POPULATION ECOLOGY OF BLAINVILLE'S BEAKED WHALES (MESOPLODON DENSIROSTRIS)

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TABLE OF CONTENTS

Chapter 1: General Introduction

Chapter 2: Comparing rates of turnover, age composition and abundance of Blainville's beaked whales on and off a navy range

TABLE OF CONTENTS continued

Chapter 3: Abundance and survival trends of Blainville's beaked whales surrounding an atypical stranding

TABLE OF CONTENTS continued

Chapter 4: Assigning age and sex classes using sighting history data

TABLE OF CONTENTS continued

<u>Chapter 5:</u> Age and sex specific population demographics

TABLE OF CONTENTS continued

<u>Chapter 6:</u> Re-sightings of beaked whales re-floated during mass stranding

<u>Chapter 7:</u> General discussion

LIST OF FIGURES

LIST OF FIGURES continued

LIST OF FIGURES continued

LIST OF FIGURES continued

LIST OF TABLES

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ABSTRACT

Quantifying population demographics is necessary to analyse the status of wildlife populations and to support effective conservation and management. Such a need exists for beaked whales which are vulnerable to anthropogenic noise, including navy sonar. Here, population demographics were estimated for Blainville's beaked whales (*Mesoplodon densirostris*) in The Bahamas and the potential population-level effects of sonar investigated. Mark-recapture models were fitted to photo-identification data collected at the US Navy's Atlantic Test and Evaluation Center (AUTEC) where sonars were used regularly and 170 km away at Abaco where sonar use was limited, with the exception of a navy exercise correlated with a stranding of beaked whales in 2000.

Life history data collected from 1997-2011 revealed that onset of sexual maturity occurred at age nine for both males and females and minimum longevities were 23 years. The annual turnover of individuals at Abaco was supported by the estimation of a larger parent population. However, adult females showed high site fidelity and survival, while adult males' occupancy patterns were different, making survival of males difficult to separate from permanent emigration. Average annual abundance was lower at AUTEC when compared to a same-sized area at Abaco. Despite a similar number of adult females at both sites, a higher female:calf ratio was found at AUTEC, suggesting lower recruitment through births may have contributed to lower abundance. Population demographics in Abaco changed after the 2000 stranding; abundance and temporary emigration increased then returned to pre-2000 levels remaining stable thereafter. Two stranded whales re-floated in 2000 were later re-sighted having survived exposure to sonar and the physiological stresses related to stranding. This work provides evidence of a possible population-level effect of sonar use at a navy range and during a multi-ship exercise, emphasising the valuable role that longitudinal studies play in monitoring impacts of anthropogenic activities.

CHAPTER 1

GENERAL INTRODUCTION

1.1 Background

The beaked whales (Ziphiidae: Cetacea) are adapted to a deep water environment, an ecological niche in which they were successful during the mid- to late Miocene (7 – 16 million years ago) (Barnes *et al.* 1985, de Muizon 1991). During this time they reached the height of their morphological diversification (Barnes *et al.* 1985, Mead 1989) and remain one of the largest mammalian groups today (Dalebout *et al.* 2002). Yet despite being a highly speciose family, beaked whales are perhaps the least known of large mammals (Wilson 1992). Most species share common behavioural characteristics making field observations difficult. They are typically found in small groups, exhibit cryptic surface behaviours, have very short surfacing intervals and can dive for extraordinarily long periods making them difficult to detect (Barlow 1999, Claridge 2006). As a result, most information on their ecology has come from beach-cast or stranded animals, and several species are only known from a few specimens (Dalebout *et al.* 2008). However, recent public and scientific concern that beaked whales may be particularly vulnerable to anthropogenic noise have focussed much attention on addressing the many gaps in our knowledge of their population and behavioural ecology.

Concern about the potential effects of noise on marine mammals has increased in recent decades (Richardson *et al.* 1995). Attention shifted from impacts of commercial shipping traffic masking baleen whale communication (e.g., Payne and Webb 1971) to behavioural responses of beaked whales to anthropogenic noise (Peterson 2003, Aguilar de Soto *et al.* 2006, Cox *et al.* 2006, Tyack *et al.* 2011, Pirotta *et al.* 2012) following a number of atypical mass strandings of beaked whales that occurred in close temporal and spatial proximity to naval exercises (Van Bree and Kristensen 1974, Simmons and Lopez-Jurado 1991, Frantzis 1998, Balcomb and Claridge 2001, Evans and England 2001, Jepson *et al.* 2003, Freitas 2004, Fernandez *et al.* 2005, Cox *et al.* 2006). Although the mechanisms directly causing the strandings remain unclear, mid-frequency sonars (2-10 kHz) used during fleet readiness training exercises have been linked to behavioural responses that in turn have led to a number of hypothesized physiological impacts (Evans and England 2001, Jepson *et al.* 2003, Fernandez *et al.* 2005, Cox *et al.* 2006, Hooker *et al.* 2009). Strandings typically involve individuals from multiple ziphiid species, but primarily of the genera *Ziphius* and *Mesoplodon*.

One of these events occurred in The Bahamas. On 15 March 2000, an antisubmarine warfare exercise involving surface ships using standard hull-mounted mid-range tactical sonars transited Northwest Providence Channel, between the islands of the northern Bahamas (Figure 1.1), correlated with the stranding of at least 14 beaked whales (Balcomb and Claridge 2001, Evans and England 2001). Two species were involved: Cuvier's beaked whale (*Ziphius cavirostris*, *n* = 11) and Blainville's beaked whale (*Mesoplodon densirostris*, *n* = 3). Eight whales stranded alive, six of which were re-floated; and six whales are known to have died. The population-level effect of this and other atypical strandings worldwide needs further investigation (Cox *et al.* 2006). For this reason, Taylor *et al.* (2007) note that beaked whales are of high conservation interest and that it would be particularly useful if studies could detect trends in beaked whale abundance.

Although direct mortalities from some sonar exercises have been accepted within the scientific community, indirect impacts are more difficult to document but also need evaluating. For example, Blainville's beaked whales regularly use the waters at the US Navy's Atlantic Undersea Test and Evaluation Center (AUTEC) in The Bahamas (DiMarzio *et al.* 2008), where mid-frequency active sonars are frequently used during fleet readiness training. During multi-ship sonar tests at AUTEC, Blainville's beaked whales move away from ships using sonar, returning to the range only when exercises cease (McCarthy *et al.* 2011, Tyack *et al.* 2011). It is unknown whether these shorter-term movements are mirrored by longer-term changes in residency or increased annual turnover of individuals or to what extent these movements affect the population demographics.

Concern has also been raised recently about how acoustic disturbances could cause chronic stress. It has been hypothesised that long-term exposure to frequent intense stressors that cause behavioural responses and displace individuals from optimal habitat could reduce fitness via mechanisms such as decreased foraging efficiency, failed reproduction, increased calf mortality, immunosuppression, and inhibited growth and metabolism (Curry 1999, Wright *et al.* 2007, Moore and Barlow 2013). This is of particular concern for lactating and pregnant females, and may result in failed reproduction and increased calf mortality (Wright *et al.* 2007). Beaked whales exhibit extreme diving behaviour (Hooker and Baird 1999, Tyack *et al*. 2006, Baird *et al*. 2006) and, as such, may be unable to enhance food intake much further during lactation. Additionally, long post-dive recovery periods are required and therefore the number of dives is limited (Arranz *et al.* 2012). As such, higher energetic cost associated with displacement combined with lower energy intake during navy exercises provides a possible mechanism to reduce fitness. Combined, these factors suggest that beaked whales inhabiting navy ranges may have lower fecundity, and perhaps calf survival.

The particular vulnerability of beaked whales to navy sonar has highlighted the need for basic data on the ecology of beaked whales to inform mitigation of the effects of such activities (Cox *et al.* 2006). Barlow and Gisiner (2006) recommend that studies of beaked whales should be conducted on varying spatial scales. Large scale systematic surveys can assess distribution, but mark-recapture methods (on a smaller scale) will be best for estimating abundance. This method also provides much needed individual-level data which can help understand population processes, including survival, movements, reproduction, development, growth, dispersal, feeding, predation, and competition. Factors affecting these processes include the distribution and abundance (density) of individuals within a population, of their prey, their predators, their competitors, where suitable habitats are found, and where disturbances may occur.

Cetaceans are long-lived, highly specialised animals with delayed reproduction and low fecundity which makes them incapable of rapid adaptation and thus particularly vulnerable to anthropogenic impacts (Bowen and Siniff 1999, Moore 2005). Marine mammals face some serious environmental threats, the scale of which is enormous and the complexity of cumulative effects equally daunting. For example, the effects of climate change on habitat alteration especially in polar regions (Tynan and DeMaster 1997), bycatch of cetaceans in fisheries (Lewison *at al.* 2004), and disturbance from noise pollution (see Hildebrand (2005) for a review). To minimise these impacts, a precautionary approach will be needed in management decisions including that management action should not require large numbers of precise estimates (Taylor *et al.* 2007). The work presented in this thesis fills some of the gaps in our knowledge about the population ecology of Blainville's beaked whales in the hope of improving mitigation of navy activities in The Bahamas and elsewhere, and to contribute to conservation strategies for this species.

1.2 Blainville's beaked whales

1.2.1 Phylogeny

The *Ziphiidae* first appeared in the early Miocene (about 24 million years ago), and reached the height of its speciation in the middle Miocene and remained through the late Miocene (7 to 10 million years ago) (Barnes *et al.* 1985, Mead 1989). Beaked whales are part of the Superfamily Ziphoidea, and their evolutionary relationship with Physeteroidea and Delphinoidea as well as the relationship between ziphiids is unclear (Rice 1998). De Muizon (1991) classified the *Ziphiidae* into three subfamilies: *Hyperoodontinae*, includes *Hyperoodon* and *Mesoplodon* (including *Indopacetus*); *Ziphiinae*, includes *Ziphius, Berardius*, *Tasmacetus* and four fossil genera; and *Squaloziphiinae.* It is estimated that the divergence of *Ziphius* and *Mesoplodon* occurred during the early Miocene (Dalebout *et al.* 2008).

With 21 recognised extant species, the *Ziphiidae* represent one of the largest mammalian groups, yet least known. In fact, two new species have been recorded within the last two decades (Reyes *et al.* 1991, Dalebout *et al.* 2002) and another possible new species or subspecies suggested recently (Dalebout *et al.* 2007). The majority of the *Ziphiidae* family comprise the genus *Mesoplodon* (*n* = 14) while the other five genera are monotypic or consist of antitropical species (Dalebout *et al.* 2008).

Three species are known from The Bahamas: Cuvier's beaked whale, *Ziphius cavirostris* (Cuvier 1823), which is also known as goose-beaked whale; Blainville's beaked whale, *Mesoplodon densirostris* (Blainville 1817), which is also known as dense- beaked whale; and, Gervais' beaked whales, *M. europaeus* (Gervais 1855), which is also known as Antillean beaked whale, Gulf Stream beaked whale or European beaked whale. These species were first recorded in The Bahamas from beach-cast specimens by Caldwell and Caldwell (1974), Moore (1958) and Balcomb (1981), respectively. There is a single record of True's beaked whale, *M. mirus* (True 1913), from The Bahamas (Anon 1981), but this record cannot be confirmed because the specimen has been lost (Claridge 2006).

1.2.2 General Characteristics

Blainville's beaked whale characteristics have been described extensively from dead or live stranded individuals (e.g., Moore 1958, 1968, McCann 1974, Mead 1989). They have a robust, cigar-like body shape with a small dorsal fin located on the posterior third of the body (Mead 2002). Pitman (2002) gives 4.7 m as a maximum recorded length for Blainville's beaked whale and no significant differences in body length by sex is known (MacLeod 2006).

Dentition in ziphiids has been reduced numerically in all but one species (*Tasmacetus sheperdi*) to only one to two pairs of teeth located in the mandible (Heyning 1984), although vestigial teeth can be found in a few species (Mead 1989). In *Mesoplodon* there is only one pair of laterally compressed teeth which are located at varying positions in the mandible depending on the species (Moore 1968). At the onset of sexual maturity the teeth erupt from the alveoli in males only (McCann 1963, Besharse 1971) and are used in male-male aggression (McCann 1974, Mead *et al*. 1982, Heyning 1984).

Although sexual dimorphism exists in all Ziphiid species, it is most pronounced in Hubbs' beaked whale (*M. carlhubbsi*) and Blainville's beaked whale (*M. densirostris*) (Heyning 1984). In these species, as males mature, ossification in the mesorostral canal results from the expansion of the vomer, premaxilla and maxilla bones which eventually fuse in older males (Moore 1963, Mead 1989). This massive rostral bone serves to reinforce the rostrum as males engage in combat (Heyning 1984), and is most developed in *M. densirostris* in which the rostral bone has the highest density (5.7 g/cm^3) of any mammalian bone tissue measured (Zotti *et al*. 2009).

Ross *et al.* (1988) and Jefferson *et al.* (2008) provide an excellent overview of beaked whale pigmentation patterns. Oval scars caused by cookie cutter sharks (*Isistius* sp.) often cover the body both dorsally and ventrally (McCann 1974), and Walker and Hansen (1999) suggest that individuals accumulated these scars with age. Scars on Blainville's beaked whales remain visible for more than 10 years (McSweeney *et al.*

2007), although re-pigmenting of scars may occur in other mesoplodonts (R. Pitman, *pers. comm.* 2008). Aggressive use of the teeth in male-male combat results in extensive intra-specific scarring or "battle scars" on males (McCann 1974).

1.2.3 Life history and behaviour

Life history data for ziphiids are very limited and are based primarily on data collected from stranded whales or from whale fisheries. Minimum age at sexual maturity for a female *M. densirostris* is reported at 9 years based on growth layer groups in the teeth (Ross 1979). Perrin and Myrick (1980) counted at least 27 growth layer groups in the tooth cementum of a Gervais' beaked whales (*M. europaeus*) which is the maximum age known for any mesoplodont.

Blainville's beaked whales in The Bahamas have been reported in small groups ranging from 1 to 11 whales (median 4 whales; Claridge 2006), similar to that reported elsewhere (Shallenberger 1981, McSweeney *et al.* 2007). This species exhibits a harem-type social organisation with a fission-fusion structure and generally low indices of association among adults (Claridge 2006, McSweeney *et al.* 2007). Group composition generally consists of a single adult male with several adult females and their young (Ritter and Brederlau 1999, Claridge 2006, McSweeney *et al.* 2007). Photo-identification studies have shown long-term site fidelity in Blainville's beaked whales (Claridge 2006, McSweeney *et al*. 2007).

1.2.3.1 Prey and feeding ecology

Foraging dives for Blainville's beaked whales have been recorded to depths of 1,599 m and dive times of 83 min (Baird *et al.* 2008). Their prey species are primarily mesopelagic or deep-water benthic fish and cephalopods, with cephalopods being the most common prey (Clarke 1996, MacLeod *et al.* 2003). Analyses of faecal samples of Blainville's beaked whales from The Bahamas suggest that their diet is quite varied and that deep-water fish are an important component (Hickmott 2005, DeRuiter *et al.* 2007).

1.2.3.2 Predation

Based on scarring patterns observed on adults and calves, beaked whales are preyed upon by large sharks, false killer whales and killer whales (McSweeney *et al.* 2007). In The Bahamas, a group of pygmy killer whales was observed harassing a young Blainville's beaked whale (*pers. obs.*). Predator avoidance may explain diel variation in diving behaviour with Blainville's beaked whales in Hawaii spending more time at the surface at night (Baird *et al.* 2008), although a diel pattern was not observed in the Canary Islands (Arranz *et al.* 2012).

1.2.4 Distribution and abundance

Blainville's beaked whale has the widest distribution of all *Mesoplodon* species, occurring circumglobally in tropical and warm temperate waters (Mead 1989). Beaked whales can be found throughout varying deep-water environments but they show a preference for topographically complex areas such as submarine canyons, shelf edges, and seamounts (Whitehead *et al.* 1997, Waring e*t al.* 2001, D'Amico *et al.* 2003, MacLeod and Zuur 2005), presumably because prey is concentrated around these features (Hui 1985, Kenney and Winn 1987, Baumgartner 1997). A steep depth gradient is an important variable in predicting Blainville's beaked whale habitat (MacLeod *et al.* 2004, Claridge 2006), which may allow access for foraging in both the deep scattering layer and near the sea floor over small spatial scales (Arranz *et al.* 2012).

Few estimates of beaked whale abundance at the species level are available but at least some species occur in small, localised populations (e.g., Gowans *et al.* 2000), and "hot spots" with higher than average densities may exist (Barlow *et al.* 2006). Using photographic mark-recapture, Gowans *et al.* (2000) reported a small population [130 (95% CI = 106-166)] of northern bottlenose whales (*Hyperoodon ampullatus*) from The Gully, Nova Scotia. All other studies to date have employed distance sampling methods. The highest ziphiid densities have been reported for Baird's beaked whale (*Berardius bairdii*) for the Japanese eastern slope waters (68.1 whales/1000 km^2, CV = 0.30; Miyashita 1986), while densities of Cuvier's beaked whale (*Ziphius cavirostris*) have been found to be an order of magnitude lower (e.g., 6.2 whales/1000 km^2, CV = 1.43; Barlow 2006).

Densities of mesoplodont beaked whales appear to be even lower, although large variation in densities supports the existence of "hotspots" in some areas (Barlow *et al.* 2006). Barlow (2006) found very low density of Blainville's beaked whales around Hawaii (1.17 whales/1000 km^2, CV = 1.25). However, using acoustic detections from the fixed hydrophone array and distance sampling methods, Marques *et al.* (2009) estimated the density of Blainville's beaked whales on the AUTEC range averaged over a 6-day period between 22.5 and 25.3 whales/1000 km^2 (depending on assumptions used, with 95% confidence intervals 15.4 – 32.9 and 17.3 – 36.9).

1.2.5 Population structure and dynamics

To date, little work has been done on beaked whale population structuring, but recent studies have presented some interesting results. Morin *et al.* (2012) found that *M. densirostris* haplotypes were divided into two clades, representing the western Atlantic and the Pacific, while for Cuvier's beaked whales, three major clades were noted. No haplotypes were shared between ocean basins for either species. Dalebout *et al.* (2005) described a high degree of isolation and low maternal gene flow among regional and oceanic populations of Cuvier's beaked whales. Similarly, studies of genetic variability and residency patterns (using photo-identification techniques) have identified separate stocks of northern bottlenose whales in the north-western Atlantic (Dalebout *et al.* 2001). However in the Morin *et al.* (2012) study, *Ziphius* samples from the Atlantic were found in all three clades identified and from the Pacific in two of the clades. This complex pattern in *Ziphius* suggests either multiple inter-ocean migration events in recent evolutionary history, or possibly current gene flow between ocean basins (Morin *et al.* 2012).

Population trends for beaked whale species have remained largely unknown because of the difficulty in obtaining precise estimates of abundance (Read and Wade 2000, Taylor *et al.* 2007). Probabilities of detecting beaked whales visually during ship-based or aerial surveys are low; resulting in high coefficients of variation in abundance estimates which can be greater than 100% (e.g., Barlow 2006). With this lack of precision, the only way to detect a change in abundance for beaked whales is through repeated annual surveys over long periods of time (Taylor *et al.* 2007, Jewell *et al.* 2012). One such study using ship-based visual survey data collected over 18 years, Moore and Barlow (2013) showed a decline in *Ziphius* and *Mesoplodon* beaked whale abundance off the west coast of the United States, including the area where the US Navy operates an underwater testing range. Using photographic mark-recapture approaches, Whitehead and Wimmer (2005) showed no significant trend in abundance for northern bottlenose whales inhabiting The Gully off the Scotian Shelf from 1988 – 2003. However, Whitehead (2013) recently showed a 21% per year increase in sighting rates for Sowerby's beaked whale (*M. bidens*) in The Gully and adjacent submarine canyons over a longer time period (23 years), which may be the result of reduced anthropogenic disturbance since this area was designated a marine protected area in 2004.

<u>1.2.6 Conservation Status</u>

The conservation status of Blainville's beaked whale is largely unknown and it is listed in the IUCN Red List of Threatened Species as data deficient (IUCN 2012). As with almost all cetaceans, these species are also listed under CITES Appendix II, signifying that they may become threatened with extinction unless trade is closely controlled (CITES 2012). One of the major problems that marine mammals face is habitat loss and alteration. Harwood (2001) predicts that marine mammal habitats are likely to continue to deteriorate as a result of commercial fishing, pollution, disturbance, and increased risks of mortality from pathogens and biotoxins. In particular, beaked whales face high potential risks with low levels of information available to monitor trends with precision (Taylor *et al.* 2007).

While there was no commercial fishery for mesoplodont whales, they are occasionally taken in other fisheries, e.g. Japan (Mead 1989) and ziphiids are taken in a small whale fishery in St. Vincent in Lesser Antilles (IWC 1989). Read and Wade (2000) reported that bycatch in pelagic driftnet fisheries exceeded the removal limits set under the US Marine Mammal Protection Act for *Mesoplodon* species in the western North Atlantic and for mesoplodonts in the North Pacific. However, total fishery-related mortality cannot be estimated for each species of *Mesoplodon* because of the uncertainty in species identification by fishery observers (Lewison *et al.* 2004).

From 1950 to 2004, after modern high-powered mid-frequency active sonar was employed, D'Amico *et al.* (2009) found 126 mass strandings of beaked whales globally. Strandings were significantly correlated with navy exercises in the Mediterranean and Caribbean Seas (Filadelfo *et al.* 2009). Assessing the impacts of navy exercises of beaked whales at the population level is greatly needed and, as such, is one of the main focuses of this thesis.

1.3 Thesis Overview

1.3.1 Study area

The Great Bahama Canyon is located in the northern Bahamas (25.5N, 77.3W; Figure 1.1). The canyon stretches over 270 km in length and 40 km in width, encompasses an area of approximately 29,000 km^2, and reaches depths of almost 5 km

(Sealey 1994). There are two branches which merge to form the canyon itself: Northwest Providence Channel and the Tongue of the Ocean. Northwest Providence Channel is a major international shipping channel providing access for vessels transiting between the northwest Atlantic Ocean and the Caribbean Sea to the southeast United States and Gulf of Mexico. In contrast, the Tongue of the Ocean (a dead-end for large draft vessels) has very little commercial shipping traffic, and for this reason was selected as the site of the US Navy's Andros-AUTEC Operating Areas which began operations in 1966. The majority of acoustic testing in the Tongue of the Ocean takes place on the weapons ranges located just offshore from the main base at the Atlantic Underwater Test and Evaluation Center (AUTEC) on Andros Island.

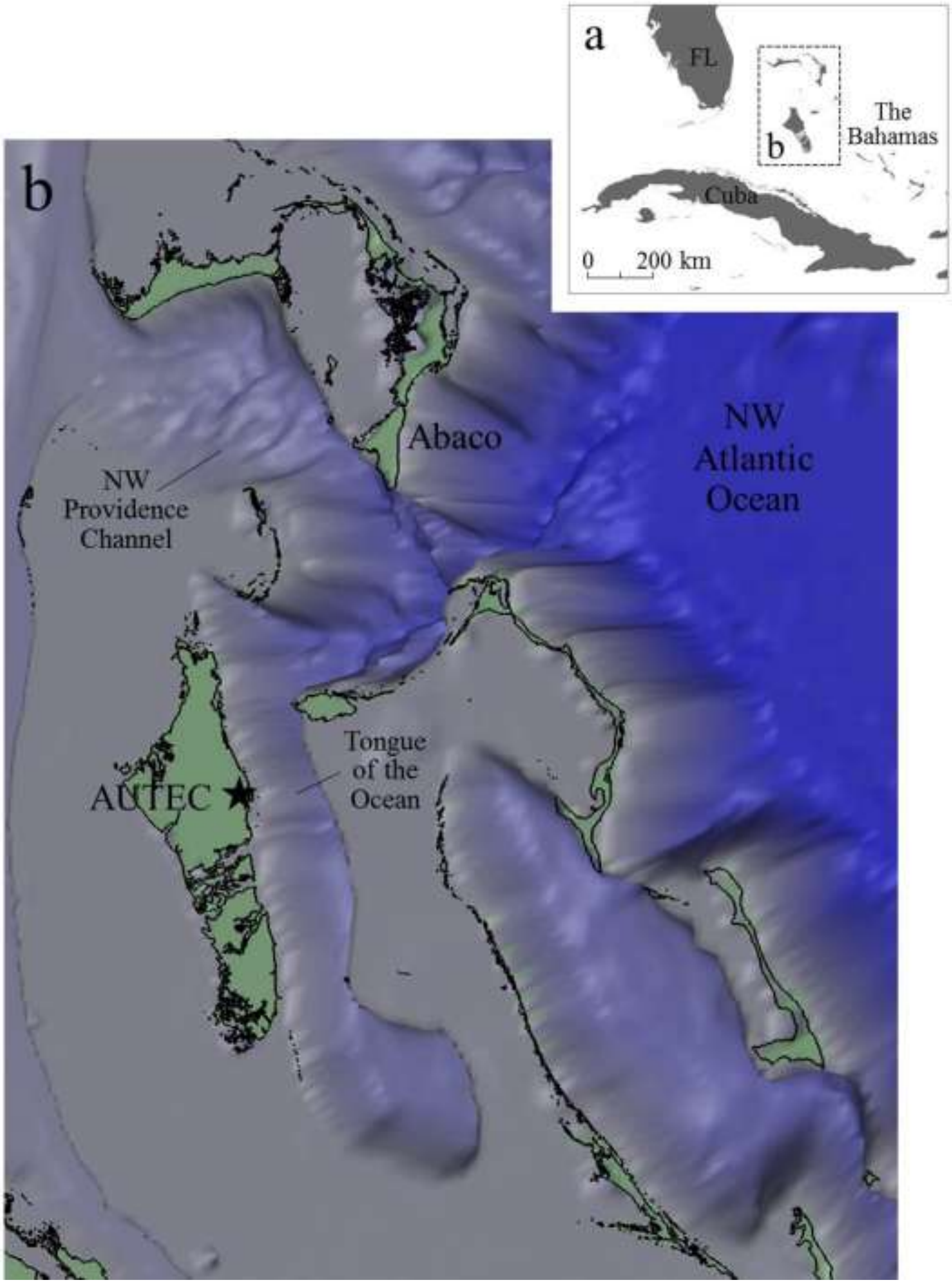

Figure 1.1. The Great Bahama Canyon is the most prominent oceanographic feature in the northern Bahamas. It consists of two branches: Northwest Providence Channel and Tongue of the Ocean. Data sources are: for bathymetry, General Bathymetric Chart of the Oceans (GEBCO 2008); and for shoreline, GSHHS (Global Self-consistent, Hierarchical, High-resolution Shoreline; NOAA National Geophysical Data Center) with 20X vertical exaggeration.

