surveys were conducted over a longer time period so, although sighting rates were lower than during line transect surveys (Chapter 2), the number of sightings of beaked whales was greater, which allowed for a more robust comparative analyses of habitat selection between species. Since this comparison was relative not absolute, the variation in effort throughout the study area did not matter because the same effort applied for each species.

The same analyses of habitat use were performed for both survey techniques, which provided an opportunity to compare the results of relative distribution. When comparing habitats selected by sperm whales and beaked whales, the general pattern of habitat use was similar from both opportunistic and line transect surveys (Figure 4.5); however, the importance of some variables differed when looking at interspecies comparisons (Table 4.4 and Table 4.6). This is because most of the opportunistic sightings of sperm whales were actually north of the transect grid, while most sightings of beaked whales were in the grid both on and off transect. Therefore, the difference in results between opportunistic and line transects may not be directly comparable between these species, because different areas were surveyed for sperm whales during opportunistic surveys than during transects.

However, univariate ANOVA tests for fixed physical variables from beaked whale sighting locations on and off transect found no significant differences for any of the variables (Table 4.7). This suggests that opportunistic surveys can provide a valuable description of general habitat selection of cetaceans, as long as the limitations are recognised. Randomised line transect surveys will always be the preferable survey technique to determine absolute distribution, and these data can be better applied to assessing and predicting habitat preferences.

CHAPTER FIVE

GENERAL DISCUSSION

This study represents a unique assessment of beaked whale distribution and habitat selection. The key characteristics of this work include: the fine spatial scale, beaked whale species identification to the species level, known age and sex classes of individuals (for Blainville's beaked whales), and the analysis of environmental parameters correlated with sightings data from both randomised and opportunistic surveys. The unique combination of these four aspects has allowed a closer examination of habitat preferences of Blainville's beaked whales and Cuvier's beaked whales, exploring relationships between species and between different age classes within a species.

There are three key biological themes that emerge from this work. The first theme is that beaked whales showed habitat preferences, with Cuvier's beaked whales found further offshore and in deeper water than Blainville's beaked whales. The second biological theme is based on habitat sharing by Cuvier's beaked whales and sperm whales, while habitat partitioning existed between beaked whale species. The third key theme is the evidence of habitat partitioning between different age classes of Blainville's beaked whales and the suggestion that occupancy of the best habitat may be driven by a dominance hierarchy.

HABITAT PREFERENCES OF BEAKED WHALES

The predominance of beaked whales on the northern side of the Great Bahama Canyon, which is characterised by rugged bottom topography with numerous canyons and gullies (Mullins *et al.* 1979), supports the findings of previous studies that beaked whales inhabit deep-water environments, and show a preference for areas that are topographically diverse (Waring *et al.* 2001, Hooker *et al.* 2002, Mead 2002, D'Amico *et al.* 2003).

It is believed that the fixed physical features influence the oceanography of an area by increasing prey biomass and creating areas of higher productivity. D'Amico *et al.* (2003) showed that Cuvier's beaked whales in the Ligurian Sea preferred waters over submarine canyons where frontal influences exist, as indicated by remote sensing data and historical oceanography. Waring *et al.* (2001) reported similar findings for beaked whales off the northeast coast of North America where beaked whales were sighted along the shelf edge and the north wall of the Gulf Stream.

Although the biological oceanography of the Abaco study area has not yet been described, based on the activities of local commercial and sport-fisheries, which concentrate their efforts along the shelf edge, prey biomass appears to be higher along the canyon wall. Throughout the year, chlorophyll *a* concentrations are highest on the shallow bank platforms (Figure 1.3), and thus the bank edge could be locally influenced by off-bank transport of these relatively nutrient-rich waters.

Within the study area, there are several topographic features which may help to concentrate biomass along the canyon wall on the northern side of the Great Bahama Canyon. The first of these is extremely high depth gradient (Sealey 1994), which increases toward the southeastern portion of the study area (Mullins 1978). Perhaps, more importantly, there are only two places along the northern margin of Northwest Providence Channel where off-bank transport of sand occurs (Hine *et al.* 1981), which has contributed to the erosion of the canyon wall, creating gullies and side canyons.

