Diving Behaviour and Foraging Ecology of Blainville's and Cuvier's Beaked Whales in the Northern Bahamas

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ABSTRACT

In recent years beaked whales have received an increased level of interest due, in part, to a number of high profile mass stranding events caused by tactical sonar (Balcomb & Claridge 2001; Fernández et al. 2005a). Such events have resulted in a demand and requirement for a greater understanding of beaked whale ecology and behaviour.

This study represents the first attempt to examine dive duration data and differences in the diving behaviour of Blainville's beaked whale (*Mesoplodon densirostris*) and Cuvier's beaked whale (*Ziphius cavirostris*) in the North-western Atlantic. Foraging behaviour is also examined using dietary and niche overlap
evidence from the northern Bahamas. Data from Blainville's beaked whales, Cuvier's beaked whales and another deep diving cetacean; the sperm whale (*Physeter macrocephalus*), were used to infer the depth of foraging dives and niches being exploited.

Data was collected during opportunistic vessel surveys conducted in the northern Bahamas between 1994 -2004. Stomach contents from stranded animals and faecal samples from free ranging whales were also collected.

Prey remains were preserved in ethanol and identified under microscopic examination.

Dive analysis was conducted using both log-survivorship plots (Fagen & Young 1978) fitted with a non-linear 'broken-stick' model (Sibly et al. 1990) and cumulative time plots (Hooker & Baird 1999).

Diet analysis revealed three prey types, cephalopods, crustaceans and fish. All prey were considered to be deep water species, principally being inhabitants of the meso- to bathypelagic zones.

Diving Analysis found evidence of different dive types. Long (considered deep) dives were not significantly different between the two beaked whale species (Mann-Whitney U test, $P = 0.09$) (Blainville's; median = 50 min, Cuvier's; median = 62.8 min). Short (considered shallow) dives were significantly different between species (Mann-Whitney U test, $P = < 0.0001$) (Blainville's; median = 6.6 min, Cuvier's; median = 18 min).

The depth range of the prey species consumed and the dive data suggest that in the Bahamas both Blainville's and Cuvier's beaked whales are diving for long periods and to great depths to forage.

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Chapter One

INTRODUCTION

In recent years beaked whales have received an increased level of interest due, impart to a number of high profile mass stranding events caused by mid frequency tactical sonar employed by the US and NATO naval forces (Balcomb & Claridge 2001; NMFS 2001).

Such events have resulted in a demand and requirement for a greater understanding of beaked whale ecology and behaviour. Equally these events have highlighted the distinct lack of published data on the 21 currently identified beaked whale species, which are typified by being long duration divers and deep water inhabitants, existing in offshore habitats, at or beyond continental shelf breaks (Hooker & Baird 1999a).

Different theories relative to the sensitivity of beaked whales to sonar, and how sonar exposure leads to strandings have been proposed (Potter 2004). One theory suggests a decompression sickness (DCS) type effect, where gas bubble emboli are a contributory factor in the death of stranded whales (Jepson et al. 2003; Jepson et al. 2005; Fernández et al. 2005a). Subsequently interest in the physiological and behavioural effects of diving to depth and for long durations has arisen.

Models of gas bubble formulation have been generated for one species of beaked whale, the northern bottlenose whale (Houser et al. 2001), but none have been generated for the two species of beaked whale that have repeatedly been representative in mass stranding events, Cuvier’s beaked whale (*Ziphius cavirostris*) and Blainville's beaked whale (*Mesoplodon densirostris*).

This study represents the first attempt to examine dive duration data and differences in the diving behaviour of Blainville's beaked whale and Cuvier's beaked whale in the North-western Atlantic.

Concomitantly, foraging behaviour is examined using dietary analysis and niche overlap evidence between Blainville's beaked whale, Cuvier's beaked whale and another deep diving cetacean the sperm whale (*Physeter macrocephalus*), inhabiting the northern Bahamas and used to infer the depth of foraging dives and niches being exploited.

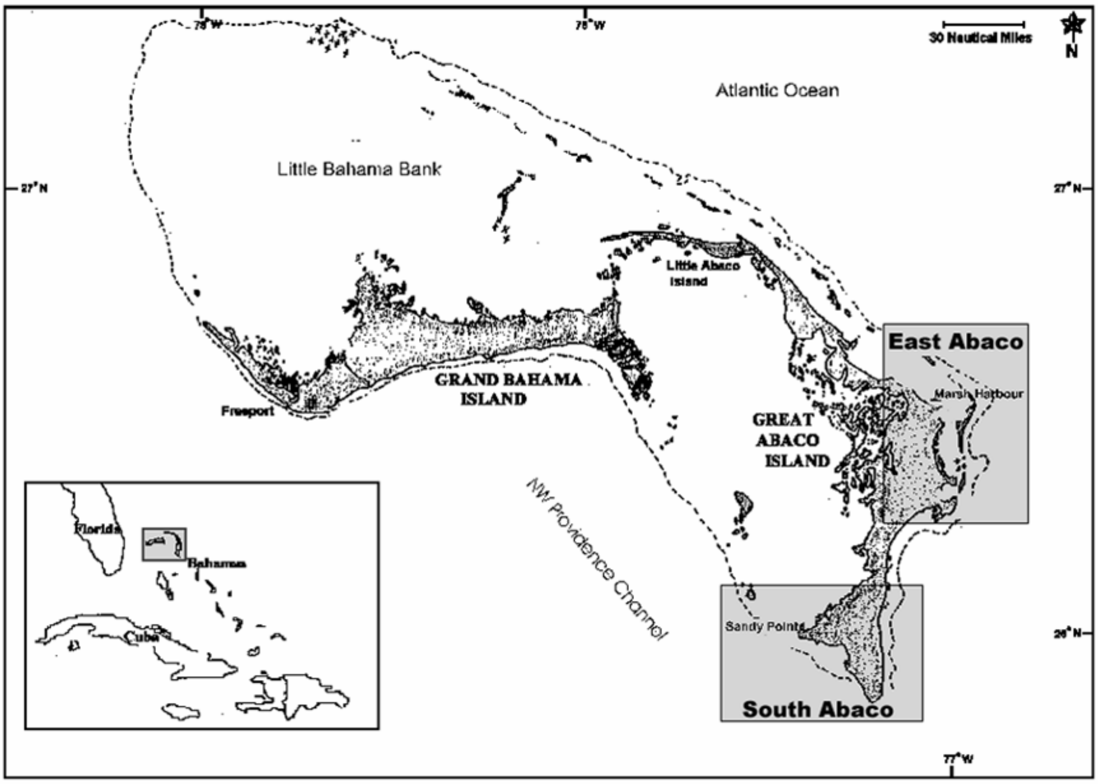


Figure 1.1. The island archipelago of the Bahamas, showing the two study areas off the eastern and southern coasts of Great Abaco Island in the northern Bahamas where studies were conducted.

Both Cuvier's beaked whale and Blainville's beaked whale were represented in the now well documented mass stranding event that took place on 15th March 2000 in the northern Bahamas (Balcomb & Claridge 2001), directly within the main study area of the Bahamas Marine Mammal Survey (BMMS), which has been studying the behavioural ecology of both Blainville's and Cuvier's beaked whales in the northern Bahamas since 1991 (Fig. 1.1).

Primary objectives were:

1. Use faecal and stomach content samples to determine foraging behaviour and infer diving depths of *M. densirostris* and *Z. cavirostris* in the Bahamas.
2. Investigate the implications of sea state on the quality of diving behaviour data collected.
3. Compare diving behaviour between *M. densirostris* and *Z. cavirostris* (dive and surface interval duration analysis (inclusive of inter-ventilation durations/respiration rates)), using different dive analysis methodologies.
4. Compare diving behaviour between age classes of *M. densirostris* (dive and surface interval duration analysis).
5. Review of the Bahamas mass stranding in 2000, relative to the species composition of the study area where the exercise took place, the composition of the stranding itself and the current proposed theories as to why beaked whales strand.

Chapter Two

INTRODUCTION

Knowledge of the diet of any species is fundamental to understanding its ecology (Hooker et al. 2001) and studies of diet and niche overlap with other deep diving species can provide an insight into the depth animals are diving to forage. As MacLeod et al. (2003) state, the distribution of preferred prey items will relate to the distribution of the predator and will, in part define the habitats in which a specific predator occurs while the abundance of preferred prey may affect the abundance of the predator within a specific habitat.

Studying beaked whales in the field is demanding and deploying devices on Blainville's and Cuvier's beaked whales, such as time-depth recorders (TDR's) that directly record dive depths is a significant challenge. To date, such studies are few in number and none have taken place in the Bahamas or central north-western Atlantic (Baird et al. 2004; Hooker & Baird 1999b; Johnson et al. 2004).

Dietary analysis from stomach contents and faecal samples provides a means to gather information on the foraging behaviour of these poorly understood species, where no other data exist.

Developing this knowledge has gained increasing importance due to recently documented mass strandings associated with tactical naval sonar.

In 1963 tactical mid frequency sonar was introduced to the world's oceans and in the same year the first incidence of a Cuvier's beaked whale mass stranding was recorded (NMFS 2001). In subsequent years beaked whales have attracted increasing attention due to a proliferation of mass strandings associated with naval sonar (Balcomb & Claridge 2001; Fernández et al. 2005a; Frantzis 1998).

Different causative factors have been proposed and investigated relating to the mechanism producing fatal effects in beaked whales exposed to tactical sonar (Crum et al. 2005; Houser et al. 2001, Jepson et al. 2003; NMFS 2001). The nature of the diving behaviour, being typically deep and for long durations (Hooker & Baird 1999a) is considered to be implicit in the factors that propagate beaked whale fatalities (Fernández et al. 2005a).

The passage of tactical sonar through the three-dimensional water column is complex and non uniform. At differing depths and distances from the sound source, animals may be exposed to very different intensities and durations of sonication (NMFS 2001).

Knowledge of the depth of dives and layers of the water column where animals are most likely to forage and thus spend increased time, is therefore of great interest and importance in understanding how animals may be impacted by sonar.

One documented stranding event involving the two beaked whale species that have been most abundant in mass strandings (Blainville's beaked whale and Cuvier's beaked whale) occurred in the Bahamas in 2000 (Balcomb &

Claridge 2001), directly within an area where the only long term study of these species in the central north-western Atlantic has been conducted (Claridge 2004).

The current paucity of data for the central north-western Atlantic and direct relevance of a naval sonar induced mass stranding in the Bahamas, make diet analysis and assessment of dive depths of foraging beaked whales in the Bahamas directly relevant to the investigation and understanding of the effects of sonar on these enigmatic animals.

Sampling prey species

In the eastern Atlantic both Blainville's and Cuvier's beaked whales have been shown to forage at depths in excess of 600 m (Johnson et al. 2004; Madsen et al. 2005). No such data exists for the western Atlantic, thus foraging depth currently can only be inferred from the known depth ranges of prey species.

Blainville's and Cuvier's beaked whales in the Bahamas are encountered in areas associated with sub-marine canyon systems with high topographic diversity (Claridge 2004), akin to other beaked whale species and as such sampling of potential prey via conventional trawl methods is potentially impractical (Hooker et al. 2001).

More conventional methodologies of collecting evidence of consumed prey in free-ranging marine mammals, such as scat collection in studies of pinipeds (Hammond and Prime 1990; Pierce et al. 1990) or more direct stomach analysis via stomach pumping of captured animals (Pierce and Boyle 1991), present obvious limitations where the study of large free-swimming cetaceans such as beaked whales are concerned.

Previously published data on the diets of Blainville's and Cuvier's beaked whales have all been based on stomach content analysis.

Faecal sample collection is another means of studying diet and has been used to study the diet of sperm whales (*Physeter macrocephalus*) (Smith & Whitehead 2000).

No published data exists for faecal sample analysis of beaked whales and it is considered that until this study no faecal samples have ever been successfully collected from any beaked whale species.

Beaked whale diet

Beaked whales, inclusive of both Blainville's beaked whale and Cuvier's beaked whale are considered to predominantly feed on squid (Mead 1989).

Studies based on stomach content analysis have revealed the presence of crustaceans and fish, in addition to squid in the diets of beaked whales (Clarke 1996; Sekiguchi et al. 1996). Preferred beaked whale prey are considered to occur predominantly between 200 and 2000 m depth, at or beyond the Continental Shelf and thus beaked whales have been considered generalist predators of deep water squid, fish and crustaceans (MacLeod et al. 2003).

Blainville's beaked whale

Previously published data on the diet of Blainville's beaked whale is scarce and of three known studies of stomach contents, two have been from the eastern Atlantic (South Africa and Wales) and the third from southern Brazil in the western Atlantic (MacLeod et al. 2003). No prey items were found in the stomach of the Brazilian whale. A single item was found in the Welsh animal, the squid *Histioteuthis reversa* and the South African animal's stomach predominantly contained fish species, including Silver scabbardfish (*Lepidopus caudatus*) and Hake (*Merluccius capensis*).

To date, no dietary data has been published for Blainville's beaked whale in the central north-western Atlantic or more specifically from the Bahamas.

Cuvier's beaked whale

Diet analysis results have been published for Cuvier's beaked whale across its cosmopolitan range. Consumed prey constituents are cephalopods, crustaceans and fish of varying prevalence dependent upon where the animals were from.

Of the cephalopod prey, MacLeod et al. (2003) reported that the squid families Histioteuthis, Cranchiidae and/or Gonatidae were the most important in terms of numbers and biomass in the diet.

In the central north-western Atlantic two published records exist for the diet of Cuvier's beaked whale. An animal from the Gulf of Mexico stranded in Texas (USA) and contained remains of the squid *Loligo peali* and unidentified cephalopods (Fertl et al. 1997) and another single animals stomach was analysed from the Leeward Dutch Antilles in the Caribbean. Unidentified cephalopods and the crustacean *Gnathophausia ingens* were found (Debrot & Barros 1994). No published records however exist for the diet of Cuvier's beaked whale in the Bahamas.

Niche Overlap

Niche overlap is a measure of the resource use among different species within a community guild (Krebs 1998) and studies of food and feeding habits can determine the position of animals within food webs and habitats (Pauly et al. 1998).

In this chapter niche overlap analysis is used to explore whether Blainville's beaked whales, Cuvier's beaked whales and sperm whales consume similar prey.

In the waters adjacent to the south west coast of Abaco Island, these three deep diving species are encountered over small spatial scales (<4 km) (Claridge 2004).

Sightings data from line transect surveys indicate that Blainville's beaked whales do not share habitat with either of the other species, but Cuvier's beaked whales and sperm whales in the area share habitat (Claridge 2004). Subsequent to the mass stranding event in March 2000, sightings of Cuvier's beaked whales decreased and none were observed for a further 20 months. Sightings of sperm whales increased significantly between 1999 and 2000, continuing to increase in the following two years (Claridge 2004). The absence of a competitor and an abundance of a shared prey type may have promoted the increase in sperm whales.

Niche overlap analysis may reveal where dietary similarities occur between these species, allowing inferences about the depth of foraging dives of one species to be applied to another where data may be absent or limited.

The aim of this chapter was to determine the depth of foraging dives of Blainville's and Cuvier's beaked whales in the northern Bahamas by (i) documenting the prey remains from stomach contents and faecal samples of Blainville's beaked whales, Cuvier's beaked whales and sperm whales, another deep diving whale found in the northern Bahamas, (ii) determine the depth distribution of prey species, (iii) investigate the diet composition of the three species, (iv) investigate evidence of niche overlap between the three whale species.

Chapter Two

METHODS

Sample Collection - Stomach Contents

Stomach contents were collected from five deep diving whales, three Cuvier's beaked whales, one Blainville's beaked whale and one sperm whale, having stranded on the islands of Abaco and Grand Bahama in the northern Bahamas between March 2000 and March 2004.

Three of the whales (two Cuvier's beaked whales and the Blainville's beaked whale) stranded in March 2000 as part of a multi-species mass stranding that took place in association with United States led naval operations in waters adjacent to both Abaco and Grand Bahama.

Necropsies were performed on all five whales and in addition to the collection of stomach contents, both tissue samples and biological data (sex, length etc.) were collected. For three of the stranded animals (one Cuvier's beaked whale, the Blainville's beaked whale and sperm whale) necropsies were performed on the day of stranding, where the animals were considered to be freshly dead.

The remaining Cuvier's beaked whales that stranded on Grand Bahama on the 15th March 2000, were buried and subsequently exhumed and necropsied on the 18th March and were recorded as being in a moderate state of decomposition.

During the necropsies prey remains were collected from both the oesophagus and stomachs of stranded animals and frozen for later analysis.

In the case of the Blainville's beaked whale, the intact gastro-intestinal system (from oesophagus to anus) was removed and frozen.

On thawing, the Blainville's beaked whales stomach was systematically opened beginning at the esophagus. The contents were removed through careful rinsing of the mucosal lining of all stomach chambers into a 5-liter dissecting pan.

In order to separate stomach content components, each of the stomach content samples were independently flushed through a series of three interlocking stainless steel screens. The screen mesh sizes from top to bottom were 2.0 mm, 1.0 mm and 0.355 mm.

Analysis of the Blainville's beaked whale stomach and the two Cuvier's beaked whales that stranded in March 2000, were conducted by Bill Walker (National Marine Mammal Laboratory, NOAA, Seattle, USA).

Sample Collection - Faecal Samples

Faecal samples were collected from free ranging beaked whales by towing a swimmer alongside the research vessel, allowing underwater observations of animals. When a defecation event was observed the swimmer would dive to collect faecal material in a sterile sample container.

Faecal samples from sperm whales were collected at the surface immediately post fluking and defecation. The research vessel was manoeuvred into the fluke print of the diving whale and the water scanned for faecal matter. Where faeces were found a swimmer entered the water and collected the sample in a sterile container. Samples were kept on ice until the vessel returned to shore where the sample was left to settle. Sterile forceps were then used to remove hard prey remains.

Stomach content and faecal sample prey remains were preserved in either 50% or 70% ethanol for later microscopic examination at 6 to 10X magnification.

Prey identification

Cephalopod beaks were identified using published reference guides (Clarke 1986) and the reference collection of Dr. M. B. Santos.

A binocular microscope fitted with an eye piece graticule was used to measure unbroken beaks, determining the lower rostral length (LRL) of squid and lower hood length (LHL) of octopods (Clarke 1986).

Mantle length (ML) and weight estimates of cephalopods were calculated using regressions from Clarke (1986) and Santos (2002).

Measurements were not possible for the beak from the family *Enoploteuthidae,* as regression models for length and weight estimation were not available.

Crustacean and fish prey remains not examined by Bill Walker, were examined microscopically and identification attempted using reference material housed at the Natural History Museum, London, UK.

Prey remains collected by Bill Walker are stored in the USA and were unavailable for cross-referencing purposes or prey measurement calculations and comparisons with the prey items recovered from the animals that stranded in 2003 (Cuvier's beaked whale) and 2004 (sperm whale).

Diet Composition

Percentages of cephalopod prey type present in the stomachs of a Cuvier's beaked whale and the sperm whale (strandings #4 and #5) were calculated and mean length and weights with standard deviations calculated for each prey species using the statistical package within Excel.

Nine prey types were identified and classified as squid (of which six family types were identified), octopods, crustaceans and fish.

Stomach content and faecal sample data were used to determine diet composition for each whale species.

Diet composition was calculated in terms of percentage of overall prey numbers recorded for each of the nine prey types.

Prey Distribution

Literature on the identified prey species from stomach contents and faecal sample analysis was reviewed in order to determine the known depth ranges in which each prey type is known to occur. This information is reviewed relating to the depths to which the three whale species may be foraging to in the Bahamas.

Niche Overlap and Competition

Niche overlap between Blainville's beaked whale, Cuvier's beaked whale and sperm whales in the northern Bahamas was calculated using a percentage overlap index (Krebs 1998),

$$P_{jk} = \left[\sum_{i=1}^{n} (\text{minimum } p_{ij},\ p_{ik}) \right] 100$$

where

P_{jk} = Percentage overlap between species *j* and species *k*

p_{ij} = Proportion resource *i* is of the total resources used by species *j*

p_{ik} = Proportion resource *i* is of the total resources used by species *k*

n = Total number of resource states.

Percentage overlap is a measure of the actual area of overlap of resource utilisation curves of the two species and is robust as it is not sensitive to how the resource states are divided (Krebs 1998).

In this study niche overlap is examined between the three whale species to make inferences about the depth of foraging dives and niches being exploited.

Chapter Two

RESULTS

Stomach Contents

Necropsies were performed on five deep diving whales from the study area: four beaked whales (three Cuvier's and one Blainville's beaked whale) and one sperm whale (Table 2.1). Prey remains were found in all the sampled stomachs, except that of the Blainville's beaked whale which was empty (Table 2.2).