The canyon is characterised by U-shaped troughs with strong turbidity currents (Schwab *et al.* 1989, Sealey 1994) and is rich in topographic complexity with numerous V-shaped submarine canyons and gullies eroded by bank-derived sediment cascading down the nearly vertical marginal escarpment (Mullins 1978, Mullins *et al.* 1979). Northwest Providence Channel is one of seven main passages between the Atlantic Ocean and the Caribbean Sea (Johns *et al.* 2002) and contributes about 1.2 Sv to the Florida Current transport (Leeman *et al.* 1995). This westward flow is influenced by the warm Antilles current and the cold Deep Western Boundary Current. The Tongue of the Ocean is characterized by net northwestward flow, originating from the area to the south and from passages between the eastern islands of The Bahamas. Satellite data show that productivity levels in this area are typical of subtropical oligotrophic environments, ranging in chlorophyll *a* concentrations from 0.05 to 7.0 mg/m^3 (SeaWiFS data from http://oceancolor.gfsc.nasa.gov).

1.3.2 Approach

Using existing and new photo-identification data and a Bayesian approach to mark-recapture model fitting, I investigated the population ecology of two localised populations of Blainville's beaked whale in the Great Bahama Canyon. Data were collected during a 15-year field study (1997 – 2011) conducted off southwest Abaco Island and a 6-year study (2005 – 2010) at the US Navy's Atlantic Underwater Test and Evaluation Center (AUTEC) in the Tongue of the Ocean. Combined, these efforts have resulted in an unprecedented dataset for this species.

In Chapter 2, I fit mark-recapture models to the photo-identification data at AUTEC and Abaco to estimate and compare key aspects of the population demographics of Blainville's beaked whale on and off a navy range. This work provides the first estimate of abundance for mesoplodont beaked whales in an area where tactical sonars are frequently used, and are reported relative to a control site (Abaco) where sonar is not used regularly. Study areas of the same size are used to facilitate a comparison of the rates of turnover of whales in each area which is considered an important factor to assessing disturbance. Here turnover is inferred from annual rates of temporary emigration and re-immigration and not from turnover in the population during the study resulting from birth and immigration (recruitment), death and permanent emigration.

In Chapter 3, a slightly more complex mark-recapture model is fitted to the full time series of photo-identification data available for Abaco, a time period which includes before and after the March 2000 stranding. Apparent survival and recruitment are estimated and trends in population parameters and abundance assessed to determine potential population level effects of the atypical stranding event. To address individual heterogeneity, in Chapter 4 I explore characteristics that can be used to assign age class and sex to individuals. Assignments are then made to each individual known from high quality identifications, including all individuals in the mark-recapture sample used in Chapter 3, and the age structure of the population is described. Age at sexual maturity is estimated by monitoring some individuals born during the study as they matured. In Chapter 5, I examine age- and sex-specific heterogeneity in the population demographics of the Abaco population by fitting a mark-recapture model which is stratified by age class and sex. Differences in probabilities of capture and survival are evident, and model fit is improved. Finally, in Chapter 6 an account is given of the successful re-floating of two whales that live-stranded during the March 2000 stranding.

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CHAPTER 2

COMPARING RATES OF TURNOVER, AGE COMPOSITION AND ABUNDANCE OF BLAINVILLE'S BEAKED WHALES (*MESOPLODON DENSIROSTRIS*) ON AND OFF A NAVY RANGE IN THE BAHAMAS

2.1 Introduction

Quantifying population demographics is necessary to diagnose the status of wildlife populations and to support effective conservation and management. However, monitoring cetaceans is difficult because complete enumeration of all individuals in a population or a sampling area is rarely possible. In many studies, experimental design is often limited by logistics and cost, resulting in temporal or geographic sampling constraints, further limiting power to assess population status. So comparing populations exposed to different natural or anthropogenic pressures can provide a valuable context in which to interpret their status.

Concerns about the effects of environmental degradation on marine mammals have become increasingly focussed on disturbances from anthropogenic noise to which some cetaceans are especially vulnerable (Richardson *et al.* 1995). In particular, atypical mass strandings and behavioural responses of beaked whales of the genera *Ziphius* and

Mesoplodon have been correlated with naval sonar exercises (e.g., Frantzis 1998, Evans and England 2001, Jepson *et al.* 2003, Peterson 2003, McCarthy *et al.* 2011, Tyack *et al.* 2011). However, it is not clear if these responses lead to population-level impacts (Moore and Barlow 2013); an issue that requires a better understanding of beaked whale population demographics and status (Cox *et al.* 2006). Visual field observations of beaked whales are difficult because most species exhibit cryptic surface behaviour, short surfacing intervals, and long dive durations (Barlow 1999, Tyack *et al.* 2006). This limits the accuracy and precision of abundance estimates based on distance sampling from line transect surveys (Barlow 1999), although mark-recapture sampling methods may be a better approach when combined with knowledge of their population demographics and structuring (Barlow and Gisiner 2006).

Mark-recapture methods are commonly used in population ecology. Individuals within a target population are captured, marked and then released, and recaptures of the marked individuals are recorded in subsequent sampling occasions. Using statistical modelling, abundance can then be estimated based on the probability of a marked individual being re-captured (Lebreton *et al.* 1992). However, for most cetacean species, capturing and marking is not feasible and an alternative approach is to "capture" individuals photographically and use naturally-occurring features (e.g., scars) as their marks (Hammond 1986, 1990; Hammond *et al.* 1990, Hammond 2009, Hammond 2010). Photographic mark-recapture methods have been used successfully to quantify the population size and demographics of multiple cetacean species (e.g., Whitehead *et al.* 1997, Wilson *et al.* 1999, Mizroch *et al.* 2004, Ramp *et al.* 2006, Durban *et al.* 2010). Additionally, photographic methods can be used to estimate rates of individual movement or turnover, which is an essential component of understanding factors contributing to changes in abundance over time (e.g., Whitehead 1990, Durban *et al.* 2000, Matkin *et al.* 2012).

Despite being difficult to find at sea, some species of beaked whale, such as Blainville's beaked whale (*Mesoplodon densirostris*) can potentially be good candidates for photographic mark-recapture studies. They possess individually distinctive natural markings including a variety of mark types caused by scars from the bites of cookie cutter sharks (*Isistius* sp.) as well as intra-specific scarring (McCann 1974). These scars are long-lasting, at least in some beaked whale species (e.g., Claridge 2006, McSweeney *et al.* 2007). Despite the utility of this approach, photographic mark-recapture methods have been used to estimate abundance for only one species of beaked whale, the northern bottlenose whale, *Hyperoodon ampullatus* (Whitehead *et al.* 1997, Gowans *et al.* 2000, Whitehead and Wimmer 2005). There is a need for similar studies to be undertaken for other beaked whale species particularly in areas where beaked whales are exposed to anthropogenic noise, such as on navy ranges (Barlow and Gisiner 2006).

Blainville's beaked whales regularly use the waters at the US Navy's Atlantic Undersea Test and Evaluation Center (AUTEC) in The Bahamas (DiMarzio *et al.* 2008), where mid-frequency active sonars are frequently used during fleet readiness training. It has recently been documented that Blainville's beaked whales will cease foraging and move tens of kilometres away from AUTEC's Weapons Range during multi-ship sonar exercises, returning days later when the testing has ceased (McCarthy *et al.* 2011, Tyack *et al.* 2011). It is unknown whether these shorter-term movements are mirrored by longer-term changes in residency or to what extent these movements affect the population demographics.

In this study, mark-recapture models were fitted to photo-identification data to estimate turnover rates (emigration and re-immigration, e.g., Whitehead 1990, Matkin *et al.* 2012) and abundance of Blainville's beaked whales at the US Navy's AUTEC range and a control area nearby, but off the range. Study sites of similar size (300 km^2) were selected in each location and the same 8-month annual sampling intervals from 2005 – 2010 were used, so that rates of turnover at the two study sites could be directly compared. Estimates of the abundance of whales using each study area were also compared, providing the first mark-recapture estimate of abundance for beaked whales on a Navy range where sonar is regularly used. The specific objectives of this study were:

(1) To estimate turnover rates of Blainville's beaked whales at two separate localities within the northern Bahamas: a control site (Abaco) where whales are not exposed to anthropogenic noise pollution from navy sonar exercises; and within a navy range (AUTEC) where whales are regularly exposed to navy sonars.

(2) To estimate average annual abundance of Blainville's beaked whales at Abaco and AUTEC.

(3) To compare age composition of Blainville's beaked whales between sites (e.g. proportion of adult male, adult female, immature, and calf).

2.2 Methods

2.2.1 Study area

Field work was conducted in two discrete study sites approximately 170 km apart in The Bahamas (one off the southwest coast of Abaco Island, and one at AUTEC off the eastern side of Andros Island; Figure 2.1a). Areas of comparable size (approximately 300 km^2), encompassing the majority of the available photo-identification data, were selected so that rates of turnover could be quantitatively compared. At Abaco, the study area was bordered on one side by a deep water contour in order to exclude shallow (<200 m), unsuitable beaked whale habitat (Figure 2.1b; Tyack *et al.* 2006). At AUTEC, the study area was a rectangular swath of deep water that is considered suitable beaked whale habitat (Figure 2.1c).

2.2.2 Data collection

Surveys for beaked whale groups were conducted from a wide variety of ship and boat platforms, ranging from 6 to 83 m in length. However, once a group was sighted, close approaches were made using small vessels (<9 m) only. At AUTEC, searches were assisted by acoustic detections, using a network of bottom-mounted hydrophones to detect the echolocation clicks of beaked whales in real time (Moretti *et al.* 2006), and the vessel was often directed to the area of vocalising whales. When approaching whales, the vessel was manoeuvred alongside the group so that the camera was perpendicular to the animals when possible. Nikon Digital SLR cameras were used with either a fixed 300 mm F4 lens or 80-200 mm F2.8 zoom lens and images were stored at a resolution of at least 6 megapixels. Photographs were taken of the entire length of the animal as it surfaced: the focal area for age class assessment was the head, and the area immediately surrounding the dorsal fin was primarily used for individual identifications (see below). When possible, photographs were taken of both the right and left sides of all individuals within a group.

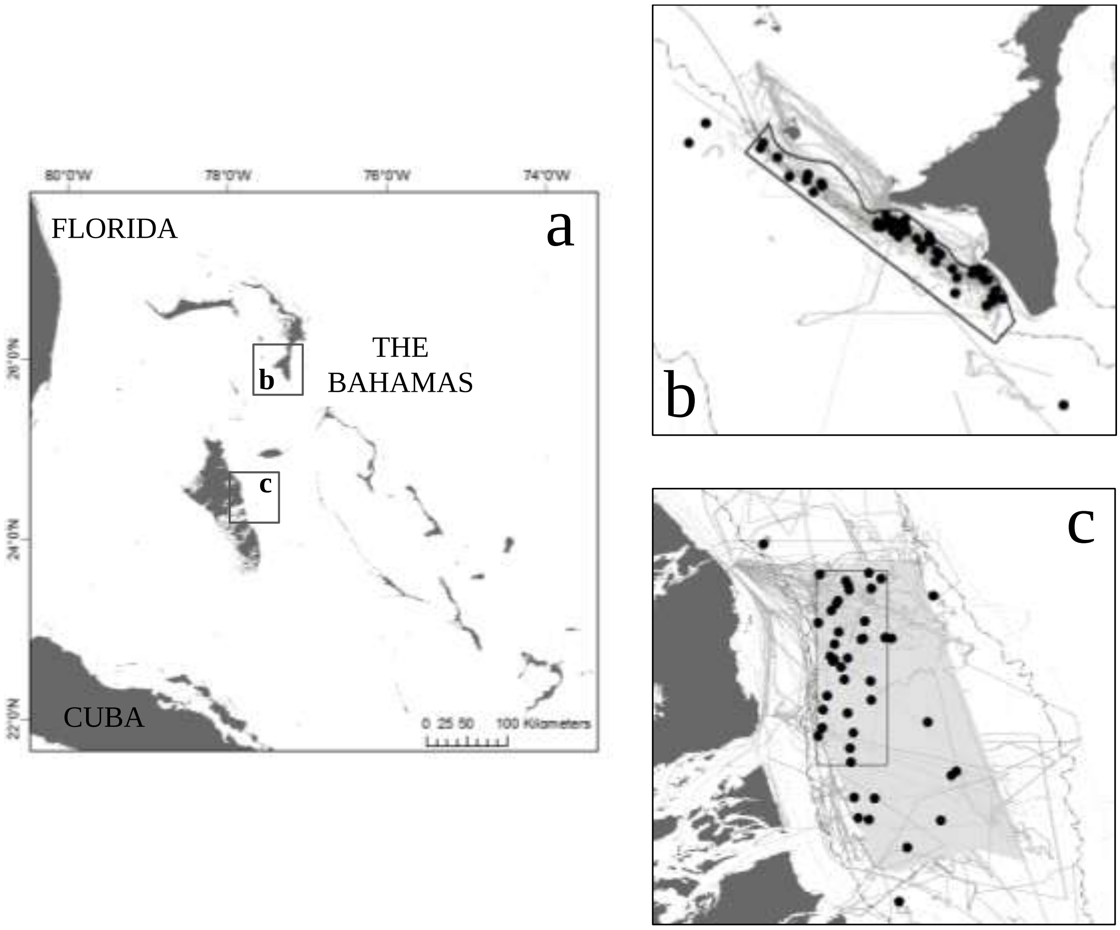

Figure 2.1. (a) Map of The Bahamas archipelago showing the two study areas: (b) Abaco and (c) AUTEC. The 300 km^2 area selected at both study sites is marked by a solid polygon; solid circles represent the locations of encounters with Blainville’s beaked whales from March through October, 2005 – 2010; vessel survey tracks are indicated by the grey lines and the 1,000 m isobaths by a dashed black line. In (c), the outer boundary of the hydrophone array at AUTEC is shown (light grey shaded area).

2.2.3 Photographic processing

Individual beaked whales were identified using the unique pattern of scarring on the body and nicks in the dorsal fin or near the base of the fin. McSweeney *et al.* (2007) found that these marks are long-lasting on *M. densirostris* in Hawaii. Longevity in marks was also observed for this species in The Bahamas (Figure 2.2).

1998 2008

Figure 2.2. Photo-identification images of Md091, an adult female Blainville's beaked whale from the Abaco study area. These photographs were taken 10 years apart demonstrating that the longevity of natural markings in this species is appropriate for this six-year study. Oval marks are scars from bites attributed to cookie cutter sharks (*Isistius* sp.).

Identification photographs were assigned a quality grade (*Q*) ranging from 0 to 3 (3 being the highest quality photograph) based on the image size, focus, lighting, angle, and exposure of the photograph (Figure 2.3). Only high quality images (*Q* > 1) were used in subsequent analyses to prevent misidentifications. A rectangular area framing the dorsal fin was defined as the "ID area". Images were each sized by cropping photographs to the measure of one dorsal fin base-width in all directions from the centre of the fin base. Additionally, individuals were assessed for presence or absence of unique markings, including any nicks or notches, on the trailing edge, leading edge or at base of dorsal fin (within the ID area). This was done for both sides of every animal and all identification photographs were pooled for the same individual, thereby increasing the number available for mark-recapture analysis. Only individuals with at least one nick were considered reliably marked or distinctive enough to include in mark-recapture analyses to ensure that all marks were unique.

Field efforts at AUTEC occurred between March and October of each year, while at Abaco photo-identification data was conducted year-round. To ensure a consistent timeframe for comparing turnover and abundance, the Abaco data were limited to only those collected from March to October. However, information was used from “out-of-sample re-sightings” (Fearnbach *et al.* 2012), additional sightings outside the annual sampling intervals, the study period, or spatially restricted study areas, to inform about survival in years when an animal was known to be subsequently alive but not seen in the previous interval.

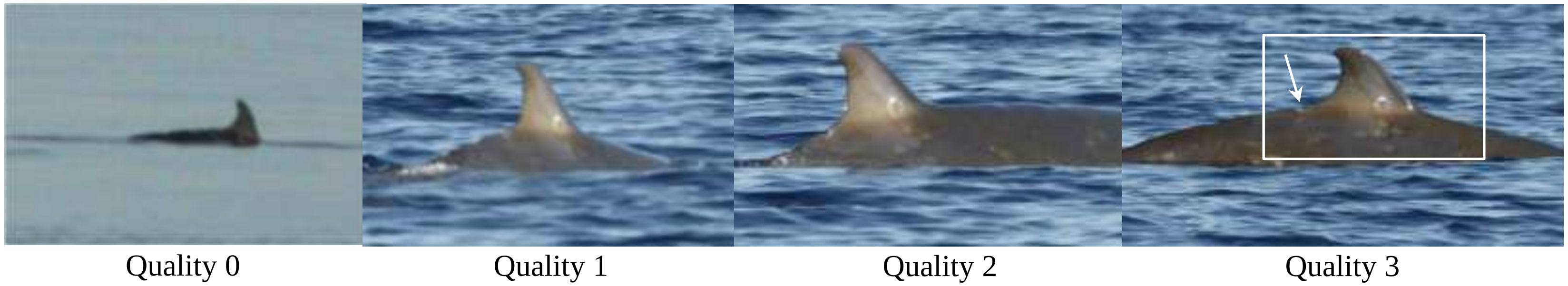

Figure 2.3. Four photographs of the same whale, Md538, but of varying image quality (*Q*), demonstrating how photographs were graded from very poor quality (0, on far left) to excellent quality (3, on far right). Only images with quality 2 and 3 were included in the analyses. The box shown in the Quality 3 image represents the "ID area", inside which the presence or absence of marks was noted.

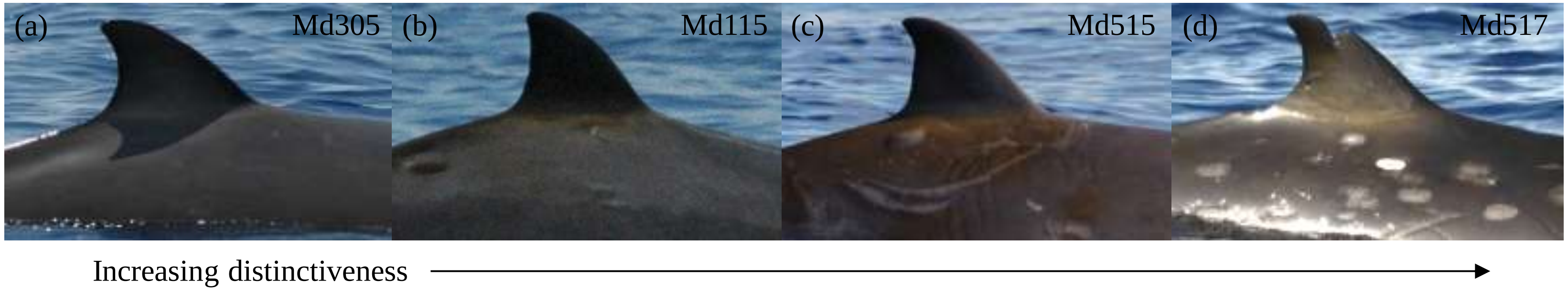

Figure 2.4. High quality photographs of four different whales, ranging from less distinctive (a) to very distinctive (d). While only Md517 (d) was included in the mark-recapture analysis (because it has a nick), all four individuals could readily be distinguished within an encounter-day by using all marks types including lightly pigmented marks (a), re-pigmented Isistius sp. scars (b), and linear scars (c).

2.2.3.1 Determining age composition

The final step in the photographic data processing was to assign a life history category to each individual based on its age class and, when known, sex. This was necessary for two reasons: (1) to determine if the age composition was the same in both areas to address bias when comparing movement patterns which may differ by age class and/or sex (e.g., Wimmer and Whitehead 2004) and (2) to exclude younger, dependent individuals (calves) from the sampling because their captures were not independent from their mother's capture. Claridge (2006) described methods for assigning age class and sex to Blainville's beaked whales based on relative body size, extent of scarring, sexual dimorphism (abruptly stepped mandibles in sub-adult and adult males), secondary sexual characteristics (erupted teeth in adult males) and close association with calves for adult females. Longitudinal monitoring of known individuals from around the time of birth through maturation has provided validation of this approach and has allowed tentative ages to now be assigned to each class (see Chapter 4 for details).

Using high quality photographs, age class and, where possible, sex was assigned to each individual documented during March – October within each 300 km^2 study area. The presence or absence of characteristics used for determining age class and sex was examined to determine the level of certainty (C) in designating an age class and sex, ranging from 0 (not certain) to 3 (extremely certain). Only individuals with $C > 1$ were included in the age composition analyses. Both distinctive and non-distinctive individuals, including calves, were included so that the age composition for each area could be completely described. To do this, it was assumed that all individuals that were documented in high quality photographs ($Q > 1$) from a single encounter-day could be readily distinguished, regardless of the presence of nicks. This was achievable because (1) group sizes are typically small (median 4 whales, range 1 – 11; Claridge 2006) and not many individuals were photographed on any one day and (2) all types of marks could be used to distinguish individuals including those that were not necessarily long-lasting, including pigmentation patterns, re-pigmented *Isistius* sp. scars, and linear scars (Figure 2.4). Individuals were separated into four different categories of age / sex class: adult female, adult male, sub-adult (sub-adult male, sub-adult female and sub-adult of unknown sex), and dependent calf.

These data were then used in several different ways with two separate goals. The first of these was to compare the age structure between the two study areas. To do this the encounter-day data were reviewed to tally the number of individuals represented by each age / sex class for each of the six years. Here it was further assumed that all individuals documented in high quality photographs could be distinguish within the same year. If an individual’s class changed during the year (e.g., a dependent calf separated from its mother), it was assigned to the class it was first seen in that year but its status was updated the following year. The mean proportion represented by each class by year was then calculated and proportions were compared between study areas.

The second goal was to compare the proportion of dependent calves to non-calves between areas. To do this, the total number of individuals documented in each class during the study was tallied. If an individual’s class changed during the study it was assigned the class when first seen. The number of calves was then taken as the proportion of the total number of individuals documented and Bailey’s test for differences in proportions was used to compare the proportions of calves to the totals in both areas (Bailey 1959):

$$d = \frac{k_1 - k_2}{\sqrt{k(1-k)(\frac{1}{n_1} + \frac{1}{n_2})}}$$

$$\text{where } k_1 = \frac{a_1}{n_1},\ k_2 = \frac{a_2}{n_2},\ k = \frac{a_1 + a_2}{n_1 + n_2}$$

and a_1 = the number of calves at Abaco, a_2 = the number of calves at AUTEC, n_1 = the total number of individuals identified at Abaco, and n_2 = the total number of individuals identified at AUTEC.

2.2.4 Mark-recapture analysis

Mark-recapture models were fitted to photographic identification data from each area separately. For each area, a matrix Y was constructed of individual identification histories with elements y_{it} of values 1 or 0 depending on whether or not each individual $i = 1,\ldots, n$ was identified during each of $t = t1_i,\ldots, T = 6$ annual sampling intervals, following the interval of first identification for each whale $t1_i$. These binary observations y_{it} were modelled as conditional on annual probabilities of capture (π), given that the whale was alive and present in the study area, and was thus available for capture. Notably, whales that were not seen in every year but were known to be alive, and may have temporarily emigrated beyond the bounds of these restricted study areas, had to be accounted for. Therefore, a mark-recapture approach that parameterized annual probabilities of emigration (λ) and re-immigration back into the study area (κ) in addition to survival (φ) was adopted (Whitehead 1990, Matkin *et al.* 2012). This is equivalent to allowing for temporary emigration to an unobservable state (e.g., Kendall and Nichols 2002, Schofield *et al.* 2009). Survival here represents “apparent survival”, which accommodates both death and any permanent emigration from the study area. The standard Cormack Jolly-Seber (CJS) model (Lebreton *et al.* 1992) with capture probability dependent only on apparent survival was reproduced by removing the emigration λ and re-immigration κ terms from the model (e.g., Whitehead 1990).

An individual state-space formulation of the model was adopted (e.g., Schofield *et al.* 2009) to allow the inclusion of individual covariates to facilitate model fitting. Specifically, binary covariates were incorporated for survival status (alive or not), which were known for years between repeated sightings and from out-of-sample re-sightings, and these data were inputted into a separate binary matrix X. When the status of a whale was unknown following the last capture, it was treated as missing data to be estimated. Similarly, the emigration /re-immigration status (available in the study area or not) was known, and entered as a binary covariate, when the whale was actually observed (Y=1), but was treated as missing data in years when the whale was not captured (e.g., Schofield *et al.* 2009).

2.2.4.1 Priors

Rather than assuming a time-invariant specification for the survival and movement parameters (e.g., Whitehead 1990), a flexible hierarchical Bayesian formulation was adopted with each annual probability specified as a function of overall mean (μ) and additive annual additive effect, b_t (following Matkin *et al.* 2012):

$$\text{logit}(\varphi_t, \lambda_t, \kappa_t, \pi_t) = \text{logit}(\mu^{\varphi,\lambda,\kappa,\pi}) + b_t^{\varphi,\lambda,\kappa,\pi}$$

$$b_t^{\varphi,\lambda,\kappa,\pi} \sim \text{N}(0, \sigma^{\varphi,\lambda,\kappa,\pi})$$

where logit(a) = log(a/(1-a)). Uniform(0,1) prior distributions were placed on each of the four mean probabilities $\mu^{\varphi,\lambda,\kappa,\pi}$ and Uniform(0,20) priors were adopted for the standard deviations $\sigma^{\varphi,\lambda,\kappa,\pi}$ for the distribution of annual effects, to allow annual departures from the mean to emerge if they were supported by the data. This hierarchical formulation therefore allowed for “borrowing strength” across years: estimates from sparse data years were smoothed towards the overall mean and annual departures were detected when sufficient data existed to support a difference from the mean (e.g. Fearnbach *et al.* 2012).