These characteristics support earlier findings that beaked whales are found in areas of rugged bottom topography, and help explain higher SPUE values for beaked whales than some other species, e.g. oceanic dolphins (Figure 4.3). However, the fact that the survey area only covered the canyon wall hampers interpretation of how important this habitat is relative to the entire canyon system.

SHARING AND PARTITIONING OF HABITATS

Sightings data from line transect surveys showed that Cuvier's beaked whales and sperm whales shared the same habitat in the study area (Table 4.4). Mead (2002) noted similarities between modern ziphiids and sperm whales because they have retained some of their ancestral characters, and also share similar ecology, both feeding at considerable depth and specialised to feed on squid and mesopelagic fish. However, previous studies have demonstrated habitat partitioning between ziphiids and sperm whales (Kenney and Winn 1986, Waring *et al.* 2001, Hooker *et al.* 2002, D'Amico *et al.* 2003).

Some of these previous studies did not identify beaked whales to the species level (Kenney and Winn 1986, Waring *et al.* 2001), whereas in this study, beaked whale sightings data were analysed at the species level. These analyses showed a highly significant difference in habitat selected by Blainville's beaked whales and both Cuvier's beaked whales (Table 4.4).

Furthermore, the spatial scale of the previous studies were more coarse; for example, Waring *et al.* (2001) used a grid scale four times the scale used in this study. The finer scale used in this study increased the chances of detecting differences in inter-specific habitat selection. This illustrates the importance of analyses based on sightings data at the species level and of fine-scale surveys in order to more accurately describe sharing or partitioning of habitats between beaked whales and other species.

Previous studies (Waring *et al.* 2001, D'Amico *et al.* 2003) used remote sensing data to identify permanent and ephemeral oceanographic features. They found that ziphiids were more associated with frontal boundaries than sperm whales, and suggested that the biological aspects of their environment influenced their partitioning of habitats more than the physical oceanography. In this study, surface environmental data was limited to sea surface temperatures recorded at the time of the sighting, and was not found to differ significantly between species (Table 4.4). So while this study analysed the physical habitat at a finer scale, it was unable to assess distribution relative to frontal boundaries because sea surface temperature data were not processed.

Waring *et al.* (2001) proposed that differences in prey selection between sperm whales and beaked whales may be important factors contributing to the habitat partitioning they reported. However, their study occurred off the northeastern US coast (40° N) just beyond the upper latitudinal limits of adult female and sub-adult male sperm whales. Since adult male sperm whales consume larger prey than females (Rice 1989) and Cuvier's beaked whales, differences in prey selection (or prey age classes) of Cuvier's beaked whales and sperms in these northern latitudes in understandable.

However, nursery groups of sperm whales, consisting of adult females and their offspring, are found in the Great Bahama Canyon year-round. Large adult males are rarely sighted in The Bahamas (BMMS, unpublished data). Although there is no direct information on prey of either sperm whales or Cuvier's beaked whales from The Bahamas, sperm whales and Cuvier's beaked whales are known to feed on the same prey species (Heyning 1989, Rice 1989), so competition between adult female sperm whales and Cuvier's beaked whales for the same prey and prey of same age class is possible. Furthermore, in a sub-tropical oligotrophic environment less prey is available than more productive waters in higher latitudes, so more competition between predators would be expected.

The change in temporal occurrence of Cuvier's beaked whales and sperm whales during the study (Figure 2.7) further suggests that competition between these species may exist. The decline in the sighting rate of Cuvier's beaked whales was following the mass stranding event, which occurred in March 2000, with no sightings of this species in the study area for 20 months. Concurrently, the rate at which sperm whales were sighted increased, with the greatest increase in sighting rates between 2000 and 2001. A possible explanation for these temporal changes is that sperm whales may have frequented the study area more in this period because there was more prey available during the absence of their competitors, Cuvier's beaked whales.