The stomach of the first Cuvier's beaked whale from Grand Bahama (Stranding #1) contained five cephalopod beaks representing three individual squid, each of which being a different squid species. Portions of crustacean exoskeletons were also found, of which the number of antennulae found indicates a minimum of eleven individuals were represented. Squid eye lenses were also found, but no fleshy portions of prey remains were present and no fish remains were found (Table 2.2).

Non-prey items encountered were twenty three anisakid nematodes (probably *Anisakis simplex*) ranging in length from 10 to 30 mm and a small quantity (<1 cc) of typical beach matrix. No anthropogenic material was found.

The second Cuvier's beaked whale from Grand Bahama (Stranding #2) contained one cephalopod beak, two squid eye lenses and portions of a crustacean exoskeleton (Table 2.2). Of the crustacean remains found, carapace portions from one individual were present. No fish remains were

Stranded Animal Stomach Content Analysis Summary of Stranding Events

Reported date of stranding	Local Time (24hr)	Species	Stranding #	Location	Latitude	Longitude	Condition	Estimated age class	Sex	Length	Disposition (examined condition code)	Date and time of stomach contents collection
15 Mar 2000	afternoon	Cuvier's beaked whale	1	Gold Rock Creek, Grand Bahama	26° 36	-78° 22	Reported as live stranding	adult	F	18 ft	found dead (code 3)	18 March 2000 12:00 (local time)
15 Mar 2000	afternoon	Cuvier's beaked whale	2	Gold Rock Creek, Grand Bahama	26° 36	-78° 22	Reported as live stranding	sub-adult	M	17 ft	found dead (code 3+)	18 March 2000 12:00 (local time)
16 Mar 2000	13:00	Blainville's beaked whale	3	Cross Harbour Creek, Abaco	25° 56.4	-77° 16.5	Reported dead	juvenile	M	11 ft	found dead (code 2)	16 Mar 2000 13:00 (local time)
18 Apr 2003	06:00	Cuvier's beaked whale	4	Hopetown, Abaco	26° 31.9	-76° 57.4	Reported dead	sub-adult	M	14 ft (missing posterior part of body including entire tail – shark damage)	found dead (code 2)	18 Apr 2003 afternoon
02 Mar 2004	morning	Sperm whale	5	Rocky Point, Abaco	26° 00.0	-77° 24.7	Reported dead	sub-adult	M	30 ft	found dead (code 2)	02 Mar 2004 morning

Condition codes: code 1 = alive; code 2 = fresh dead; code 3 = moderate decomposition; code 4 = advanced decomposition; code 5 = mummified/skeletal; code 6 = dead condition unknown (NMFS 2001).

Table 2.1. Summary of stranded animal data where stomach contents were removed and analysed.

found and no fleshy remains of prey remains were present. Non-prey items encountered were five fragments of a marine plant (probably s*argassum* sp.) the largest of which was approx. 10 x 25 mm. No parasitic nematodes were present and no anthropogenic material was found.

The stomach of the Blainville's beaked whale from Abaco (Stranding #3) contained no prey remains. Non–prey items found included fourteen small anisakid nematode worms (probably *Anisakis simplex*) ranging in length from 10-24 mm. One approximately 10 x 120mm marine plant fragment (*Zostera* sp.) and approximately 8 cc of beach matrix consisting mainly of tiny coral fragments and Foraminifera. The mucosal lining of the stomach contained no visible lesions or ulcerations. No anthropogenic material was found.
(Report prepared by William A. Walker, June 6, 2000).

The stomach of the Cuvier's beaked whale stranded on Abaco (Stranding #4) contained two squid beaks, representing two squid species (Table 2.2). Crustacean exoskeleton remains were found, representing at least one individual from the suborder *Dendrobranchiata*, possibly being *Caridea*. No fish remains were present.

The stomach of the Sperm whale (Stranding #5) contained twenty nine lower and thirty five upper cephalopod beaks. Five squid species are represented and one deep water octopus species (*Haliphron atlanticus*). No crustacean or fish remains were found (Table 2.2).

	Whale Species and ID				
Sample # / Stranding #	**1**	**2**	**3**	**4**	**5**
Species	Cuvier's	Cuvier's	Blainville's	Cuvier's	Sperm
Sex	female	male	male	male	male
Age Class	adult	sub-adult	juvenile	sub-adult	sub-adult
Total Prey Types found	**4**	**2**	**0**	**3**	**6**
Cephalopoda					
Histioteuthidae					
Histioteuthis hoylei	✓ (1 UB, 1 LB)	✓ (1LB)	-	-	-
Histioteuthis 'type A'	-	-	-	✓ (1 LB)	✓ (13 LB)
Chiroteuthidae					
Chiroteuthis sp.	✓ (1 UB, 1 LB)	-	-	-	-
Chiroteuthis 'Type 1'	-	-	-	-	✓ (1 LB)
Chiroteuthis 'Type 2'	-	-	-	-	✓ (3 LB)
Octopoteuthis	-	-	-	-	✓ (1 LB)
Cranchiidae		-	-	-	✓ (6 LB)
Megalocranchia sp.	✓ (1 LB)	-	-	-	
Ommastrephidae	-	-	-	✓ (1UB)	-
Octopoda					
Haliphron atlanticus	-	-	-	-	✓ (5 LB)
Unknown Upper beaks	-	-	-	-	35
Crustacea					
Order – Decapoda			-		-
Suborder – Dendrobranchiata				✓ (min. of 1 individual) (possible infraorder of the above decapod)	
Infraorder – Caridea			-		-
Superfamily - Oplophoridae					
Acanthephyra sp. cf. A. curtirostris	✓ (min. of 11 individuals)	✓ (1 individual)	-	-	-
Fish	-	-	-	-	-

UB – Upper beaks, LB – Lower beaks

Table 2.2. Summary of prey species found in the stomachs of three deep diving whales inhabiting waters surrounding Abaco Island, The Bahamas.

Faecal Samples

Eleven faecal samples containing hard prey remains were collected between June 2002 and 23 August 2004 during encounters with free ranging whales in the South Abaco study area (Fig 1.1). Two samples were collected from Blainville's beaked whales and nine from sperm whales (Table 2.3).
Of the two Blainville's beaked whale's samples, one contained small fragments of crustacean exoskeleton and the other, two fish vertebral bones which could not be further classified.

From the nine Sperm whale samples, eight contained cephalopod remains from which eleven squid beaks were collected (eight lower beaks and three upper beaks). These beaks represented three squid species (*Histioteuthis meleagroteuthis*, *Histioteuthis* 'type A' and a member of the family *Enoploteuthidae*) (Table 2.3). The remaining faecal sample contained two portions of crustacean exoskeleton.

Prey Identification

Stomach and faecal sample analysis revealed the presence of five squid species represented in the diet of Cuvier's beaked whales from the Northern Bahamas.
Of the species found, regression analysis to determine prey size and weight was only possible for one squid type, *Histioteuthis* 'type A' (from stomach sample #4) (Table 2.4).

Date	Local Time (24hr)	Species	Specimen #	Location	Latitude	Longitude	Estimated age class	Sex	No. prey items in sample	Prey Type	Prey Identification	LRL	Length (squid) mm	Weight (squid) grams
06 Jun 2002	morning	Blainville's beaked whale	1	South Abaco	25° 56	77° 21	sub-adult	-	2	crustacean	unidentifiable	-	-	-
07 Jun 2002	14:03	Sperm whale	2	South Abaco	25° 55	-77° 21	adult	F	1	squid beak (LB)	Histioteuthis meleagroteuthis	4.6	89.5	170.8
08 Jun 2002	14:12	Sperm whale	3	South Abaco	25° 57	- 77° 26	adult	F	1	squid beak (UB)	unidentifiable	-	-	-
05 Jul 2002	15:00	Sperm whale	4	South Abaco	25° 52.21	-77° 16.29	sub-adult	-	1	squid beak (LB)	Enoploteuthidae	3.8	-	-
10 Jun 2003	14:46	Sperm whale	7	South Abaco	25° 57.371	-77° 24.307	- (group)	-	1	squid beak (LB)	Histioteuthis 'type A'	5.2	101.4	219.8
10 Jun 2003	15:37	Sperm whale	8	South Abaco	25 57.046	-77° 22.886	- (group)	-	1	squid beak (UB)	unidentifiable	-	-	-
10 Jun 2003	15:58	Sperm whale	9	South Abaco	25° 57.063	-77° 21.981	adult	F	3	squid beak (LB)	Histioteuthis 'type A'	(1) 4.8 (2) 5.9 (3)N/A	93.5 117.3 -	186.4 296.3 -
31 Jul 2003	15:44	Sperm whale	10	South Abaco	26° 03.561	-77° 34.002	adult	F	1	squid beak (UB)	unidentifiable	-	-	-
13 Mar 2004	11:13	Blainville's beaked whale	14	South Abaco	25° 54.75	-77° 17.55	calf	-	2	fish bones (vertebrae)	indeterminate fish	-	-	-
19 Jun 2004	09:43	Sperm whale	15	South Abaco	-	-	-	-	2	crustacean	unidentifiable	-	-	-
23 Aug 2004	10:58	Sperm whale (Pm14)	17	South Abaco	25° 56.19	-77° 21.92	adult	F	2	squid beak (LB)	Histioteuthis 'type A'	(1) 4.3 (2) 6.1	81.6 121.2	142 317.4

LRL = Lower rostral length, LB = Lower beak, UB = Upper beak

Table 2.3. Summary of faecal samples containing hard prey remains, collected from free ranging animals in south Abaco.

The sperm whale stomach and faecal sample analysis found the presence of seven squid and one octopod species in the diet of sperm whales in the southern study area.

Beak measurement was possible for seven of the eight cephalopod species represented in the sperm whale samples.

Of the squid species, estimates of size and weight revealed the *Cranchiidae* squid to be the largest squid species consumed (Tables 2.3 & 2.4).

In the stranded sperm whale (stranding #5) the most abundant prey species was *Histioteuthis* ‘type A’, representing 45% of the prey items consumed. The estimated mean size of the *Histioteuthis* ‘type A’ consumed was to 136 mm ML and of similar size and weight to the single specimen found in the stomach of the Cuvier’s beaked whale (stranding #4) (Table 2.4).

Prey mass estimates revealed that 79% of the estimated weight of consumed prey was represented by the octopod, *Haliphron atlanticus,* having a mean weight of 7941 grams (Table 2.4).

Prey Distribution

The prey analysis revealed the presence of nine principle prey types or components in the samples from the three whale species.

Six squid families were represented in the diet of the three whales, the *Histioteuthidae*, *Chiroteuthidae*, *Octopoteuthidae*, *Cranchiidae*, *Ommastrephidae* and *Enoploteuthidae*. A single octcopod species was represented, *Haliphron atlanticus*. Decapod crustaceans were found from the suborder *Dendrobranchiata*, and indeterminate fish bones were found.

	Number of lower beaks	No. of upper beaks	% of sample	No. measured	**LRL**/mm		**LHL**/mm		**Length**/mm		**Weight**/grams	
					Mean (S.D.)	Range	Mean (S.D.)	Range	Mean (S.D.)	Range	Mean (S.D.)	Range
Cuvier's Beaked Whale												
Histioteuthidae												
Histioteuthis 'type A'	1	-	1	1	6.96	-	-	-	**141.08**	-	**435.82**	**-**
Ommastrephidae		1	-	0	-	-	-	-	-	-	-	-
Sperm Whale												
Histioteuthidae												
Histioteuthis 'type A'	13	-	0.448		6.72 (0.81)	5.18 – 8.21	-	-	**135.59** (18)	101.42 – 168.84	**409.04** (111.09)	219.83 – 638.15
Chiroteuthidae												
Chiroteuthis 'Type 1'	1	-	0.034	1	6.96	-	-	-	181.75	-	148.29	-
Chiroteuthis 'Type 2'	3	-	0.103	3	4.23 (0.81)	3.39 – 5.00	-	-	114.77 (19.70)	94.39 – 133.70	40.62 (19.68)	21.27 – 60.61
Octopodaeties	1	-	0.034	1	11.43	-	-	-	197.66	-	328.14	-
Cranchiidae	6	-	0.207	6	10.77 (3.56)	6.61 – 15.18	-	-	663.12 (242.31)	379.24 – 963.22	716.11 (539.85)	155.50 – 1506.11
Octopoda												
Haliphron atlanticus	5	-	0.172	5	-	-	13.43 (3.15)	8.75 – 16.61	-	-	7941.30 (4745.08)	1757.42 – 13658.17
Unknown Upper beaks	-	35	-	-	-	-	-	-	-	-	-	-

LRL = Lower rostral length, LHL = Lower hood length

Table 2.4. Cephalopod size and weight analysis from stomach contents of a Cuvier's beaked whale and a sperm whale stranded on the island of Abaco, Bahamas (strandings #4 & #5).

Prey analysis revealed the presence of nine principle prey components in the samples from the three whale species. Six squid families were represented in the diet of the three whales, the *Histioteuthidae*, *Chiroteuthidae*, *Octopoteuthidae*, *Cranchiidae*, *Ommastrephidae* and *Enoploteuthidae*.
A single octcopod species was represented, *Haliphron atlanticus*.
Decapod crustaceans were found from the suborder *Dendrobranchiata* and for two of the stomach samples identified down to species level. The specimens found were a species of peaked shrimp (*Acanthephyra curtirostris*), a deep water shrimp living at depths greater than 500 metres (Table 2.5).
Two fish bones were found in a single faecal sample from a Blainville's beaked whale and on analysis, considered to originate from the same prey item. The bones could only be identified as indeterminate fish; as such no depth range could be determined.

All the prey types are considered to be deep water species, principally being inhabitants of the mesopelagic (200 – 700 m) to bathypelagic (700 – 2000 m) zones (200 – 2000 m depth range) (Nybakken 1997).

Diet Composition in the northern Bahamas

Diet composition in Blainville's beaked whale is considered to consist of 50% crustacean and 50% fish species. Cuvier's beaked whale diet as being comprised of 68% benthic invertebrates and 32% squid species. The sperm whales diet was divided into 2.3% benthic invertebrates, 86.3% squid and 11.4% octopods (Fig. 2.6).

Prey Species	Depth Range (metres)
Cephalopoda	
Histioteuthidae	
Histioteuthis hoylei (arcturi)	0->1000 (Voss et al. 1998)
Histioteuthis meleagroteuthis	100 – 2020 (Voss 1969)
Histioteuthis 'type A'	Some Histioteuthis beaks could not be identified to species but belong to the 'type A' group (Clarke 1986)
Chiroteuthidae *Chiroteuthis sp.* *Chiroteuthis 'Type 1'* *Chiroteuthis 'Type 2'*	0-2000 (Guerra 1992)
Octopoteuthidae Octopodaeties	0-2000 (Guerra 1992)
Cranchiidae *Megalocranchia sp.*	meso-bathypelagic and benthic zones (Nesis 1987)
Ommastrephidae	0->600 (Young 2005)
Enoploteuthidae	0-300 (Diekmann 2004)
Octopoda Haliphron atlanticus	Up to 3180 (Guerra 1992)
Crustacea Order – Decapoda Suborder – Dendrobranchiata Infraorder – Caridea Superfamily - Oplophoridae *Acanthephyra sp. cf. A. curtirostris*	>500 1000-1250 (highest abundance) (Foxton 1972)
Fish	-

Table 2.5. Depth range and distribution information of prey species.

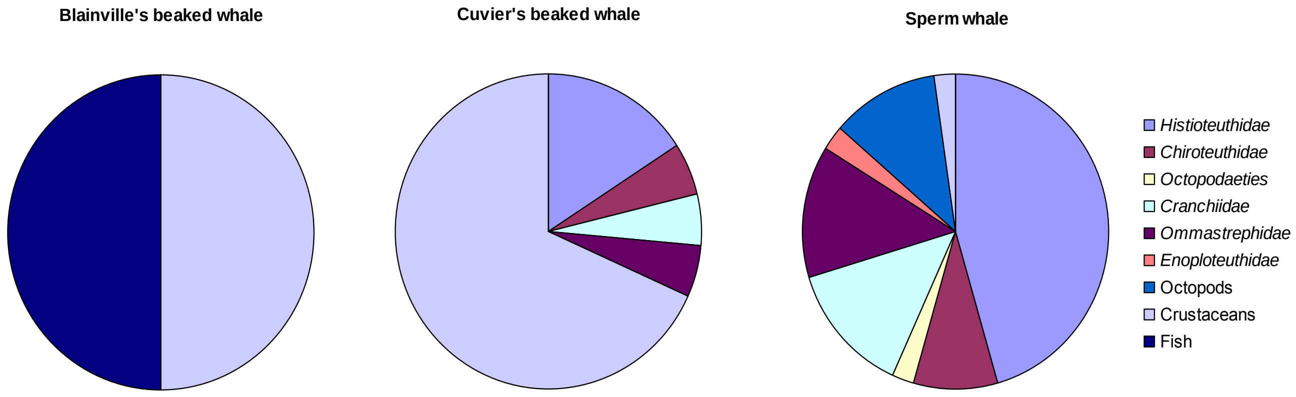


Figure 2.6. Percentage by abundance, of the prey types identified in the diet of Blainville's beaked whale, Cuvier's beaked whale and the sperm whale in the northern Bahamas.

Niche Overlap and Competition

Percentage niche overlap analysis using the data from the faecal samples and stomach contents of Blainville's beaked whale, Cuvier's beaked whale and sperm whales collected in the Bahamas, suggests virtually no overlap between Blainville's beaked whales and sperm whales. A 50% overlap between Cuvier's and Blainville's beaked whales and 33.9% overlap between Cuvier's beaked whales and sperm whales (Table 2.7).

Attention must be drawn to the sample sizes used to determine levels of overlap between these whale species in the Bahamas. Only two prey items were present for the Blainville's analysis. A total of 19 prey items were represented in the three Cuvier's samples and 44 items of prey were present in the 10 sperm whale samples.

Species	Squids						Octopods	Crustaceans	Fish	Percentage overlap with **Blainville's beaked whale**	Percentage overlap with **Cuvier's beaked whale**	Percentage overlap with **Sperm whale**
	Histioteuthidae	Chiroteuthidae	Octopodaeties	Cranchiidae	Ommastrephidae	Enoploteuthidae						
Mesoplodon densirostris Blainville's beaked whale (stomach n=1) (faecal n=2) **(Total food items, n=2)**	0 (0) **0**	0 (0) **0**	0 (0) **0**	0 (0) **0**	0 (0) **0**	0 (0) **0**	0 (0) **0**	0 (1) **0.5**	0 (1) **0.5**	100	50	2.3
Ziphius cavirostris Cuvier's beaked whale (stomach n=3) (faecal n=0) **(Total food items, n=19)**	3 (0) **0.157**	1 (0) **0.053**	0 (0) **0**	1 (0) **0.053**	1 (0) **0.053**	0 (0) **0**	0 (0) **0**	13 (0) **0.684**	0 (0) **0**	50	100	33.9
Physeter macrocephalus Sperm whale (stomach n=1) (faecal n=9) **(Total food items, n=44)**	13 (7) **0.455**	4 (0) **0.090**	1 (0) **0.023**	6 (0) **0.136**	6 (0) **0.136**	0 (1) **0.023**	5 (0) **0.114**	0 (1) **0.023**	0 (0) **0**	2.3	33.9	100

Values in brackets are those collected from faecal samples. Figures in bold are percentages of the diet represented by each prey type.

Table 2.6. Diet composition and percentage niche overlap between three deep diving whales found in the Northern Bahamas.

Chapter Two

DISCUSSION

This study used three techniques, stomach contents, faecal samples and niche overlap to make inferences about the diet and diving/foraging depths of Blainville's and Cuvier's beaked whales in the northern Bahamas.

The results of the stomach and faecal analysis show that dietary components from Bahamian Cuvier's beaked whales and sperm whales are consistent with those from stomach content studies from elsewhere in the Atlantic (MacLeod et al. 2003; Santos et al. 2001).
Principle prey components are cephalopods, crustaceans and fish, all of which being considered to be distributed within the meso- to bathypelagic depth ranges.

The lack of stomach content data for Blainville's beaked whale is disappointing and unfortunately consistent with a general trend of few or no prey items being found in analysed *Mesoplodon* stomachs (MacLeod et al. 2003).

Faecal collection and analysis has been proven possible for Blainville's beaked whale in this study and it is again unfortunate that the crustacean and fish remains collected could not be fully identified.
Blainville's beaked whale diet is considered to be comprised of primarily squid and deep water fish (Mead 1989).

Dietary evidence of squid consumption was not found in this study, but cephalopod prey is considered to be consumed by Blainville's beaked whales in the northern Bahamas, as high quality photo identification images taken during encounters with these animals have revealed the presence of cephalopod tentacle sucker scars on the rostrums of whales (pers. obs.).