In addition to parameters of the mark-recapture model, derived parameters related to abundance were also estimated. Specifically, estimates of capture probability π_t were used to derive estimates of distinctive animal abundance, N_t, using the study area during each annual interval. These parameters were linked to the observed data by specifying the number of individuals actually observed in the study area each year, $O_t = \sum y_{1:n,t}$, as a binomial sample from the abundance N_t with the binomial proportion given by the estimated π_t. As with the other parameters, a hierarchical prior was adopted to smooth abundance estimates across years:

$$\log(N_t) = \log(\mu^N) + b_t^{\,N}$$

$$b_t^{\,N} \sim \mathrm{N}(0, \sigma^N)$$

A Uniform (min[O_t],100) prior was set for the average annual abundance, μ^N, with the lower boundary set as the minimum number of distinctive whales that were actually observed in any year. Annual effects were drawn from a Normalized prior with mean zero and standard deviation $\sigma^N \sim$ Uniform(0,20).

To produce estimates of the abundance of all whales using the study area in each interval, A_t, annual estimates of abundance for distinctive whales (N_t) were rescaled to include non-distinctive individuals, including calves. Using methods described by Durban *et al.* (2010), the distinctive proportion of the population in each year, m_t, were estimated as the binomial proportion given by the number of whales identified that were judged to be distinctive relative to all whales that could be distinguished in high quality photographs ($Q > 1$) during each encounter-day. The proportion therefore represented the overall average across days within each year. The proportion of the population that was distinctive, m_t, was assigned the same hierarchical prior structure to borrow strength across years:

$$\mathrm{logit}(m_t) = \mathrm{logit}(\mu^m) + b_t^{\,m}$$

$$b_t^{\,m} \sim \mathrm{N}(0, \sigma^m)$$

with a flat Uniform(0,1) prior on the average distinctiveness proportion, μ^{m}, and a Uniform(0,20) prior on the standard deviation of annual effects, σ^{N}. The overall annual abundance, A_t, was then defined as N_t / m_t.

2.2.4.2 Inference and model fitting

WinBUGS software (Lunn *et al.* 2000) was used for parameter estimation, drawing upon three Markov Chain Monte Carlo (MCMC) sequences from the posterior distribution of each model parameter. Inference was based on 60,000 iterations, after discarding an initial burn-in of 20,000 iterations for each chain, using the method of Brooks and Gelman (1998) to determine convergence of the multiple chains. **S**ummary statistics for the posterior distributions were then estimated from the sampled values.

To assess the degree of difference between the estimated posterior distributions of parameters measured at Abaco and AUTEC, the model was fitted to both area datasets using the same MCMC simulation and the proportion of the post burn-in MCMC values for which the parameter (e.g. abundance A_t) for Abaco exceeded that for AUTEC was compared. Over the full MCMC sequence this long-run proportion equated to the probability p that the parameter estimates from the two areas were different, while accounting for the full uncertainty encompassed by the posterior distribution for each estimate. If the two distributions completely overlapped (i.e. there was no difference in a parameter estimate between areas), then p would equal 0.50. The percentage of iterations where the parameter for Abaco is greater than that for AUTEC estimates the probability that the true difference between the areas is greater than zero.

This is similar to a two-tailed test, and values close to one mean that Abaco's parameter is greater than that of AUTEC, and vice-versa for values close to zero.

Model selection was accomplished by comparing the fit of the re-immigration model to a reduced-parameter CJS model using a minimum posterior predictive loss approach (Gelfand and Ghosh 1998, Durban *et al.* 2010, Matkin *et al.* 2012, Fearnbach *et al.* 2012). The same MCMC simulation was used to generate predictive binary observations from the posterior distribution of the fitted model parameters to compare the competing models. For each model, a new set of data (Y^{new}) with the same dimensions as the observed data (i in 1, …n and t in 1, …T) was predicted by generating samples from the posterior distributions of the fitted model parameters. The loss function then measured the discrepancy between the observed data, Y, and the predicted data, Y^{new} and used the sum of the predicted errors (PE):

$$\mathrm{PE} = \sum_{i=1}^{n} \sum_{t=1}^{T} [y_{it}^{new} - y_{it}]^2$$

The Mean Squared Predictive Error (MSPE) was then used as a measure of the discrepancy between the observed and predicted data. The model with the smallest MSPE was considered to best predict a replicate set of the observed data and was thus selected as the model which best fit the data.

To ensure that the model selected was a reliable fit to the observed data, a posterior predictive approach for goodness-of-fit checking was adopted (Gelman *et al.*

1996). A simulation model was run by drawing 60,000 replicates (20,000 from each chain) from the posterior predictive distribution, π_t, which was based on posterior estimates of model parameters. A discrepancy measure, D, was then calculated for both the simulated Y^{new} and observed data Y (as described by Durban and Elston 2005):

$$\mathrm{D}(Y) = \sum_{i=1}^{n} \sum_{t=1}^{T} |y_{it} - \pi_{it}|$$

$$\mathrm{D}(Y^{new}) = \sum_{i=1}^{n} \sum_{t=1}^{T} |y_{it}^{new} - \pi_{it}|$$

The discrepancy measures themselves had posterior distributions, and so could be compared by estimating the exceeding tail area probability as the percentage of MCMC draws for which $D(Y^{new}) > D(Y)$. The result is a Bayesian (or posterior predictive) *p*–value: values close to 0.5 indicate that the simulated discrepancy of the data is similar to what is expected from replication under the model (Gelman *et al.* 1996); if the model is a poor fit to the data, the Bayesian *p*–value will be close to 0 or 1 (Brooks *et al.* 2000).

2.3 Results

2.3.1 Photo-identification Data

During the study period (2005 – 2010) more than twice as many vessel surveys for beaked whales occurred in the Abaco study site (235 surveys) than at AUTEC (102 surveys), resulting in a larger photographic dataset at Abaco (Table 2.1). During the chosen sampling interval (March – October), there were a total of 34 and 20 encounter-days at Abaco and AUTEC, respectively within each 300-km^2 study area. Using only high quality photographs, at Abaco 73 whale-by-year identifications were collected and inputted into the Y matrix, comprising 44 distinctive individuals, excluding calves. At AUTEC there were 43 whale-by-year identifications which represented 29 distinctive, non-calf individuals. Out-of-sample re-sightings resulted in 18 and 19 additional entries inputted to the X matrices for Abaco and AUTEC, respectively.

Table 2.1. Summary of effort and photographic data collected for Blainville's beaked whales from the control site (Abaco) and the US Navy's Atlantic Test and Evaluation Center (AUTEC). These data were selected for use in the mark-recapture analysis following restrictions on annual sampling interval, size of study area, image quality and individual distinctiveness.

	Control Site **Abaco**	**Navy Range** **AUTEC**
No. vessel surveys	235	102
No. encounter-days	34	20
Total identifications by year	73	43
Total individuals (including calves)	48	30
Total non-calf individuals	44	29

At both sites, there was annual variation in the number of distinctive whales photo-identified (Figure 2.5), which may reflect annual variation in survey effort. In all years, more whales were identified each year at Abaco (median = 10 whales, range 6 – 19) than at AUTEC (median = 5 whales, range 3 – 18). Most notable is the lack of photographic matches of any whales between the two areas.

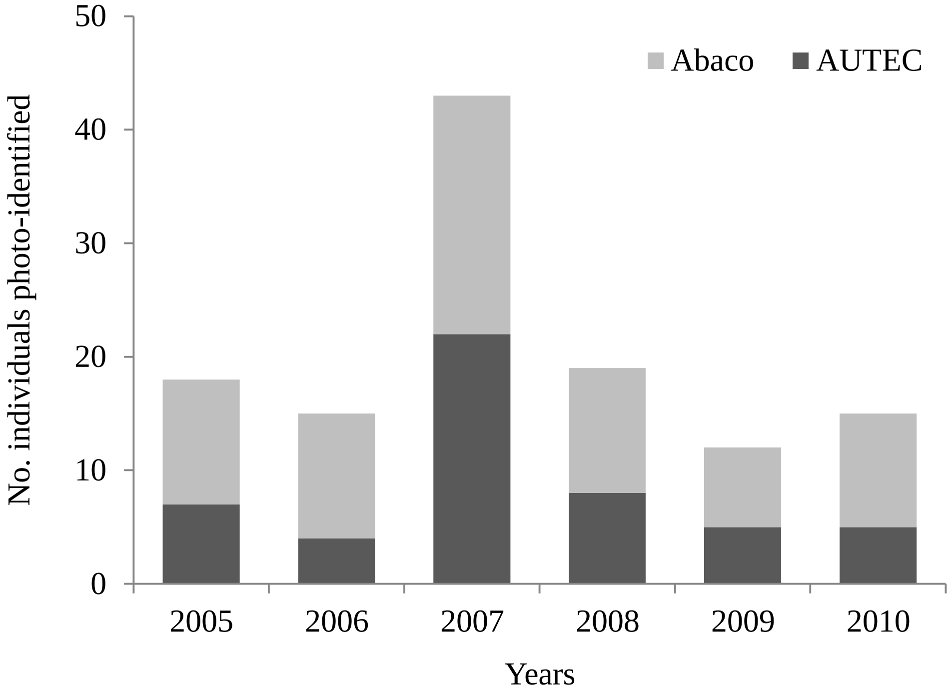

Figure 2.5. The number of distinctive, non-calf Blainville's beaked whales identified from high-quality photographs during the annual sampling interval in years 2005 – 2010 for both study areas.

The majority of whales were only seen in one year (median = 1, maximum = 5 at Abaco; median = 1, maximum = 4 at AUTEC) (Figure 2.6). However, some individuals were seen in multiple years (15 whales at Abaco, 34% of the total; and 10 whales at AUTEC, 35% of the total), suggesting some level of site fidelity.

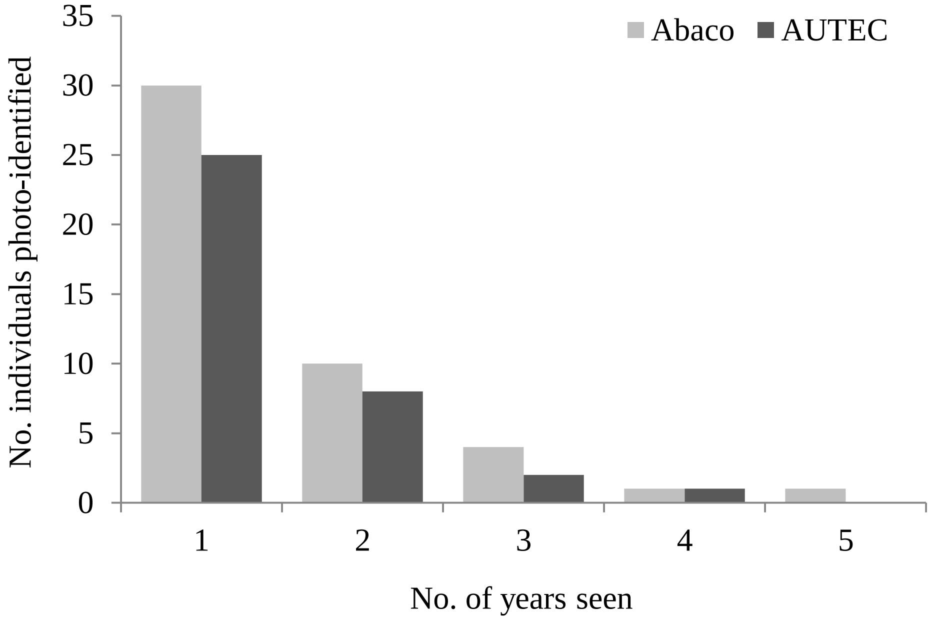

Figure 2.6. The number of years that individual, distinctive non-calf Blainville's beaked whales were photo-identified from high quality photographs during the annual sampling interval in years 2005 – 2010 for each area.

2.3.2 Age composition

Using the mean annual proportions represented by four different categories of age / sex classes (adult female, adult male, sub-adult, calf), an unequal proportion of adults to immature animals was found between the two sites with fewer sub-adults and calves at AUTEC (Figure 2.7; $t = 3.28$, df = 10, $p < 0.005$). However, this difference was primarily due to a higher proportion of adult females at the navy range ($t = 4.37$, df = 10, $p < 0.001$), while the proportion of males was similar at both sites ($t = 0.08$, df = 10, $p = 0.46$). Notably, the annual mean adult female-to-calf ratio was higher at AUTEC ($t = 2.81$, df = 10, $p < 0.01$), yet when immature classes were compared separately between the two areas, although apparent, differences were not significant (sub-adults: t

= 1.22, df = 10, $p = 0.12$; calves: $t = 1.11$, df = 10, $p = 0.15$), possibly due to small sample sizes.

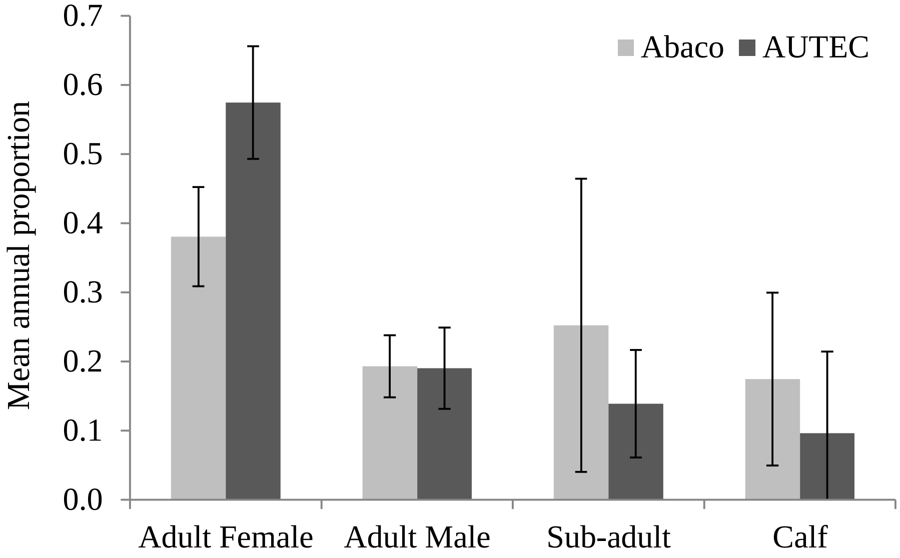

Figure 2.7. A comparison of the mean annual proportion represented by age / sex classes in Abaco and AUTEC. The error bars represent standard deviations.

Despite a difference in the mean annual proportion, there was a similar number of adult females documented at both sites during the study, but with apparently differing reproductive success. Thirteen of 25 adult females were documented with 17 calves at Abaco (4 neonates), compared to only five of 23 adult females at AUTEC documented with five calves (1 neonate). However, the Bailey test found only limited support for a difference in the proportion of calves relative to the total number of individuals identified in each area [$d = 1.61$, $n_1 = 65$ (Abaco), $n_2 = 39$ (AUTEC), $p < 0.10$].

2.3.3 Mark-recapture model results

For both areas, model selection showed some support for use of an open population model with re-immigration rather than the standard CJS model. For Abaco, there were 30 discrepancies between 264 observed and predicted data points for the re-immigration model, compared to 33/264 data points for the CJS model, resulting in MSPE values of 0.11 and 0.12, respectively. For AUTEC, there were 14/174 discrepancies for the re-immigration model compared to 17/174 for the CJS model, resulting in MSPE values of 0.08 and 0.10, respectively. The Bayesian *p*-value to test model fit was close to 0.5 for both models ($p = 0.58$ for both areas, Figure 2.8) suggesting that the re-immigration model fitted both data sets adequately.

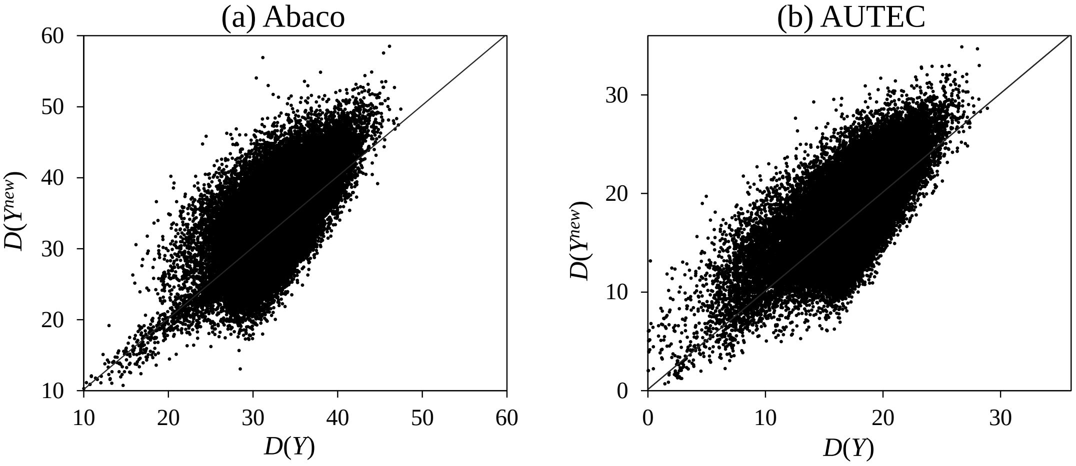

Figure 2.8. Discrepancy plots for the re-immigration model for Abaco and AUTEC. Points are the 60,000 MCMC samples of a discrepancy function (*D*, Durban and Elston 2005) calculated for both observed data and data simulated by the model. The diagonal line represents the line $y = x$ and the posterior predictive value is the proportion of points that lie below the line, corresponding to Bayesian *p*–value statistics of 0.58 for both areas.

Inference was therefore based on the full posterior probability distributions for each model parameter using the re-immigration model (Figure 2.9). Estimates of average annual capture probabilities were more precise for the Abaco dataset (posterior median $\mu^{\pi} = 0.23$, 75% Highest Posterior Density Interval [HPDI] = 0.19 – 0.30) than the AUTEC dataset ($\mu^{\pi} = 0.25$, 75% HPDI = 0.18 – 0.37), and there was no support for a difference between the posterior distributions ($p = 0.45$).

The probabilities of apparent survival were very similar [$p = 0.50$; at Abaco, $\mu^{\varphi} = 0.86$ (75% HPDI = 0.60 – 0.97); at AUTEC, $\mu^{\varphi} = 0.85$ (75% HPDI = 0.59 – 0.97)]. The estimated annual probabilities of emigration away from the study area were also similar at Abaco (posterior median $\mu^{\lambda} = 0.21$, 75% HPDI = 0.09 – 0.39) and AUTEC ($\mu^{\lambda} = 0.28$, 75% HPDI = 0.12 – 0.50), and probability tests did not support a difference between areas ($p = 0.43$). The data provided very little information about annual re-immigration at either site with the posterior distributions showing little deviation from the flat prior distributions; at Abaco, posterior median $\mu^{\kappa} = 0.48$ (75% HPDI = 0.24 – 0.74), and at AUTEC, $\mu^{\kappa} = 0.50$ (75% HPDI = 0.26 – 0.75), and the probability that these were similar was high ($p = 0.48$).

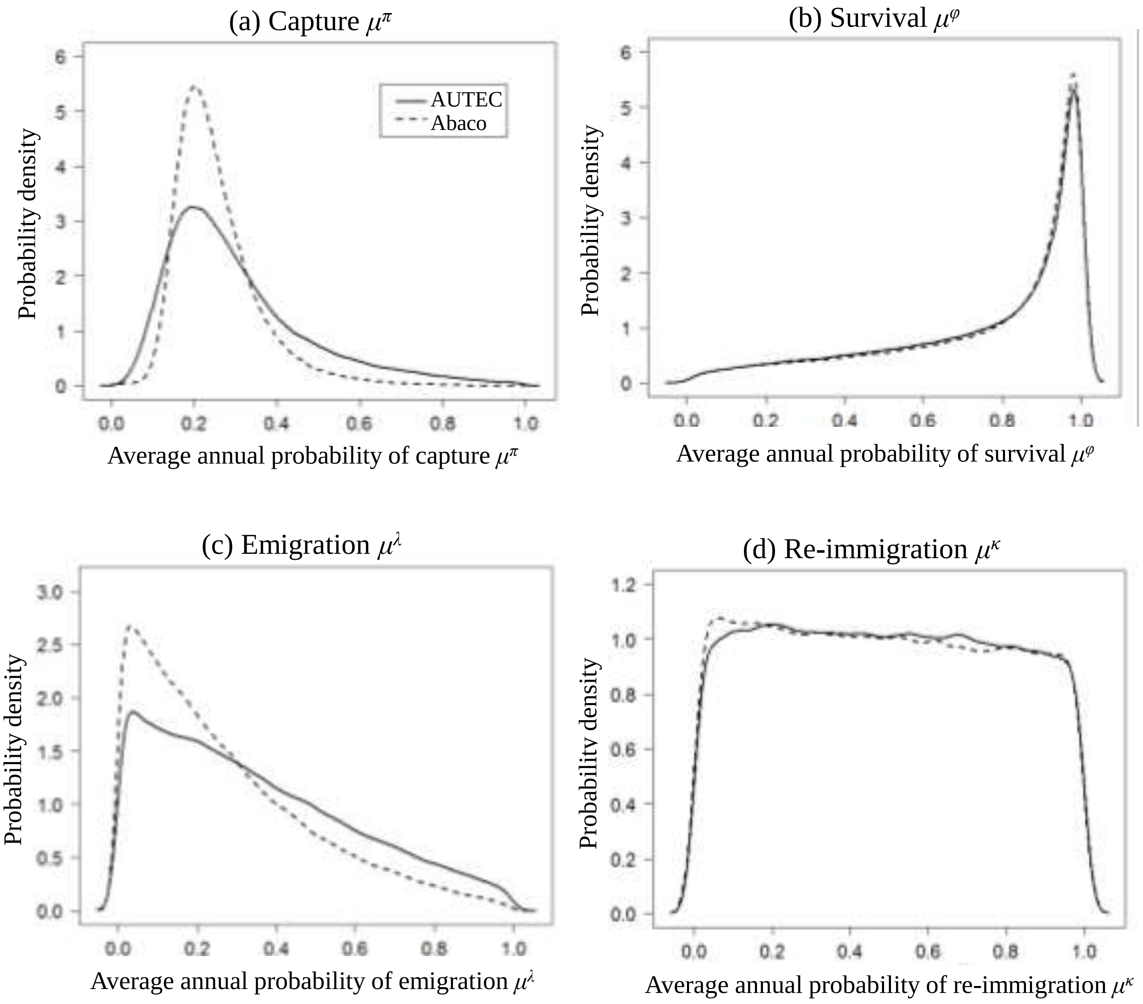

Figure 2.9. Plots of the posterior probability distribution for annual means of (a) capture μ^{π}, (b) apparent survival μ^{φ} (c) temporary emigration μ^{λ} and (d) re-immigration μ^{κ}. Dashed and solid lines represent the full posterior distributions for Abaco and AUTEC, respectively. The higher posterior densities shown in plots a and c suggest higher precision in these estimates for Abaco than AUTEC.

The average annual abundance for distinctive whales (*N)* differed between areas ($p = 0.77$). At Abaco, average annual abundance, posterior median $\mu^{N} = 49$ whales (75% HPDI = 38 – 62) while at AUTEC, $\mu^{N} = 31$ whales (75% HPDI = 22 – 42). The most precise estimate for Abaco was in 2008 [posterior median $\mu^{N} = 47$ whales (75% HPDI =

36 – 61] and for AUTEC in 2007 [posterior median μ^N = 35 whales (75% HPDI = 25 – 48)]. Additionally, the proportion of the population that was estimated to be distinctive was substantially lower at Abaco than at AUTEC [p = 0.17; for Abaco, posterior median μ^m = 0.63 (75% HPDI = 0.58 – 0.67), for AUTEC, μ^m = 0.74 (75% HPDI = 0.68 – 0.80)]. After accounting for this difference by re-scaling, probability tests revealed a high probability that total average annual abundance (μ^A) at Abaco was greater than at AUTEC, p = 0.88. The posterior median for total average annual abundance at Abaco was 80 whales (75% HPDI = 63 – 99) compared to 42 whales at AUTEC (75% HPDI = 32 – 55) (Figure 2.10). However, posterior probability distributions were skewed, and the modes for each area were 101 and 34 whales, respectively. The most precise estimates were in 2007 for both areas; for Abaco posterior median μ^A was 90 whales (75% HPDI = 69 – 117), and for AUTEC posterior median μ^A was 45 whales (75% HPDI = 33 – 64).

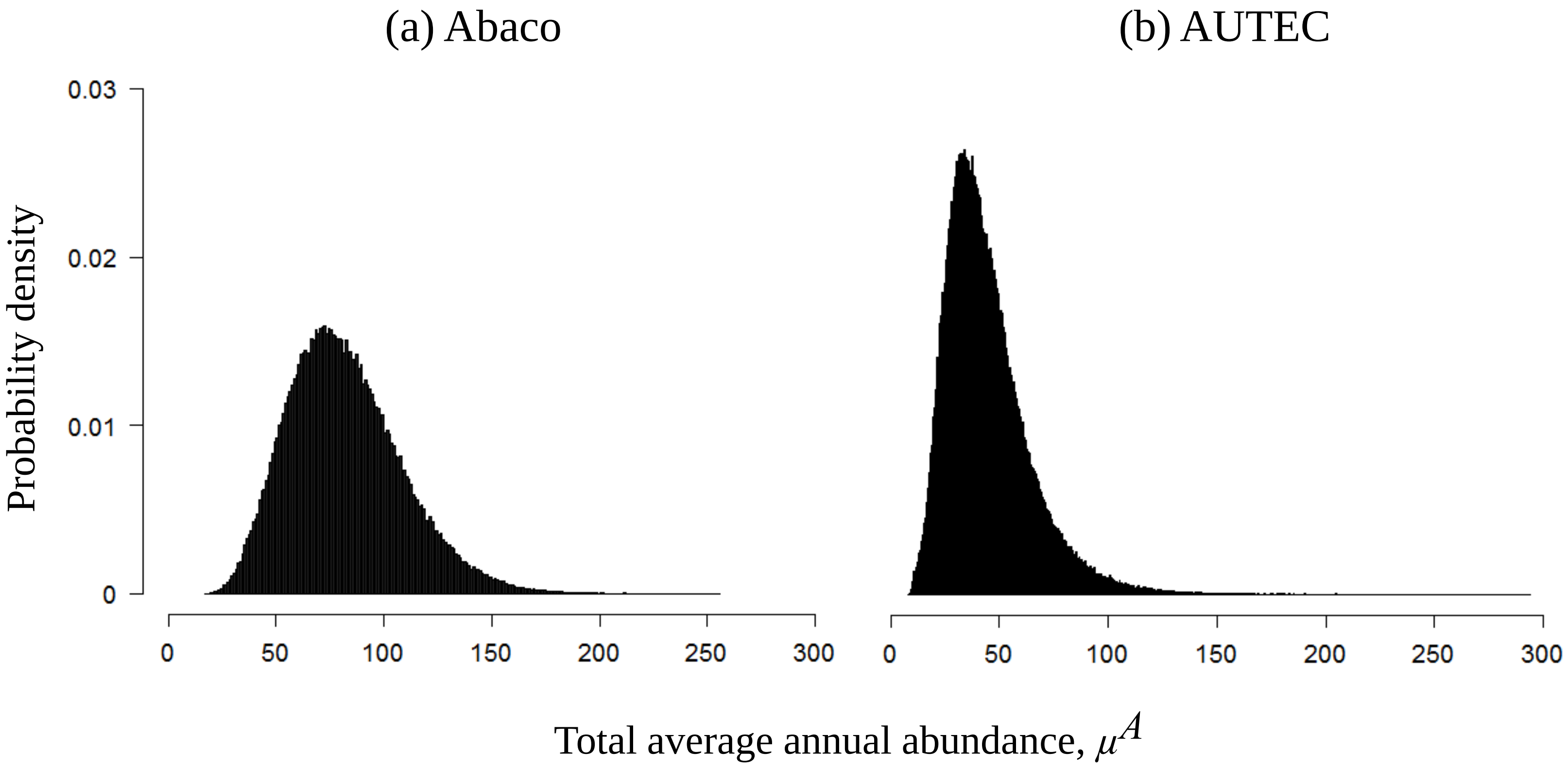

Figure 2.10. Plots of the posterior probability distribution for the total average annual abundance, μ^A, in (a) Abaco and (b) AUTEC from 2006 – 2010.