There are, however, other potential reasons for the difference in sighting rates throughout the study period. The data used in this analysis included opportunistic survey data, which became more biased as the study progressed. Knowledge of "hot spots" increased with time, and during opportunistic surveys, when the aim was to maximise encounters with species, these areas were preferentially surveyed. The land base from which surveys initiated also changed in 1999, resulting in closer access to the 1000 m isobath, thereby increasing our chances of sighting sperm whales.

Beaked whales and *Kogia* species appeared to utilise different habitats (Table 4.4). MacLeod *et al.* (2004) found partitioning by water depth between Blainville's beaked whales and dwarf sperm whales (*K. sima*) off the eastern side of Great Abaco Island. However, in this study, there was no significant difference found in the water depths at which Blainville's beaked whales and *Kogia* species were sighted.

The finer spatial resolution of this study shows stratification in habitat use of cetaceans, with larger species found in deeper water and further offshore, presumably feeding on larger prey and at greater depths. However, the high frequency of sightings along the bank edge of the two most commonly sighted cetaceans in the study area, *Kogia* species and Blainville's beaked whales, implies that this area is likely a productive feeding area.

DOMINANCE HIERARCHY IN BLAINVILLE'S BEAKED WHALES

Resource-defence and/or female-defence systems can be factors in the evolution of sexually selected traits, such as dimorphism in size and in specialised morphological features like tusks (Campagna 2002). Beaked whales, and especially Blainville's beaked whales, provide an excellent example of sexual dimorphism. The importance of male-male competition for females is suggested by the male's larger size, the teeth (or tusks) erupting through the gums only in adult males and the intra-specific scarring caused by tooth-rakes, which are much more extensive on males than females (McCann 1974).

Sub-adult and adult Blainville's beaked whales were distributed differently in the study area (Figure 4.6), with sub-adults found in deeper water ($p < 0.01$) and at a greater distance from land ($p < 0.05$) (Table 4.8). Adults occupied the more productive feeding areas along the bank edge, while sub-adults were found in less optimal habitat within the study area. In Chapter 2, it was shown that all adult males had low photo-resighting rates, with the exception of one male which was photographed in the study area more often than any other whale. This particular male (Md75) may have established a dominance hierarchy within the study area which could limit other males, including sub-adult animals, from gaining access to the more productive, inshore waters where adult female groups were found.

Dominance hierarchies have been well documented for elephant seals (*Mirounga* spp.), in which males aggressively establish a dominance hierarchy, and only the highest ranking males have undisturbed access to reproductive females (LeBoeuf and Laws, 1994). Young male elephant seals are excluded to the outside of rookeries, while adult males guard groups of adult females. The harem-like social structure described for Blainville's beaked whales in Chapter 3 supports a female-defence mating system based on a dominance hierarchy, with single adult males having an association with particular groups of females of reproductive status, while sub-adults form separate groupings.

When hierarchies are being established, male elephant seals intimidate each other with vocal displays but if neither male retreats, violent fights ensue, resulting in bloody wounds and multiple lacerations, and sometimes even death (Campagna 2002). Various forms of female-defence mating systems have been described for cetaceans and male-male competition is fairly common; for example, agonistic behaviour between humpback whales on the breeding grounds (Tyack and Whitehead 1983). Male-male interactions in cetaceans can become very aggressive, such as a near fatal fight between male bottlenose dolphins described by Parsons *et al.* (2003). Although fighting between male Blainville's beaked whales has never been observed, the extensive deep furrowed, overlapping intra-specific scarring patterns are clear evidence of extremely violent aggressive interactions within this species. During this study, two adult males were never sighted in the same group, suggesting that, to reduce the risk of injury, subordinate males challenge dominant males infrequently. The low resighting rates of all but one adult male demonstrates that the majority of males did not remain in the study area for long periods of time. By forcing sub-adult whales to occupy different habitat, challenges to the dominant animals are further reduced.

In their study of individual distribution and ranging patterns of northern bottlenose whales, Hooker *et al.* (2002) found no difference in positions of different age-sex classes within the Gully, but did note separation between different adult males. (This study used slightly different age-sex classes, separating adult females and adult males, and grouping adult females with unknown immature whales.) The relative spatial differences between adult males was believed to be based on preference for locations that provided the best mating opportunities as females moved in and out of the Gully (Hooker *et al.* 2002).