On two occasions during encounters with Blainville's beaked whales, specimens of the big eyed scabbard fish (*Benthodesmus elongates*) have been found at the time when animals have resurfaced after performing long duration foraging dives (Claridge & Hickmott, unpublished data). Specimens showed signs of gas expansion of the swim bladder and physical disfigurement consistent with pressure related effects induced by rapid ascent from depth. This species is known from the western Atlantic and found at depths up to 1600 metres (ITIS 2005; Whitehead et al. 1987).

The specimens found may have been brought to the surface by foraging whales and might constitute part of the diet of Blainville's beaked whale in the Bahamas. Although this association and evidence of these fish being actual prey is speculative, a member of the same family of fishes, the *Trichiuridae* (Cutlassfishes, hairtails and ribbon fishes) was found to be the main component of the stomach of a stranded Blainville's beaked whale in South Africa (MacLeod et al. 2003).

Bias in diet studies

Dietary studies of consumed prey can be subject to bias and both stomach and faecal analysis are no exception. Both methodologies provide evidence of only the most recently consumed prey, and variability in the digestion rates of prey and retention of indigestible prey material in the gut can generate bias in results (Clarke 1980; Bigg & Fawcett, 1985; Clarke 1988). Equally some ingested prey items may be the result of consumption of “secondary prey items”, being prey of prey (Best 1999; Pierce & Boyle 1991) and others may be taken incidentally whist ingesting more typical prey (Whitehead 2003).

Specific to faecal sample collection, excretion rates, rates of dispersal and sinking, and detectability of smaller prey items, may all influence the outcome of diet studies (Whitehead 2003).

Genetic techniques using stable isotope analysis and fatty acid signatures from skin and blubber samples have been used to infer diet choice in two species of beaked whales (Ostrom et al. 1993; Hooker et al. 2001), reflecting diet choice over time periods of days to months. Hence overcoming some of the issues relating to bias in stomach and faecal analysis. Currently no such analysis has been published for Blainville’s and Cuvier’s beaked whales.

Niche Overlap

Diet analysis of sperm whales in the Bahamas was included in this study as stomach and faecal samples were available from the same geographic location as the beaked whale samples. Equally as sperm whales are known to conduct deep foraging dives for the same prey types as beaked whales (Whitehead 2003; Whitehead & MacLeod 2003).

Niche overlap was used to determine whether inferences made about the depth of foraging dives of sperm whales could also be applied to beaked whales if the level of dietary niche overlap was sufficiently high.

Niche overlap based on the stomach and faecal samples from the Bahamas would suggest that niche overlap is relatively low between the study species, being particularly low between Blainville's beaked whales and sperm whales. The level of overlap could be considered too low to allow inferences about dive depths based on foraging and prey distribution to be made about beaked whales based on sperm whale diet analysis.

It is worthy of mention that the sample sizes used to establish levels of niche overlap were small. This was particularly true for Blainville's beaked whale and the lack of data is likely to be the major factor in the levels of niche overlap presented in this thesis, rather than the results providing a clear indication of true levels of overlap.

Where larger datasets of diet have been used to determine diet composition (Pauly et al. 1998) and niche overlap analysed (Whitehead 2003) between these species, levels of overlap are far higher (Table 2.8).

In the south Abaco study site the dwarf sperm whale (*Kogia sima*) is the most commonly sighted deep diving whale species in pelagic waters (Claridge 2004). Data from Pauly et al. (1998) and Whitehead (2003) show in addition to sperm whales, the dwarf sperm whale has a high niche overlap with Blainville's and Cuvier's beaked whales. Stomach analysis have also shown that it consumes similar prey, from the meso- and bathypelagic zones

Species	Benthic Invertebrates	Squids		Fish			Percentage overlap with **Blainville's beaked whale**	Percentage overlap with **Cuvier's beaked whale**	Percentage overlap with **Sperm whale**
		Small	Large	Small Pelagics	Meso-pelagics	Miscellaneous fishes			
Mesoplodon densirostris Blainville's beaked whale	0	0.2	0.3	0	0.3	0.2	100	80	60
Ziphius cavirostris Cuvier's beaked whale	0.1	0.3	0.3	0	0.15	0.15	80	100	65
Physeter macrocephalus Sperm whale	0.05	0.1	0.6	0.05	0.05	0.15	60	65	100
Kogia sima Dwarf sperm whale	0.1	0.4	0.4	0	0.05	0.05	60	80	65

Diet data from Pauly et al. (1998), Percentage niche overlap from Whitehead (2003) using Krebs (1998) percentage overlap index of niche overlap.

Table 2.8. Diet composition of the four most frequently sighted deep diving whale species known to inhabit waters of South-West Abaco island, the Bahamas.

(Cardona-Maldonado & Mignucci-Giannoni 1999; Hűckstädt & Antezana 2001; McAlpine et al. 1997) and as such may also be used to aid the understanding of the foraging behaviour and dive depths of some beaked whale species.

Whitehead & MacLeod (2003) have shown that niche breadth is greater in sperm whales than Cuvier's beaked whales, indicating an increased level of specialisation in the dietary choice of Cuvier's beaked whales. This would suggest that making inferences about all the prey types consumed by sperm whales and similarities in depths of foraging dives of sperm whales and beaked whales would be inappropriate.
It could be argued however, that where no data exists for a species, information from another that shares similar behavioural, habitat and foraging traits may be employed with due caution to infer the depths of foraging dives of another species.
The high levels of niche overlap (based on the data of Pauly et al. (1998)) and depth distributions of the identified prey remains from Cuvier's beaked whales and sperm whales in this study, imply that both Blainville's and Cuvier's beaked whales in the northern Bahamas are deep water foraging animals of the meso- to bentho-pelagic zones (200 – 2000 m)

Diet studies can provide valuable insights into the probable dive depths of species. Hooker and Baird (2001) do however, highlight that such techniques can be important in interpreting studies of diving but can not replace detailed descriptions of diving behaviour, like those gained from the deployment of time-depth recorders (TDR’s) on animals (Hooker & Baird 1999).

Only recently has such data been gathered for Blainville’s and Cuvier’s beaked whales (Baird et al. 2004; Johnson et al. 2004).

Johnson et al. (2004) have deployed acoustic TDR tags that have provided highly detailed data on foraging behaviour, showing that both species dive to depths within the meso- and bathy-pelagic zones. Tags have shown that Blainville’s beaked whale begin echolocating at a mean depth of 400 m and Cuvier’s beaked whale, at 475 m. Changes in echolocation from regular clicks to buzzes and impact sounds with possible prey have been recorded, along with bottom echo’s from the sea floor indicating that some near benthic foraging occurs.

The presence of sand in a faecal sample from a free swimming Blainville’s’ beaked whale collected in the south Abaco study site during the summer of 2005 (Claridge, pers. comm.) may provide additional evidence that at times these animals forage benthically.

Madsen et al. (2005) have shown that a foraging Blainville’s beaked whale spent most of its time during foraging dives between 650 and 725 m depth, where it produced the most echolocation buzzes, considered to be associated with targeting and attempts to catch prey items.

Although the TDR data are from the eastern Atlantic and Pacific and only a small number of Blainville's and Cuvier's beaked whales have been tagged with TDR's, the highly detailed data on foraging depth and behaviour clearly compliment the inferences made about the foraging behaviour and dive depths from diet analysis of these species in the Bahamas.

In conclusion, this study has demonstrated that dietary analysis can be used as a tool to aid the understanding of dive depth and foraging behaviour in two, difficult to study, beaked whale species in a geographic area where previously no dietary analysis has taken place.

Chapter Three

INTRODUCTION

This chapter investigates the role of diving behaviour in studying the ecology of Blainville's and Cuvier's' beaked whales, where the term 'diving behaviour' is used to describe the pattern of surfacing, where dive durations are known but dive depths are not (Hooker and Baird 2001).

Studying diving behaviour is considered important because knowledge of three-dimensional habitat use can aid understanding of a species ecology (Hooker & Baird 2001). Relative to the number of species of beaked whales (Ziphiidae) and their near global distribution, very little is known about their ecology or abundance.

Beaked whales, perhaps more than any other cetacean group spend the greatest preponderance of their daily lives submerged beneath the surface in offshore habitats. This coupled with their cryptic, inactive surface behaviour and typically small group sizes, make them difficult to detect and study (Barlow 1999; Claridge 2004; Hooker & Baird 1999a).

Blainville's and Cuvier's beaked whales are considered the most cosmopolitan of beaked whale species (Mead 1989; Heyning 1989) and yet both are listed as data deficient (sufficient data on abundance and distribution is absent) on the IUCN Red List of Threatened Species (1996).

Incidental catches of both species have been recorded, associated with pelagic driftnet fisheries in the western North Atlantic and are considered to exceed potential biological removal levels (Read & Wade 2000).
Data on diving behaviour and knowledge gained from different geographic locations may be used in generating improved detection functions for line-transect surveys. These techniques are commonly employed to quantify distributions and generate abundance estimates, which can then be directly applied in conservation strategies and management plans (Barlow et al. 1997; Barlow & Sexton 1996).

Knowledge of the diving behaviour of these species is of further importance because disruption to what may be considered ‘normal’ diving behaviour in these species has been proposed as an influential factor in their vulnerability to acoustic trauma (Fernández et al. 2005a). Quantifying what the diving behaviour is in these species and within specific populations and geographical areas may assist in understanding whether the theories relating to acoustic trauma are relevant.

Records of diving behaviour in Blainville’s’ and Cuvier’s beaked whales have until recently been limited to data on surfacing patterns (Barlow and Sexton 1996; Barlow et al. 1997).
Hooker and Baird (1999b) were the first to deploy time-depth recorders (TDR’s) on a beaked whale species (northern bottlenose whale, *Hyperoodon ampullatus*), gathering comprehensive information on three-dimensional ranging of ziphiid whales. Subsequently, TDR’s have been deployed on both

Blainville's and Cuvier's beaked whales (Baird et al. 2004; Johnson et al. 2004), but the number of deployments remains low due to the difficulties associated with working with beaked whales and deploying TDR devices.
To date, no specific data has been published on diving behaviour of these species in the central western Atlantic (surfacing patterns or TDR data). Observations by Balcomb (1981) are perhaps the first records of diving behaviour of beaked whales in the Bahamas, yet the animals were only identified as *Mesoplodon* sp.

Both whale species are known to be deep and long duration divers (Mead 1989) and published dive duration records of these species vary, Miyazaki and Wada (1978) reported Cuvier's beaked whale dive durations of 30-40 min, Barlow (1999) recorded median dive durations of 28.6 min and TDR results have shown median durations of 22.5 min with a maximum of 87 min (Baird et al 2004). Tyack et al. (2005) found that deep foraging dives had a mean of 58 min and maximum of 85 min.
In the case of Blainville's beaked whale, Barlow et al. (1997) presented data for *Mesoplodon* sp., inclusive of Blainville's beaked whale where median dive duration was 18.7 min in the Gulf of California. Baird et al. (2004) recorded shallow dives with a mean of 7.47 min in Hawaii and deep foraging dives in the Canary Islands had a mean duration of 50 min (Tyack et al. 2005).

Diving behaviour can be subdivided into categories of dives considered to be for specific behaviours (e.g. deep long duration foraging dives and shallow short duration recovery/respiration dives) and analysis of recovery dives and extended surface intervals can provide insights into whether animals are diving within their aerobic dive limits (Hooker & Baird 1999b). Categorisation of dive data may account for differences observed in some of the published data on dive duration in the study species.

Investigating the existence of different dive types and differences between age classes, and whether these species are diving within their aerobic dive limits may aid the understanding of how beaked whales cope with the effects of diving repeatedly to depth and the physiological impact of such behaviour. Insights into the durations of dives, surface recovery periods and inter-ventilation durations (respiration rates), are important in determining the significance of proposed theories of the causative factors that lead to beaked whales stranding when exposed to navy sonar.

Diving behaviour data is analysed here, to establish whether different dive types exist for the study species. The diving behaviour of groups of Blainville's beaked whales where group composition differed, in terms of presence or absence of juveniles or calves was also investigated to examine whether any strategies to care for young during long foraging dives are employed by this species, as alloparental care has been shown in the sperm whale, another deep diver (Whitehead 1996).

Additionally, inter-ventilation durations are examined between the two beaked whale study species to provide an additional insight into the differing physiological requirements of these whales and see if hyperventilation type behaviour was evident prior to diving.

Analysis of the respiratory pattern of an animal that stranded during the Bahamas 2000 event is also included to compare physiological differences between a stressed sonar exposed animal and free swimming animals considered to be healthy and unexposed to sonar.

The aim of this chapter was to determine the diving behaviour of Blainville's and Cuvier's beaked whales in the northern Bahamas by (i) investigating the relationship between the duration of dives recorded and sea state (Beaufort scale), relative to the detectability of animals, (ii) applying different analysis methods to determine whether these species perform different dive types, (iii) determine whether animals are diving aerobically by investigating relationships between dive duration and surface interval, (iv) look for differences in diving behaviour between age classes in Blainville's beaked whale, (v) investigate differences in inter-ventilation durations between species as an additional insight into physiological differences between species.

Chapter Three

METHODS

Opportunistic vessel surveys were conducted off the southern and eastern side of Great Abaco Island in the northern Bahamas between 1994 - 2004. Surveys were conducted throughout the year, depending on the weather conditions, and more frequently in the summer months. When at sea, vessels conducted non-random searches for beaked whales, frequently returning to areas that had previously yielded a high probability of encounters. 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 long dives. During the course of an encounter visual observers were employed to monitor 360 degrees around the vessel. Searching was conducted using both the naked eye and 7X binoculars and the time recorded each time an animal or synchronously diving group dived and surfaced. Opportunistic surveys were conducted in sea state conditions between Beaufort 0 and 4.

All fieldwork was conducted under The Bahamas Marine Mammal Survey (BMMS) research permit issued by The Bahamas Department of Fisheries (permit # MAF/FIS/12A).

When animals were sighted and encounters begun, data were collected on the location, species, group size and composition, and direction of travel (if any). Every 15 minutes the time, location, sea state and behavioural state were recorded until the encounter ended.

In order to document the species, group composition and study the diving behaviour of different age classes, high quality photographs of the head, thoracic region and dorsal fins of beaked whales were taken during encounters. These were later examined and individuals were separated into different age classes. Group sizes were established via the number of individuals visually identified by experienced observers and subsequently confirmed by photographic analysis.

Age class characteristics are here taken from those presented by Claridge (2004) stating,

"Sexual dimorphism has been described for dense-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 3."

Encounter Summary information

Blainville's beaked whale encounters

On 13 occasions diving and surfacing behaviour was not considered to be synchronous within groups of Blainville's beaked whales. In these cases, surface intervals and dive durations were recorded for individually identified animals within the group. This meant that 146 surface interval and diving profiles were recorded for Blainville's beaked whales and used in the analysis presented.

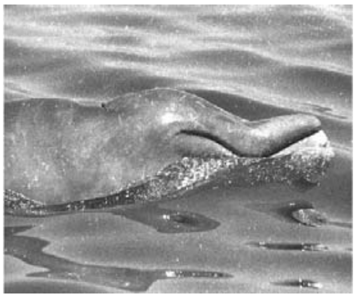
Adult male

- 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

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

Figure 3. Sexual dimorphism in dense-beaked whales makes it possible to readily distinguish five different age and sex classes from high quality photographs of the head and thoracic region (Figure recreated from Claridge 2004).

Definition of diving in this study

In this study the term ‘diving behaviour’ is used to describe the pattern of surfacing, where dive durations are known but dive depths are not (Hooker and Baird 2001).

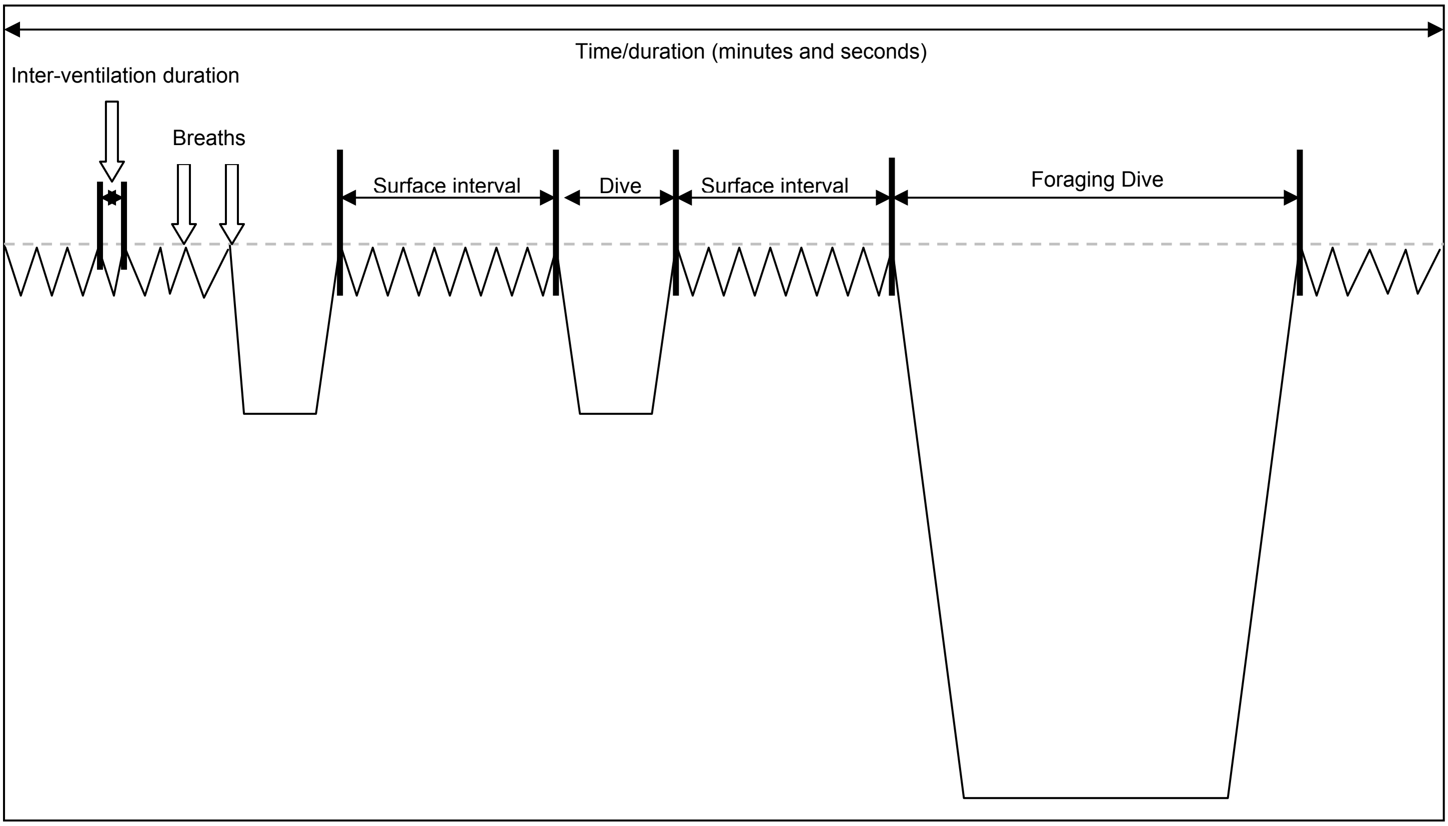


Figure 3.0. Hypothetical dive profile of a beaked whale, indicating the nature and types of data presented and analysed in this study.

Data Analysis

The diving behaviour datasets (dive durations and surface interval (SI) durations) for both Blainville’s and Cuvier’s beaked whales and the data split by age class, were analysed and compared for the presence of different dive or surface interval types. Log-survivorship plots (Fagen & Young 1978) were generated and fitted with a non-linear ‘broken-stick’ model to determine break points within the data. The sums of the mean squared errors of the three fitted regression lines were calculated and the data divided at the durations (either dive or SI) that resulted in the minimum sum of mean squared errors (minimum mse) (Sibly et al. 1990). Cumulative time plots (cumulative time spent in dives or SI's of different durations) were also used; where it is assumed that bimodality within the data defines the presence of different data types and that the trough in the data indicates the break point between types (Hooker & Baird 1999b).

Surface Interval Analysis

In order to investigate whether animals dive within their aerobic dive limits, data series of were split and paired to allow comparison of the duration of a dive compared to the duration of a surface interval prior to it. The raw data was then used again to split series into pairs of times where a dive duration could be compared to the duration of the surfacing interval that followed it. Scatter plots were then generated and linear regression lines plotted to assess the degree of correlation between pairs of data.

This method was also applied to study the inter-ventilation durations.

Median dive and surface interval times were used during the analysis. Median durations are considered to be a better estimate of expected dive or surface interval duration than mean durations, because they are less affected by extreme outliers that may represent errors (Barlow & Sexton 1996).

All statistical analyses and modelling were performed using the statistical packages 'R' and 'StatsDirect'.