For each of the five years for which abundance estimates were derived, estimates of abundance for distinctive whales, N_t, was consistently higher for Abaco than AUTEC (Figure 2.11). This difference became even more apparent for total abundance, A_t, because the proportion of whales estimated to be distinctive was lower at Abaco in each year.

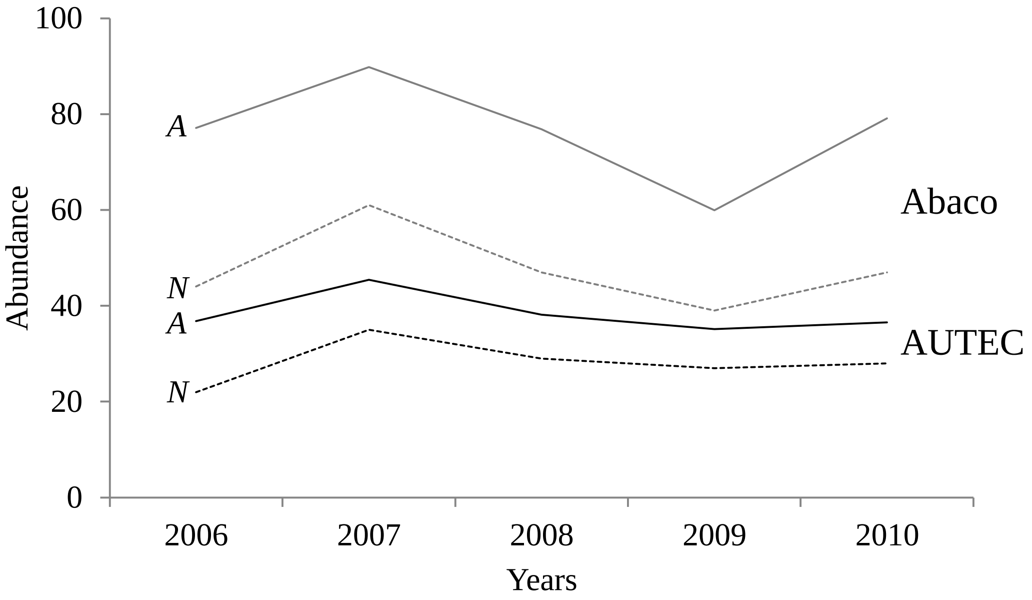

Figure 2.11. For each area, abundance was estimated annually for distinctive whales (N_t, dashed lines) and then rescaled for the proportion of non-distinct individuals (m_t) to determine the overall annual abundance (A_t, solid lines). Here the posterior median of each annual estimate is presented: distinctive and total abundance was higher for the Abaco study site (light grey lines) than for AUTEC (black lines).

2.4 Discussion

2.4.1 Population structuring

Based on satellite telemetry studies (e.g., Schorr *et al.* 2009, Tyack *et al.* 2011, Durban unpublished data), Blainville's beaked whale movements appear to be similar to those of coastal bottlenose dolphins (Scott *et al.* 1990) and northern bottlenose whales (Wimmer and Whitehead 2004), where individual movement may be on spatial scales in the range of tens of kilometres. In this study, no photographic matches of Blainville's beaked whales were found between the two study areas, separated by 170 km, suggesting that regular home ranges of whales from both sites do not overlap and that there is population structuring of this species in the northern Bahamas.

Location data from satellite tags deployed on *M. densirostris* at AUTEC and Abaco provide support for limited exchange between the two areas as the tagged whales remained in the general area in which tagging occurred, on a time scale of up to several weeks (Tyack *et al.* 2011, Durban unpublished data). Differences in chemical markers measured in skin and blubber biopsy samples taken from Blainville's beaked whales at both sites provide further support that these whales are foraging in small and distinct localised areas over periods of months (Claridge *et al*. 2012). The lack of photographic matches as reported here suggests that this spatial separation may be evident over periods of years. Population structuring between the navy range and the control site allowed the comparison of population demographics for a subpopulation of Blainville's beaked whales regularly exposed to navy sonars to a subpopulation rarely exposed.

2.4.2 Similar rates of turnover

The data were too limited to inform precisely about turnover, but annual rates of temporary emigration of Blainville's beaked whales at the Navy range and the control site may be low. Nonetheless, estimates of apparent survival were lower than one might expect based solely on mortalities as compared to other cetaceans (e.g., Mizroch *et al.* 2004, Ramp *et al*. 2006, Ford *et* al. 2007), suggesting some permanent emigration occurred, at least over the time period of this study. Future monitoring will enable better identification of parameters and therefore a greater understanding of movement processes.

However, estimation of these parameters was based solely on distinctively marked whales (likely adults), which have accumulated scars as they matured (Walker and Hanson 1999, Chapter 4). Analyses of age class and sex confirmed that they were mostly adult females, particularly at AUTEC. Therefore, the relatively low annual rates of movement primarily reflect site fidelity of adult females and not necessarily other age and sex classes. Long-term site fidelity of adult female Blainville's beaked whales has been reported previously for Abaco (Claridge 2006) and Hawaii (McSweeney *et al.* 2007). This study provides further evidence of adult female site fidelity near Abaco and at AUTEC.

Residency patterns can, however, vary by age class and sex (see Chapter 5, also Wimmer and Whitehead (2004) for northern bottlenose whales) and there may be some evidence of limited site fidelity by some whales in this study. The majority of whales at both sites were only seen in one year of the study. The mark-recapture model fitted the data well overall, suggesting that many of these single observations could be explained by the inherent processes of capture probability and apparent survival (including permanent emigration). However, the model may not fit all the data well. One explanation is that although adult females appear resident, other age / sex classes may exhibit different movement patterns, at least during the duration of the study. Low estimates of apparent survival may suggest permanent emigration of adult males and young dispersers (a hypothesis examined later in Chapter 5).

2.4.3 Abundance estimates for *M. densirostris*

Few estimates of beaked whale abundance at the species level are available, but from what is currently known, at least some species occur in small, localised populations (e.g., Gowans *et al.* 2000), and "hot spots" with higher than average densities may exist (Barlow *et al.* 2006). Using photographic mark-recapture and an open population model similar to this study (although not within a Bayesian framework), Gowans *et al.* (2000) reported a small population estimate [130 (95% CI = 106-166)] for northern bottlenose whales from the Gully, Nova Scotia and noted the need for effective management to protect this small population from the negative impacts of human activities. Using visual survey data and distance sampling methods, the highest Ziphiid densities have been reported for Baird's beaked whale (*Berardius bairdii*) for the Japanese eastern slope waters (68.1 whales/1000 km^2, CV = 0.30; Miyashita 1986), while densities of Cuvier's beaked whale (*Ziphius cavirostris*) have been found to be an order of magnitude lower (e.g., 6.2 whales/1000 km^2, CV = 1.43; Barlow 2006). Densities of mesoplodont beaked whales appear to be even lower, although large variation in densities may validate the existence of “hotspots” in some areas (Barlow *et al.* 2006).

In this chapter, the first estimates of abundance for Blainville’s beaked whales are presented both on and off a navy range using photographic mark-recapture approaches. Total average annual abundance was lower at Abaco than on the navy range, but the estimate reported here at AUTEC was higher than that made previously on the range by Marques *et al.* (2009) or elsewhere (Barlow 2006). Using acoustic detections from the fixed hydrophone array and distance sampling methods, Marques *et al.* (2009) estimated the density of Blainville’s beaked whales on the AUTEC range averaged over a 6-day period between 22.5 and 25.3 whales/1000 km^2 (depending on assumptions used, with 95% confidence intervals 15.4 – 32.9 and 17.3 – 36.9). The density/abundance of whales estimated from a 6-day survey are expected to be lower than a mark-recapture average annual estimate simply because of individual movements in and out of the area. However, abundance/density estimates at AUTEC (and Abaco) appear to be much higher than Barlow (2006) found for Blainville’s beaked whales around Hawaii (1.17 whales/1000 km^2, CV = 1.25) using visual survey data. Moore and Barlow (2013) have suggested that because navy ranges tend to be located in high-quality beaked whale habitat because of the topography, they could actually be serving as population sinks, further emphasising the need for effective management in areas where impacts are likely to occur, such as navy ranges.

In this study biases in the mark-recapture estimates may have been introduced that should be considered, especially when making a comparison between abundance at AUTEC and Abaco. To address assumptions that all individuals possess unique marks and that those marks are not lost, only high quality photographs of well-marked individuals were included here. However, it was assumed that unmarked individuals behaved in a similar way to marked ones which may have not been true. Furthermore, differences found in residency patterns by age / sex class will introduce heterogeneity of capture probabilities, potentially violating the assumption that the probability of capture is equal for all individuals in the population, including both marked (older whales) and unmarked (typically younger whales), and bias the estimates of abundance (Seber 1982). This is complicated by the possibility that individuals that spend more time in the study area are not only more available for capture, but also may have become habituated to the research vessel, becoming “trap happy” and further contributing to this heterogeneity. Future work should attempt to minimise heterogeneity by maximising capture probabilities through increased sampling effort, which will allow use of more realistically complex models to account for individual heterogeneity (e.g., Fearnbach *et al.* 2012).

2.4.4 Why lower abundance on the navy range?

The comparison to the Abaco site during the same time period, using the same size for the study areas, allowed the lower estimation of abundance for beaked whales at AUTEC to be placed in a local geographically relevant context. A comparison of average annual abundance of Blainville’s beaked whales on and off a navy range revealed a substantially higher abundance at the control site than on the navy range. The reason for this difference is unknown although some possible explanations can be immediately dismissed. By-catch mortality in pelagic net fisheries such as reported elsewhere (e.g. Forney 2004) does not occur on or off the navy range because all pelagic net fisheries are illegal in The Bahamas and vessel activity is monitored closely on the range so illegal fishing is highly unlikely. Due to their high site fidelity and the lack of photographic matches of the AUTEC whales outside the Tongue of the Ocean, it is highly improbable that individuals are moving to areas where they would be at risk of incidental take in fisheries. A low human population and lack of industry at both sites means that ecosystem changes caused by overfishing or chemical contaminants are unlikely. Studies of persistent organic pollutants in *M. densirostris* sampled from both AUTEC and Abaco show levels similar to those found in undeveloped regions, such as the Aleutian Islands (Claridge *et al.* 2012). Larger-scale impacts of other anthropogenic activities (e.g. global climate change) are unlikely to occur at a scale that would affect whales residing in only one of the two areas, a distance of only 170 km.

However, there are two other possible explanations for the difference in abundance of Blainville's beaked whales at the control site and on the navy range. The first is that prey availability is lower at AUTEC than at Abaco due to bio-oceanographic variation between the study areas. Beaked whale habitat preferences are generally characterised by complex bottom topography (Waring *et al.* 2001, D'Amico *et al.* 2006), such as canyon walls which are likely to be more productive and to support higher prey abundance. However, Ferguson *et al.* (2006) provided evidence for high population densities in diverse habitats including abyssal plains, and suggested that beaked whales are not narrowly restricted to highly productive areas typical of coastal and upwelling areas of the continental slope. Although both sites lie within the Great Bahama Canyon, the fine-scale habitat of the two areas is somewhat dissimilar, which could result in differences in productivity, although it is unknown which area is more productive. The Abaco site is located on the lee shore while the AUTEC site lies on the windward side of the island (Figure 1), although differences in up-welling as the result of land orientation have not been documented for the region, e.g., island-effects. The Abaco site primarily encompasses the canyon wall, whereas the AUTEC site is centred on the western side of the U-shaped trough which forms the Tongue of the Ocean.

Blainville's beaked whales generally forage at depths in excess of 800 m (Johnson and Tyack 2005, Tyack *et al.* 2006, Baird *et al*. 2006, Durban unpublished data) where they feed primarily on mesopelagic fish and squid (MacLeod *et al.* 2003, Johnson *et al.* 2004). Little is known about beaked whale prey densities and distributions at these depths, although Hazen *et al.* (2011) conducted prey field mapping to depths of 500 m on the AUTEC range and to a much lesser extent at the Abaco site, and reported that prey distribution is not spatially uniform. Hazen *et al.* (2011) found the highest prey densities along the western side of the AUTEC range, the exact area included here in this study, suggesting this area provides good foraging habitat for beaked whales. However, Hazen *et al.* (2011) were unable to sample prey at the depth that Blainville's beaked whales forage so it remains unclear whether or not variation in productivity between sites influenced the substantial difference in abundance but there is no supporting evidence that prey availability in the western portion on the navy range is less than at Abaco. Prey mapping studies, at appropriate depths, could provide a quantitative comparison between the two sites.

Another possible explanation for differences in abundance of beaked whales on and off the navy range is that there are population-level effects of exposure to navy sonars. Beaked whales in both areas may be exposed to man-made noise, but the acoustic environments of the two sites differ. The Abaco study area lies within Northwest Providence Channel, a major international shipping lane, while noise associated with shipping traffic at AUTEC is minimal. Aguilar de Soto *et al.* (2006) describe interruption of a foraging dive by a beaked whale when a ship passed overhead. In Northwest Providence Channel, shipping traffic is concentrated mid-channel approximately 20 km outside the study area so disruption of foraging activity within the study area is not expected to be a common disturbance. However, an extreme acoustic disturbance to beaked whales has occurred in Northwest Providence Channel. In March 2000 an atypical stranding of 14 beaked whales was caused by an anti-submarine warfare exercise transiting the Channel (for details, see Balcomb and Claridge 2001, England and Evans 2001). It is unknown to what extent the Abaco subpopulation was impacted, but recent analyses of abundance trends suggests the population in Abaco has remained stable (see Chapter 3). However, since 2000 military sonar has not been regularly used in Northwest Providence Channel, while sonar is frequently used at AUTEC. Indirect impacts associated with chronic stress from acoustic disturbance could be affecting reproductive success, resulting in lower abundance at the navy range.

Direct impacts of certain sonar exercises are well known (e.g., Simmonds and Lopez-Jurado 1991, Frantzis 1998, Balcomb and Claridge 2001, Jepson *et al.* 2003, Cox *et al*. 2006), but the indirect impacts such as those that may be related to chronic stress are more difficult to document. It has been hypothesised that long-term exposure to frequent intense stressors that cause behavioural responses and displace individuals from optimal habitat could reduce fitness via mechanisms such as decreased foraging efficiency, failed reproduction, increased calf mortality, immunosuppression, and inhibited growth and metabolism (Curry 1999, Wright *et al.* 2007, Moore and Barlow 2013). Observations of beaked whale behavioural responses to sonar exercises at AUTEC and apparent low reproductive rates and recruitment through births on the navy range present some reasons for concern about potential impacts of chronic stressors.

During multi-ship sonar tests at AUTEC, Blainville's beaked whales move away from ships using sonar, returning to the range only when exercises cease (McCarthy *et al.* 2011, Tyack *et al.* 2011). Data recorded from depth-recording satellite tags on Blainville's beaked whales during multi-ship exercises at AUTEC are currently being analysed to investigate whether foraging is disrupted (Durban, unpublished data). Higher energetic costs associated with displacement combined with lower energy intake during these navy exercises provides a possible mechanism to reduce fitness. This is of particular concern for lactating and pregnant females, and may result in failed reproduction and increased calf mortality (Wright *et al.* 2007). Furthermore, younger animals (calves and even foetuses) may be particularly vulnerable as novelty may induce hypothalamic-pituitary-adrenal responses which may cause permanent neurological alterations to their still-developing brain (Curry 1999, Wright *et al.* 2007). Photo-identification data in this study revealed an unequal proportion of adults to immature animals between the two study sites, with a higher female:calf ratio at AUTEC, suggesting a lower reproductive rate and/or calf survival at the navy range than the control site. Lower recruitment through births at AUTEC may provide an explanation as to why abundance is lower than at Abaco.

Although information currently available cannot provide a quantitative answer to whether frequent sonar use at AUTEC is causing stress to resident beaked whales, this is a hypothesis that is being tested. Studies underway include comparative measurements of individual pregnancy and stress hormone levels in whales at AUTEC and Abaco (following methods developed by Rolland *et al.* 2005, Hunt *et al.* 2006, Kellar *et al.* 2006, 2009) which may provide a context for interpreting low recruitment at AUTEC. Results of the depth-recording satellite tags deployed on whales displaced during sonar exercises are key to investigating potential changes in foraging behaviour. Although not currently underway, prey sampling to assess potential foraging efficiency of displaced whales would also be valuable. Photo-identification surveys should be continued with sampling intensified to monitor the population demographics at AUTEC. The outcome of these studies is a critical component to understanding if there are population-level effects of frequent exposure to navy sonar.

2.4.5 Conclusions

The lack of photographic matches between the selected control site off Abaco Island and the navy range at AUTEC suggests that population structuring of Blainville's beaked whales is a feature of the northern Bahamas. Including Abaco as a control site and comparing aspects of the population demographics between these two areas was thus a robust and effective experimental design. Rates of estimated turnover were similar at both sites with possibly low rates of temporary emigration; however, results were based only on distinctive whales, which were mostly adult females, suggesting that high site fidelity of adult females on a relatively fine scale may be a key feature of the population ecology of this species (e.g., Baird *et al.* 2009).

Average annual abundance of Blainville's beaked whales was lower on a navy range where mid-frequency active sonars are used regularly when compared to a control site with limited sonar use. Of particular concern is that, despite a similar number of adult females at both sites, a higher female:calf ratio was found on the navy range. Combined, these results suggest lower recruitment through births at AUTEC than at the control site contributing to the lower overall abundance. Although there may be other unknown differences between the sites, lower reproductive rates (or calf survival) may be attributed to exposure of adult females to stressors associated with frequent and repeated use of navy sonars at AUTEC. As such, this work may provide preliminary evidence of population level effects of the regular use of navy sonars on Blainville's beaked whales in The Bahamas – a hypothesis that should be tested further.

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CHAPTER 3

ABUNDANCE AND SURVIVAL TRENDS OF BLAINVILLE'S BEAKED WHALES (MESOPLODON DENSIROSTRIS) SURROUNDING AN ATYPICAL STRANDING IN THE BAHAMAS

3.1 Introduction

Impacts of human activities on wildlife can range from minor disturbance to direct mortalities but evaluating the population consequences of these effects, even when direct, can be one of the most difficult challenges facing wildlife conservationists (Karanth and Nichols 1998, Blaustein and Kiesecker 2002, Wilson 2003). This is particularly true for marine mammal species where baseline data on population dynamics are often lacking and the statistical power to detect trends in abundance is limited (Taylor *et al.* 2007, Jewell *et al.* 2012). Estimates of abundance and trends are constrained by uncertainty over population definition (e.g., Fearnbach *et al.* 2012), heterogeneous capture probabilities (Corkrey *et al.* 2008), and sparse data (Lonegan *et al.* 2007).

Among the most difficult marine mammals to study are the beaked whales (Family Ziphiidae). This is primarily due to their diving behaviour; foraging dives are long in duration yet surfacing intervals are extremely short, limiting their availability for detection while at the surface (Barlow 1999, Tyack *et al.* 2005, Baird *et al.* 2006). For this reason, probabilities of detecting beaked whales visually during ship-based or aerial surveys are low, resulting in high coefficients of variation in abundance estimates which can be greater than 100% (e.g., Barlow 2006). With this lack of precision, the only way to detect a change in abundance for beaked whales is through repeated annual surveys over long periods of time (Taylor *et al.* 2007, Jewell *et al.* 2012). Moore and Barlow (2013) recently reported on a decline in beaked whale abundance off the west coast of the United States using ship-based visual survey data collected over 18 years. Whitehead (2013) recently showed a 21% per year increase in sighting rates for Sowerby's beaked whale (*M. bidens*) in The Gully and adjacent submarine canyons off the Scotian Shelf over a longer time period (23 years), which may be the result of a reduction in anthropogenic disturbance since this area was been designated a marine protected area in 2004. However, the difficulties and cost of collecting multi-year time series make this approach generally impractical. The use of passive acoustic methods for estimating abundance of beaked whales has proven promising (Marques *et al.* 2009) but, as yet, trends in abundance have not been reported using this technique.

An alternative approach has been to use mark-recapture methods. Populations of beaked whales have been shown to occur reliably in some areas and long-term photo-identification studies have been possible in these locations [e.g., The Gully, off the Scotian Shelf (Whitehead *et al.* 1997), Hawaii (McSweeney *et al.* 2007), Canary Islands (Aguilar de Soto 2006), and The Bahamas (Claridge 2006 and this study)]. Most species of beaked whales possess natural markings consisting of scars and nicks which can be used to distinguish individuals (see Chapter 2 for details) providing a valuable tool for studying populations (Hammond 1986, Hammond *et al.*1990). Using mark-recapture methods and photo-identification data, estimates of population size and abundance trends have been reported for the northern bottlenose whale (*Hyperoodon ampullatus*) in The Gully (Whitehead *et al.* 1997, Gowans *et al.* 2000, Whitehead and Wimmer 2005), but studies of beaked whale population dynamics are still lacking. Nonetheless, there is a current and pressing requirement for beaked whale population assessments.

Behavioural responses of beaked whales to anthropogenic noise have raised concern that beaked whales may be particularly vulnerable to loud underwater sounds (Peterson 2003, Aguilar de Soto *et al.* 2006, Cox *et al.* 2006, Tyack *et al.* 2011, Pirotta *et al.* 2012). Most attention has been focussed on atypical mass strandings of beaked whales that have occurred in close temporal and spatial proximity to naval exercises (Van Bree and Kristensen 1974, Simmons and Lopez-Jurado 1991, Frantzis 1998, Balcomb and Claridge 2001, Evans and England 2001, Jepson *et al.* 2003, Fernandez *et al.* 2005, Cox *et al.* 2006). Although the mechanisms directly causing the strandings remain unclear, mid-frequency sonars (2-10 kHz) used during fleet readiness training exercises have been linked to behavioural responses that in turn have led to a number of hypothesized physiological impacts (Evans and England 2001, Jepson *et al.* 2003, Fernandez *et al.* 2005, Cox *et al.* 2006, Hooker *et al.* 2009). Strandings typically involve individuals from multiple ziphiid species, but primarily of the genera *Ziphius* and *Mesoplodon*.

One of these events occurred in the Bahamas. On 15 March 2000, an antisubmarine warfare exercise involving surface ships using standard hull-mounted mid-range tactical sonars transited Northwest Providence Channel, between the islands of the northern Bahamas (Figure 3.1), causing the stranding of at least 14 beaked whales

(Balcomb and Claridge 2001, Evans and England 2001). Two species were involved in the stranding: Cuvier's beaked whale (*Ziphius cavirostris*, *n* = 11) and Blainville's beaked whale (*Mesoplodon densirostris*, *n* = 3). Eight whales stranded alive, six of which were re-floated, and six whales are known to have died (see Chapter 6 for further details). The population-level effect of this and other atypical strandings worldwide needs further investigation (Cox *et al.* 2006).

Using a similar approach as in Chapter 2, this chapter provides the first time series for mark-recapture abundance estimates of a *Mesoplodon* species. Longitudinal photo-identification data collected from 1997 – 2011 were used to investigate the population dynamics of Blainville's beaked whales off SW Abaco Island, the site of all of the *Mesoplodon* strandings in 2000 along the north-eastern edge of NW Providence Channel (Figure 3.1). Using a Bayesian modelling framework, mark-recapture models were fitted to the photo-identification data to estimate a time series of abundance, rates of emigration and re-immigration, survival, and recruitment (e.g., Whitehead *et al.* 1997, Gowans *et al.* 2000, Whitehead and Wimmer 2005, Matkin *et al.* 2012). Of particular note, this time series encapsulates the time period before and after the stranding.

There were three specific objectives of this chapter:

(1) To examine population dynamics before and after the 2000 stranding by estimating trends in abundance, survival, and recruitment.

(2) To investigate rates of turnover by estimating the rates of individual movement out of the study area (temporary emigration) and back into the study area (re-immigration) during the study period.

(3) To provide the first survival estimate for a *Mesoplodon* species.

3.2 Methods

3.2.1 Field sampling

From 1997 – 2011, randomly placed line transects and opportunistic vessel surveys for beaked whale groups were conducted off the south-western coast of Great Abaco Island, in the northern Bahamas (26.0N, 77.3W). The study area encompassed approximately 300 km^2 along the north-eastern edge of a submarine canyon wall that lies within Northwest Providence Channel where the March 2000 stranding occurred (Figure 3.1). The study area was the same as that presented in Chapter 2 to allow comparison between estimates made during this 15-year study to those made in Chapter 2 using a shorter temporal scale (2005 -2010). A variety of vessel platforms were used during the study, but the majority of data were collected from small vessels (<9 m).

There were 236 sightings of Blainville's beaked whales over the 15 years of study but survey effort was not consistent throughout the year with the majority of encounters (67%) occurring during summer months (Figure 3.2). To allow the consistent interpretation of annual probabilities of capture in the mark-recapture design, a sampling interval was selected from May through August, which represented the time period when effort was most consistent annually.