Intra-sexual competition between adult male northern bottlenose whales has been suggested by Gowans and Rendell (1999). However, some males are also known to form long-term social bonds (Gowan, 1999), suggesting differences in the mating strategy between Blainville's beaked whales in this study area (see Figure 2.9) and northern bottlenose whales in the Gully. Generally speaking though, both species demonstrate similar behavioural ecology with the spatial distribution of females resulting from resource distribution, predation pressure, and the costs and benefits of group living, while the spatial distribution of males results from the distribution patterns of females (Davies 1991, Hooker *et al.* 2002).

FUTURE ANALYSES AND FIELDWORK

Additional analysis of data collected during this study will contribute further to our understanding of beaked whale population and behavioural ecology, as the analyses conducted represents only some applications of the data collected. From the photo-identification data collected during Blainville's beaked whale sightings, additional analyses to be done in the future include: calculating abundance estimates, assessing population demographics, such as calving intervals and survival rates, and documenting individual life histories. Analysis of 80 hours of field observation data gathered for Cuvier's beaked whales and Blainville's beaked whales during this study will help describe beaked whale behaviour, including their diving patterns.

Both the opportunistic and line transect sightings data could be applied to Generalised Linear Models (GLMs) and Generalised Additive Models (GAMs) to see how well they predict Blainville's beaked whale habitat. Substantial data were collected on other species during this study, which also deserves analysis, particularly dwarf sperm whales, the most frequently sighted species, as so little is known about their population ecology.

Future fieldwork should include genetic sampling, larger scale surveys and prey analyses. Genetic sampling in combination with photo-identification work will help to assess population structuring and further our understanding of the social organisation of ziphiids. To relate the findings in this study to beaked whale habitat preferences within the Great Bahama Canyon and to understand the significance of the canyon wall within the study area, transects should be designed to cover more area within the entire canyon system. Oceanographic data should be collected during these surveys to help understand which topographic features are influencing local productivity. And finally, an investigation into the diet of beaked whales in The Bahamas would contribute towards understanding their role ecologically.

CONCLUSIONS

This study has contributed valuable information on beaked whale distribution and habitat selection, which can be applied to the conservation of these rare, deep-diving whales through the establishment of protected areas and mitigation of impacts of anthropogenic disturbances in The Bahamas and elsewhere.

Protected areas for marine mammals have primarily been coastal where the land-water interface is most actively used by humans. Examples include: Crystal River, Florida for manatees; Moray Firth, Scotland for bottlenose dolphins; Robson Bight, British Columbia for killer whales; and, Glacier Bay National Park, Alaska for humpback whales. As human encroachment extends further offshore, oceanic habitats are becoming threatened, and the establishment of marine protected areas (MPAs) may be the only approach to protecting marine mammal species, as recommended by Hooker *et al.* (1999) for protecting northern bottlenose whales in The Gully, off Nova Scotia. The Bahamas is currently establishing an MPA system, which is focussed primarily on fisheries stock replenishment on the shallow banks. But threats to the deep-water environments through oil exploration, inter-island fast ferries and increased shipping traffic through the deep-water passages, demonstrate a growing need for the MPA system to extend offshore. By documenting species occurrence and distribution, this study will contribute information towards determining where these future protected areas should be.

Blainville's beaked whales and Cuvier's beaked whales have been the two primary species involved in mass strandings associated with anthropogenic sound, such as military sonar and seismic airguns. The impact of these events at the population level is entirely unknown, although they are believed to have a disproportionate effect on sub-adult whales. For example, during the stranding event in The Bahamas, 14 beaked whales stranded, 12 of which the age class was determined and 8 of these (67%) were sub-adult whales. Further understanding of the distribution of beaked whales is essential to know where and when to apply mitigation measures to protect them.