Study of a stranded Cuvier's beaked whale

On March 15th 2000 a juvenile Cuvier's beaked whale live stranded at Rocky Point, Abaco (25°59.802, -77°24.344) in association with a naval sonar exercise. Whilst stranded and prior to the animal being refloated and assisted back out to sea, inter-ventilation durations were recorded. The data are presented in this study purely due to the novel and unique nature of the data.

Chapter Three

RESULTS

Encounter Summary information

Blainville's beaked whale encounters

Diving behaviour information was recorded during 133 encounters with groups of Blainville's beaked whales between 1994 and 2004, in all seasons of the year (Table 3.1). Eight encounters took place in the east Abaco study area and the remainder were in south Abaco (Appendix 1, Table 1.1).

On 13 occasions diving and surfacing behaviour was not considered to be synchronous within groups of animals and surface interval and dive durations were recorded for individually identified animals within the group. This meant that 146 surface interval and diving profiles were recorded for Blainville's beaked whales and used in the analysis presented.

Year	Spring	Summer	Autumn	Winter	Total
1994	-	-	-	1	1
1995	-	1	-	-	1
1996	-	1	-	-	1
1997	1	1	-	-	2
1998	3	6	-	-	9
1999	7	6	-	2	15
2000	6	16	-	6	28
2001	8	6	7	5	26
2002	-	11	-	7	18
2003	1	4	6	4	15
2004	3	11	-	3	17
Total	29	63	13	28	**133**

Table 3.1. Frequency of Blainville's beaked whale encounters between 1994 and 2004, inclusive of the season during which encounters occurred (n=133) (Spring = March, April and May; Summer = June, July and August; Autumn = September, October and November; Winter = December, January and February).

Group size ranged from one to 11 animals (Table 3.3) of mixed composition, but where no group ever contained more than one adult male.

The total duration of encounters with Blainville's beaked whale ranged from 0.3 to 274.5 minutes (Table 3.3).

The summed totals of the durations of dives and surface intervals conducted during each encounter were calculated (Appendix 1, Table 1.1) and are summarised in Table 3.3.

On average Blainville's beaked whales spent approximately half the duration of an encounter submerged on dives (Table 3.3).

Cuvier's beaked whale encounters

Dive duration data was recorded during sixteen encounters with Cuvier's beaked whale between 1995 and 2004 and encounters occurred in all seasons (Table 3.2). Only one encounter occurred in the east Abaco study area.

The average group size was half that of Blainville's beaked whale (Table 3.3).

Year	Spring	Summer	Autumn	Winter	Total
1995	-	-	-	1	1
1996	-	-	-	-	-
1997	2	-	-	1	3
1998	-	-	-	-	-
1999	-	1	-	2	3
2000	2	-	-	-	2
2001	-	-	-	-	-
2002	1	-	-	2	3
2003	-	-	1	-	1
2004	-	3	-	-	3
Total	5	4	1	6	**16**

Table 3.2. Frequency of Cuvier's beaked whale encounters between 1995 and 2004, inclusive of the season during which encounters occurred (n=16).

Total encounter durations ranged from 3.5 to 156 minutes (summarised in Table 3.3) (Appendix 1, Table 1.2) and the average was approximately double that of Blainville's beaked whale encounters.

In comparison with Blainville's beaked whale, Cuvier's beaked whale spent a considerably greater percentage of the total encounter duration diving. The total time performing surface intervals during encounters was also very different, being approximately half that of Blainville's beaked whales (Table 3.3).

The percentage of time spent diving during encounters was significantly different between the two species (Mann-Whitney U test; P = < 0.0001), as was the percentage of time conducting surface intervals (Mann-Whitney U test; P = < 0.0001).

Species	No. of Encounters n	Group size Mean (S.D.)	Summed total Enc. Duration /min Mean (S.D.)	Summed total duration of dives performed during an encounter /min Mean (S.D.)	Summed total duration of surface intervals performed during an encounter /min Mean (S.D.)	% of encounter spent diving Mean (S.D.)	% of encounter performing surface intervals Mean (S.D.)
Blainville's beaked whale	133	4 (1.9)	36.7 (42.3)	22.4 (34)	14.3 (12.7)	0.44 (0.3)	0.56 (0.3)
Cuvier's beaked whale	16	2 (1.3)	61.5 (46.6)	53.7 (44.3)	7.9 (6.9)	0.75 (0.3)	0.25 (0.3)

Table 3.3. Comparison of encounter summary statistics between Blainville's beaked whales and Cuvier's beaked whales.

Dive Duration vs. Sea state

Blainville's beaked whale

The effects of sea state on the frequency of dives recorded and the duration of dives was examined and the results presented in Fig. 3.4. A total of 376 dive durations were recorded, of which 73% were recorded in Beaufort (B) sea states 0 to 1. The least number of dives were recorded in sea state 4 (2%).

A non-parametric Kruskal-Wallis squared rank test revealed that sea state did not affect the dive durations recorded (Chi-square = 5.54, df = 4 P = 0.2361), as such all dives recorded in each sea state were used in the subsequent diving analysis.

Although statistical analysis suggests that no difference exists between the dive durations recorded in the five different sea states, it is evident that maximum dive durations are much larger in sea states B0 to B3, ranging between 60 and 73 minutes compared to that recorded in B4, being 18 minutes.

The number of dives recorded in excess of 20 minutes varied with sea state (Fig. 3.4), possibly being a function of the number of dives recorded in each sea state.

Cuvier's beaked whale

Dive durations were recorded in all five sea states, with 69% (n = 27) of dives being recorded in B0 - B1, with only one record in B4 (Fig. 3.5). A Kruskal-Wallis test showed that sea state did not affect the durations of dive records (P = 0.2901, df = 3 (N.B. only sea states B0 to B3 could be analysed, as only one record existed for B4)).

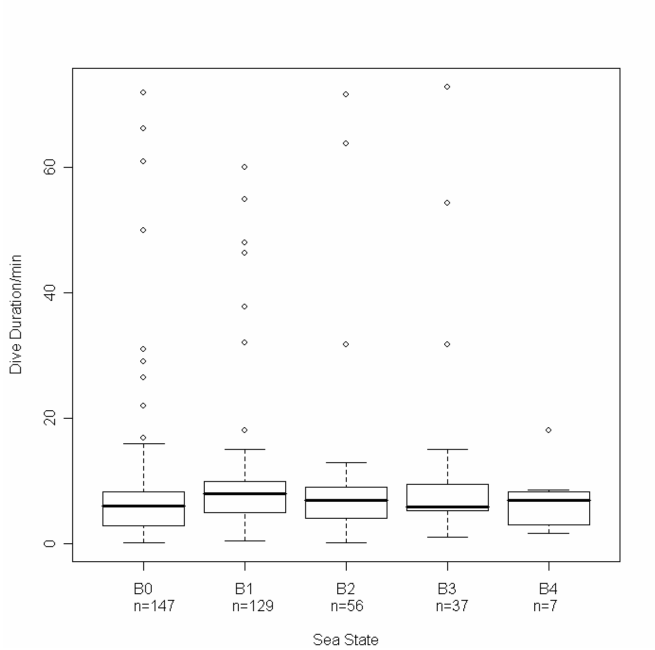


Figure 3.4. Box plot of dive durations recorded for Blainville's beaked whale in five different sea states. Median values are shown with upper and lower quartiles, range (range of data values multiplied by the interquartile range) and outliers.

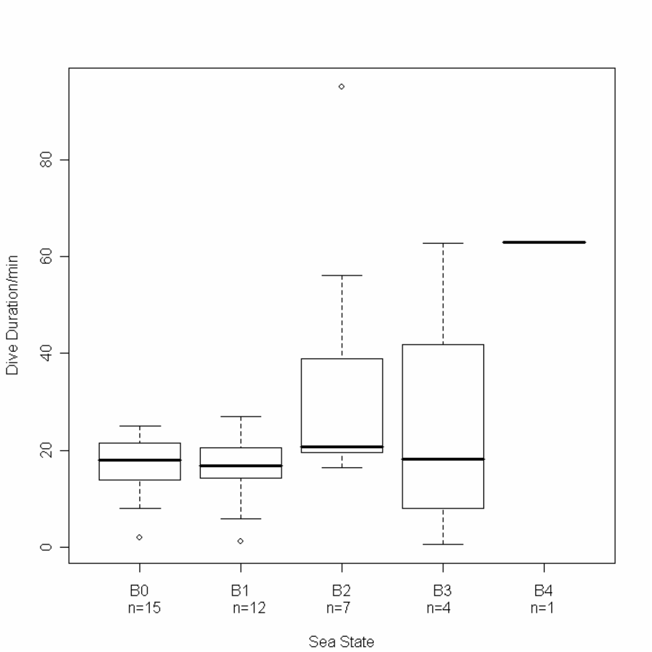


Figure 3.5. Box plot of dive durations recorded for Cuvier's beaked whale in five different sea states. Median values are shown with upper and lower quartiles, range (range of data values multiplied by the interquartile range) and outliers.

Frequency of Dives

Blainville's beaked whale

A total of 376 dives were recorded between 1994 and 2004, and dive durations had a median of 7 minutes (mean = 8.7 min, S.D. = 10.7) (Fig. 3.6).

Cuvier's beaked whale

A total of 39 dives were recorded between 1995 and 2004 (Fig. 3.7). Dives had a median duration of 19 minutes (mean = 22 min, S.D. = 17.9).

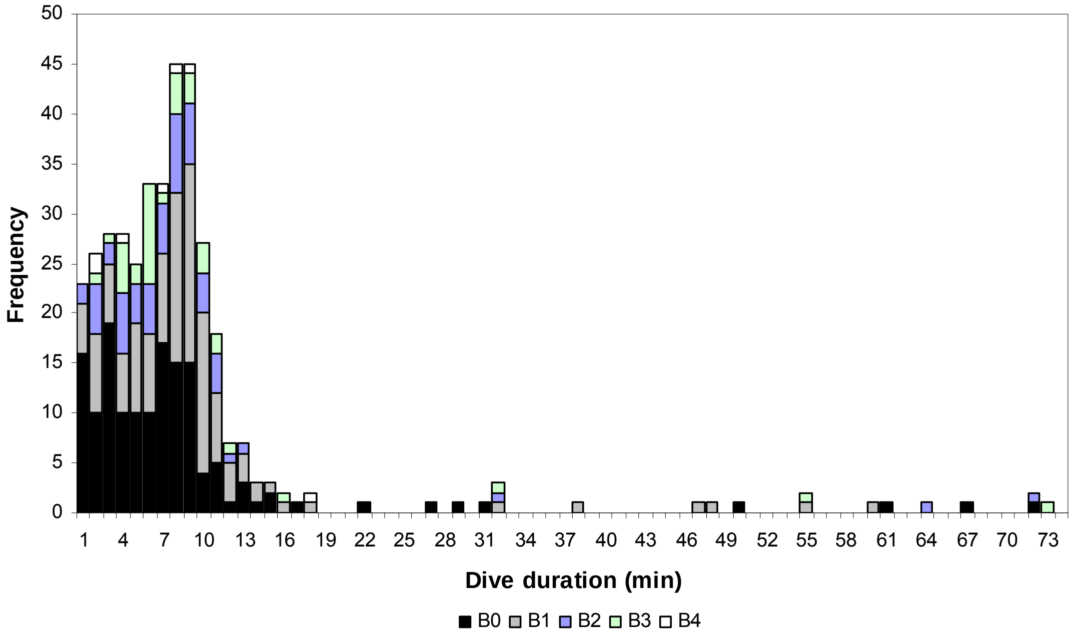


Figure 3.6. Frequency histogram plot of Blainville’s beaked whale dive durations occurring in one minute bins, inclusive of the sea state during which dives occurred (n=376).

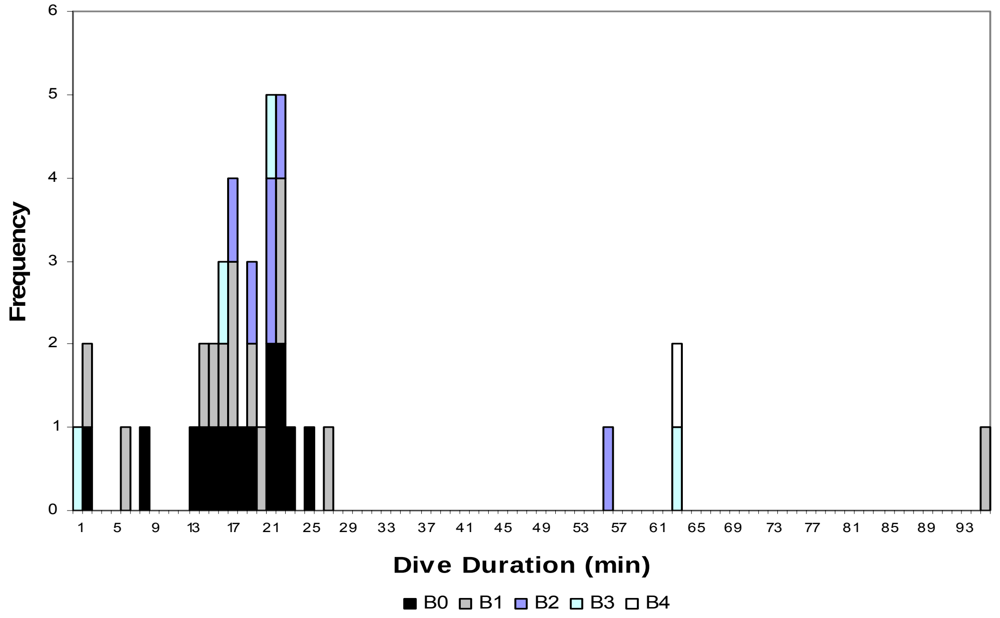


Figure 3.7. Frequency histogram of Cuvier’s beaked whale dive durations occurring in one minute bins, inclusive of the sea state during which dives occurred (n=39).

Bout Analysis

Log-survivorship analysis of Blainville's and Cuvier's beaked whale dive durations

The log-survivorship plot and broken stick model clearly defined two distinct breaks in the dive duration data for both species. These breaks were at 8 and 13 minutes for Blainville's beaked whale (minimum mse = 0.025) (Fig 3.8) and 16 and 23 minutes for Cuvier's beaked whale (minimum mse = 0.017) (Fig 3.9).

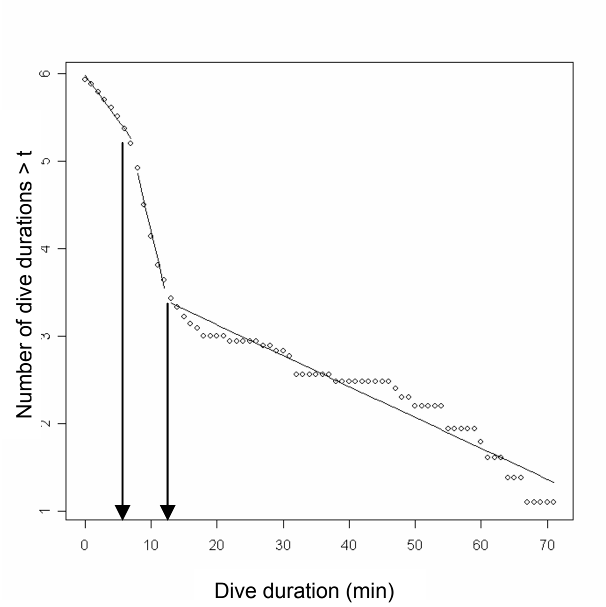


Figure 3.8. Log-survivorship plot of Blainville's beaked whale dive durations (n= 376), fitted with a broken stick model to define dive types.

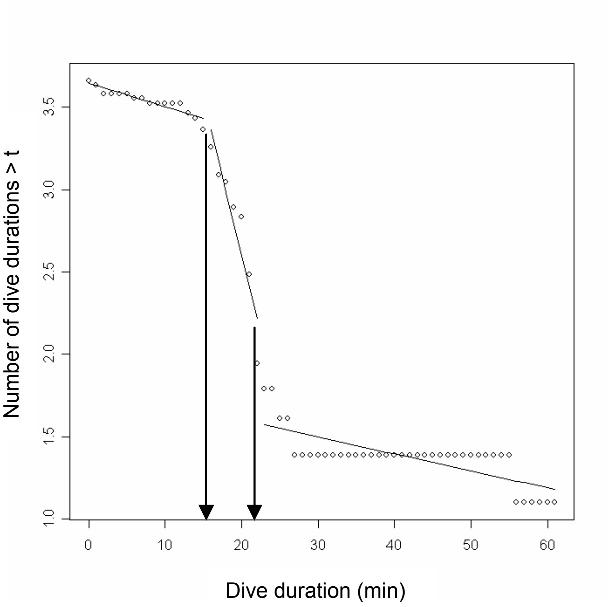


Figure 3.9. Log-survivorship plot of Cuvier's beaked whale dive durations (n= 39), fitted with a broken stick model to define dive types.

Log-survivorship analysis broke the data into three different dive types. These were defined as short, medium and long dives (Table 3.12).

The duration of the three dive types were compared between species. Short dive durations were significantly different (Mann-Whitney U test; P = 0.001), as were medium duration dives (Mann-Whitney U test; P = <0.0001).

Long duration dives however were not significantly different (Mann-Whitney U test; P = 0.113).

Cumulative time analysis of Blainville's and Cuvier's beaked whale dive durations

Cumulative time analysis broke both species data sets into short and long dives. Blainville's beaked whale data was broken at 22 minutes (Fig. 3.10) and the Cuvier's beaked whale data at 44 minutes (Fig. 3.11). Dive types of both species are summarised in Table 3.12.

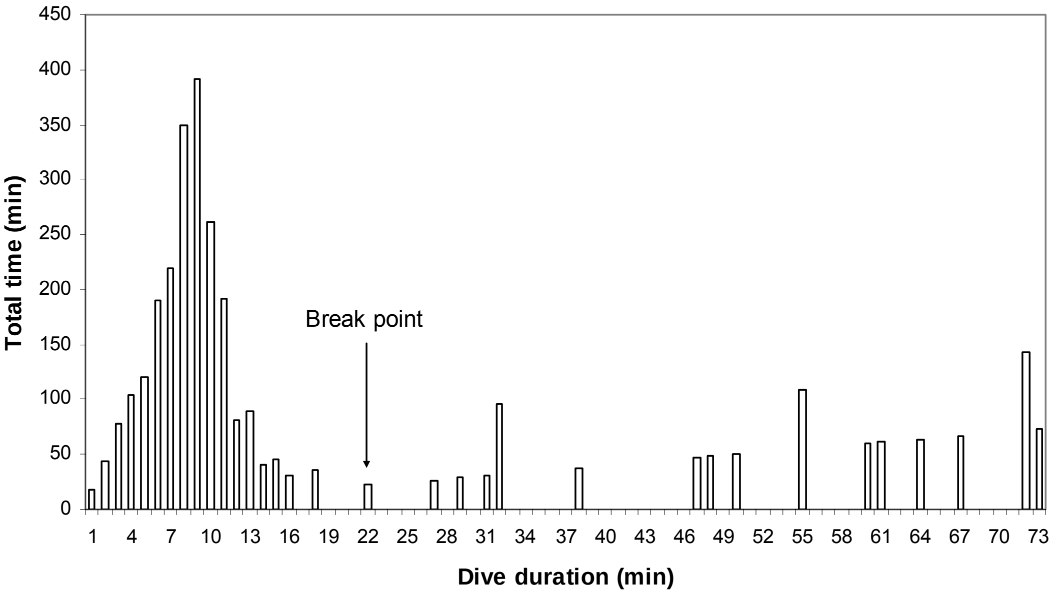


Figure 3.10. Cumulative time spent in dives of different duration for Blainville's beaked whales (n = 376).

The duration of short dives of each species were significantly different (Mann-Whitney U test; P = < 0.0001). Where as long dives were not (Mann-Whitney U test; P = 0.097).