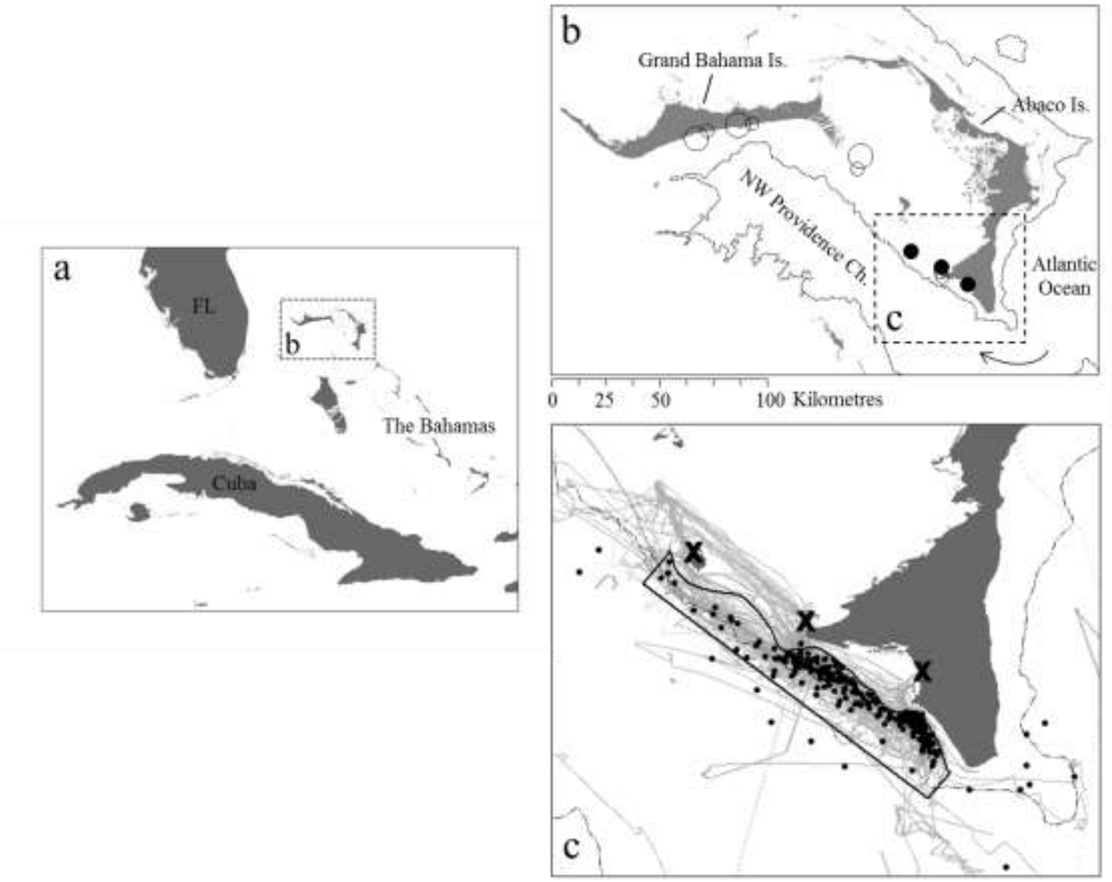

Figure 3.1. (a) Map of The Bahamas showing: (b) the area where a stranding of beaked whales occurred on 15 March 2000 on Abaco and Grand Bahama Islands as navy ships transited from the Atlantic Ocean through Northwest Providence Channel (as indicated by the arrow) conducting an antisubmarine warfare exercise. Small circles represent stranding locations of a single whale and large circle represent two whales that stranded together in the same location. Blainville’s beaked whales (*n* = 3) are shown in black and Cuvier’s beaked whales in white (*n* = 11). In (c), the Abaco study area is enlarged showing vessel tracks (grey lines) and sighting locations for Blainville’s beaked whales (small solid circles) from May – August, 1997-2011. The stranding location for each of the three Blainville’s beaked whales are shown again here as a black “X”. The 1000 m isobath is shown by the black dotted line.

During these annual sampling intervals, surveys covered more than 40,500 km of trackline in the study area (Figure 3.1), resulting in 157 sightings of groups of Blainville's beaked whale, summarised in Table 3.1. In addition, 79 sightings occurred outside the sampling interval ("out-of-sample" sightings between September and April) from which identification data could be used to inform on survival status, and therefore helped to separate mortalities from the movement and capture processes across the annual intervals.

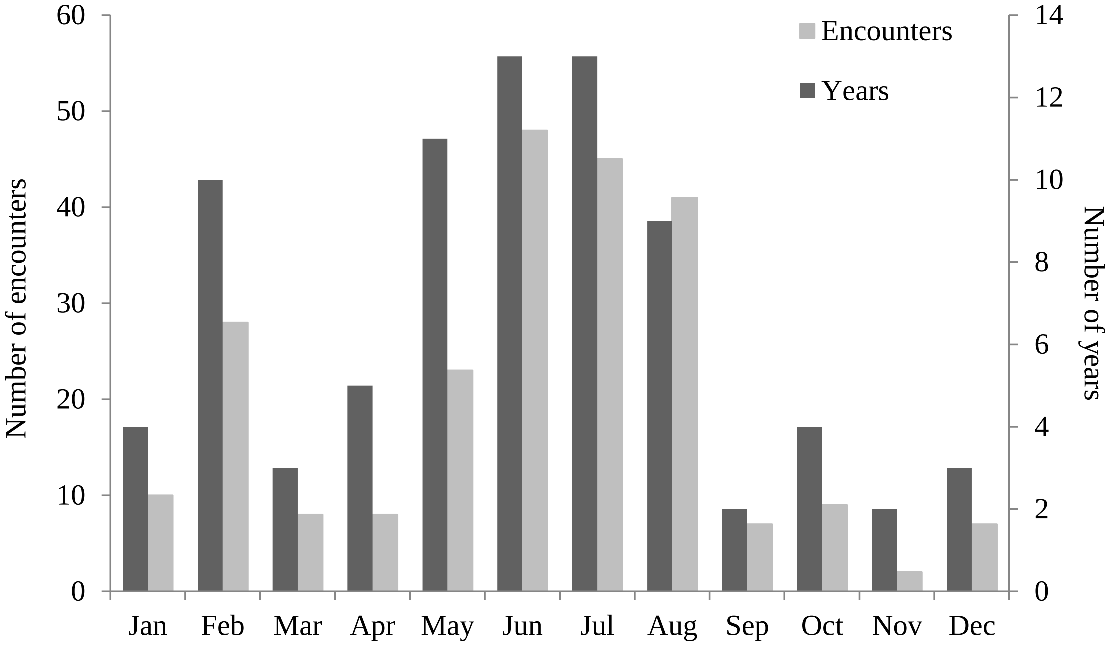

Figure 3.2. Variation in survey effort shown by the number of encounters by month over the entire study period (light bars) and the number of years with encounters during each month (dark bars).

Table 3.1. Summary of survey effort and encounters with Blainville's beaked whales during the annual May – August sampling intervals with the number of "out of sample" encounters given in parentheses.

Year	Survey effort (km)	No. encounters
1997	1021	5 (1)
1998	311	6 (0)
1999	1661	14 (3)
2000	4039	15 (14)
2001	2470	9 (19)
2002	4200	11 (7)
2003	3017	5 (10)
2004	4100	22 (6)
2005	4128	10 (3)
2006	3305	12 (5)
2007	2488	7 (2)
2008	2981	9 (0)
2009	1935	5 (1)
2010	1226	8 (2)
2011	3617	19 (6)

3.2.2 Photographic mark-recapture

Photographic sampling of whales was carried out using protocols described in detail in Chapter 2. Between 1997 and 2003, black and white film (Ilford HP5 or Fujifilm) was shot using Nikon 35 mm cameras. The film was later push-processed to 1600 ASA to increase contrast and help reveal markings on the whale's dorsal fin and body. Between 2004 and 2011, Nikon digital SLR cameras were used to shoot high-resolution images of at least 6 megapixels. Photographs were taken of the entire length of the animal as it surfaced, but the focal area was a rectangular area defined as the “ID area”, sized by one dorsal fin base-width to the anterior, posterior and below the fin. Attempts were always made to photograph all individuals within a group on both right and left sides.

Each identification image was visually examined either using a light table and magnifying eyepiece (for the black and white negatives) or a high-resolution computer monitor (for the digital images). Individual beaked whales were identified using the unique pattern of scarring on the body and nicks in the dorsal fin or at the base of the fin. However, only those individuals with at least one nick within the ID area were considered reliably-marked, or distinctive, and therefore included in the mark-recapture analyses. This ensured that unique whales could be identified from photographs of either side of the animal. Identification photographs were assigned a quality grade (Q) ranging from 0 to 3 (3 being the highest quality photograph) based on the image size, focus, lighting, angle, and exposure (see Figure 2.3), and only high quality images ($Q > 1$) were used in subsequent analyses to prevent misidentifications. To further limit identification errors, two researchers separately confirmed all identifications of new whales.

3.2.3 Mark-recapture model

Owing to the limited extent of the study area, and that it is known that whales move beyond the survey area and an open population model was chosen that parameterises emigration and re-immigration, in addition to survival and recruitment (e.g. Whitehead 1990, Ford *et al*. 2007, Matkin *et al*. 2012). To fit this model, sighting history data were compiled for each individual *i*, starting from the time of first capture (i.e. photo-identification) through each annual interval *t*. These data were inputted into three different binary matrices based on whether the whale was captured ($Y_{it} = 1$) or not captured ($Y_{it} = 0$), whether the whale was known to be alive ($X_{it} = 1$) or not alive ($X_{it} = 0$), and whether the whale was in the study area and available for capture ($F_{it} = 1$) or outside the study area and unavailable for capture ($F_{it} = 0$) (e.g. Schofield *et al.* 2009). Whales were inputted as alive (X=1) whenever they were seen (Y=1) and in years between repeated sightings. Additionally, out of sample sightings were used to inform whether or not a whale was alive in years following the last interval of sighting. After its last sighting, and prior to its first sighting, the whale's status was unknown and X_{it} was treated as missing data about which inference could be made. Similarly, when a whale was not observed in the study area (Y=0), its availability state was unknown and F_{it} was treated as missing data to be estimated.

Using the same model as in Chapter 2 model parameters included the annual probabilities of survival φ_{it}, emigration λ_{it}, re-immigration κ_{it}, and capture π_{it}. However, in addition to estimating survival and movement of beaked whales, trends in non-calf recruitment were also of interest. Using the approach of Pradel (1996), the same identification histories (all three matrices) were also read backwards, to estimate seniority γ_{it}, in place of survival, starting at the time of last observation (e.g., Ford *et al.*

2007). The probability of seniority (or the inverse of recruitment) is the probability that individual i present at interval t was already present in the population at time $t – 1$.

3.2.3.1 Priors

As described in detail in Chapter 2, a flexible hierarchical formulation was adopted with the annual vectors for each parameter set modelled in terms of an overall mean μ and an annual additive effect b_t. For example, the prior specification for capture probabilities π was:

$$\text{logit}\ (\pi_t) = \text{logit}\ (\mu^{\pi}) + b_t^{\pi}$$

$$b_t^{\pi} \sim N(0, \sigma^{\pi})$$

where logit(a) = log(a/(1-a)). Uniform(0,1) prior distributions were placed on each of the five mean probabilities $\mu^{\varphi,\lambda,\kappa,\pi,\gamma}$. Annual effects ($b_t$) were drawn from a Normal prior with mean zero and standard deviation $\sigma^{\varphi,\lambda,\kappa,\pi,\gamma}$. Uniform(0,20) priors were placed on each σ to allow non-zero annual effects to emerge (e.g., Fearnbach *et al*. 2012). This hierarchical formulation allows for the borrowing of strength from information in the full vector of annual estimates to improve estimates in individual years, smoothing estimates more towards the mean in years with sparse data (little information), thereby improving the precision of each year, but allowing departures from the mean when supported by the data.

Estimates of abundance were determined following the same approach as described in Chapter 2. Capture probabilities π_t were used to estimate abundance of distinctive marked whales using the area each year, N_t, by linking these parameters to the observed data. Specifically, the number of individuals actually observed in the study area in each year, $O_t = \sum y_{1:n,t}$, was treated as a binomial sample from the abundance N_t with the binomial proportion given by the estimated π_t. As with the other parameters, we adopted a hierarchical prior to smooth abundance estimates across years:

$$\log(N_t) = \log(\mu^N) + b_t^N$$

$$b_t^N \sim N(0, \sigma^N)$$

A Uniform (min[O_t],100) prior was set on the average annual abundance μ^N, with the lower bound set to the minimum number of distinctive whales observed in any annual interval and annual effects b^N drawn from a Normal prior with mean zero and standard deviation $\sigma^N \sim$ Uniform(0,20).

To produce estimates of the abundance of all whales using the study area in each year, A_t, annual estimates of abundance for distinctive whales (N_t) were rescaled to include non-distinctive individuals, including calves. Using methods described by Durban *et al.* (2010), the distinctive proportion of the population in each year, m_t, were estimated as the binomial proportion given by the number of whales identified that were judged to be distinctive relative to all whales that could be distinguished in high quality photographs ($Q > 1$) during each encounter-day. The proportion therefore represented the overall average across days within each year. The proportion of the population that was distinctive, m_t, was assigned the same hierarchical prior structure to borrow strength across years:

$$\text{logit}(m_t) = \text{logit}(\mu^m) + b_t^m$$

$$b_t^m \sim N(0, \sigma^m)$$

with a flat Uniform(0,1) prior on the average distinctiveness proportion, μ^m, and a Uniform(0,20) prior on the standard deviation of annual effects, σ^N. The overall annual abundance was then defined as $A_t = N_t / m_t$.

Additional derived parameters estimated by the model were estimates of the parent population size, (P_t), or the number of whales using the study area during the entire year (including those not remaining in the study area). For both distinctive whales,

$$NP_t = N_t \Big/ \frac{\kappa_t + \lambda_t}{\kappa_t},$$

and after rescaling to include all whales, $AP_t = NP_t / m_t$.

3.2.3.2 Inference and model fitting

WinBUGS software (Lunn *et al.* 2000) was used to implement Markov Chain Monte Carlo (MCMC) sampling with three sequences used to make repeated draws from the posterior distribution of each parameter. The three sequences were compared to identify and discard initial burn-in iterations prior to convergence (Brooks and Gelman 1998). Summary statistics and kernel density plots for the posterior distributions were then based on 20,000 sampled values for each chain after burn-in.

Model selection was accomplished by comparing the re-immigration model to the standard Cormack-Jolly-Seber model with reduced parameterisation (no emigration or re-immigration) using a minimum posterior predictive loss approach (Gelfand and Ghosh 1998; Durban *et al.* 2010; Matkin *et al.* 2012; Fearnbach *et al.* 2012). The loss function measured the discrepancy between observed and predictive errors and then used the Mean Squared Predictive Error (MSPE) as a measure of the discrepancy; the model with the lowest MSPE was determined as the best fit. Additionally, to test if the model selected was a reasonable fit to the data, a further posterior predictive test was used (as described in Chapter 2; Gelman *et al.* 1996). The result is a Bayesian *p*-value where values close to 0 or 1 indicate poor fit while values close to 0.5 indicate the model fit is adequate (Gelman *et al.* 1996, Brooks *et al.* 2000).

Monitoring parameter values across MCMC iterations allowed probabilistic statements about parameter differences to be made. Over the full MCMC sequence the probability that an annual probability for a particular parameter was greater than the average for that parameter was estimated from the proportion of iterations for which the annual additive effect did not equal zero (b_t < > 0). If this probability was high, p would be close to 1; contrarily, p would be close to 0 if the estimated parameter in that particular year was less than the average, while if there was no deviation from the overall average, i.e., $b_t = 0$, p would equal 0.5.

3.3 Results

3.3.1 Mark-recapture sample

Photo-identification data were collected from 157 groups of Blainville’s beaked whales encountered in the study area during the annual sampling interval of May –

August from 1997 – 2011 (Figure 3.1). Despite selection of the time period with the majority of survey effort, the number of encounters each year ranged from only 5 to 22 (median = 9 encounters, Table 3.1).

Table 3.2. The total number of captures of identified individuals and number of distinctive individuals identified from high-quality photographs during the annual May-August sampling interval. Out-of-sample captures are shown in parentheses.

Year	No. identifications May-Aug	No. individuals
1997	8 (0)	6
1998	11 (0)	8
1999	33 (2)	15
2000	50 (6)	17
2001	23 (12)	10
2002	39 (6)	16
2003	11 (11)	7
2004	36 (5)	13
2005	24 (2)	11
2006	19 (9)	11
2007	16 (1)	12
2008	19 (0)	13
2009	7 (1)	7
2010	14 (4)	8
2011	29 (5)	17

Using only high-quality photographs and after removing capture histories for dependent calves (because their capture probabilities were not independent), 75 different distinctive individuals were identified. There were 339 identifications (captures) of these whales during the annual sampling intervals and an additional 64 identifications collected from out-of-sample encounters (Table 3.2). The total number of individuals identified each year ranged from 6 to 17 (median = 11), which generally reflected the variation in annual survey effort; years with highest effort resulted in the highest number of encounters and usually the highest number of individuals photo-identified.

A discovery curve of cumulative number of individuals against the cumulative number of whale-by-year identifications confirms that this is an open population with regular recruitment of new individuals (Figure 3.3), despite re-sightings of many individuals (56% of 171 cumulative identifications).

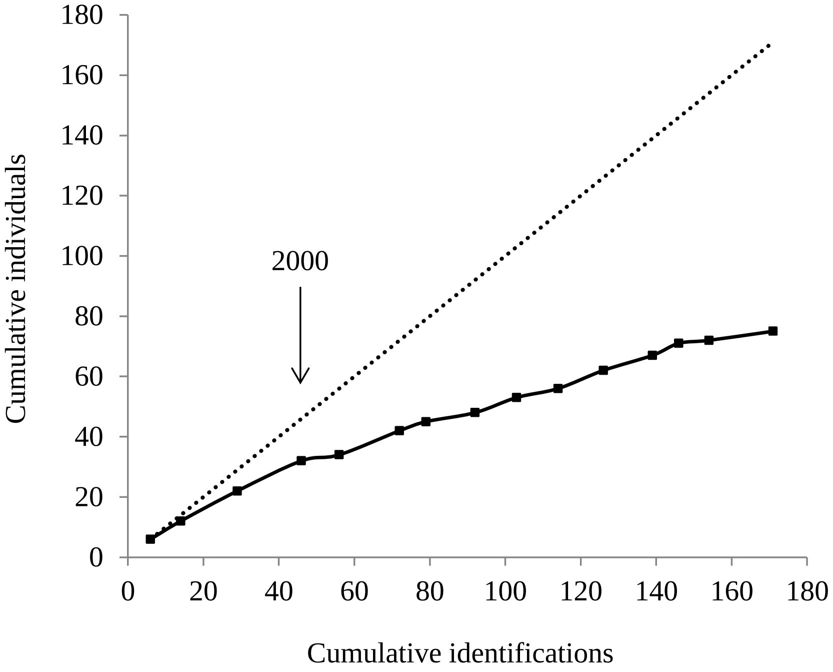

Figure 3.3. Rate of discovery curve for distinctive Blainville's beaked whales in southwest Abaco from 1997-2011 (May – August only). The cumulative number of individuals is plotted against the cumulative number of whale-by-year captures, for each annual sampling period. The dashed line represents a hypothetical 1:1 discovery rate for reference and the year of the atypical stranding is shown.

Although the majority of whales were seen in more than one year of the 15-year study (median 2, maximum 11, Figure 3.4), almost half of the individuals were seen in only one year (37 whales, 48% of the total). Notably, all of the individuals seen in more than 6 years were adult females.

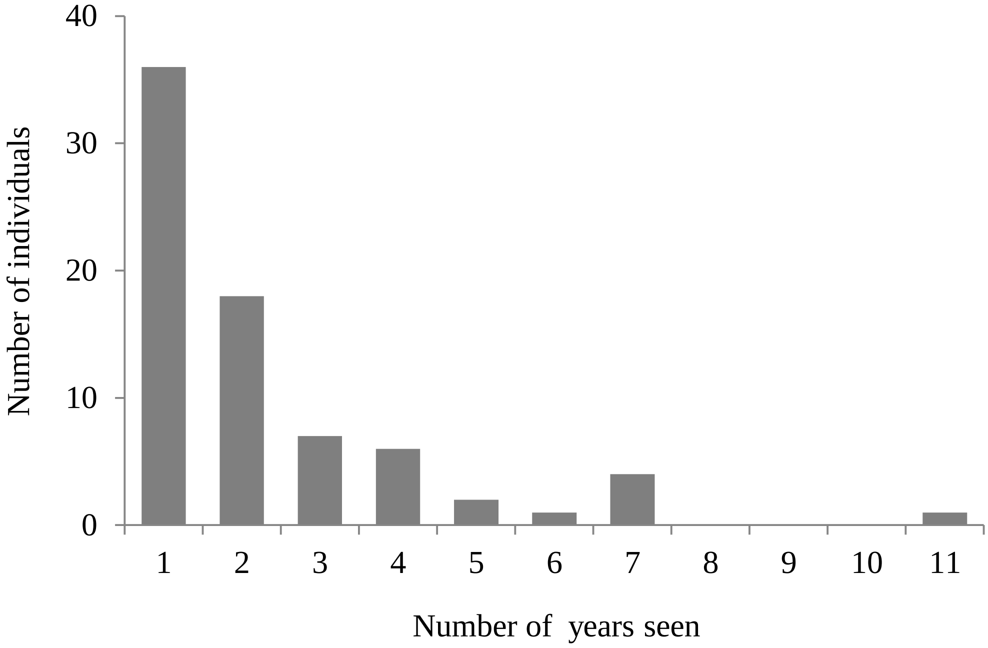

Figure 3.4. The number of years in which distinctive individual Blainville’s beaked whales (non-calf) were identified from high-quality photographs during the annual sampling interval from 1997 – 2011.

These photo-identification data were used to populate the matrices inputted into the re-immigration mark-recapture model. Specifically, the mark-recapture sample consisted of n = 75 individuals, representing 171 non-zero entries inputted as an individual capture in the sightings history matrix ($Y_{it} = 1$). There were long periods of absence in the sighting record for multiple individuals; notably, three whales had absences lasting for 5 years, two for 6 and 8 years, and one whale was absent for 10 years. During these absences the individuals may have left the study area and later returned, or may have remained but were not captured. This provided valuable data to inform the survival/alive matrix and an additional 121 entries were inputted as alive (X_{it} = 1) for those years when whales were not seen between years of repeated captures. Finally, from the out-of-sample captures, there were 47 records of individuals that occurred after the annual interval of their last capture or outside the boundaries of the study area that provided extended information on an individual's survival status for a specific year. These were also included as X_{it} = 1 (alive) beyond the time the whale was actually last seen within the annual interval. Likewise, there were 22 records before first captures which were included to inform on recruitment.

3.3.2 Mark-recapture model

3.3.2.1 Model selection and fitting

Model selection supported the use of an open population model with re-immigration rather than the standard CJS model as determined by the lowest number of discrepancies between the observed and predicted data. For the re-immigration model, there were 93 discrepancies between 1,125 observed and predicted data points, compared to 139 for the CJS model, resulting in MSPE values of 0.08 and 0.12, respectively. However, the Bayesian *p*-value to test the re-immigration model fit was 0.82 (Figure 3.5) suggesting that, there was additional variability in the data not accounted for by the chosen model (Brooks *et al.* 2008, King *et al.* 2010).

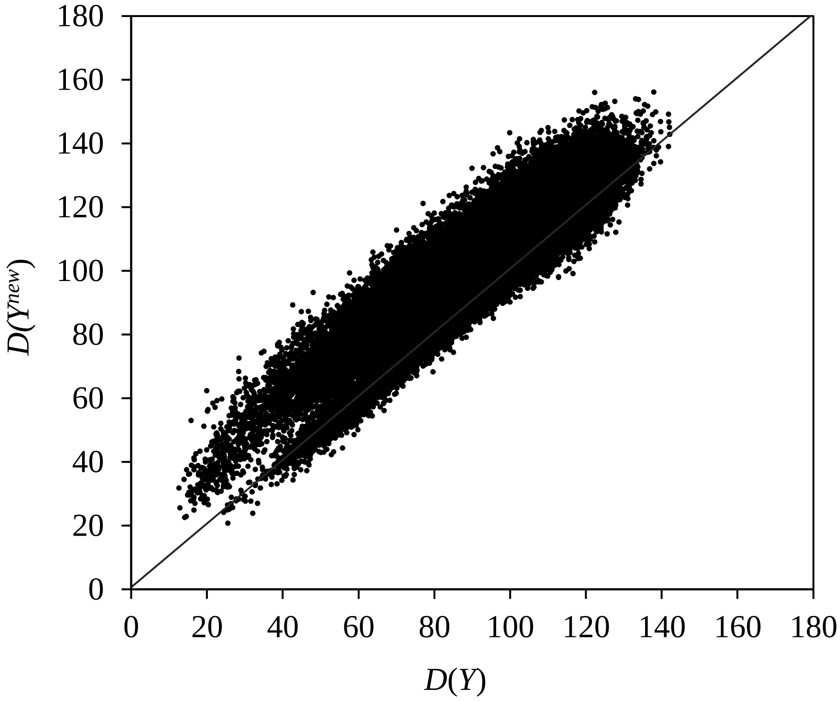

Figure 3.5. Discrepancy plot for re-immigration model with recruitment. Points are the 60,000 MCMC samples of a discrepancy function (*D*, Durban and Elston 2005) calculated for both observed data and data simulated by the model, corresponding to Bayesian *p*–value of 0.82.

3.3.2.2 Probability of capture

Inference was based on the full posterior probability distributions for each model parameter using the re-immigration model. Estimates of average annual capture probability were high (posterior median μ^{π} = 0.47, 95% Highest Posterior Density Interval [HPDI] = 0.32 – 0.73, Figure 3.6).

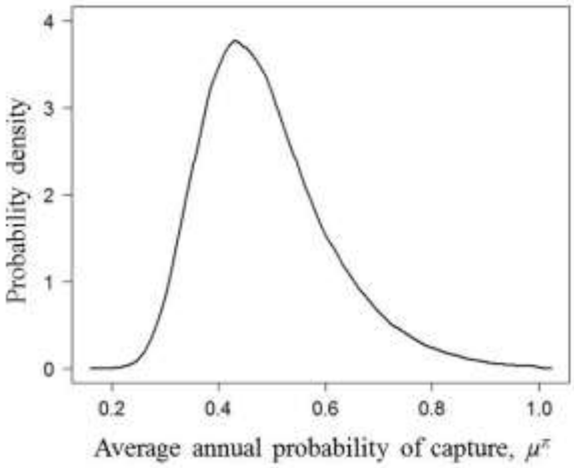

Figure 3.6. Posterior probability distribution plot for average annual capture μ^{π} for the re-immigration model.