Ziphiids were one of the most common species sighted during this study, further demonstrating the importance of submarine canyons as primary habitat for beaked whales (Waring *et al.* 2001, D'Amico *et al.* 2003). Mitigation should begin by excluding military exercises and seismic surveys from submarine canyons, until more is known about exactly which activities are harmful. No policies currently exist in The Bahamas to mitigate military exercises or seismic surveys, other than those self-imposed by the military and oil industry while operating in Bahamian waters. This study will help provide background information to apply towards local mitigation policies.

The unique aspects of this study have allowed a more detailed assessment of beaked whale distribution and habitat selection. The differences found in habitat preferences between species and different age classes add to the complexity of effectively mitigating disturbances from loud sound sources. These differences in distribution may be driven by both the social constraints of a dominance hierarchy system in Blainville's beaked whales and interspecies competition, but are believed to be primarily influenced by prey concentrations. It is not realistic to conduct fine-scale surveys throughout the range of beaked whale species, but studies at this resolution are necessary to evaluate the impacts at the population level and may provide useful data for extrapolating elsewhere.

APPENDIX I

List of marine mammal species recorded in The Bahamas. Species sighted at sea by the Bahamas Marine Mammal Survey are designated by (S) following the scientific name.

Atlantic bottlenose dolphin	*Tursiops truncatus* (S)
Atlantic spotted dolphin	*Stenella frontalis* (S)
Pan-tropical spotted dolphin	*Stenella attenuata* (S)
Striped dolphin	*Stenella coeruleoalba* (S)
Rough-toothed dolphin	*Steno bredanensis* (S)
Fraser's dolphin	*Lagenodelphis hosei* (S)
Risso's dolphin	*Grampus griseus* (S)
Short-finned pilot whale	*Globicephala macrorhynchus* (S)
Melon-headed whale	*Peponocephala electra* (S)
Pygmy killer whale	*Feresa attenuata* (S)
False killer whale	*Pseudorca crassidens* (S)
Killer whale	*Orcinus orca* (S)
Dense-beaked whale	*Mesoplodon densirostris* (S)
Antillean beaked whale	*Mesoplodon europaeus* (S)
Cuvier's beaked whale	*Ziphius cavirostris* (S)
Dwarf sperm whale	*Kogia sima* (S)
Pygmy sperm whale	*Kogia breviceps* (S)
Sperm whale	*Physeter macrocephalus* (S)
Minke whale	*Balaenoptera acutorostrata* (S)
Fin whale	*Balaenoptera physalus*
Humpback whale	*Megaptera novaeangliae* (S)
West Indian manatee	*Trichechus manatus* (S)
Hooded seal	*Cystophora cristata*
Caribbean monk seal (extinct)	*Monachus tropicalis*

APPENDIX II

BMMS Survey Protocols

1) The driver of the vessel is responsible for the safe manoeuvring of the vessel at all times.
2) When marine mammals are sighted, determine their direction of travel and approximate speed, and the formation of the group before the first close approach.
3) Have a plan for approaching which matches the specific objectives for the encounter, e.g. photo-id, faecal collection, biopsy, tagging, etc., and which also matches the species encountered.
4) Approach the group slowly, from the side and slightly behind.
5) When within the distance deemed necessary for the specific objective, follow parallel to the animal(s) and group, whenever possible.
6) If obtaining fluke photographs, stay directly behind the whale and maintain the same speed as the whale.
7) Do not to drive within a group, unless individuals are separated by more than 5 body lengths, and do so slowly.
8) Never separate mother/calf pairs.
9) Try not to change RPMs unless necessary, but when necessary slowly increase or decrease the speed of the vessel.
10) If it is necessary to re-engage the gears, try to do so when the animal being followed exhales, especially when with sperm whales.
11) Pay attention to the entire group throughout the encounter.
12) Respond to any behavioural responses that may mean the animal or group is disturbed (e.g. chuffing, tail slaps & breaching near the boat), by slowly increasing the distance between the vessel and the animal(s), and in some cases, terminating the encounter.
13) When the objectives are accomplished, slowly move away from the group.
14) Do not increase speed until well away from the group.
15) Continue to keep track of the group as you leave, in case their direction of travel has changed.

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