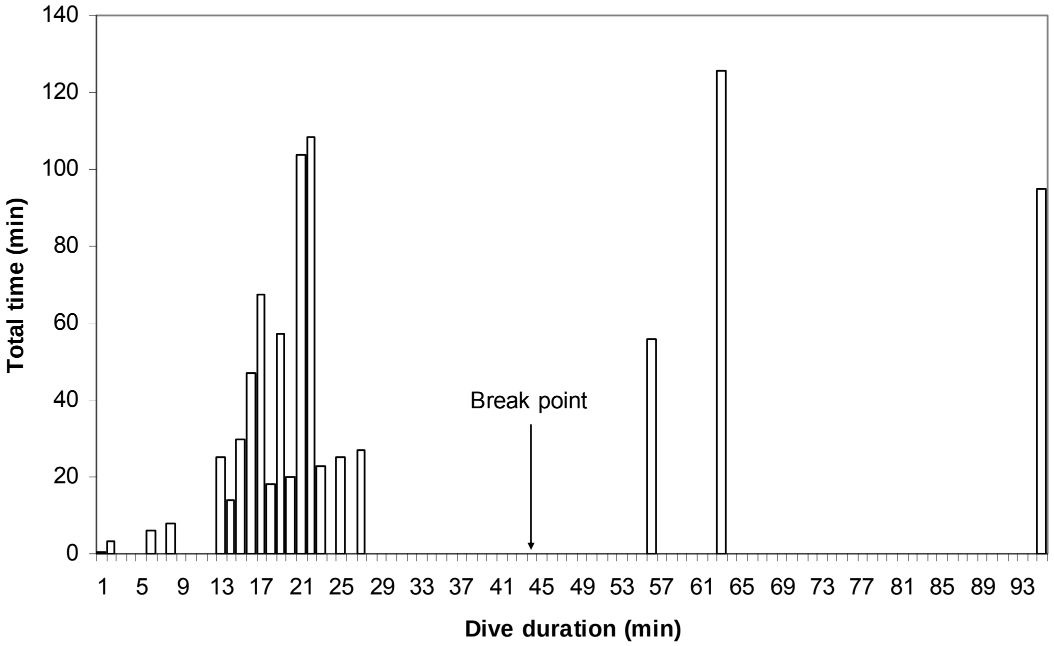


Figure 3.11. Cumulative time spent in dives of different duration for Cuvier's beaked whale (n = 39).

		Log-survivorship						Cumulative time					
Species	Dive type	Breaks	n	mean	median	S.D.	Range	Breaks	n	mean	median	S.D.	Range
Blainville's	Short	0-8	241	4.7	5	2.4	0.1-8	0-22	257	6.5	6.6	3.6	0.1-22
	Medium	9-13	104	9.8	9.5	1.3	8.1-13	-	-	-	-	-	-
	Long	14+	31	36.5	31.7	20.9	13.4-72.9	23+	19	49.5	50	16.2	26.5-72.9
Cuvier's	Short	0-16	13	10.3	13	5.9	0.6-16	0-44	35	16.7	18	6.4	0.6-27
	Medium	17-23	20	19.9	20.6	2	16.5-22.7	-	-	-	-	-	-
	Long	24+	6	54.8	59.4	26.1	25-95	45+	4	69.2	62.8	17.5	56-95

Table 3.12. Summary of dive duration data (minutes) of both beaked whale species analysed using two forms of bout analysis, log-survivorship and cumulative time plots.

Dive duration vs. age class in Blainville's beaked whale

Dive records with juveniles or calves present

A total of 257 records were recorded when juvenile or calves were present and dives had a median duration of 7 min (mean = 8.7 min, S.D. = 10.7) (Fig. 3.13).

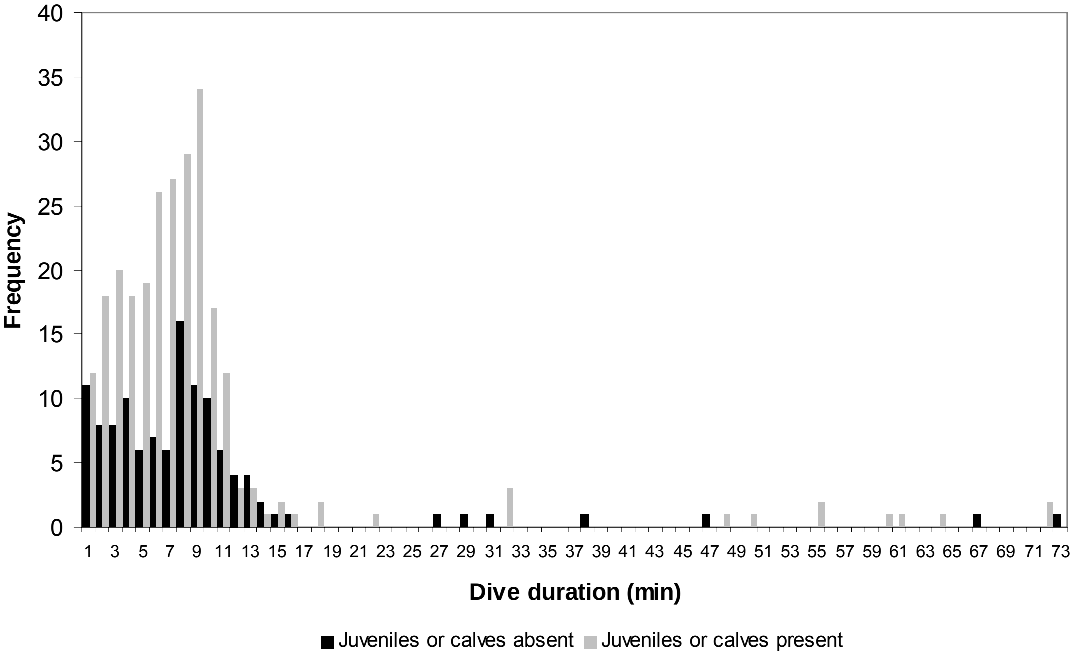


Figure 3.13. Frequency histogram of Blainville's beaked whale dive durations occurring in one minute bins, where juveniles and calves were present (n=257) or absent (n=118).

Dive records with juveniles or calves absent

118 dive durations were recorded where juveniles and calves were absent, with a median duration of 7.6 minutes (mean = 8.7 min, S.D. = 10.6) (Fig. 3.13).

Bout analysis of age class divided dive data for Blainville's beaked whale

Log-survivorship analysis

The log-survivorship plot and broken stick model clearly defined two distinct breaks within the data for both the presence and absence data sets. These breaks were at 8 and 13 minutes where juveniles and calves were present (minimum mse = 0.051) and 8 and 15 minutes where they were absent (minimum mse = 0.029). Data are summarised in Table 3.15.

Statistical analysis showed that there was no significant difference between the presence and absence short dive data (Mann-Whitney U test; P = 0.184). A difference between the data sets was more evident for the medium duration dives, just missing the 5% significance level (Mann-Whitney U test; P = 0.054).

There was no significant difference between long dives (Mann-Whitney U test; P = 0.805).

Cumulative time analysis

Based on the plot (Fig. 3.14), the data were split into short and long dives. Where juveniles and calves were absent the break was at 26 minutes and where they were present, at 22 minutes. The data are summarised in Table 3.15.

No significant differences were found for either short dives (Mann-Whitney U test; P = 0.910) or long dives (Mann-Whitney U test; P = 0.251) when the two data sets were compared.

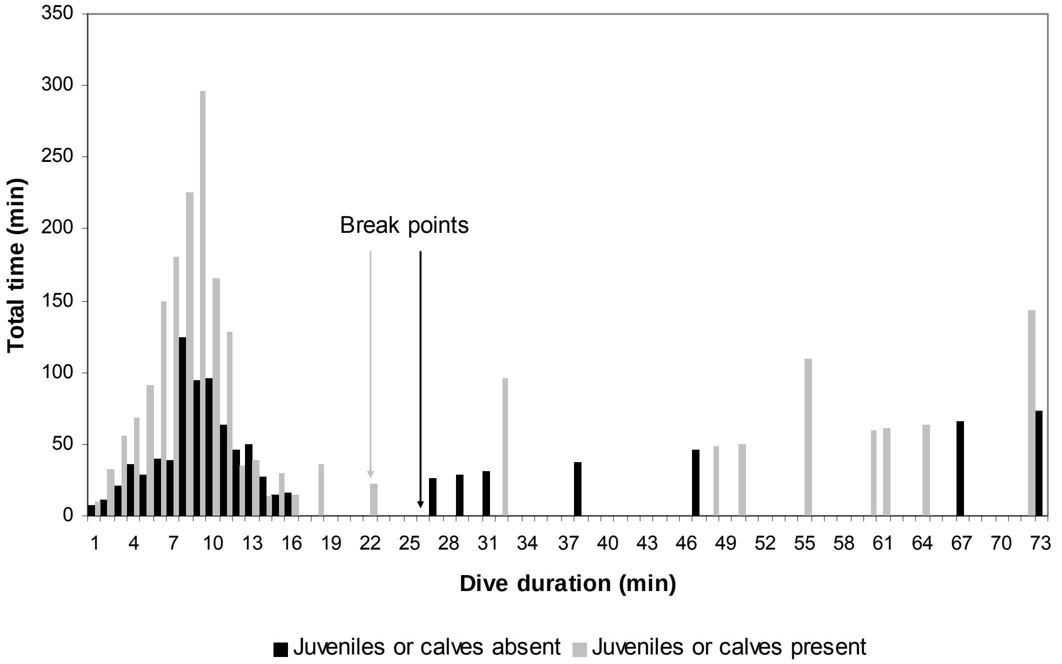


Figure 3.14. Cumulative time spent in dives of different duration for Blainville's beaked whale, where juveniles and calves were either present or absent in encountered groups.

		Log-survivorship						Cumulative time					
Group Composition	Dive type	Breaks	n	mean	median	S.D.	Range	Breaks	n	mean	median	S.D.	Range
Juveniles or calves absent	Short	0-8	72	4.3	4	2.6	0.2-8	0-26	111	6.5	6.7	3.8	0.2-15.9
	Medium	9-15	38	10.4	9.9	1.7	8.1-15	-	-	-	-	-	-
	Long	16+	8	40.7	34.4	19.9	15.9-72.9	27+	7	44.3	37.8	18.6	26.5-72.9
Juveniles or calves present	Short	0-8	169	4.8	5	2.2	0.1-8	0-22	245	6.5	6.5	3.4	0.1-22
	Medium	9-13	69	9.6	9.1	1.2	8.2-13	-	-	-	-	-	-
	Long	14+	19	39.4	32	21.2	13.7-72	23+	12	52.6	54.7	14.5	31.7-72

Table 3.15. Summary of dive duration data (minutes) of Blainville's beaked whales where juveniles and calves were either present or absent in encountered groups, analysed using two forms of bout analysis, log-survivorship and cumulative time plots.

Surface Interval Analysis

Frequency of Surface Intervals

Blainville's Beaked Whale

483 surface intervals were recorded between 1994 and 2004, having a median duration of 3 minutes (mean = 4.3 min, S.D. = 5.7) (Fig. 3.16).

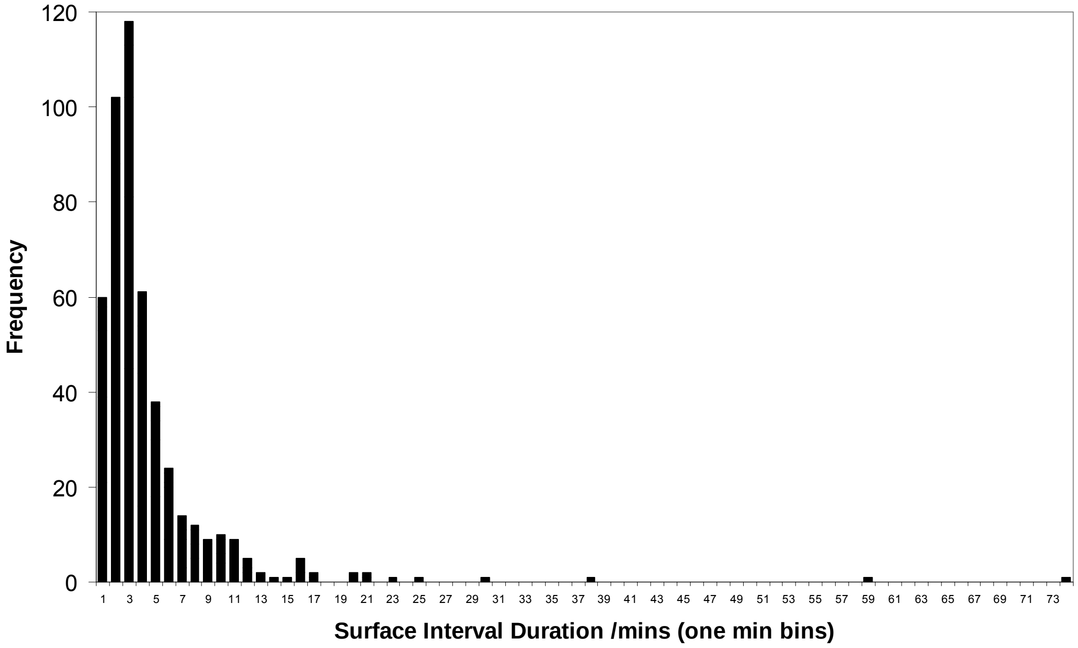


Figure 3.16. Frequency histogram of Blainville's beaked whale surface interval durations (n=483).

Cuvier's Beaked Whale

48 surface intervals were recorded between 1995 and 2004 with a median duration of 2 minutes (mean = 2.6 min, S.D. = 2.1) (Fig. 3.17).

Surface interval durations were found to be significantly different between the two species (Mann-Whitney U test; P = 0.002).

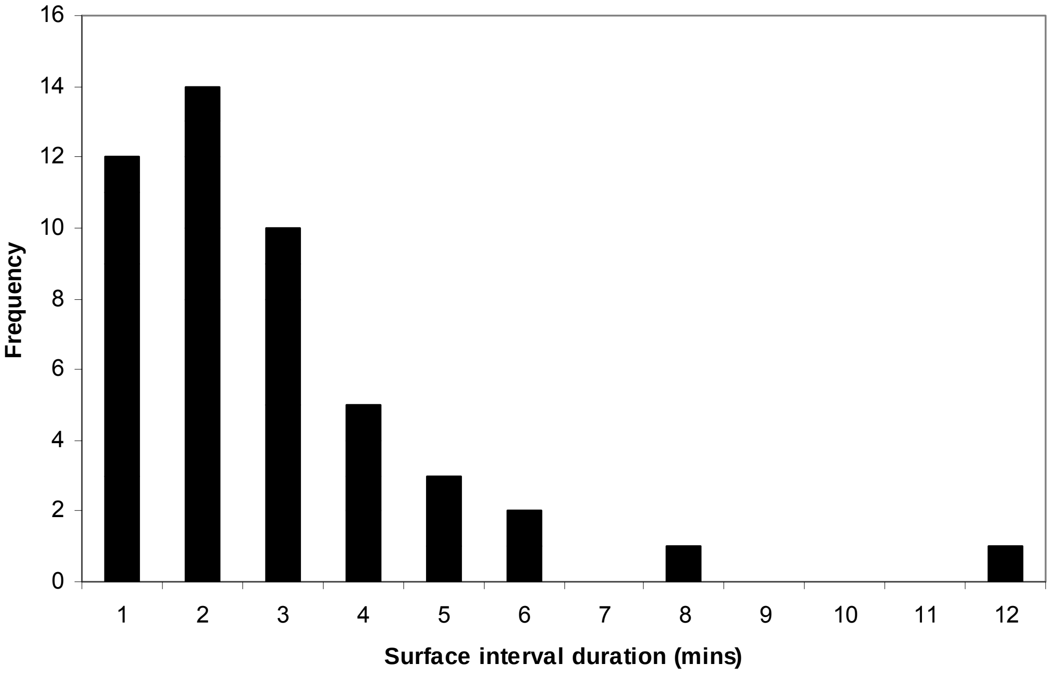


Figure 3.17. Frequency histogram of Cuvier's beaked whale surface interval durations (n=48).

Bout Analysis

Log-survivorship and cumulative time analysis

Log-survivorship plots showed no breaks and no discernable bimodality was observed in the cumulative time plots for either the Blainville's or Cuvier's beaked whale datasets, indicating that different surface interval duration types were not present for either species.

Surface interval duration vs. dive duration

Surface interval duration vs. subsequent dive duration

350 pairs of data (surface interval duration followed by the subsequent dive duration) were recorded for Blainville's beaked whale and 38 pairs for Cuvier's beaked whale (Fig. 3.18).

Simple linear regression showed that for both Blainville’s beaked whale ($r^2 = 0.0018$, df = 348, P = 0.418) and Cuvier’s beaked whale ($r^2 = 0.0039$, df = 36, P = 0.718), that the duration of a surface interval was not correlated to the duration of the subsequent dive.

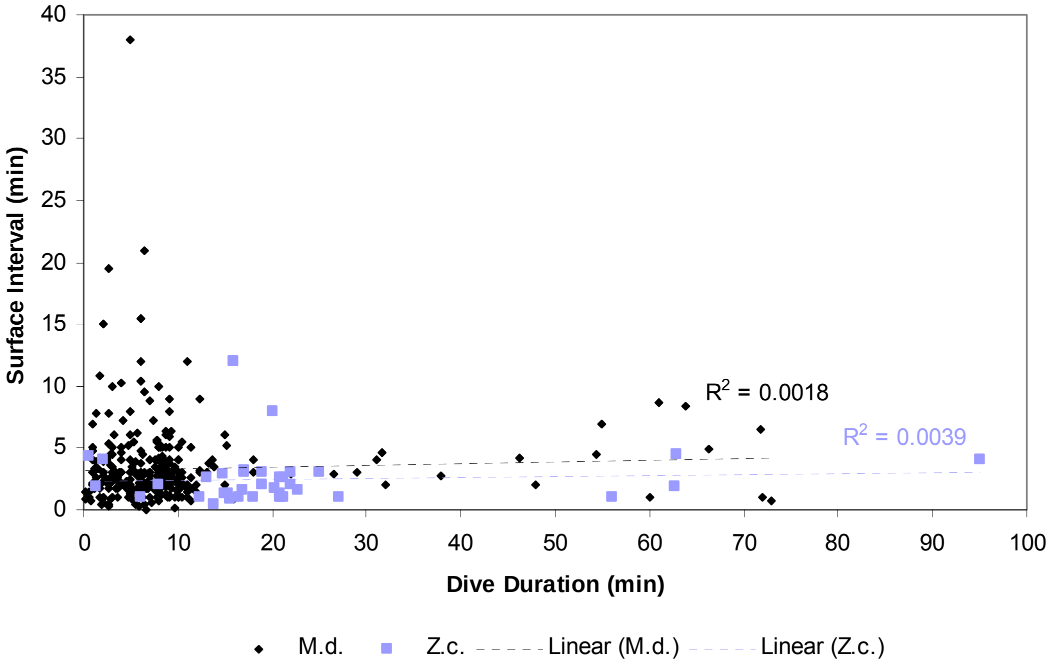


Figure 3.18. Scatter plots and linear regression lines for surface interval durations followed by the subsequent dive durations, of Blainville’s (M.d.) and Cuvier’s (Z.c.) beaked whales.

Surface interval duration vs. the preceding dive duration

341 pairs of data (surface interval duration and the preceding dive duration) were recorded for Blainville’s beaked whale and 33 pairs for Cuvier’s beaked whale (Fig. 3.19).

Simple linear regression showed that for both Blainville’s beaked whale ($r^2 = 0.0014$, df = 339, P = 0.499) and Cuvier’s beaked whale ($r^2 = 0.0076$, df = 31, P = 0.625), that surface interval duration was not correlated to the duration of the preceding dive.

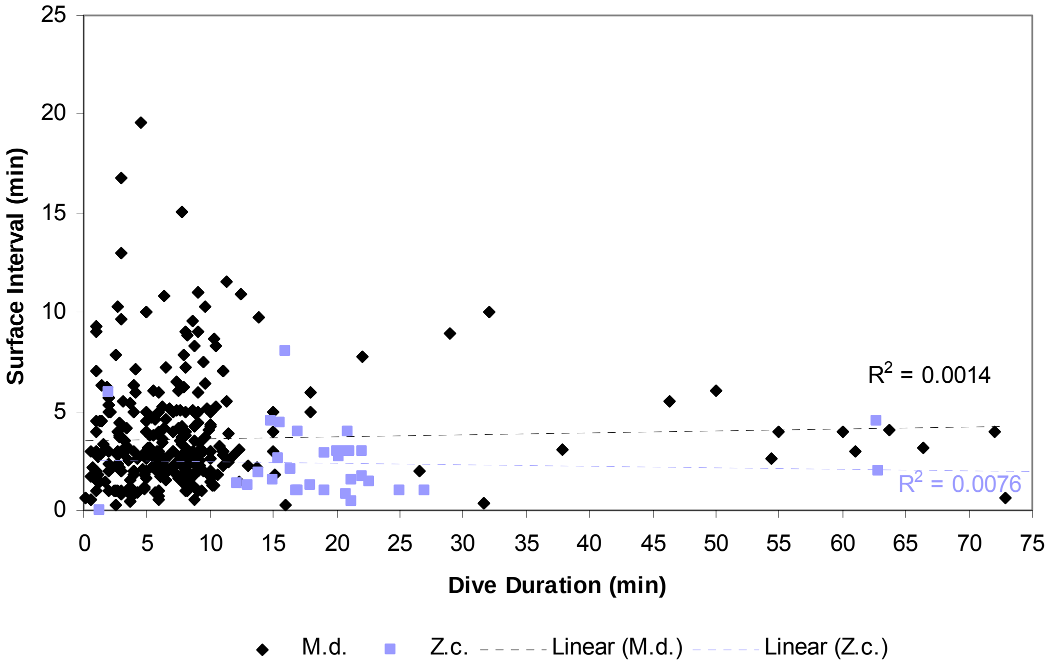


Figure 3.19. Scatter plots and linear regression lines for surface interval durations vs. the duration of the preceding dives, of Blainville's (M.d.) and Cuvier's (Z.c.) beaked whales.