Some annual variability in capture probabilities during the study period was evident (Figure 3.7), with departures away from the mean capture estimates (b_t < > 0) in the majority of the years (9 of 14 years).

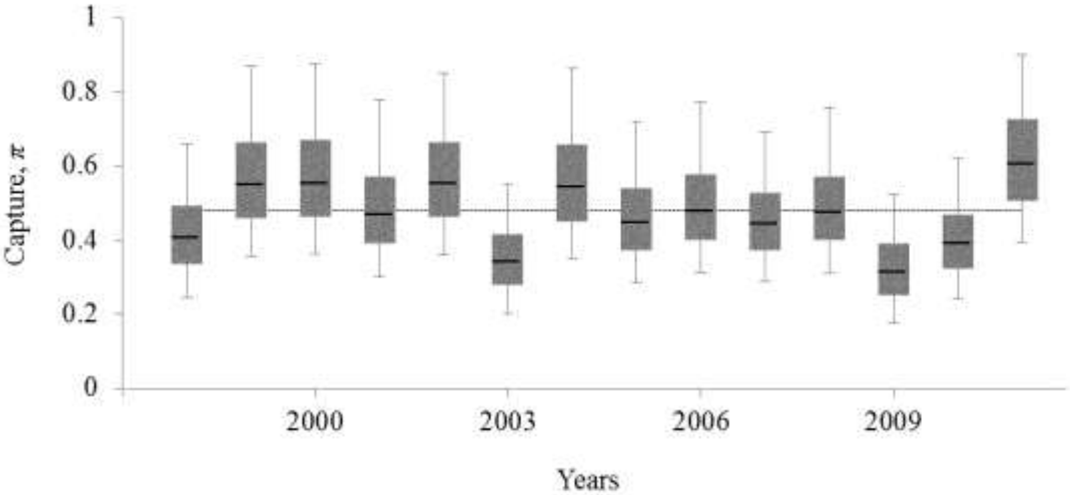

Figure 3.7. Annual capture probability estimates (π_t) during the time series for non-calf and distinctive whales. Estimates are presented as posterior medians (solid black line within bars), with 75% (grey bars) and 95% (vertical whiskers) HPDI. The dashed horizontal line represents the posterior median estimate for average annual capture (μ^{π}).

3.3.2.3 Rates of turnover

Concordant with the multi-year absences in the capture record of some individuals, estimates of temporary emigration and re-immigration showed support for some annual turnover. There was a relatively low probability of annual temporary emigration out of the study area (posterior median μ^{λ} = 0.28, 95% HPDI = 0.14 – 0.47), while estimated re-immigration rates were even lower (posterior median μ^{κ} = 0.08, 95% HPDI = 0.02 – 0.17; Figure 3.8).

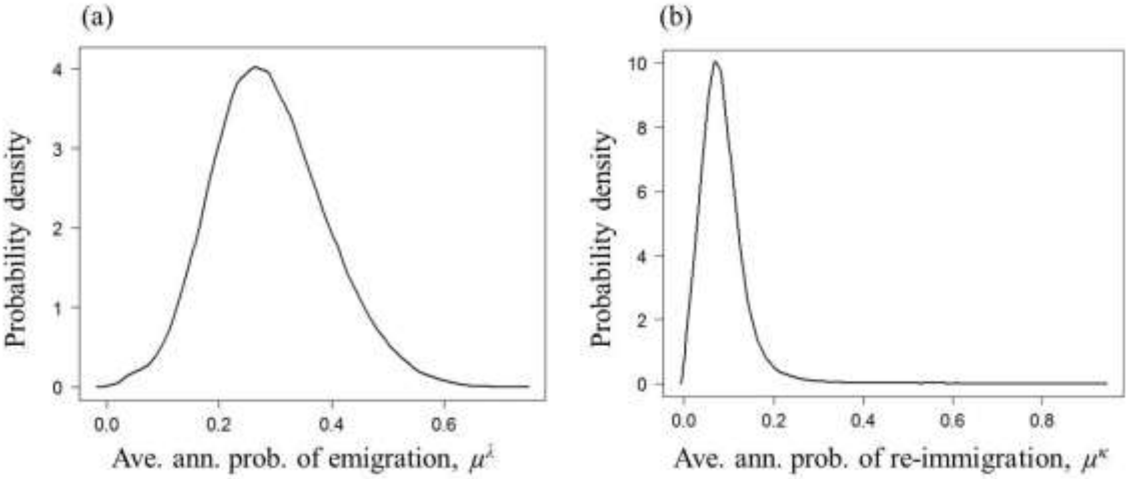

Figure 3.8. Posterior probability distribution plots for the parameters contributing to turnover in the population; (a) average annual probability of emigration μ^{λ} and (b) average annual probability of re-immigration μ^{κ}.

Over the period of the study there was no trend evident for either annual temporary emigration or re-immigration (Figure 3.9).

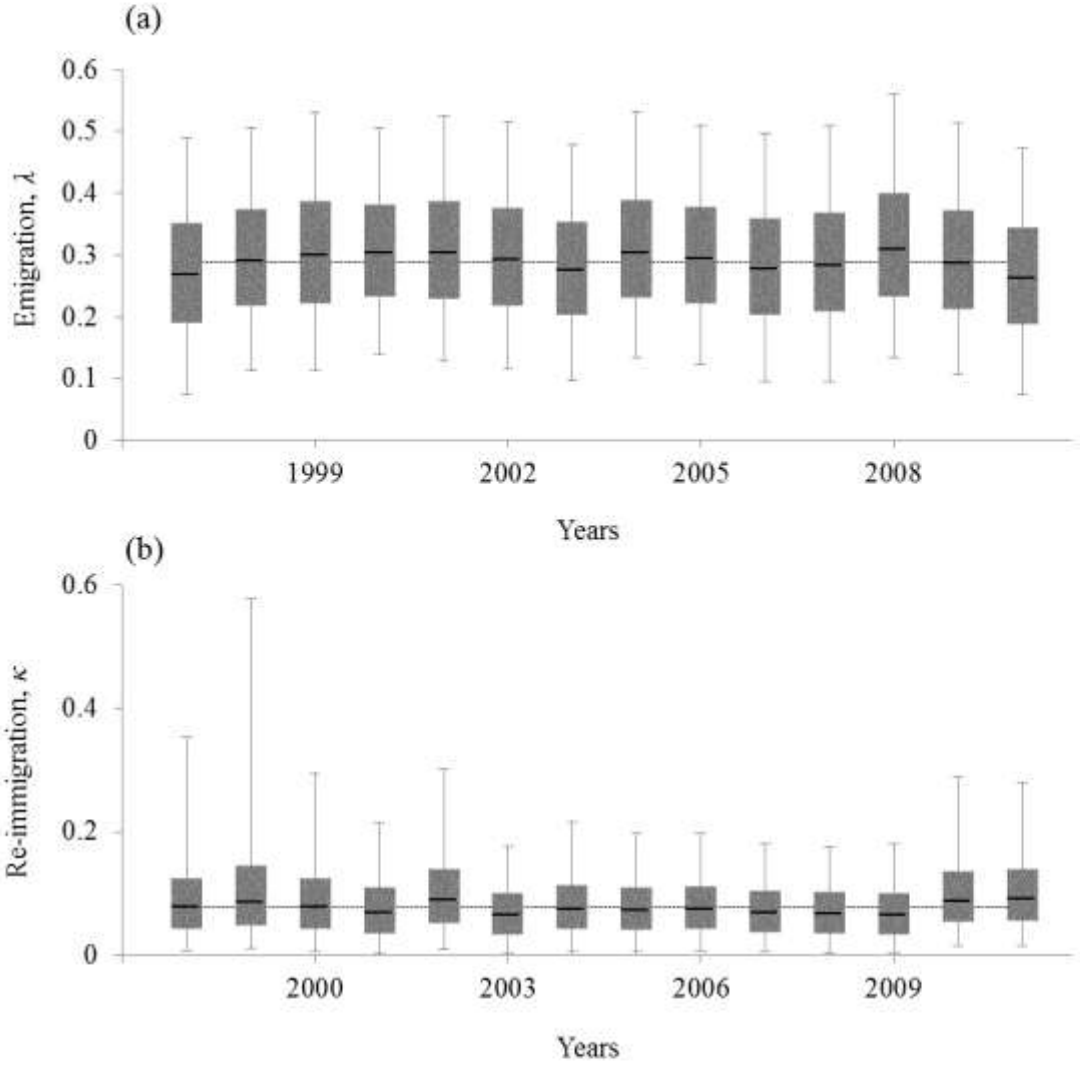

Figure 3.9. Annual probability estimates for (a) temporary emigration (λ_t) and (b) re-immigration (κ_t) during the time series for non-calf and distinctive whales. Estimates are presented as posterior medians (solid black line within bars), with 75% (grey bars) and 95% (vertical whiskers) HPDI. The dashed horizontal line represents the posterior median estimates for average annual emigration and re-immigration (μ^{λ} and μ^{κ}, respectively).

3.3.2.4 Survival and recruitment

Average annual probability of survival was high (posterior median $\mu^{\varphi} = 0.990$, 95% HPDI = 0.949 – 1.000), while probability of recruitment was low (posterior median $\mu^{1-\gamma}$ = 0.003, 95% HPDI = 0.000 – 0.071). However, the skewness apparent in both plots of the posterior probability distributions (Figure 3.10) suggests that the median may not be an appropriate measure of central tendency for either estimate. The posterior mean estimate for average annual survival was very similar to the median estimate (posterior mean = 0.983, SD = 0.024), and the mode was 0.999. Unlike survival, for average annual recruitment, the posterior mean estimate was not the same as the median because these estimates were even more skewed (posterior mean = 0.014, SD = 0.029), so the posterior mode estimate (0; i.e., no recruitment) is used here instead.

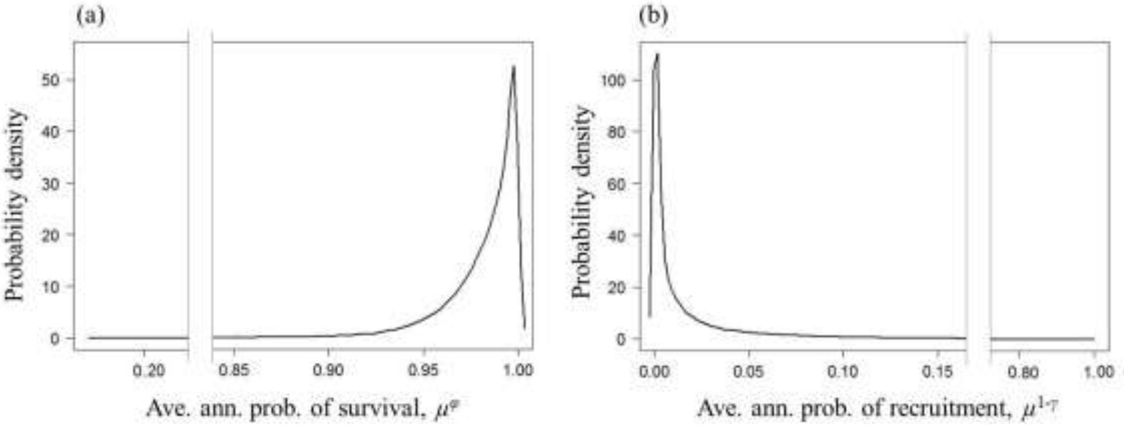

Figure 3.10. Posterior probability distribution plots for (a) average annual probability of survival μ^{φ} and (b) average annual probability of recruitment $\mu^{1-\gamma}$.

Annual survival estimates (1997 – 2010) were computed for the 15-year study and no trend in non-calf survival was noted throughout the time series (Figure 3.11).

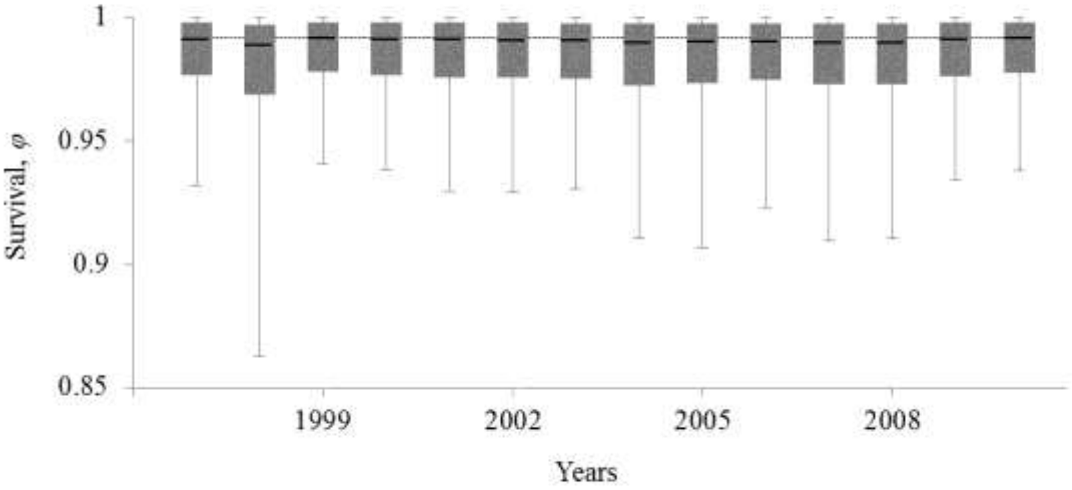

Figure 3.11. Annual survival estimates (φ_t) during the time series for non-calf distinctive whales. Estimates are presented as posterior medians (solid black line within bars), with 75% (grey bars) and 95% (vertical whiskers) HPDI. The dashed horizontal line represents the posterior median estimate for average annual survival (μ^{φ}).

Estimates of recruitment remained low and relatively consistent throughout the study with two exceptional years. In 2005, recruitment was higher than the average annual estimate (p = 0.93; Figure 3.12), and recruitment appeared to remain high in 2006, but support for a departure from the average was less (p = 0.78). However, the estimates in both of these years had the lowest precision of all years.

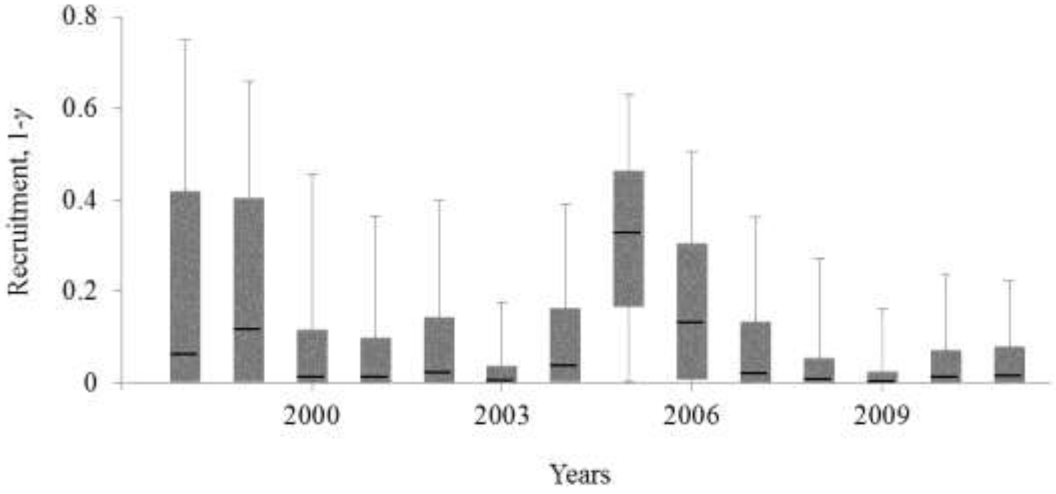

Figure 3.12. Annual recruitment estimates (1-γ_t) during the time series for distinctive whales, not including calves. Estimates are presented as posterior medians (solid black line within bars), with 75% (grey bars) and 95% (vertical whiskers) HPDI. The posterior mode estimate (= 0) was the best measure of central tendency for these estimates.

3.3.2.5 Abundance of distinctive whales

The posterior median estimate for the average annual abundance of distinctive whales (μ^N) was 25 whales (95% HPDI = 17 – 35; Figure 3.13).

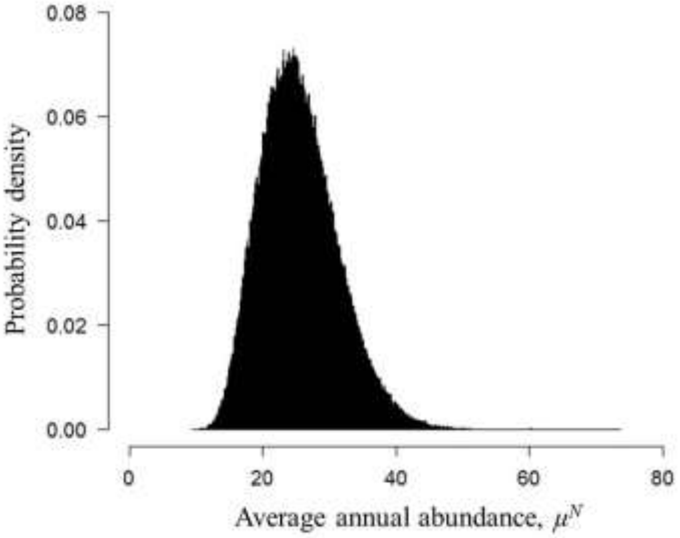

Figure 3.13. Plot of the posterior probability distribution for average annual abundance of distinctive whales (μ^N).

The annual abundance for distinctive whales (N_t) varied little during the study (Figure 3.14). The highest estimate was in 2000 when it was estimated that 28 distinctive whales (95% HPDI = 19 – 42) used the study area during the annual sampling interval. The most precise estimate was in 2011: posterior median $N_t = 27$ whales (95% HPDI =18 – 40).

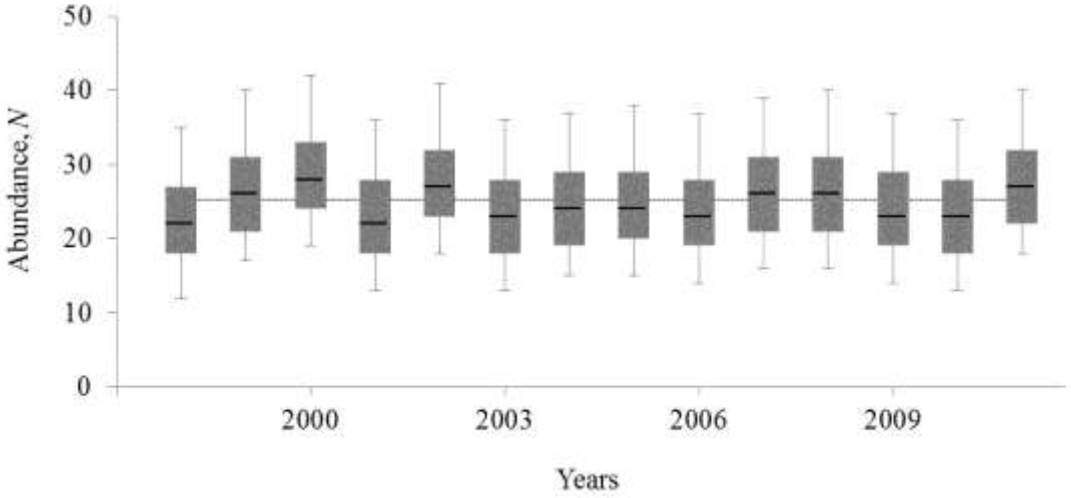

Figure 3.14. Time series for the annual abundance estimates for distinctive whales (N_t) Estimates are presented as posterior medians (solid black line within bars), with 75% (grey bars) and 95% (vertical whiskers) HPDI. The dashed horizontal line represents the posterior median estimates for average annual abundance (μ^N).

3.3.2.6 Proportion distinctive

The posterior median for the proportion of the population that was estimated to be distinctive (μ^m) was 0.60 (95% HPDI = 0.56 – 0.65; Figure 3.15).

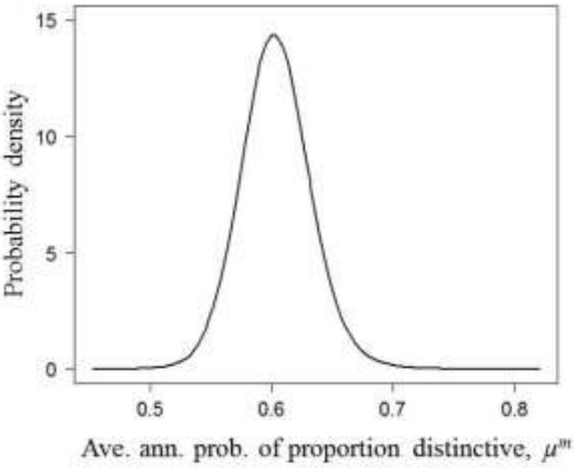

Figure 3.15. Plot of the posterior probability distributions for average annual proportion of the population representing distinctive whales (μ^m).

The annual proportion of the population that was distinctive (m_t) showed some variability during the time series of the study (e.g., in 2011; Figure 3.16), but there were no evidence for departure from the mean throughout (i.e., b_t was close to 0 for all years). The annual estimates for m_t were used to rescale annual abundance (N_t) to include all whales in the population, i.e., distinctive, non-distinctive whales, including dependent calves in the estimate of total abundance (A_t).

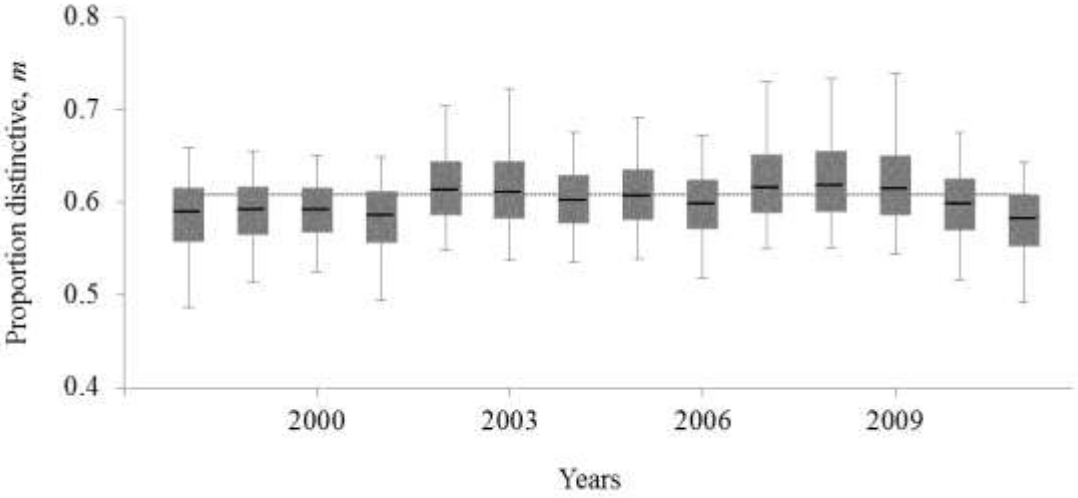

Figure 3.16. Annual estimates for the proportion of distinctive whales in the population (m_t). Estimates are presented as posterior medians (solid black line within bars), with 75% (grey bars) and 95% (vertical whiskers) HPDI. The dashed horizontal line represents the posterior median estimates for average annual abundance (μ^m).

3.3.2.7 Total abundance

After rescaling to include non-distinctive whales and calves, the posterior median estimate for total average annual abundance was μ^A = 42 whales (95% HPDI = 28 – 58; Figure 3.17).

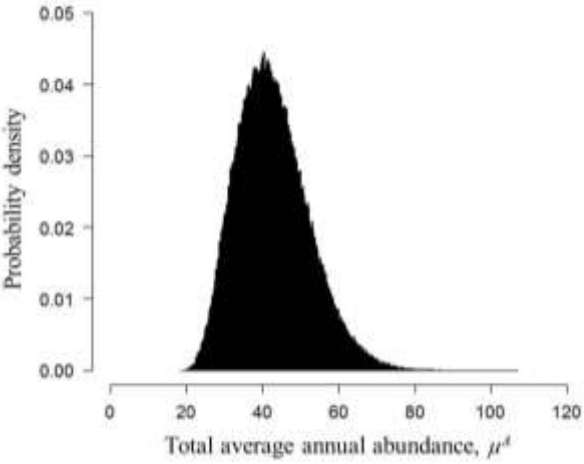

Figure 3.17. Plot of the posterior probability distribution for total average annual abundance (μ^A), after rescaling to include non-distinctive whales and calves.

Total annual abundance (A_t) appeared relatively stable over the time series (Figure 3.18). The highest and most precise estimate was in 2000, when the posterior median for total annual abundance was 48 whales (95% HPDI = 31 – 73).

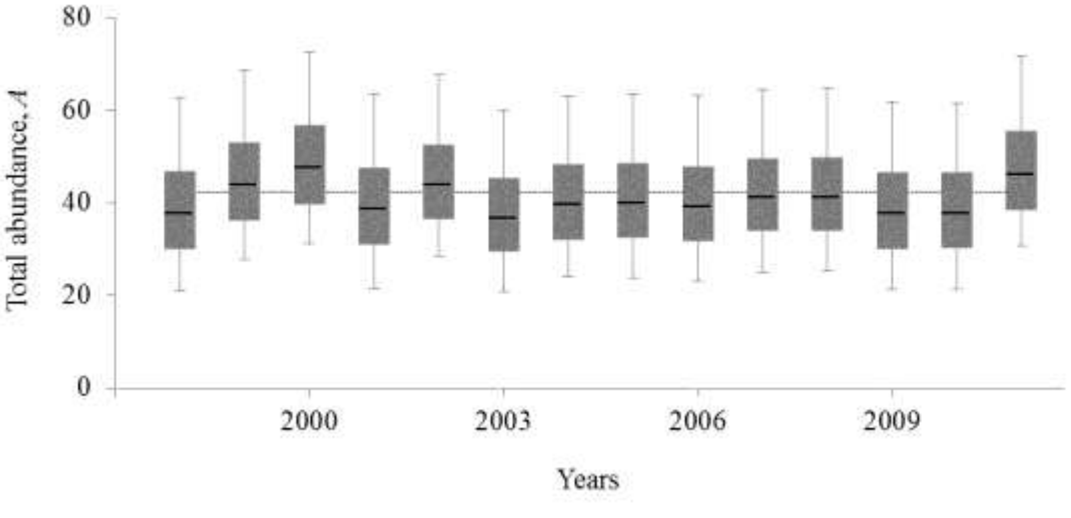

Figure 3.18. Total annual abundance estimates (A_t) for Blainville's beaked whales off SW Abaco from 1998 to 2011. This estimate includes indistinctive whales and calves. The mean overall abundance (μ^A = 42 whales) is shown as the dashed horizontal line. Estimates are presented as posterior medians (solid black line within bars), with 75% (grey bars) and 95% (vertical whiskers) HPDI.

3.3.2.8 Parent population size

Additional derived parameters estimated by the model were estimates of the parent population size, P_t, the number of whales using the study area during the entire year (including those not remaining in the study area), for both distinctive whales only (μ^{NP}) and for the all whales (μ^{AP}). For both parameters, the range of the posterior distributions were large, so 75% HPDIs are presented instead of 95% HPDIs as well as the year with the most precise estimate. The posterior median estimate for the size of the parent population of distinctive whales, μ^{NP} was 135 whales (75% HPDI 101 – 221), with a mode of 100 whales. The most precise estimate was in 2001 when the posterior median estimate NP = 108 whales (75% HPDI 73 – 180). The estimated size of the total parent population after rescaling, μ^{AP} was 230 whales (75% HPDI 171 – 390), with a mode of 155 whales. The most precise estimate was in 2011, posterior median AP = 169 whales (75% HPDI 120 – 250).

3.4 Discussion

<u>3.4.1 *M. densirostris* abundance</u>

This study has shown that using mark-recapture methods with photo-identification data is a tractable approach for a species that presents challenges in using more conventional ship-based surveys for abundance estimations. The estimates of abundance reported here are seemed reasonable (42 whales) relative to the number of individuals actually observed each year (median 11 whales). However, these whales are part of a larger parent population size (~155 whales), indicating that not all individuals were in the study area at any one time; only about 27% of this larger population used the study area during a given 4-month sampling interval, supporting turnover of individuals in the study area. Indeed, estimates of abundance using data over an 8-month sampling interval (Chapter 2) revealed much higher average annual abundance (80 whales), although precision in the estimates from the shorter time period (only 6 years) was much less. The area sampled was quite small (300 km^2) relative to potential home ranges of these whales as suggested by satellite telemetry data for Blainville's beaked whales (Schorr *et al.* 2009, Durban unpublished data) so it was not surprising to find that whales seem to range beyond its bounds. Future analyses should investigate individual home ranges, using both photo-identification and telemetry data, which would also allow a closer look at rates of temporary emigration and re-immigration to better inform the re-immigration model.

3.4.2 Model fitting: need to account for heterogeneity

Model selection supported the re-immigration model over a standard CJS, yet the measure of fit (Bayesian *p*-value 0.82) for the re-immigration model was not optimal (Brooks *et al.* 2008), although values even more distant from 0.5 have been deemed adequate (King *et al.* 2010). Convergence of the three MCMC chains was achieved quickly advocating good model performance, but the discrepancy plot (Figure 3.5) shows some indication of clustering which suggests that the model may not have fit all the data well. Initial data exploration revealed that long-term site fidelity could be documented for some individuals, namely adult females, yet almost half of the whales were seen in only one year (Figure 3.4) This indicates heterogeneity in capture probabilities, perhaps based on age/sex differences in site-fidelity, which may compromise model fit and lead to negative biases in abundance estimates (e.g. Hammond 1986, Hammond *et al.* 1990).

To address the critical assumptions that all individuals possess unique marks and that those marks are not lost (Seber 1982), as recommended by Friday *et al.* (2000) and Stevick *et al.* (2001) only high quality photographs of distinctively-marked individuals were included in the dataset used for parameter estimation in this study. This approach assumed that non-distinctive individuals behaved in a similar way to distinctive ones which may have not been true. Most non-distinctive whales were younger (see Chapter 4 for details). Immature whales may have occupied different habitat than adult females (Claridge 2006), potentially resulting in differences in capture probabilities as well as turnover rates, and apparent survival (Whitehead and Wimmer 2005). Incorporating age- and sex-structured heterogeneity into the model would be an important advancement of this work (see Chapter 5).

3.4.3 Rates of turnover

Unlike in Chapter 2 where inference about movement rates was data limited due to a shorter time series of annual intervals, the longer term dataset used here was more useful. Despite high site fidelity of adult females, estimates of rates of movement suggested that the same whales did not remain in the study area across the annual sampling interval. While it was estimated that 28% of whales may temporarily emigrate from the study area on an annual basis, the probability of re-immigration was low, thus supporting turnover of whales in the study area. It is possible that the relatively short sampling interval (4 months) did not allow enough time for temporary emigrants to reimmigrate during the year sampled, and it would be a very useful exercise to determine the temporal scale at which turnover occurs. However, the existence in differences in residency patterns by age / sex class (as discussed above) will make it difficult to interpret turnover unless stratification by age class and sex can also be integrated.

3.4.4 Survival estimate for a *Mesoplodon* species

The survival estimates reported here are the first survival estimates for Blainville's beaked whale and, in fact, for any *Mesoplodon* species. However, the parameter estimated in this study is "apparent" survival rate, which is a product of unknown components of true survival and permanent emigration. Despite this, high non-calf survival was found in this study, as is expected for long-lived mammalian species with low reproductive potential. *M. densirostris* survival was higher than that for northern bottlenose whales off Nova Scotia; survival and permanent emigration was estimated to be approximately 0.90, after accounting for an annual rate of mark change of ~0.03 in the initial estimate (φ = 0.87, 95% CI = 0.83 – 0.91; Gowans *et al.* 2000).

Blainville's beaked whale survival was also higher than non-calf survival reported for baleen whales [e.g., φ = 0.951 (SE 0.014) for western grey whales, *Eschrichtius robustus* (Bradford *et al.* 2006); φ = 0.96 (SE 0.008) for humpback whales, *Megaptera novaeangliae* (Barlow and Clapham 1997); φ = 0.975 (SE 0.006) for blue whales, *Balaenoptera musculus* (Ramp *et al*. 2006)]. Average survival was more comparable to odontocete populations with stable or increasing population growth [e.g., φ = 0.98 (95% HPDI 0.95 – 0.99) for US west coast transient killer whales, *Orcinus orca* (Ford *et al.* 2007)], and slightly higher than that reported for a population of coastal bottlenose dolphins, *Tursiops truncatus*, from the same geographic region, but possibly in decline [$\varphi = 0.95$ (95% HPDI 0.92-0.97) Fearnbach *et al.* 2012]. Buckland (1990) made two recommendations to ensure reliable survival estimation for cetaceans, both of which have been met in this study; capture probabilities were greater than 0.20 in any given year and the field effort lasted longer than 10 years. However, potential age- and sex-structured heterogeneity (as mentioned above) may have biased survival estimates upwards, favouring adult females.

3.4.5 Population trends around an atypical stranding

One of the primary objectives of this study was to investigate the potential impact on local populations of beaked whales of the anti-submarine warfare exercise that took place on 15 March 2000 in the Abaco study area. The use of mid-frequency active sonars by surface ships during the exercise resulted in the stranding of 14 beaked whales; the majority were Cuvier's beaked whales ($n = 11$) but three Blainville's beaked whales also stranded (Balcomb and Claridge 2001, Evans and England 2001). At least six whales died (one of the three Blainville's beaked whales) and evidence of acoustic traumas was documented in the freshest carcasses examined (Evans and England 2001). Two (one *Ziphius* and one *M. densirostris*) of six whales that live stranded and were assisted back out to sea by rescuers, were later re-sighted (as detailed in Chapter 6), providing an indication that some whales survived the event, yet the population level impact remained unknown.

During the period 1997 – 2011, the population dynamics of Blainville's beaked whales were remarkably stable with no obvious trends in abundance or survival. The only anomaly around the time of the stranding comes from observation of the empirical data. The discovery curve (Figure 3.3) showed an entry of 10 “new” whales into the study area in the months after the stranding (during the May – August sampling in 2000). It is unknown whether this represented natural variation in the number of whales using the area related to prey availability or lagged recruitment from births, individuals first acquiring a nick, or actual recruitment. The discovery curve reached closer to a horizontal asymptote in 2001 than any other time during the study emphasising the relatively high contribution of new whales after the stranding. However, there was not a significant increase in estimated recruitment once effort was accounted for in the mark-recapture model, perhaps indicating that the discovery of new whales was at least partly a function of increased effort.

3.4.6 Conclusions

This work has filled some key gaps in our knowledge about the population demographics of Blainville’s beaked whales. While long-term site fidelity of adult females in the Abaco study area was apparent, these whales were part of a larger parent population suggesting some annual turnover occurs. The first survival estimates for a mesoplodont were provided, which showed high non-calf survival of Blainville’s beaked whales off southwest Abaco, comparable to estimates for other odontocetes. This work represents the first use of mark-recapture models with longitudinal photo-identification data to produce a time series of abundance estimates for a *Mesoplodon* species. Notably, no change in the population dynamics of the Abaco population of Blainville’s beaked whales was detected following the March 2000 sonar exercise, but this species was not predominant in the stranding. This study has demonstrated a useful method applied to a species that is otherwise difficult to study and provided excellent baseline for future monitoring of direct and indirect (e.g., increased cyclone activity due to climate change) anthropogenic impacts on this and other populations.

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CHAPTER FOUR

ASSIGNING AGE AND SEX CLASSES TO BLAINVILLE'S BEAKED WHALES USING SIGHTING HISTORY DATA

4.1 Introduction

Information about an individual's age and its sex is critical to understanding a species' reproductive biology (Boyd 1985, Heimlich-Boran 1986, Plavcan and van Schaik 1998), evolutionary biology (e.g., reproductive costs, Tolley *et al*. 1995), social organisation (Bigg *et al.* 1990, Whitehead *et al.* 1991), conservation biology (Perrin and Reilly 1984, Newsome *et al.* 2007, Wells 2012), and population demographics (Olesiuk *et al.* 1990). Data on the age class and sex of individuals can add a new element to an existing investigation, while lack of this information may render the study less useful. For example, age- and/or sex-specific heterogeneity can lead to serious biases in estimates of abundance (Seber 1982, Hammond 1990). Furthermore, conservation actions applied to one age class may not be effective for another. Of particular importance to population biologists is that the assessment of age class and sex allows investigation into age and sex specific demography, leading to a better understanding of population dynamics.

In mammals, relative age can be inferred based on an individual's increase in size (Lee and Moss 1995, Clark and Odell 1999), structural degradation and growth changes (e.g. tooth wear and development, Severinghaus 1949). Absolute age, a more important metric, is determined by counting growth layers, also called growth layer groups (GLGs), in teeth (Scheffer 1950, Laws 1952, Linhart and Knowlton 1967), bone (Marmontel *et al.* 1996), and horns or claws (Hemming 1969) which are known to accumulate at a rate correlated with seasonal patterns. In mysticetes, GLGs in the ear plug from the auditory meatus and in baleen plates are counted to determine absolute age (Purves1955, Laws and Purves 1956, Lockyer 1972), although there is still some debate about the rate at which GLGs in ear plugs of baleen whales accumulate (Gabrielle *et al.* 2007, Best 2012). Absolute age in odonotocetes has been determined by counting GLGs in the dentine layers in teeth (Nishiwaki *et al*. 1958, Kasuya 1972, Perrin and Myrick 1980, Kasuya and Marsh 1984, Hohn *et al.* 1989). Problems with counting GLGs in teeth with closed pulp cavities from older animals have been overcome by counting cemental instead of dentinal layers (Kasuya 1976, Kasuya and Marsh 1984). More recent methods have also been developed using the racemization rate for aspartic acid in the eye lens nucleus (George *et al.* 1999, Garde *et al.* 2007). However, with very few exceptions (e.g., Myrick *et al*. 1983, Hohn *et al*. 1989), determining age using these methods is only possible using dead specimens collected either from strandings, incidental takes in fisheries or directed catches.

Indeed, catch data have provided a large amount of information on age structure in cetacean populations, and the relationship between age, size and sexual maturity (e.g., Lockyer 1972, Kasuya and Marsh 1984, Martin and Rothery 1993, Tormosov *et al.* 1998). An individual's maturity state can be readily determined through direct examination of the reproductive organs using testes weight, and the presence or absence of sperm in the testes of males and the presence of a corpus albicans or corpus luteum in the ovaries of females as indications of sexual maturity (McMaster 1984). Age at the onset of sexual maturity can then be determined for individuals which have concurrently been aged (e.g., Hohn *et al.* 1985).

Examination of beaked whales from two species taken in whaling operations has contributed information on life history traits for ziphiids, including the age at sexual maturity, gestation length and longevity. Kasuya (1977) reported on Baird's beaked whales (*Berardius bairdii*) taken in the Japanese whaling industry. Females attained sexual maturity at 10 – 15 years and males at 6 – 10 years (assuming one GLG is equivalent to one year's growth). The gestation period was estimated to be 17 months. The oldest female was 54 and the oldest male was 84 years old. Thus, males apparently attained sexual maturity at a younger age and lived 30 years longer than females. Life history data for northern bottlenose whales (*Hyperoodon ampullatus*) commercially harvested off Iceland and Norway have also been collected. Benjaminsen and Christensen (1979) reported that this species attained sexual maturity at 7 – 11 years for both sexes. The gestation period was 12 months (Benjaminsen 1972) and mean calving interval was given as 2 years (Benjaminsen and Christensen 1979). Christensen (1973) reported maximum ages of 27 for females and 37 for males. However, the value of whaling data to inform about age structure of a population is limited as larger animals were generally targeted in fisheries and inconsistencies between whaling data and stranding data have been noted (Stevick 1999). Additionally, while information from these two species is valuable, of the 21 extant ziphiid species (Dalebout *et al*. 2004), these were the only two hunted commercially, therefore reproductive data and age structure for beaked whales are still lacking.

For *Mesoplodon* species, almost all information on age and sexual maturity has come from the examination of carcasses from stranded animals (Mead 1989, Heyning 1989) and is limited by the rarity of strandings of the majority of the species. In a summary of reproductive data for beaked whales, Mead (1984) gave maximum size data for 11 *Mesoplodon* species, but only had enough data to present size at sexual maturity for *M. europaeus* females (mean body length 450 cm). Age data are even sparser with data for only two species given by Mead (1984): assuming one GLG is equivalent to one year's growth, maximum age of 27 years for *M. europaeus* (from Perrin and Myrick 1980); and minimum age at sexual maturity for a female *M. densirostris* with one corpus albicans, indicating this animal had recently become sexually mature at age 9 years (from Ross 1979). Confounding problems of small sample sizes is the potential for bias in basing life history parameters on data from naturally stranded animals because these individuals do not necessarily represent the population as a whole (e.g., differences may exist in body lengths, age at sexual maturity and longevity between sick and healthy individuals). Yet gathering life history data from living cetacean populations is challenging and can be exceptionally difficult for beaked whales.

In studies of free-ranging cetacean populations, several different characteristics have been used to aid in determining life history parameters of individuals. Body length can be measured either directly using aerial (Perryman and Lynn 1993, Fearnbach *et al.* 2011) or underwater photogrammetry (Spitz *et al.* 2000, Pack *et al*. 2012), or can be derived from measurements of body features visible above the surface (e.g., dorsal fin, Durban and Parsons 2006; or fluke, Jacquet 2006). Photographs and observations of sexually dimorphic features have been used to identify the sex in some species, such as the size and head shape of sperm whales (*Physeter macrocephalus*) (Gordon 1987), dorsal fin height of male killer whales (*Orcinus orca*) (Olesiuk *et al.* 1990, Durban and Parsons 2006), and melon morphology in northern bottlenose whales (Gowans *et al*. 2000). Individuals have been identified as female if they are observed in close association with calves (e.g., Clapham and Mayo 1987, Slooten *et al*. 1993, Knowlton *et al*. 1994), but alloparental care does exist in some species (e.g., sperm whales, Whitehead 1996) which can lead to mistaken sex assignment. More recently, Herman *et al.* (2008) described new methods to determine age of killer whales by measuring specific lipids, endogenous fatty acids and fatty acid ratios in blubber obtained from remote biopsy sampling. While the data described above can be collected instantaneously, determining age structure of the population generally requires longitudinal studies.

Individual whales can be aged with certainty if first photo-identified in the first year of life. Neonates can be distinguished by the presence of foetal folds: lighter pigmented linear “folds” orientated dorsoventrally as a result of the foetus folding *in utero*, which in tropical waters disappear within 1 month after birth (Fearnbach *et al.* 2011), thus providing an even finer measure of date of birth. Longitudinal monitoring of young cohorts within a population can then provide information on age at sexual maturity (e.g., Olesiuk *et al*. 1990, Herzing 1997, Hamilton *et al.* 1998, Gowans *et al.* 2000, Gabrielle *et al*. 2009). Age at first parturition in females can be confirmed when viable offspring have been documented, although long periods between sightings may result in incomplete histories if documentation of the first calf is missed.

Determining age at sexual maturity in males can be more difficult but, in sexually dimorphic species, the age at which the development of secondary sex characteristics begins can provide evidence of attaining sexual maturity in males [e.g., for killer whales, when the fin height to base ratio exceeds that of its mother (Olesiuk *et al*. 1990)]. Behaviour in males may change when they reach sexual maturity especially for species in which male competition for mates leads to combat; individuals engaged in behaviours associated with breeding suggest they may have reached sexual maturity, otherwise why undergo the risk of injury (e.g., Clapham *et al*. 1992)? For many odontocete species, the amount of intraspecific scarring increases with the onset of sexual maturity in males [e.g., in ziphiids (Mead *et al.* 1982, Heyning 1984), sperm whales (Gordon 1987), and narwhals (*Monodon monoceros*) (Silverman and Dunbar 1980)]. Scarring in both sexes also provides insight into the relative age of individuals (young versus old adults) as scars from parasites or predators accumulate with age. For example, Walker and Hanson (1999) found increasing numbers of scars from cookie cutter shark (*Isistius brasiliensis*) bites on female *M. stejnegeri* with increasing numbers of corpus albicans. For some species, changes in colour phase has been correlated to age (e.g., Herzing 1987) but information on relative age may not always be sufficiently precise. What are needed are datasets that span a greater portion of an animal's life history to allow reliable sex identification of all age–sex classes retrospectively (e.g., Olesiuk *et al*. 1990); however, for cetaceans this requires studies spanning a decade or more.

Although beaked whales are challenging to study because of their diving behaviour (Barlow 1999), some populations have been shown to occur reliably in localised areas where they have been the focus of long-term photo-identification studies.

These include northern bottlenose whales in The Gully, off the Scotian Shelf (Whitehead *et al*. 1997); Cuvier's beaked whales (*Ziphius cavirostris*) off San Clemente Island, southern California (Falcone *et al.* 2009) and in Hawaii (McSweeney *et al*. 2007); and Blainville's beaked whales in Hawaii (McSweeney *et al*. 2007), the Canary Islands (Aguilar de Soto 2006), and The Bahamas (Claridge 2006 and this study). Life history data from photo-identifications of beaked whales have been augmented in these studies because ziphiids exhibit sexual dimorphism causing the development of external characteristics, which have been used to determine age class and, in some species, sex of individuals based on field observations (e.g., Gowans *et al.* 2000, Claridge 2006, McSweeney *et al*. 2007, Falcone *et al.* 2009).

Dentition in ziphiids has been reduced numerically in all but one species (*Tasmacetus sheperdi*) to only one to two pairs of teeth located in the mandible (Heyning 1984), although vestigial teeth can be found in a few species (Mead 1989). In *Mesoplodon* there is only one pair of laterally compressed teeth which are located at varying positions in the mandible depending on the species (Moore 1968). At the onset of sexual maturity the teeth erupt from the alveoli in males only (McCann 1963, Besharse, 1971) and are used in male-male aggression so may be better described as "tusks" (Mead *et al*. 1982, Heyning 1984) or "battle teeth" (McCann 1974). Although sexual dimorphism exists in all Ziphiid species, it is most pronounced in Hubbs' beaked whale (*M. carlhubbsi*) and Blainville's beaked whale (*M. densirostris*) (Heyning 1984). In these species, as males mature, ossification in the mesorostral canal results from the expansion of the vomer, premaxilla and maxilla bones which eventually fuse in older males (Moore 1963, Mead 1989). This massive rostral bone serves to reinforce the rostrum as males engage in combat (Heyning 1984), and is most developed in *M.*

densirostris in which the rostral bone has the highest density (5.7 g/cm^3) of any mammalian bone tissue measured (Zotti *et al*. 2009).

Male Blainville's beaked whales also undergo massive development of the mandible posterior to the mandibular symphysis and the teeth are located on this elevated part of the ramus such that the crown of the teeth project above the rostrum (Moore 1968, Besharse 1971). Aggressive use of the teeth in male-male combat results in extensive intra-specific scarring or "battle scars" on males (McCann 1974) which take the form of either a singular line or two parallel lines, depending on whether one or both attacker's teeth engage, and are one of the most striking external characteristics (Heyning 1984). In contrast, females of this species do not undergo development of the mandible and the teeth typically remain un-erupted from the alveoli (Besharse, 1971), and little or no intraspecific scarring is visible (Heyning 1984, Mead 1989, Claridge 2006). Distinguishing adult male Blainville's beaked whales from adult females is thus relatively easy from high quality photographs of the head (Figure 4.1).

Figure 4.1. Sexual dimorphism in Blainville's beaked whales makes it possible to readily distinguish (a) adult females from (b) adult males using high quality photographs of the head. The oval light coloured marks visible on the female's head are scars caused by deep crescent-shaped bites from cookie cutter sharks (*Isistius* sp.), while the linear scarring on the male is evidence of intra-specific combat. The brown colouration on both animals is due to diatoms (Bacillariophyta) on their skin.

Other features visible externally in Blainville's beaked whales have been identified as aids in distinguishing age class and sex, some of which may be useful in field observations. Variation in pigmentation patterns noted in stranded animals have been suggested as a means of distinguishing immature and mature individuals, but may not be representative of true colouration because pigmentation changes quickly upon death (Allen *et al.* 2011). Furthermore, diatoms (Bacillariophyta) often cover portions of the skin sometimes making it difficult to distinguish pigmentation of free-swimming whales. Distinguishing the sexes of younger Blainville's beaked whales based on field observations can also be problematic, but relative age of individuals can be ascertained based on the extent of scarring. Oval scars attributed to cookie-cutter sharks (*Isistius* sp.) are often scattered over the body (McCann 1963) and are accumulated with age (Walker and Hanson 1999). For males, intraspecific scars also accumulate from repetitive aggressive social interactions; scarring is heaviest on the oldest and lightest on the youngest males (Heyning 1984). Besharse (1971) noted differences in rostral length between adult and sub-adult females, but this would likely be difficult to assess in photographs of free-ranging animals; however, the length of the tooth in adult males, if photographed, could be a good indicator of relative age (Mead *et al.* 1982).

In this chapter, longitudinal photo-identification records were used to designate age class and sex to individuals with the following specific objectives:

1. To assess accuracy of photographic sex designations for individual Blainville's beaked whales by comparing with molecular genetics techniques.
2. To determine the age at sexual maturity for this species.
3. To examine and use characteristics from individuals of known age and sex to assign age and sex classes to other whales of unknown age when first sighted.
4. To describe the age structure for the Abaco Blainville's beaked whale population.

4.2 Methods

4.2.1 Data collection

Field work was conducted off the southwest coast of Abaco Island in The Bahamas (see Figure 3.1) between 1997 and 2011. Encounters were not restricted to a sampling interval or the 300km^2 study area used in the mark-recapture analyses (Chapters 2 and 3) but included all encounters off the southwest coast of Abaco Island. When a group of beaked whales was sighted, the vessel was manoeuvred alongside the group so that the photographs were taken perpendicular to the animals when possible. Between 1997 and 2003, black and white film (Ilford HP5 or Fujifilm) was shot using Nikon 35 mm cameras equipped with high-speed motordrives and a fixed 300-mm F4 lens. The film was later push-processed to 1600 ASA to increase contrast and help reveal markings on the whale's fin and body. Between 2004 and 2011, Nikon digital SLR cameras were used to shoot high-resolution images of at least 6 megapixels. Photographs were taken anterodorsally and dorsolaterally, beginning from the tip of the rostrum, and as the animal rolled during its surfacing, through the entire length of the body. In this way, photographs of the head, thorax, dorsal fin, and tailstock could be assigned to one individual. Attempts were made to photograph both the right and left sides of all individuals within a group.

During some encounters between 2009 and 2011, tissue samples were collected from photo-identified individuals using remote biopsy methods. Specifically, biopsy darts with 40 mm stainless steel tips (manufactured by Ceta-Dart, Copenhagen, Denmark) were fired from a 85-lb crossbow (Barnett RX150 or Wildcat, Barnett International, Odessa Florida, USA). Samples were taken from the flank region near the dorsal fin. Individuals from all age classes were targeted, except dependent calves. All individuals biopsied were photo-identified. Additionally, one sample consisted of sloughed skin obtained opportunistically from a live-stranded whale (Md149) before it was re-floated and pushed back out to sea. This individual was photographed anterodorsally and dorsolaterally during the rescue. Tissue samples were stored in a preservation solution [20% dimethyl sulphoxide (DMSO), supersaturated in NaCl] immediately after collection and were later transported to the Southwest Fisheries Science Center, La Jolla, California, USA where molecular sexing was completed by personnel at the Marine Mammal Genetics Program (see Morin *et al.* 2005 for genetic methods used). To test the reliability of sexing by photographs, a direct comparison was made for individuals that were assigned to an age / sex class photographically and for which tissues had been collected for genetic analysis.

4.2.2 Photo-identification analysis

Each identification image was visually examined using either a light table and magnifying eyepiece (for the black and white negatives) or a high-resolution computer monitor (for the digital images). Individual beaked whales were identified using the unique pattern of scarring on the body and nicks in the dorsal fin or at the base of the fin within a rectangular area measuring one dorsal fin base-width in all directions from the centre of the fin base, which was defined as the “ID area”. Identification photographs were assigned a quality grade (Q) ranging from 0 to 3 (3 being the highest quality photograph) based on the image size, focus, lighting, angle, and exposure (e.g., see Figure 2.3), and only high quality images ($Q > 1$) were used in subsequent analyses to prevent misidentifications. To further limit identification errors, two researchers separately confirmed all new identifications.