Surface interval duration vs. age class in Blainville's beaked whale

Surface interval records with juveniles or calves present

326 surface interval durations were recorded where juveniles or calves were present in encountered groups of whales. The median duration of surface intervals was 3 minutes (mean = 4.2 min, S.D. = 5.4) (Fig. 3.20).

Surface interval records with juveniles or calves absent

157 surface interval durations were recorded where juveniles or calves were absent from encountered groups. The median duration was 3 minutes (mean = 4.6 min, S.D. = 6.4) (Fig. 3.20).

Surface interval durations were not significantly different between the two datasets (Mann-Whitney U test; P = 0.495).

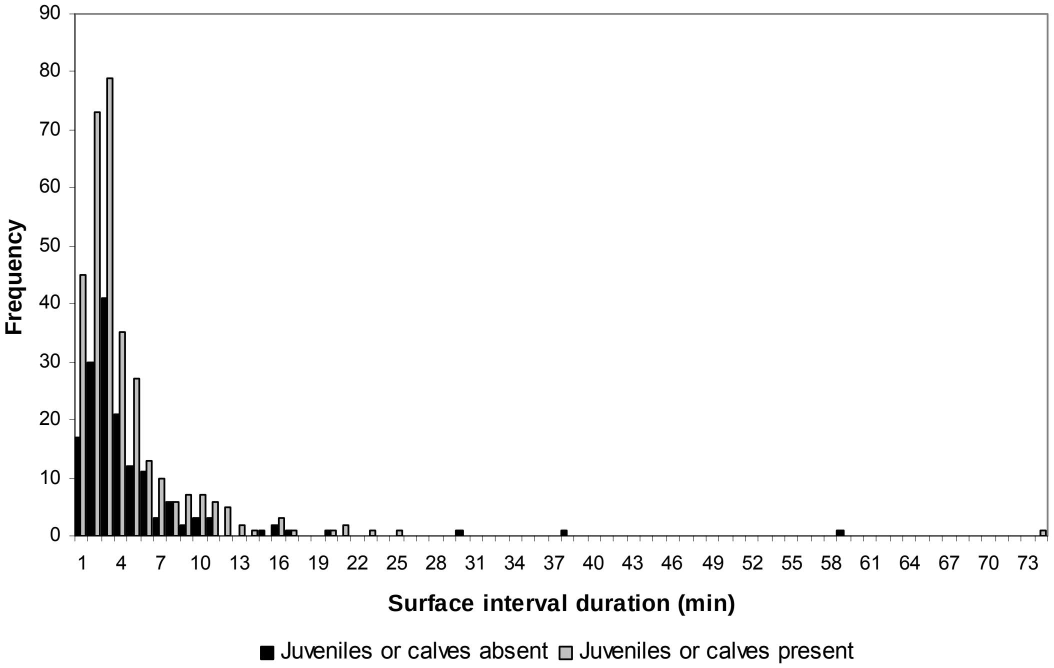


Figure 3.20. Frequency histogram of Blainville's beaked whale surface interval durations where juveniles or calves were either present (n = 326) or absent (n = 157) from encountered groups.

Bout Analysis

Log-survivorship and cumulative time analysis

Log-survivorship plots showed no breaks and no apparent bimodality was observed in the cumulative time plots for each of the datasets where juveniles or calves were either present or absent during encounters.

Surface interval duration vs. dive duration

Surface interval duration vs. subsequent dive duration

244 pairs of data (surface interval duration followed by the subsequent dive duration) were recorded for groups where juveniles or calves were present and 106 pairs where both were absent (Fig. 3.21).

Simple linear regression showed that for the presence data the correlation coefficient was significantly different from zero ($r^2 = 0.0207$, df = 242, $P = 0.025$).

Where juveniles and calves were absent, the surface interval duration was not correlated to the duration of the subsequent dive ($r^2 = 0.0055$, df = 104, $P = 0.455$).

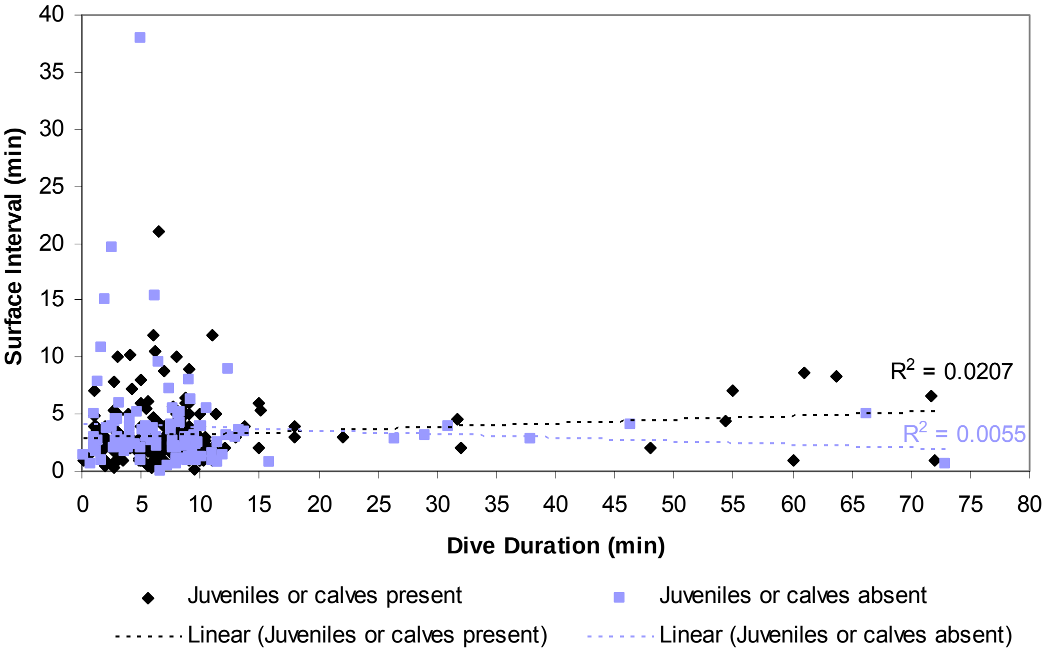


Figure 3.21. Scatter plots and linear regression lines for surface interval durations vs. the duration of the subsequent dives, of Blainville's beaked whale groups where juveniles or calves were either present or absent.

Surface interval duration vs. the preceding dive duration

243 pairs of data (surface interval duration and the preceding dive duration) were recorded for groups where juveniles or calves were present and 100 pairs where both were absent (Fig. 3.22).

Simple linear regression showed that for both presence (r² = 0.0059, df = 241, P = 0.238) and absence data (r² = 0.0015, df = 98, P = 0.706), that surface interval duration was not correlated to the duration of the preceding dive.

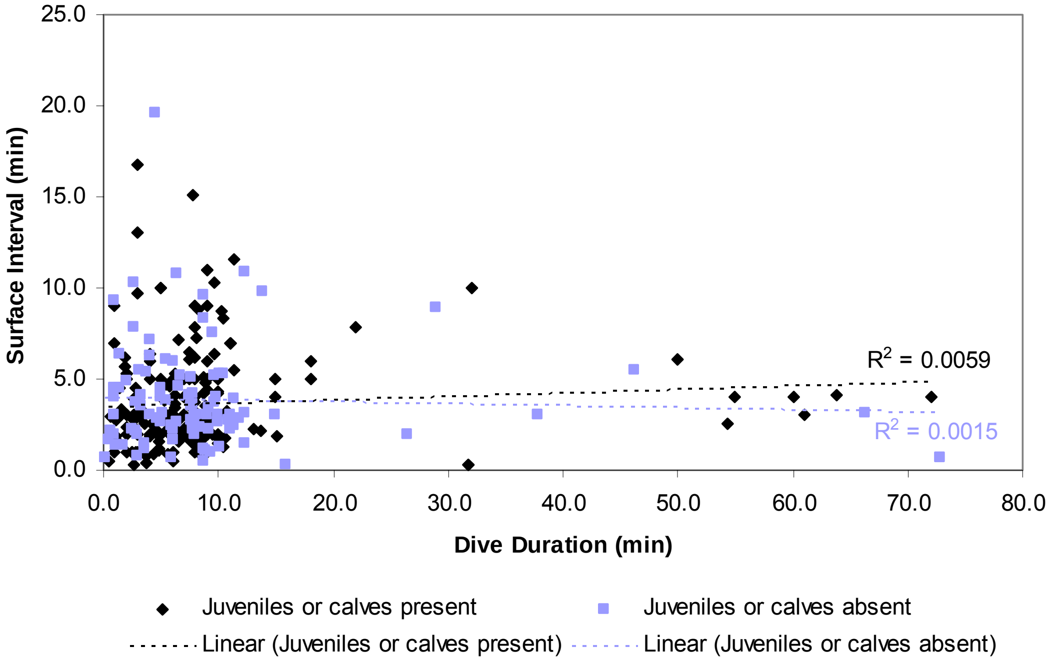


Figure 3.22. Scatter plots and linear regression lines for surface interval durations vs. the duration of the preceding dives, of Blainville's beaked whale groups where juveniles or calves were either present or absent.

Respiration rates

Frequency of inter-ventilation durations

Blainville's Beaked Whale

215 inter-ventilation durations were recorded on 15 occasions (15 different individual animals) between August 2003 and August 2004. The median inter-ventilation duration was 11 seconds (mean = 15.4 sec, S.D. = 14.2) (Fig. 3.23).

Cuvier's Beaked Whale

42 inter-ventilation durations were recorded on 3 occasions (3 different individual animals) between April 1997 and July 2004. The median inter-ventilation duration was 9 seconds (mean = 12.7 sec, S.D. = 14.2) (Fig. 3.23).

Inter-ventilation durations of the two species were found to be significantly different (Mann-Whitney U test; P = 0.004).

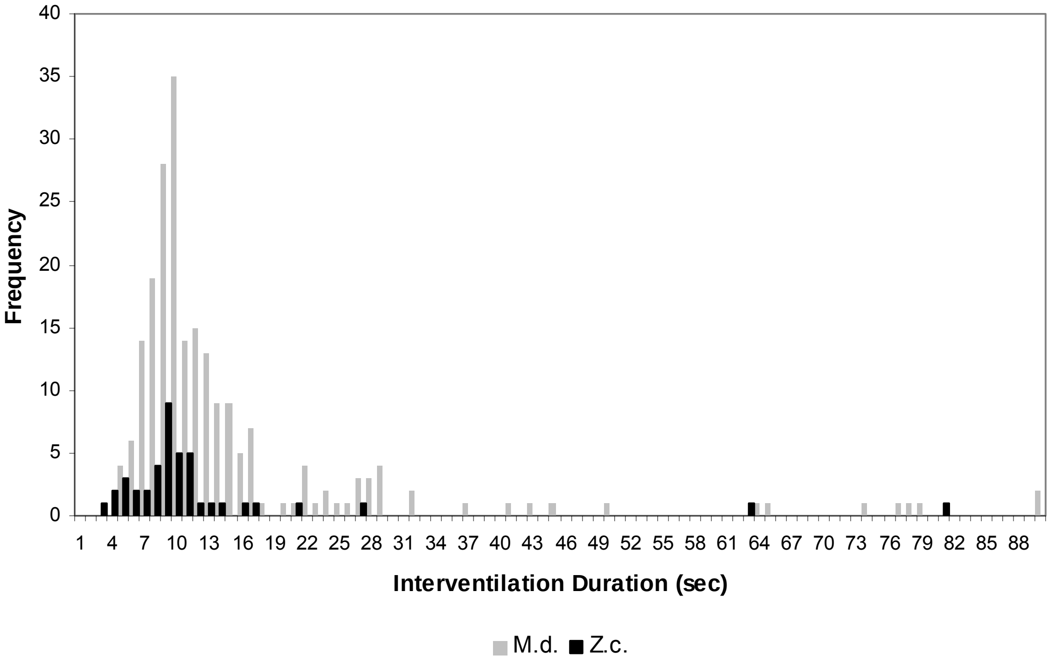


Figure 3.23. Frequency histogram of Blainville's beaked whale (M.d.) (n = 215) and Cuvier's beaked whale (Z.c.) (n = 42) inter-ventilation durations.

Gaseous Exchange

Using the median inter-ventilation and surface interval durations for each beaked whale species, the number of possible breaths per surface interval were calculated.

Blainville's = 10 sec (approx. 18 breaths possible in 3 min surface interval)

Cuvier's = 9 sec (approx. 13 breaths possible in 2 min surface interval)

Blainville's beaked whales have the opportunity to breathe 28% more times than Cuvier's beaked whales during surface intervals, potentially providing the chance for more gaseous exchange.

Inter-ventilation duration vs. the preceding and subsequent duration

Blainville's Beaked Whale

Inter-ventilation duration vs. subsequent inter-ventilation duration in a series and inter-ventilation duration vs. the preceding inter-ventilation duration in a series

71 pairs (inter-ventilation duration followed by the subsequent inter-ventilation duration in a series) and 74 pairs (inter-ventilation duration and the preceding inter-ventilation duration) of data were recorded for individual Blainville's beaked whales (Fig. 3.24).

Simple linear regression showed that neither dataset displayed any correlation between inter-ventilation durations (inter-ventilation duration followed by the subsequent inter-ventilation duration in a series; $r^2 = 0.0014$, df = 69, $P = 0.755$) (inter-ventilation duration and the preceding inter-ventilation duration; $r^2 = 0.033$, df = 72, $P = 0.119$).

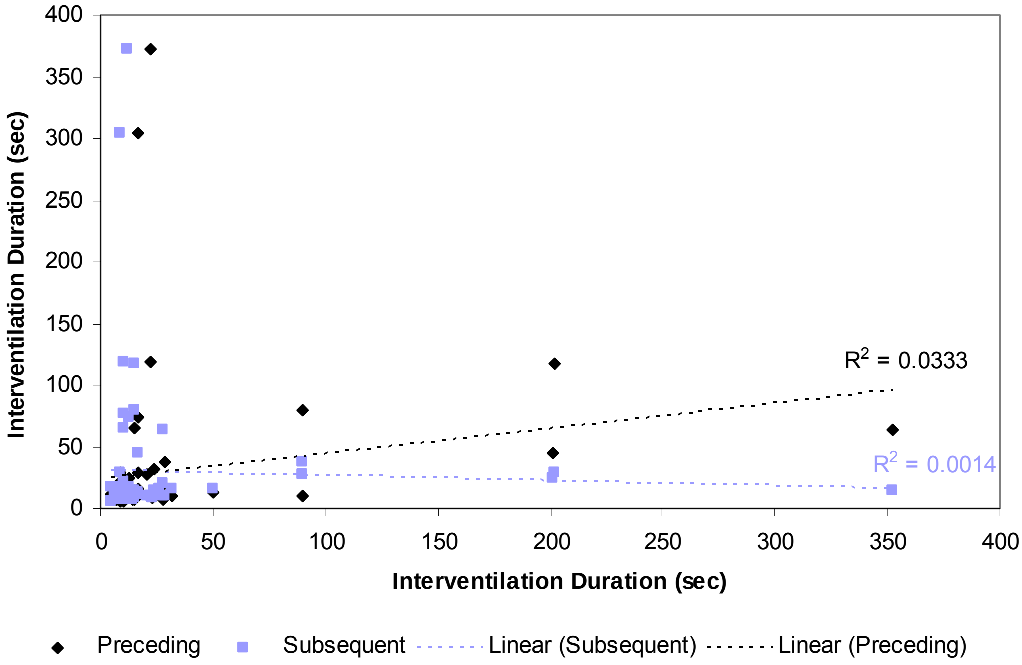


Figure 3.24. Scatter plots and linear regression lines for inter-ventilation durations vs. the preceding inter-ventilation duration and inter-ventilation durations vs. the subsequent inter-ventilation duration of Blainville's beaked whales.

Cuvier's Beaked Whale

Inter-ventilation duration vs. subsequent inter-ventilation duration in a series and inter-ventilation duration vs. the preceding inter-ventilation duration in a series

19 pairs (inter-ventilation duration followed by the subsequent inter-ventilation duration in a series) and 20 pairs (inter-ventilation duration and the preceding inter-ventilation duration) of data were recorded for individual Cuvier's beaked whales (Fig. 3.25).

Simple linear regression showed that neither dataset displayed any correlation between inter-ventilation durations (inter-ventilation duration followed by the subsequent inter-ventilation duration in a series; $r^2 = 0.0061$, df = 17, $P = 0.751$) (inter-ventilation duration and the preceding inter-ventilation duration; $r^2 = 0.0004$, df = 18, $P = 0.931$).

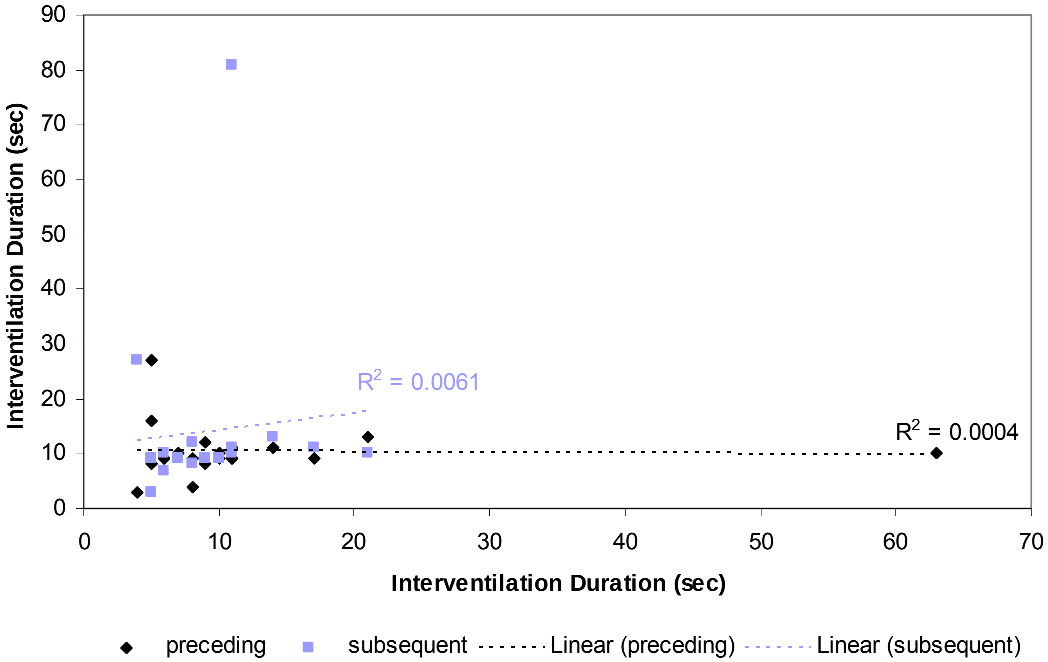


Figure 3.25. Scatter plots and linear regression lines for inter-ventilation durations vs. the preceding inter-ventilation duration and inter-ventilation durations vs. the subsequent inter-ventilation duration of Cuvier's beaked whales.

Blainville's beaked whale inter-ventilation analysis

On the 13th June 2004 the longest series of inter-ventilation durations was recorded for Blainville's beaked whale; 91 breaths during 53.75 minutes. During the series, 9 inter-ventilation durations were recorded that were 90 seconds or longer. These are considered here as dives (longest = 6.2 min) (Fig. 3.26).

Between the dives 8 periods of breathing are evident, during which the mean number of breaths was 10 (median = 10, S.D. = 2.6).

Pairs of breaths preceding and subsequent to the dives were analysed to see if breathing differed pre or post dive. E.g. Breath 1 compared with Breath 2, Breath 2 compared with Breath 3…..etc (excluding durations ≥ 90 secs).

Across the whole dataset the median difference in duration between pairs of breaths was 4.5 seconds (S.D. = 15.7) (excluding durations $\geq$ 90 seconds).

Of the pairs of post diving breaths (identified in Figure 3.26) the duration difference between breaths had a median of 9.5 seconds (S.D. = 4.3), 100% of which demonstrated that the time duration until the next breath occurs, was longer for the immediate post dive breath than the second post dive breath. The pre-dive pairs of breaths had a median of 13 seconds (S.D. = 21.5), where 75% of the immediately preceding breaths were longer than the breath prior to this.

A Kruskal-Wallis squared ranks of variance test showed that both the durations between breaths before and after dives were significantly different to one another and significantly different to the durations between breaths across the whole series of data (Chi-square = 13.410034 df = 2 P = 0.0012).

The duration between breaths directly after a dive are longer on average than across the rest of the series (excluding dives). Preceding a dive the trend is for duration between breaths to increase and for durations to be longer than across the rest of the dataset.

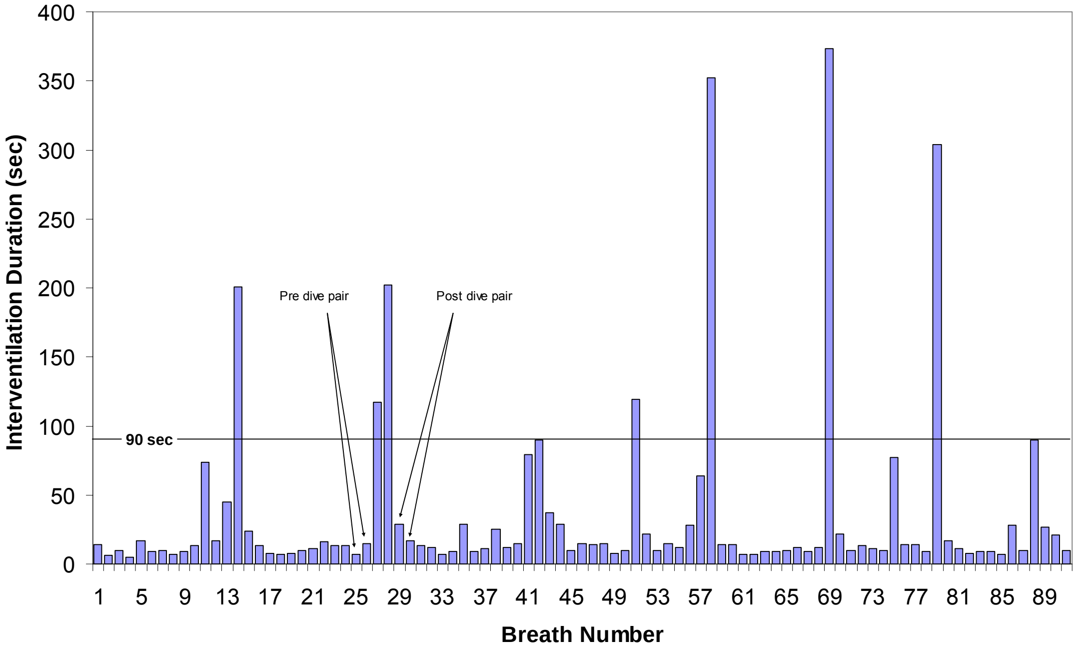


Figure 3.26. Histogram of Blainville's beaked whale inter-ventilation durations.

Stranded vs. free ranging Cuvier's beaked whales

On 15th March 2000 a sub-adult Cuvier's beaked whale live stranded at Rocky Point, Sandy Point, South Abaco. During the rescue and refloating process inter-ventilation durations of the animal were recorded.

227 inter-ventilation durations were recorded, having a median duration of 4 seconds (mean = 6.9 sec, S.D. = 19.9). During the 26.4 minutes of recording the animal only performed breath holds greater than 20 seconds twice (71 and 78 seconds) (Fig. 3.27).

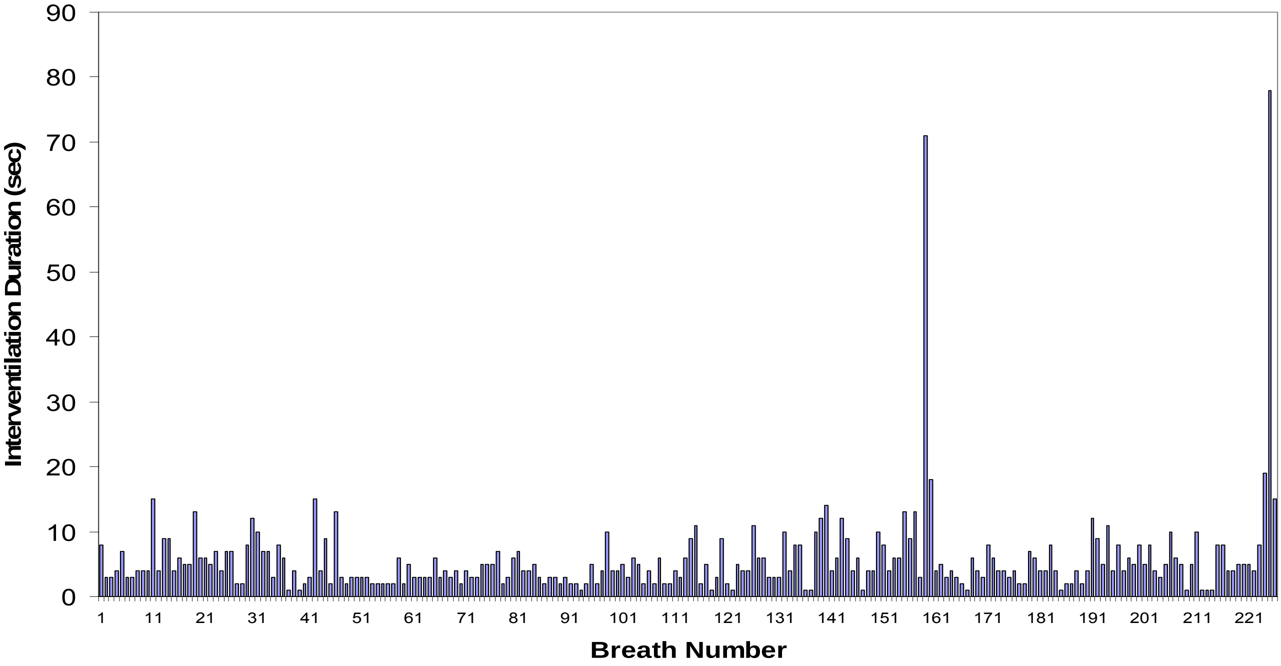


Figure 3.26. Histogram of a stranded Cuvier's beaked whale inter-ventilation durations.

The breathing behaviour of the stranded animal was significantly different to the breathing records of free-ranging Cuvier's beaked whales (data presented earlier) (Mann-Whitney U test; P = <0.0001).

Chapter Three

DISCUSSION

Results presented here show that the average dive duration recorded by observers did not vary with sea state for either species.

The number of dives recorded was however correlated to sea state, decreasing as sea state increased.

Claridge (2004) also found a negative correlation between the number of sightings and increasing sea state, as well as a reduction in the effective sighting strip width of line transects. Based on data presented by Claridge (2004) it may be considered that Beaufort (B) 3 should be the cut off point for recording dive durations. Above this sea state the effective observation and recording of every surfacing an animal makes becomes less likely (height of viewing platform and distance to the animals being studied are also relevant to the ability to observe animals and the robustness of the data collected).

Barlow et al. (1997) report excellent survey conditions as being B2 or less, but included data collected in sea states up to and including B4 in their analysis of *Mesoplodon* sp. and Cuvier's beaked whales in the Gulf of California.

B4 data were retained in this study, both in keeping with the Barlow et al. (1997) study and because at the time of collection observers were confident that recorded observations were a true representation of the behaviour of study animals.

The trend of decreasing detectability as sea state worsens is highly relevant to the conservation of beaked whales. One proposed mitigation measure being employed by naval operators whilst using tactical sonar, is the use of visual observers to detect whales, allowing ships to alter or cease operations. Inability to detect animals in what are (to naval ships) very moderate sea states (B3>) may mean that the potential for groups of beaked whales to be missed by observers and exposed to sonar is high.

Barlow (1999) indicates that detection functions for beaked whales are low. Although not as low as data presented by Barlow et al. (1997), the percentage of time spent at the surface (during bouts of breathing) during encounters, were low for Cuvier's beaked whales in this study.
The percentage of time at the surface was not dissimilar to that spent diving in Blainville's' beaked whales. This result may be an artefact of many of the encounters with Blainville's beaked whales being prematurely shortened by researchers, where, upon performing a deep foraging dive (signified by a more pronounced forceful exhalation and inhalation immediately prior to diving and then a high arch role exposing the tailstock, but not flukes (Claridge & Hickmott pers. obs.)), encounters are ended either to continue searching for other species or to complete line transect surveys.
This bias in leaving groups means the percentage of time animals spend at the surface is mostly representative of when they are performing surface intervals only and not of the full diving cycle (where deep foraging and shallow dives are performed).

The apparent seasonality of encounters with animals is also likely a result of bias. Field effort is based around ‘Earthwatch’ volunteer seasons which are split into winter and summer (Jan – Apr) (Jun – Aug), hence the bias in the field effort during these months. In addition, there is generally a reduction of effort between August and November during the main hurricane season.

The visual recording of dive duration times is unquestionably subject to the risk of error if surfacing events are missed and thus generate bias. Missing an entire surfacing series can cause two dives to be counted as a single longer dive. Confusing groups of animals where multiple groups are present in an area and misreporting the diving behaviour is also possible (Barlow et al. 1997).

In this study all efforts were made to collect the most accurate data possible and high quality photo identification shots were taken of all group members during dive behaviour studies to avoid the risk of confusing animal groups.

The dive data were explored with different analysis methods in an attempt to more accurately investigate diving behaviour by determining whether different types of dive were present in the data and establishing where breaks in the data were.

Dive type analysis

The two methods employed are considered to be almost entirely objective compared with other methods (Hooker and Baird 2001).

It is acknowledged that where cumulative time analysis was used in this study, there was a lack of data for long duration dives in Blainville's beaked whales and a general lack of data for Cuvier's beaked whales to clearly define bi-modal distributions. As such the break points applied, although following the trend of the data, are somewhat subjective in their placement. It is hoped that the collection of additional data will allow more objective break points to be determined.

Log-survivorship analysis broke the dives into three categories. In other studies of beaked whale diving (Hooker and Baird 1999b, Baird et al. 2004), dive types have been categorised as 'short and shallow' and 'long and deep', where 'long and deep' dives are considered to have a foraging function.

The median long dives of both species were found to be comparable with TDR average durations for Blainville's beaked whales tagged in the Canary Islands and Cuvier's beaked whales in the Ligurian Sea (Tyack et al. 2005).

Comparable data were also available for the shallow dives of Blainville's beaked whale from an animal tagged in Hawaii (Baird et al. 2004), where the average duration was 7.47 minutes.
The results presented here fall within the range of the data from the Hawaiian animal.

The results, however, are very different to those presented by Barlow et al. (1997), another study whereby dive durations were recorded visually at the surface. These results appear to have been analysed as one dataset and not separated by dive type.

The differences observed, may serve to highlight the importance of trying to determine whether dive types occur and subsequently analysing the split data separately.

Log-survivorship analysis split both Blainville's beaked whale and Cuvier's beaked whale data into three dive types. The question can be posed, what is the function of these three dive types?

Long dives are considered foraging dives and the short dives may be respiratory dives during a surfacing interval. Underwater observations (pers. obs.) in the Bahamas suggest that these dives are shallow, within 50 metres depth of the surface.

In Hawaii shallow dives also average less than 50 metres (Baird et al. 2004). These dives may have a travelling as well as respiratory function. Study of the ranging behaviour may provide some insight into this hypothesis.

The function of the medium duration dives is unknown, if not related to respiration or foraging. The requirement of 'bounce' dives as a form of decompression stop to recover from deep foraging dives has been proposed (Potter 2004) and the medium duration dives may provide such a function. Both the short and medium dives, as well as having potential physiological related roles may also be used as travelling dives. This is considered, as during deep foraging dives both species have been observed to resurface within the approximate location of the place they dived (Claridge and Hickmott, pers. obs.).

The higher prevalence of Cuvier’s beaked whale in strandings and it’s assumed sensitivity to anthropogenic sound, warrants investigation.
Data presented in this thesis and data from other studies (Baird et al. 2004; Johnson et al. 2004; Tyack et al. 2005), suggest that Cuvier’s beaked whales may be a more extreme diver than Blainville’s beaked whales, the second most common species in mass strandings.
Diving deeper and performing shorter surface intervals may act to contribute to sensitivity of this species.
It is noteworthy also that these are the most cosmopolitan beaked whale species and their reported prevalence in strandings may in part reflect their distribution and possible abundance compared with other species.

Are animals diving aerobically?

Concurrent with findings of Hooker and Baird (1999b) for northern bottlenose whales (*Hyperoodon Ampullatus*), the results from the Bahamas for Blainville’s and Cuvier’s beaked whales indicate that both these species show no correlation between the duration of dives and surface intervals and hence are diving within their aerobic dive limits.

Surface interval durations were significantly different between the two species. Again, as with the dive data, Cuvier’s beaked whale appears to be the more extreme species, having significantly shorter surface intervals than Blainville’s beaked whales and thus has less time for gaseous exchange. Although these shorter surfacing intervals may indicate that this species is diving within it's aerobic dive limits to a greater extent than Blainville's beaked whales and as such requires even less surface time. Equally it may be considered that this is a species that is indeed extreme and is pushing its physiological limits more than other species. More in depth dive analysis using TDR data may provide answers to these considerations.

Age class differences

This study allowed the investigation of age class differences in the diving behaviour of Blainville's beaked whales in the Bahamas.

No significant differences were found in either the diving or surfacing interval data for groups of whales where juveniles and calves were present or absent. This result is reflected in a study from the Gulf of California, where no apparent differences were found between groups with or without calves (Barlow et al. 1997).

No correlation between dive and surface interval durations was found for groups where juveniles and calves were absent, indicating that animals were diving within their aerobic limits.

Where juveniles and calves were present, a correlation was evident between the length of dives and the duration the group spent at the surface prior to diving.

No correlation was evident between the length of dive and the time spent at the surface after a dive.

This evidence may indicate that young animals need to load oxygen or prepare differently to adults in some way prior to diving.

The lack of difference in the actual duration of dives and surface intervals, may suggest that although young animals may need to prepare somewhat differently to adults before diving, they are capable of diving for durations on par with adults and as such are able to accompany their mother and conspecifics during both short dives and long foraging dives and subsequently do not require extended recovery surface intervals after dives. This may make the requirement for alloparental care as a necessity, based on the physiological capabilities of the calves redundant in this species.

As it is inappropriate to tag mothers or calves, fully understanding the diving behaviour of young animals is difficult, but warrants further investigation. Johnson et al. (2004) tagged an adult male in a group of Blainville's beaked whales containing mother/calf pairs with an acoustic TDR in the Canary Islands. The whales dived synchronously and echolocation clicks of conspecifics were recorded. Such methods and data may provide the means to determine the diving abilities of young animals and conclusively prove whether they display different diving behaviour.

Inter-ventilation durations

The lack of correlation between the times of breaths in a series suggests that durations between them are relatively consistent and thus do not indicate that animals hyperventilate prior to diving.

However, where the longest data set of inter-ventilation durations was analysed for Blainville's beaked whale, the times between breaths before and after a dive did differ when compared to the data set as a whole. A trend was evident that the time between breaths increased before a dive.
This may be further evidence that animals do not hyperventilate prior to diving as it would be expected that durations between breaths would decrease in a period of hyperventilation.

It is noteworthy that the longest dive duration whilst recording inter-ventilation rates was only 6.2 minutes. In order to clearly determine whether animals hyperventilate prior to diving, data where both short and long dives occur is required.

For the Blainville's beaked whale a mean of 10 breaths were recorded between short shallow dives. The only known published respiration records from beaked whales in the Bahamas were recorded in 1978 and 1980. Data were collected from a single whale and a group of 6 whales, all of which were only identified only as *Mesoplodon* sp. The group were recorded taking 10 breaths between dives and the single animal took seven breaths between dives (Balcomb 1981). This data is consistent with the respiration rates presented in this study.

Further analysis of respiration rates between species, age and sex classes are worthy of study and may provide additional insight into the extreme deep diving capabilities of these animals.

Chapter Four

REVIEW

In this chapter a multi-species mass stranding event which occurred in the Bahamas and was associated with naval sonar is reviewed in the light of current theories relating to why Blainville’s and Cuvier’s beaked whales are so vulnerable to anthropogenic sound. This is then further discussed relative to data and findings presented in this thesis, specifically concerning diving and foraging behaviour of these animals.

Mass Strandings

Mass strandings, defined as two or more animals (excluding mother/calf pairs) found stranded alive or dead (Wilkinson 1991), containing beaked whales are considered to occur as a result of anthropogenic sound production.

Both naval sonar and seismic survey operations have been reported as causing mass strandings, with the first record of a Cuvier’s beaked whale mass stranding occurring in 1963, the year mid-frequency tactical sonar was first deployed (NMFS 2001; Potter 2004; Simmonds & Lopez-Jurado 1991).

The deep and long duration diving behaviour and physiology of beaked whales have been suggested as factors in why these species are so sensitive to anthropogenic sound (Crum et al. 2005; Jepson et al. 2003).

Here, proposed theories of injury are discussed relative to a deep water habitat in the Bahamas where both species have been studied for over a decade and where a mass stranding took place in March 2000.

Bahamas mass stranding

The mass stranding event of March 15th and 16th 2000 in the northern Bahamas has been well documented (Balcomb & Claridge 2001; NMFS 2001).

Here a summary of the findings of the Balcomb and Claridge (2001) and NMFS (2001) reports are presented.

17 animals from 4 species of cetacean (11 Cuvier's beaked whales, 3 Blainville's beaked whales, 2 minke whales (*Balaenoptera acutorostrata*), and one Atlantic spotted dolphin (*Stenella frontalis*) (N.B. the 2 unidentified beaked whales recorded in the NMFS report were confirmed as mother calf pair of Cuvier's beaked whale by Diane Claridge from photographs taken by a witness to the stranding)) were reported stranded within a 36 hour period along the coasts of Abaco, Grand Bahama and North Eleuthera islands, flanking the North West and North East Providence channels in which US naval ships transited propagating sonar.

During 16 hours of operations five naval ships engaged in an anti-submarine warfare exercise using tactical mid-frequency sonar. The sonar's used had duty cycles of 24 seconds and these cycles were staggered in time so as not to coincide.

Seven animals are known to have died, 5 Cuvier's beaked whales, a Blainville's beaked whale and the Atlantic spotted dolphin. The remaining animals were assisted back to sea. Survival rates are unknown.

Acoustic models generated by the Office of Naval Research (ONR) of the emitted sonar revealed the presence of a surface duct that would have concentrated the sound in the top 200 m of the water column.

Reverb from the sides and bottom of the canyon were not considered critical as the models demonstrated most of the sound energy was trapped near the water's surface.

At the time of stranding, calm seas may have aided the propagation of sound at the surface as the sound waves were unimpeded. A lack of surface water mixing meant few bubbles were present in the water and thus did not act to dissipate the sound.

Species composition in the area of naval operations

By coincidence, the naval operations were conducted in an area of the Bahamas where a study of marine mammals has been conducted since 1991. Around S.W. Abaco where five of the strandings occurred (three Blainville's beaked whales and two Cuvier's beaked whales, detailed distribution and habitat studies have been conducted for deep diving toothed whales (Claridge 2004). In the years prior to and at the time of the stranding, dwarf sperm whales (*Kogia sima*) were the most frequently sighted toothed whale, followed by Blainville's beaked whale, Cuvier's beaked whale and the sperm whale (*Physeter macrocephalus*).

Theories of why beaked whales strand

Acoustic trauma

Necropsy results from the stranded animals that died, showed significant cranial lesions consisting of intra cochlear and unilateral temporal subarachnoid haemorrhage (blood in the inner ear and bleeding around and in the brain), patterns of damage consistent with acoustic trauma (NMFS 2001). The actual sound levels that the whales experienced is not known, but received levels are considered to have been in the range of 160-165 dB (decibels). These levels are below those proposed by the US navy to cause direct haemorrhagic acoustic trauma (180 dB) (Potter 2004). As such, acoustic trauma alone is not considered to be the sole cause of the stranding of animals.

Resonance

Resonance in the body cavities and other structures was one of the first theories relating to the cause of injury in the whales and their subsequent stranding. This theory has since been reviewed and the conclusion drawn that resonance is not a contributing factor in strandings. Due, in part, to what is known as the resonance enhancement factor ‘Q’, the tissue of marine mammals is not great enough for resonance to occur (Potter 2004).

Decompression (DCS) type syndrome

A DCS type syndrome has been proposed as a reason why animals are affected by sonar and strand (Fernández et al. 2005a; Jepson et al. 2003). It has been hypothesised that the diving behaviour of beaked whales leads to supersaturation of muscle tissues with nitrogen (N_2) (Houser et al. 2001). Sonar exposure of such supersaturated tissue at depth, is considered to cause pre-existing bubbles to rapidly expand causing DCS type effects. Different theories have been proposed as to how pre-existing microscopic bubbles grow.

Houser et al. (2001) propose rectified diffusion as the mechanism for macroscopic bubble growth, but this is only considered to be significant at high pressure levels that exceed the anticipated received sound levels in stranded animals (Potter 2004).

Potter (2004) proposes that normally stabilised, pre-existing microbubbles that typically do not allow gaseous exchange across their surfaces are acoustically activated by sonar and grow via static diffusion resulting in DCS type symptoms. Crum et al. (2005) suggests a similar scenario, where quasi-static diffusion allows macroscopic bubbles to grow.

Why beaked whales?

It has been suggested that if susceptibility to stranding is caused by acoustic triggering of microbubble activation, resulting in bubble growth and physiological disruption, it might be expected that the problem affects marine mammal species that share common crucial diving behaviour traits, rather than simply to be related taxonomically (Potter 2004).

As previously mentioned, two other deep diving whales are known from the area where beaked whales stranded in S.W. Abaco, with the dwarf sperm whale being the most abundant of the four species.

Diet analysis based on review of published literature and niche overlap with other deep divers in the Bahamas presented in this thesis, suggests the dwarf sperm whale is a deep diver, comparable with the two beaked whale species. MacLeod et al. (2004) does report that dwarf sperm whales were found in shallower waters on the east coast of Abaco, but Claridge (2004) found no significant difference in the distribution related to depth, between dwarf sperm whales and the two beaked whale species on the south-west coast of the island.

Dive data suggests maximum dive durations are consistent with those of both Blainville's and Cuvier's beaked whales presented in this study and that surface intervals are on average shorter (mean = 1.5 min) (Barlow et al. 1997), than those of the two beaked whales presented here.

This evidence of the possible diving behaviour of dwarf sperm whales, would make it a candidate for being susceptible to microbubble activation in supersaturated tissues on exposure to an acoustic source.

Gas bubble emboli have been reported in this species (Fernández et al. 2005b). Yet in spite of this species being the most commonly observed whale in the area, no dwarf sperm whales were reported to have stranded in association with the naval exercise.

Diving and Surfacing Intervals

Irregardless of the manner in which bubble growth is proposed, the theory of a DCS type syndrome causing animals to strand is reliant on the body tissues being supersaturated with N_2.

Houser et al. (2001) demonstrated that different surface intervals and dive patterns would have dramatic effects on the levels of supersaturation. Potter (2004) indicates that a series of short shallow dives would improve the safety margin of mammals with high supersaturation levels of N_2 in their bodies after long deep dives, as they would be de-saturating under higher ambient pressures that reduce saturation levels.

Both dwarf sperm whales and sperm whales are observed resting (logging) at the waters surface between dives in the study area. Neither beaked whale species however has been seen resting in this manner around S.W. Abaco (pers. obs).

Data presented in this thesis indicate that the duration of long foraging dives between the two beaked whale species were not significantly different in the study area, but the short dives did differ significantly, with Cuvier’s beaked whales diving for approximately twice the duration of Blainville’s beaked whales. Surface interval durations, inter-ventilation durations and the number of breaths per surfacing were all significantly different and in each case, shorter or fewer for Cuvier’s beaked whale than for Blainville’s beaked whale and such data may help provide an insight as to why Cuvier’s are the most abundant species in mass strandings.

The surface intervals of both beaked whale species presented here are longer than those used by Houser et al. (2001) when modelling beaked whale N_2 saturation levels. The longer surface intervals and a different diving pattern where more short shallow dives were performed are likely to reduce the predicted saturation levels markedly and may be sufficient to make the risk of DCS via supersaturation unlikely in these species.

Tyack et al. (2005) used models of breath-hold diving to demonstrate that the natural diving behaviour is inconsistent with problems of N_2 supersaturation and DCS. They propose an abnormal behavioural response as the most likely risk factor for stranding when exposed to sonar.

Animals displaying a flight response away from a sound source may not follow their normal diving patterns. A series of shallow dives after a long deep dive may reduce the risk of DCS type symptoms, acting like the decompression stops used by human SCUBA divers (Potter 2004).

In the case of the Bahamas stranding, the surface duct where the sonar was most intense may have acted to disrupt the natural pattern of shallow dives. The Lloyd’s mirror effect may have reduced the sound pressure level very close to the surface (Potter 2004) and animals may have remained in this area whilst fleeing the sound making them prone to DCS type effects. It is possible that dwarf sperm whales for whom spending time right at the waters surface is part of the natural diving behaviour were untroubled by prolonged surface periods and hence were not affected in the same deleterious manner.

Conclusion

Based on the dietary evidence and diving behaviour data presented in this thesis, it has been possible to deduce that in the Northern Bahamas where no previous data existed, that both Blainville's and Cuvier's beaked whales display different dive types, that may have differing behavioural and physiological roles. Where deep, long duration dives are performed, it is considered that these whales are foraging within the meso- and bathypelagic zones for cephalopod, crustacean and fish prey. These results are consistent with other diet and diving analysis studies from other regions of the Atlantic and Pacific oceans (Baird et al. 2004; Johnson et al. 2004; MacLeod et al. 2003).

Foraging dives are considered to be conducted in association with areas of high topographic variation such as canyon walls for Blainville's beaked whale and less so for Cuvier's beaked whales. Additionally, distribution data on these species in the Bahamas indicates that Cuvier's beaked whales are typically found further offshore than Blainville's beaked whales. Dive depth data from studies elsewhere would suggest that both species may be considered to forage at or near the seafloor (Baird et al. 2004; Claridge 2004; Johnson et al. 2004; MacLeod & Zuur 2005).

Both of the beaked whale species studied here were represented in a mass stranding associated with the use of naval sonar that took place within the study site. Other deep diving odontocetes (dwarf sperm whales and sperm whales) are known to inhabit the study area and proposed hypotheses for the nature of how sonar impacts beaked whales should be applicable to other deep diving whales. Yet, neither, dwarf sperm whales nor sperm whales were present in the mass stranding records in the Bahamas.

The understanding of why this was the case is to date unknown.

Further investigation of the diving behaviour of all three of these species and where possible the deployment of TDR tags may aid the understanding of why beaked whales are so prone to stranding when exposed to sonar.

Future work

TDR tagging attempts on the study species in the Bahamas research sites have been conducted by the author in 2003 and 2004 and have, as yet, proved unsuccessful. Future attempts are planned, with the aim of collecting TDR dive data on Blainville’s beaked whales, Cuvier’s beaked whales and sperm whales off the south-west coast of Abaco. The purpose: to determine the fine-scale foraging and diving behaviour of all three species (within the same geographic location) to complement the dietary and diving behaviour (surfacing patterns) studies outlined in this thesis.

Study Area	Date	Enc Seq #	Seq #	Group size	Total Enc. Duration/min	Total duration of Dives/min	Total surface interval duration/ min	% of encounter spent diving	% of encounter being surface intervals
East Abaco	08-Dec-94	1	1	6	29	22	7	0.76	0.24
East Abaco	30-Jun-95	1	1	6	20	8	12	0.40	0.60
East Abaco	24-Aug-96	1	1	7	28.7	17.7	11	0.62	0.38
South Abaco	19-Apr-97	1	1	4	31.5	24.5	6.9	0.78	0.22
South Abaco	18-Jul-97	3	1	4	6.4	6.4	0	1	0
East Abaco	19-May-98	4	1	4	15.7	0	15.7	0.00	1.00
East Abaco	20-May-98	2	1	1	18.5	14.3	4.2	0.77	0.23
East Abaco	21-May-98	2	1	5	58.1	39.4	18.7	0.68	0.32
South Abaco	12-Jun-98	1	1	4	61.5	33.2	28.3	0.54	0.46
South Abaco	08-Jul-98	1	1	2	12	12	0	1	0
South Abaco	02-Aug-98	7	1	6	5.2	4.3	0.9	0.83	0.17
South Abaco	02-Aug-98	7	2	6	5.3	4.4	0.9	0.84	0.16
South Abaco	03-Aug-98	2	1	3	40.7	31.9	8.9	0.78	0.22
South Abaco	03-Aug-98	5	1	3	29.5	21.2	8.4	0.72	0.28
South Abaco	04-Aug-98	3	1	4	8.5	4.9	3.6	0.57	0.43
South Abaco	10-Feb-99	3	1	4	62.6	24.7	37.9	0.39	0.61
South Abaco	10-Feb-99	1	1	5	57.3	32.6	24.7	0.57	0.43
South Abaco	06-Apr-99	2	1	5	35	20.6	14.4	0.59	0.41
South Abaco	24-Apr-99	2	1	2	18	15	3	0.83	0.17
South Abaco	18-May-99	3	1	4	64.6	48.9	15.7	0.76	0.24
South Abaco	19-May-99	6	1	3	29.8	27.1	2.8	0.91	0.09
South Abaco	19-May-99	2	1	5	69	58.8	10.3	0.85	0.15
South Abaco	20-May-99	6	1	2	16.9	16.9	0	1	0
South Abaco	20-May-99	3	1	5	30.2	16.8	13.4	0.56	0.44
South Abaco	23-Jun-99	7	1	2	19.4	6.4	13	0.33	0.67
South Abaco	23-Jun-99	5	1	2	44	32	12	0.73	0.27
South Abaco	24-Jun-99	8	1	5	19.5	7	12.5	0.36	0.64
South Abaco	24-Jun-99	7	1	2	56.2	41.7	14.5	0.74	0.26
South Abaco	25-Jun-99	2	1	4	33	18	15	0.55	0.45
South Abaco	21-Jul-99	3	1	6	48	33	15	0.69	0.31
South Abaco	01-Feb-00	4	1	2	1	0	1	0	1
South Abaco	01-Feb-00	1	1	4	3.8	0	3.8	0	1
South Abaco	08-Feb-00	1	1	4	14	5	9	0.36	0.64
South Abaco	16-Feb-00	1	1	4	14	8	6	0.57	0.43
South Abaco	29-Feb-00	1	1	2	11	8	3	0.73	0.27
South Abaco	18-Mar-00	1	1	5	35	27.6	7.4	0.79	0.21
South Abaco	21-Mar-00	2	1	4	16	3	13	0.19	0.81
South Abaco	21-Mar-00	5	1	4	29.9	20.3	9.5	0.68	0.32
South Abaco	22-Mar-00	2	1	6	117	72.8	44.2	0.62	0.38
South Abaco	22-Mar-00	2	2	6	117	72.5	44.5	0.62	0.38
South Abaco	17-Apr-00	3	1	2	4	0	4	0	1
South Abaco	21-Apr-00	1	1	2	35	12.5	22.5	0.36	0.64
South Abaco	13-Jun-00	4	1	3	10	0	10	0	1
South Abaco	06-Jul-00	1	1	7	44.8	31	13.8	0.69	0.31
South Abaco	09-Jul-00	4	1	1	5	0	5	0	1
South Abaco	09-Jul-00	7	1	4	37	22	15	0.59	0.41

South Abaco	09-Jul-00	3	1	7	16	5	11	0.31	0.69
South Abaco	09-Jul-00	3	2	7	28	13	15	0.46	0.54
South Abaco	09-Jul-00	7	2	4	46	25	21	0.54	0.46
South Abaco	11-Jul-00	7	1	1	10.5	1	9.5	0.10	0.90
South Abaco	09-Aug-00	8	1	3	7	1	6	0.14	0.86
South Abaco	09-Aug-00	5	1	7	232	183.1	49	0.79	0.21
South Abaco	09-Aug-00	8	2	3	7	1	6	0.14	0.86
South Abaco	10-Aug-00	6	1	11	43	21	22	0.49	0.51
South Abaco	14-Aug-00	2	1	7	39	19	20	0.49	0.51
South Abaco	14-Aug-00	1	1	7	4	0	4	0	1
South Abaco	14-Aug-00	3	1	7	27	18	9	0.67	0.33
South Abaco	14-Aug-00	2	2	7	39	17	22	0.44	0.56
South Abaco	15-Aug-00	4	1	7	18	12	6	0.67	0.33
South Abaco	15-Aug-00	2	1	5	44	19	25	0.43	0.57
South Abaco	19-Aug-00	1	1	7	101	83	18	0.82	0.18
South Abaco	20-Aug-00	1	1	7	13	7	6	0.54	0.46
South Abaco	18-Dec-00	3	1	5	8	0	8	0	1
South Abaco	18-Dec-00	3	2	5	20	0	20	0	1
South Abaco	16-Jan-01	1	1	5	35	27	8	0.77	0.23
East Abaco	15-Feb-01	3	1	4	2	0	2	0	1
South Abaco	21-Feb-01	1	1	6	116.2	93.5	22.8	0.80	0.20
South Abaco	21-Feb-01	2	1	5	36.6	23.2	13.5	0.63	0.37
South Abaco	22-Feb-01	1	1	5	81.5	60.1	21.5	0.74	0.26
South Abaco	22-Feb-01	1	2	5	79.8	60.1	19.8	0.75	0.25
East Abaco	02-Mar-01	1	1	2	3	0	3	0	1
South Abaco	08-Mar-01	4	1	2	13	8	5	0.62	0.38
South Abaco	08-Mar-01	1	1	2	2	0	2	0	1
South Abaco	13-Apr-01	2	1	1	3	0	3	0	1
South Abaco	26-Apr-01	1	1	6	57	38.2	18.8	0.67	0.33
South Abaco	27-May-01	3	1	5	0.3	0	0.3	0	1
South Abaco	27-May-01	1	1	5	32.7	9.2	23.5	0.28	0.72
South Abaco	27-May-01	1	2	5	32.7	10.2	22.5	0.31	0.69
South Abaco	29-May-01	2	1	3	21	0	21	0	1
South Abaco	01-Jun-01	1	1	5	10.7	0	10.7	0	1
South Abaco	15-Jun-01	1	1	3	60.9	23.8	37.2	0.39	0.61
South Abaco	17-Jun-01	2	1	3	7.9	3.9	4	0.49	0.51
South Abaco	08-Jul-01	4	1	4	36.3	14.2	22.1	0.39	0.61
South Abaco	08-Jul-01	5	1	2	19.7	16.5	3.2	0.84	0.16
South Abaco	18-Jul-01	3	1	9	12	0	12	0	1
South Abaco	18-Jul-01	3	2	9	20	6	14	0.30	0.70
South Abaco	11-Sep-01	1	1	3	25.3	15	10.3	0.59	0.41
South Abaco	28-Sep-01	1	1	7	38	22.8	15.3	0.60	0.40
South Abaco	06-Oct-01	1	1	7	10	0	10	0	1
South Abaco	07-Oct-01	1	1	3	10.2	3.3	6.8	0.33	0.67
South Abaco	07-Oct-01	2	1	1	43	5	38	0.12	0.88
South Abaco	25-Oct-01	3	1	4	15	11	4	0.73	0.27
South Abaco	26-Oct-01	1	1	2	13	0	13	0	1
South Abaco	17-Jan-02	1	1	3	146.8	111.8	35	0.76	0.24
South Abaco	27-Jan-02	3	1	2	6	0	6	0	1
South Abaco	27-Jan-02	2	1	2	43	30	13	0.70	0.30
South Abaco	02-Feb-02	2	1	5	84	59.3	24.7	0.71	0.29
South Abaco	03-Feb-02	2	1	5	274.5	222.7	51.8	0.81	0.19
South Abaco	13-Feb-02	2	1	4	15	2.7	12.3	0.18	0.82

South Abaco	13-Feb-02	1	1	2	25.8	18.9	7	0.73	0.27
South Abaco	04-Jun-02	2	1	6	32.8	8	24.8	0.24	0.76
South Abaco	06-Jun-02	1	1	2	74	0	74	0	1
South Abaco	07-Jun-02	1	1	5	14	0	14	0	1
South Abaco	11-Jul-02	4	1	4	32.8	18.8	14.1	0.57	0.43
South Abaco	05-Aug-02	2	1	5	54.7	29.7	25	0.54	0.46
South Abaco	05-Aug-02	4	1	7	89	66	23	0.74	0.26
South Abaco	05-Aug-02	6	1	5	5	0	5	0	1
South Abaco	05-Aug-02	5	1	1	4	0	4	0	1
South Abaco	11-Aug-02	2	1	3	13.4	7.8	5.7	0.58	0.42
South Abaco	12-Aug-02	4	1	4	8	0	8	0	1
South Abaco	25-Aug-02	2	1	4	17	2	15	0.12	0.88
South Abaco	06-Feb-03	2	1	6	44	28	16	0.64	0.36
South Abaco	06-Feb-03	3	1	3	2	0	2	0	1
South Abaco	06-Feb-03	1	1	4	103	87	16	0.84	0.16
South Abaco	26-Feb-03	1	1	5	42	32	10	0.76	0.24
South Abaco	20-May-03	1	1	2	16	0	16	0	1
South Abaco	09-Jun-03	2	1	2	56	45.9	10.1	0.82	0.18
South Abaco	24-Aug-03	2	1	3	25	0	25	0	1
South Abaco	24-Aug-03	1	1	1	58.9	0	58.9	0	1
South Abaco	24-Aug-03	3	1	1	2.6	0	2.6	0	1
South Abaco	10-Sep-03	1	1	4	46.6	24.4	22.2	0.52	0.48
South Abaco	10-Sep-03	3	1	7	5.6	0	5.6	0	1
South Abaco	12-Sep-03	2	1	4	160.3	108.9	51.3	0.68	0.32
South Abaco	12-Sep-03	3	1	5	192.6	148.6	44	0.77	0.23
South Abaco	25-Sep-03	2	1	1	3	0	3	0	1
South Abaco	13-Oct-03	3	1	2	30	0	30	0	1
South Abaco	02-Feb-04	2	1	5	58.5	36	22.5	0.62	0.38
South Abaco	02-Feb-04	3	1	5	51	36.7	14.4	0.72	0.28
South Abaco	03-Feb-04	1	1	5	82.5	67.5	15	0.82	0.18
South Abaco	12-Mar-04	2	1	5	2	0	2	0	1
South Abaco	13-Mar-04	1	1	5	50	36.6	13.4	0.73	0.27
South Abaco	25-May-04	2	1	2	35	31	4	0.89	0.11
South Abaco	25-May-04	2	3	2	27.6	18.3	9.3	0.66	0.34
South Abaco	12-Jun-04	4	1	3	3	0	3	0	1
South Abaco	13-Jun-04	2	1	2	2.1	0	2.1	0	1
South Abaco	13-Jun-04	4	1	1	8	8	0	1	0
South Abaco	13-Jun-04	4	3	1	2.7	1.7	1	0.63	0.37
South Abaco	22-Jul-04	1	1	2	6	0	6	0	1
South Abaco	22-Jul-04	2	1	2	8.9	0	8.9	0	1
South Abaco	22-Jul-04	4	1	6	22.9	0	22.9	0	1
South Abaco	18-Aug-04	2	1	4	6	0	6	0	1
South Abaco	20-Aug-04	2	1	2	26.6	7.5	19.1	0.28	0.72
South Abaco	20-Aug-04	1	1	3	2	0	2	0	1
South Abaco	20-Aug-04	4	1	5	119.2	90.1	29.1	0.76	0.24
South Abaco	20-Aug-04	2	2	2	103.1	81.1	22	0.79	0.21
South Abaco	22-Aug-04	1	1	4	7.8	1.4	6.4	0.18	0.82

App. Table 1.1. Summary table for all Blainville's beaked whale encounters.

Study Area	Date	Enc Seq #	Seq #	Group size	Total Enc. Duration/min	Total duration of Dives/min	Total surface interval duration/min	% of encounter spent diving	% of encounter being surface intervals
East Abaco	08-Dec-95	1	1	3	3.5	0	3.5	0	1
South Abaco	23-Jun-99	2	1	1	6	0	6	0	1
South Abaco	07-Feb-99	4	1	3	10	8	2	0.8	0.2
South Abaco	01-May-97	3	1	1	21	19	2	0.90	0.10
South Abaco	02-Feb-02	5	1	4	32	19	13	0.59	0.41
South Abaco	01-Mar-00	1	1	4	35	33	2	0.94	0.06
South Abaco	26-Jul-04	2	1	1	41.2	36.3	4.9	0.88	0.12
South Abaco	08-Jul-04	3	1	1	43.1	36.9	6.2	0.86	0.14
South Abaco	21-Jan-97	1	1	2	49	44	5	0.90	0.10
South Abaco	09-Apr-97	1	1	1	71.5	63.1	8.4	0.88	0.12
South Abaco	03-Feb-02	3	1	2	81	73.4	7.6	0.91	0.09
South Abaco	13-May-00	1	1	2	94	84.8	9.3	0.90	0.10
South Abaco	26-Feb-99	1	1	5	100.2	69.8	30.4	0.70	0.30
South Abaco	12-Jun-04	2	1	2	107.4	95.1	12.3	0.89	0.11
South Abaco	11-Sep-03	1	1	2	133.8	125.5	8.3	0.94	0.06
South Abaco	15-Mar-02	2	1	3	156	151	5	0.97	0.03

App. Table 1.2. Summary table for all Cuvier’s beaked whale encounters.

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