4.2.3 Assessing *Isistius* sp. scarring patterns in females

The amount of scarring from cookie cutter shark bites was quantified to determine the validity of using counts when assigning age class to individuals; specifically, the objective was to compare the amount of scarring on adult and sub-adult females. Using only photographs of the highest quality ($Q = 3$), the number of scars found within the ID area was counted on mature and immature individuals by two experienced observers, independently. Females were considered mature if seen with the same calf travelling in echelon position, and immature if they were not seen with a calf, on at least three encounter-days over two years. The difference in the number of scars on adult and sub-adult females using counts from each independent observer was examined and the averaged counts of both observers were evaluated.

4.2.4 Assigning age class and sex

External characteristics previously reported for Blainville's beaked whales which may be useful to distinguish age classes and sex from field observations are summarised in Table 4.1.

Table 4.1. Previous descriptions of external characteristics that can be used to differentiate Blainville’s beaked whales by age class and sex.

Age / sex class		**Body length (cm)**	**External Characters /Osteology**	**Pigmentation***	***Isistius* scars**	**Intraspecific scars**
Dependent calf	Neonate	Longest foetus 190, 40-48% length of mother[1]	Foetal folds[2]	White blaze on dorsal fin, dark border along its trailing edge[3]	None[2]	None[2]
	Calf	Shortest calf 261[1]; less than 60% adult body length[3]	No foetal folds[2]	Darker dorsally, paler ventrally than adults[3], dorsal “cap” on head[3]	Few[2]	Not likely, but possible[2,4]
Sub-adult	Unknown	Longest immature 415[3]	No massive development of mandible[2,5]	Dorsal “cap” on head[3]	<10 in area 4Xs length of dorsal fin base[4]	Possibly[2,6]
	Female		No massive development of mandible[7], rostrum shorter than adult female[7]	Dorsal “cap” on head[3]	<10 in area 4Xs length of fin base[4]	Possibly[2,6]
	Male	352[3] 390[8]	Teeth not yet erupted above gum, extremely stepped mandible[2,5]; teeth barely erupted, jawline relatively straight[4]	Dorsal “cap” on head[3]	<10 in area 4Xs length of fin base[4]	Some scarring but less than adult male[2,5,9] mainly on head and dorsum[2]; some parallel scars[10]
Adult	Female	Mean 444[3], 470[11]	Lack of tooth eruption[2,4,5,7], longer rostral length than male[2], no massive development of mandible[2]	No “cap” on head[3]; medium grey dorsally, lighter ventrally[12]	More than sub-adult[2]; >10 in area 4Xs length of fin base[4]; extensive[5,10]; increase with age[13]	May have some[2,4,6,9]
	Male	Mean 443[3], 470[11]	Mandibular arch[14,15,16]; teeth erupted[5,16,17]; deeper, wider, shorter rostrum[7,17]	No “cap” on head[3]; dark grey dorsally and ventrally[18]	>10 in area 4Xs length of fin base[4]	More extensive scarring[5,9,18,19]; concentrated on head and dorsum[2,6]

Sources: [1]Mead 1984, [2]Claridge 2006, [3]Ross *et al.* 1988, [4]McSweeney *et al.* 2007, [5]Mead 1989, [6]MacLeod 2002, [7]Besharse 1971, [8]Caldwell and Caldwell 1971, [9]Heyning 1984, [10]Leatherwood *et al.* 1982, [11]Pitman 2008, [12]Allen *et al.* 2011, [13]Walker and Hanson 1999, [14]Van Beneden and Gervais 1880, [15]Raven 1942, [16]Moore 1958, [17]Moore 1968, [18]McCann 1963, [19]McCann 1974.
*Pigmentation described here are from observations of dead animals only.

In this study, individual whales were monitored over a 15-year period and ontogenetic changes between observations were noted. Using high quality photographs, age class and sex (hereafter called “class”) was assigned to each individual based on the following: (1) body length relative to other animals in the photograph, (2) external sexual dimorphic characteristics, (3) pigmentation pattern, (4) number of cookie cutter shark scars, and (5) extent of intraspecific scars. Three different age classes were used: dependent calf, sub-adult, and adult. These classes were further divided; dependent calves were separated into neonates and older calves, and sub-adults and adults were separated by sex. Calves were assigned an estimated age at first sighting which was based on the five characteristics listed above as well as the presence of foetal folds and the date of the last sighting of the mother (following Gowans *et al.* 2000). Calves with foetal folds were considered to be very young; Fearnbach *et al*. (2012) reported foetal folds remaining visible for only one month in neonate bottlenose dolphins (*Tursiops truncatus*) from the northern Bahamas. Direct measurements using standardised metrics (Geraci and Lounsbury 2005) were taken of two calves that stranded during the study, which provided body length data for reference.

4.2.4.1 Determining age at sexual maturity

There were six individuals first observed as calves that were re-sighted repeatedly over 9 – 14 years, four of which (three females, one male) were monitored until sexually mature, which provided information on the minimum age at sexual maturity. Detailed examination of the individual sighting histories of these six whales was undertaken.

Once the age of each of these calves was assigned, this formed the timeline on which to assign ages at the different stages of their maturity. Males were considered sexually mature at the age at which their teeth had erupted above the epidermis of the mandibular arch, a feature that could readily be documented in photographs. For various reasons, defining age at sexual maturity was more difficult for females, particularly minimum age. During pregnancy, no change in external characteristics was evident in this study so attainment of sexual maturity was undetected until a female was observed with calf. Furthermore, a foetus may be aborted or a calf may die before first observation. Also, no data existed on gestation time for *Mesoplodon* so assumptions had to be made. Mead *et al.* (1982) and Walker and Hanson (1999) assumed a gestation period of 12 months for *M. carlhubbsi* and *M. bidens* so, following this lead, a female was considered to be sexually mature one year before the estimated birth date of her first observed calf. The estimated age of the female's calf when first observed was important in determining the age of the mother at sexual maturity.

For the females, an extended interval of no re-sightings or only one sighting in a year made determination of minimum age at sexual maturity problematic. In these cases, behavioural observations of association patterns were used to inform on maturation status based on reported segregation by age in social groupings in this species (see Claridge 2006). However, inference made using this approach needed to be interpreted with some caution because the method was somewhat circular; that is, assignment of the age class of associates was partially based on the results from monitoring the individuals of known ages through their maturation stages. To aid in resolving this problem, three critical observations of individuals of known ages in 2012 (just after this study's end date) were included because of their valuable contribution of additional information on the observed age at first calving and inter-birth interval for females as well as the minimum age at maturity for males.

4.2.4.2 Assigning classes to all individuals

Classes were then assigned to all whales observed in this study. If the individual was first observed as a calf, the initial step was to estimate the age of the calf using methods described above. Relative size of a calf at first sighting was the most important characteristic but difficult to quantify. General relative measures were used: individuals less than 1 year old were approximately 1/2 the mother's length, 1-2 year olds were 1/2 to 3/4 the mother's length, and 3-4 year olds were greater than 3/4 the mother's length. Next, using the age at sexual maturity determined for known individuals (above), if re-sightings of calves extended post-separation from the mother, age classes were updated accordingly. If an individual was first seen as a sub-adult, characteristics identified in this study from known-age individuals and the comparison in cookie cutter shark scarring patterns between adult and sub-adult females were used to inform on the most likely class assignment.

Each class assignment was rated using a certainty factor (C) ranging from 0 – 3 (3 being the highest certainty level) based on the extent to which relevant features could be seen in photographs and thus evaluated. Only class assignments with high certainty ratings ($C > 1$) were included in the summary analyses presented for the study population. Analyses were further restricted to include only those individuals seen on more than one occasion to ensure classes were assigned correctly as certainty ratings were likely to increase with an increased number of sightings. The average number of re-sightings and sighting span times for each class were reported (median and ranges). Sighting span times were defined as the time in years between the first and last sighting record, and the number of sightings of each individual was counted by encounter-day.

4.2.5 Determining population age structure

To describe the age structure of the population, the number of individuals in each class was tallied annually and averages across years were calculated. If an individual's class changed within a year, the class when it was first sighted during the year was used.

Sightings data were also used to calculate the proportion of dependent calves (neonates and older calves) to non-calves in each encounter-day to provide a reference for interpreting the comparison between Abaco and AUTEC reported in Chapter 2, which included a subset of the Abaco data (2005 – 2010). The data used here included all calves and non-calves from Abaco over the 15-year study with photo quality $Q > 1$ and certainty rating $C > 1$, and were not restricted to only those individuals re-sighted (as above).

4.3 Results

During the 15-year study, 35,272 photographs were obtained from 236 sightings of Blainville's beaked whale groups. There were 1,284 whale identifications by encounter-day from high quality photographs ($Q > 1$), from which 153 individuals were identified.

4.3.1 Comparison between molecular and photographic sexing

Fourteen skin biopsy samples were collected from 12 different whales (two whales were sampled twice, in different years). Additionally, tissue from sloughed skin was collected opportunistically from a whale which live stranded and was refloated (ID: Md149). Thus there were 13 individuals for which both tissue samples and photographs were collected. Sex was assigned photographically for 12 of the 13 whales (seven females, five males, and one unknown). For all of these 12 individuals, the designation was correct 100% of the time when compared to molecular sexing (Table 4.2). There was one animal (Md191) for which sex was designated as unknown based on photographs, and was determined to be a male using molecular sexing; so although it was not possible to determine sex photograhically for this individual, it also was not assigned incorrectly.

Table 4.2. Comparison of results of sex determination made for Blainville's beaked whales using photographic and molecular genetic techniques.

Sample Field ID	Ind ID	Photographic sexing	Molecular sexing	Age class
000315_Md2	Md149	Female	Female	Adult
080608_Md1	Md231	Male	Male	Adult
080608_Md2	Md091	Female	Female	Adult
080613_Md1	Md143	Male	Male	Adult
080614_Md1	Md209	Male	Male	Adult
080614_Md2	Md183	Female	Female	Sub-adult
080614_Md3	Md234	Male	Male	Sub-adult
080614_Md4	Md070	Female	Female	Adult
080614_Md5	Md094	Female	Female	Adult
090505_Md1	Md191	Unknown	Male	Sub-adult
110223_Md2	Md121	Female	Female	Adult
110223_Md3	Md130	Male	Male	Adult
110223_Md4	Md134	Female	Female	Adult

4.3.2 Comparing cookie cutter shark scars on female age classes

Eight individuals from these age classes met the selection criteria; i.e., seen at least three times with or without a calf over a two-year period. Five of the eight sub-adult females were known to be between 5 – 8 years old at the time that the scars were counted. Using the mean counts from both observers, there was a significant difference in the number of cookie cutter scars in the "ID area" for adult (n = 8) and sub-adult (n = 8) females (t = 3.5, df = 14, p < 0.005). The number of cookie cutter shark scars on adult females ranged from 2 – 6 (mean 3 scars, SD 1.6) and on sub-adult females from 0 – 2 (mean 1, SD 0.6). Differences in the amount of scarring on adult and sub-adult females were significant for all counts; those made by the two observers independently and their mean counts (Table 4.3). Differences in counts between observers were significant for adult females (t = 2.3, df = 14, p < 0.05), but not for sub-adult females (t

= 1.4, df = 14, p = 0.09), although the small number of scars for sub-adults would have made it difficult to find significant differences. It is noteworthy that all of the adult females and half of the sub-adult females had evidence of intraspecific scarring within the ID area.

Table 4.3. A comparison of the number of cookie cutter shark scars counted within the ID area on adult and sub-adult females by two experienced observers using high-quality photographs (Q = 3). (SD = standard deviation).

	Adult female counts					**Sub-adult female counts**					***t* stat**	***p* value**	
Observer	**Mean**	**SD**	**Median**	**Min.**	**Max.**	**Mean**	**SD**	**Median**	**Min.**	**Max.**			
1	4.1	1.8	4.0	2.0	8.0	1.3	0.7	1.0	0.0	2.0	4.2	4.5E-04	***
2	2.1	1.6	1.5	0.0	4.0	0.8	0.7	1.0	0.0	2.0	2.2	0.024	*
Mean	3.1	1.6	2.8	1.5	6.0	1.0	0.6	1.0	0.0	2.0	3.5	0.002	**

*p <0.05, **p <0.005, ***p <0.001, 14 degrees of freedom

4.3.3 Age at sexual maturity

Sightings histories were compiled for six calves monitored over 9 – 14 years as they advanced through the different stages of maturation (Table 4.4). For females, first known parturition occurred at ages 10 – 15 years, and minimum ages at sexual maturity were estimated to be between 8 – 9 years (based on 12-month gestation times). One male attained sexual maturity at age 9 years, while minimum ages at sexual maturity for males ranged from 9 to greater than 10 years.

Table 4.4. Sighting histories of Blainville’s beaked whales monitored from calves to or near the age at sexual maturity. (C) = calf born before year first seen (year estimated), C = dependent calf, S = sub-adult [separated from mother, and not seen with calf (females), or teeth not erupted (males), not associated with known adults], A? = poss. adult female (≥ 9 yr old but not seen with calf), A = confirmed adult (for females includes 1 year before parturition, and for males year in which observation of teeth erupted), M = observed with calf, (M) = not seen in that year but observed the following year with a 1-year old calf , T = teeth erupted, X = not seen. Obs. age first calving = female's age at first observation with a calf. Min. age first calving = female’s minimum age at first calving. Obs. age first teeth = male's age at first observation of teeth erupted above mandibular arch. Min. age first teeth = male’s minimum age at eruption of the teeth.

FEMALES	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	Obs. age first calving	Min. age sexual maturity
Md107	(C)	(C)	C	C	X	X	S	S	X	X	A?	X	X	X	A	(M)	15	?
Md134			(C)	C	C	C/S	X	S	X	S	A?	A?	X	A	(M)	M	12	8 - 9
Md135			(C)	C	C	S	X	S	S	X	S?	A	M	X	X	A	10	9
MALES	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	Obs. age first teeth	Min. age sexual maturity
Md115				C	C	C	S	X	X	S	X	S	X	X	X	X	> 8	> 8
Md143				(C)	C	C	S	X	S	S	S	X	T	X	A	A	9	9
Md191							(C)	C	C	X	S	X	X	S	X	X	> 10	> 10

Detailed examination of the sighting histories for each of these calves was undertaken. For the females, although all three were resighted throughout the study, the most detailed sighting histories were compiled for Md135. Based on Md135's size at first observation and earlier sightings of her mother in which the calf was absent, Md135 was estimated to be 1 year old when first sighted. She was sighted on 6 separate encounter-days as a dependent calf, until separation from her mother at age 3. Following separation, there were eight re-sightings of Md135 between 2001 – 2007 during which time she was not observed with a calf. First known parturition for Md135 occurred at age 10 when she was seen with a neonate in echelon position (group size = 2). Assuming a gestation time of 12 months (following Mead *et al.* 1982 and Walker and Hanson 1999), Md135 would have reached sexual maturity at age 9.

Minimum age at sexual maturity was also estimated to be 9 years old as it did not seem reasonable that Md135 had lost a calf previously based on behavioural observations of her associations. Although there was a interval of 16 months between re-sightings in 2004 and 2006, in each of the three encounters in 2004, Md135 did not associate with known adults, but only with individuals presumed to be sub-adults. She was re-sighted only once in 2006 with only one other whale: Md107, who was 10 years old at the time and may have recently attained sexually maturity although she had not been documented with a calf (see description of her sighting record below). Md135 was only sighted once in 2007, but this was the first encounter in which her associates included known adults since separation from her mother. These observations provide some support for Md135 not attaining sexual maturity until 2007, at the minimum age of 9 years. In 2012, Md135 was observed with a second neonate, demonstrating an inter-birth interval of 4 years.

The sighting histories for Md134 and Md107 were not as detailed. Md134 was 1 year old when first sighted, was seen on 6 different encounter-days as a dependent calf, and first observed separated from her mother at the end of 2001, when age 3. She was re-sighted on 13 occasions post-separation between 2001 and 2010, but not observed with a calf until 2011. Her calf was estimated to be 1 year old at the time of first sighting which implies that the age at first known parturition for Md134 was 12 years, and thus age at sexual maturity was 11 years. However, the minimum age at sexual maturity for Md134 may have been earlier based on observed changes in her association patterns at a younger age. Prior to 2006, Md134’s associates were sub-adults only but, in 2006, she was re-sighted on six occasions and during all of these encounters her associates included adults. She was re-sighted only once in 2007, again with adult associates. It is possible that Md134 was sexually mature in 2006 and lost a foetus/calf before the 2007 re-sighting, resulting in an inter-birth interval of 3 years. Or she may not have reached maturity until 2007 but then lost a foetus/calf soon after (she was not seen in 2008), resulting in an inter-birth interval of 2 years. If either scenario were true, her minimum age at sexual maturity could have been 8 – 9 years.

The third female, Md107, was 2 years old when first sighted, seen five times as a dependent calf, and separated from her mother at a minimum age of 4 years. After a 2 year gap in sightings she was re-sighted again in 2002 and 2003 when she was not associated with known adults. After this period her sighting history became even more scant. At age

10, she was re-sighted again (in 2006) but only once; during this encounter her only associate was Md135, who at that time was 8 years old and not quite sexually mature. Md107 was not re-sighted again until 2010 at which time she was not observed with a calf but associated with mother-calf pairs. When she was next re-sighted (in 2012), she had a 1 year old calf, so her known age at first parturition was 15 (in 2011), and age at sexual maturity was 14 years. With such a limited number of post-separation observations of Md107, determining the minimum age at sexual maturity was not attempted.

Although all three males were first documented as calves and observed post-separation from their mothers, only one of these matured during the study (Md143). Md143 was a 1 year old when first observed, was seen 13 times as a dependent calf, and separated from his mother at age 3. Post-separation, Md143 was re-sighted five times between 2002 and 2006. He did not associate with known adults until age 6 at which time his associates included adult males, females with calves and Md115 (another sub-adult male, also age 6) in mixed groups. By age 7, Md143's jawline showed only minimal enlargement of the mandibular arch, but he then had one heavy intra-specific scar behind the blowhole, and had accumulated numerous short linear scars. None of the intraspecific scars were parallel suggesting they resulted from contact with only one tooth. However by age 9, photographs of Md143 showed the apex of his teeth above the epidermis of the mandible, and his head and dorsum were marked with a multiple overlapping scars, including parallel scars. Based on these observations it was determined that Md143 reached sexual maturity at age 9. Even though Md143 was not re-sighted in 2007 (age 8), his teeth were just barely visible in 2008 and thus recently erupted, so 9 years was also considered to be the minimum age at sexual maturity for Md143.

The other two males were not sexually mature when last sighted but provided further information on minimum ages at sexual maturity in males. One of these (Md115) was first seen as a neonate and observed nine times as a dependent calf. He was first observed separated from his mother at age 3, and then four times post-separation. His pattern of associations was very similar to that of Md143; at age 6 he began associating in mixed groups with adult males, females with calves (including his mother), and other sub-adult males. Photographs taken during the last sighting in 2007, at age 8, showed that, although the mandible had developed extensively, his teeth had not yet erupted. Md115 was not seen again so, although the age at which he reached sexual maturity was not determined, the minimum age of maturity was greater than 8 years.

Md191 (a younger sibling of Md143) was first observed when 1 year old, and seen seven times as a dependent calf. Separation from his mother occurred at a minimum age of 3 years old. Post-separation Md191 was only seen two more times; once in 2006 (age 5), when he was associated with his mother and her new calf, and again in 2009 (age 8), when his associates included an adult male, Md134 (pregnant with her first viable offspring) and a known sub-adult female. There was no evidence of development of the mandibular arch at this time. However, photographs from 2012 showed massive mandibular development but the teeth had not yet erupted. Thus the minimum age for attainment of sexual maturity for Md191 was greater than 10 years of age.

4.3.4 Characteristics used to assign age class and sex

4.3.4.1 Dependent calves

4.3.4.1.1 Neonate: In this study, individuals were designated as neonates only if foetal folds were observed. One neonate (Md115) was first sighted when very small, the dorsal fin leaned to one side, and deep grooves formed the foetal folds. Md115 was re-sighted 29 days later and the foetal folds were faint, but were still visible, therefore the age at which dependent calves would no longer be considered neonates using the definition here appeared to be around 6 weeks of age. Other characteristics observed for neonates included the presence of a light blaze of pigmentation on dorsal fin, with dark leading and trailing edges and their very small size (Figure 4.2), estimated to be 1/3 the length of their mother.

An additional characteristic unique to neonates was different pigmentation of the rostrum and lower jaw to other age classes. In individuals with foetal folds, the rostrum was pigmented a dark grey colour which became increasingly dark anteriorly. This was contrasted against the creamy-white colouration of the lower jaw, which was uniform throughout with the exception of dark grey lips. Within several months after birth, the rostrum became medium grey, the same colour as the remainder of the animal dorsolaterally. Pigmentation changed to medium grey in the lower jaw as well but only posteriorly, in the region of the mandibular arch characteristic of this species; anteriorly, it remained creamy-white (Figure 4.3).

Figure 4.2. Photographs of three different neonates showing a pair of the foetal folds on each whale (the black arrows in each picture point to the foetal folds) as well as other characteristics unique to this age class. The light blaze of pigmentation in the central part of the dorsal fin with dark leading and trailing edges is a clear feature in (a) and (b), but only the darker edges are visible in (c), which is an indication that it is older. Their small size is referenced by the two green dots visible anterolaterally on the whale in (b), from lasers mounted parallel and 10 cm apart on the camera lens, and also compared to the relative size of the mother in (c).

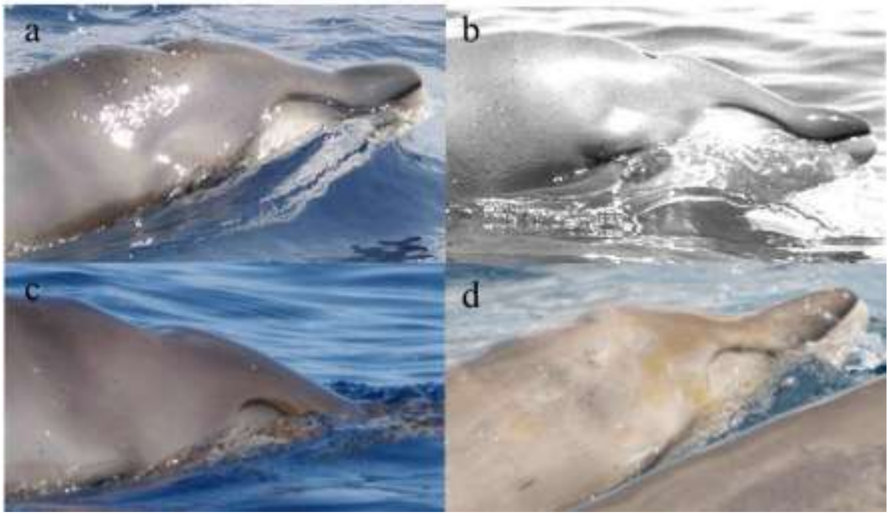

Figure 4.3. Comparison of the pigmentation patterns on the rostrum of two neonates (a) and (b), and two older calves, (c) 3-months old and (d) 1-year old.

4.3.4.1.2 Calf: In this study, a young individual was designated a calf if foetal folds were not visible. The age of the calf (birth year) was more difficult to determine than that of a neonate but was based on several features, including pigmentation, the amount of scarring, and its size relative to its mother, the latter two increased with increasing age (Figure 4.4). The darker pigmentation around the edges of the dorsal fin could be discerned in some calves of less than 1 year old, but some individuals known to be younger than 1 year (based on the mother's sighting history) did not show this. Similarly, the number of scars from *Isistius* bites varied individually but still provided a useful feature for distinguishing young calves from older calves. At age 3-4 years, calves separated from the mother, at which time their external characteristics included having adult pigmentation (medium grey dorsally and laterally, creamy-white ventrally), scarring generally included more than one cookie cutter bite dorsolaterally, as well as possible intraspecific scarring, and they often had acquired a nick in the dorsal fin or tailstock, and their length was greater than 3/4 the length of the mother.

Figure 4.4. Pigmentation and *Isistius* sp. scarring in dependent calves of varying ages: (a) 3 months, (b) 6 months, (c) 1 year, (d) 2 years, (e) 3 years.

Total length measurements taken from two immature whales that stranded during the study provided some insight for using relative size as a determinant for age in calves. The first of these was a male with a total body length of 336 cm (using standard measurements as per Geraci and Lounsbury 2005). This animal stranded coincident with an anti-submarine warfare exercise on March 15, 2000. The necropsy report for this individual (and all others in this atypical stranding) indicated it was healthy at the time of stranding (see Evans and England 2001 for details) but, unlike the other sub-adult and adult whales which also stranded, no prey remains (e.g., cephalopod beaks) were found in the stomach of this individual (Hickmott 2005). For this reason it was judged to be a dependent calf. Externally, there was no evidence of intraspecific scarring but multiple cookie cutter shark scars were noted both dorsally and ventrally. The second individual was a female with a total length measurement of 250 cm. There were no foetal folds visible and two cookie cutter shark bites were noted ventrally, near the genital region, but none dorsally. This whale was severely emaciated but cause of death was never determined. Based on its small size (smaller than previously reported for a *M. densirostris* calf), and lack of scarring dorsally, it was considered to be approximately 6 months old. The younger calf was 53 – 56% of the mean lengths for adult females given by Ross *et al.* (1988) and Pitman (2008), while the older calf was 71 – 76% of reported adult female length which provided some support for the general relative measures used in this study to estimate calf age.

4.3.4.2 Sub-adults

Sub-adults were those individuals which were no longer dependent calves but did not show characteristics known for adults. Specifically, these individuals had few cookie cutter shark scars and lacked erupted teeth or did not have a calf. Additionally, intraspecific scarring was absent or minimal. Young sub-adults were notably smaller than adults but size was difficult to use to differentiate older sub-adults from adults. Based on known ages of separation and onset of sexual maturity, sub-adults were considered to be between 4 – 8 years old.

<u>4.3.4.2.1 Sub-adult female:</u> Sub-adults were assigned as females retrospectively. There were no external characteristics that could be used to distinguish a sub-adult female from a sub-adult male until they were approximately 6 – 8 years old, the age at which morphological changes associated with sexual dimorphism became evident. Therefore, an individual was designated the sub-adult female class if its age was known and, if it had reached age 8, it had not developed morphological characteristics of a sub-adult male, and/or if it was later re-sighted with a calf. If it was never re-sighted, its designation was sub-adult of unknown sex (Figure 4.5).

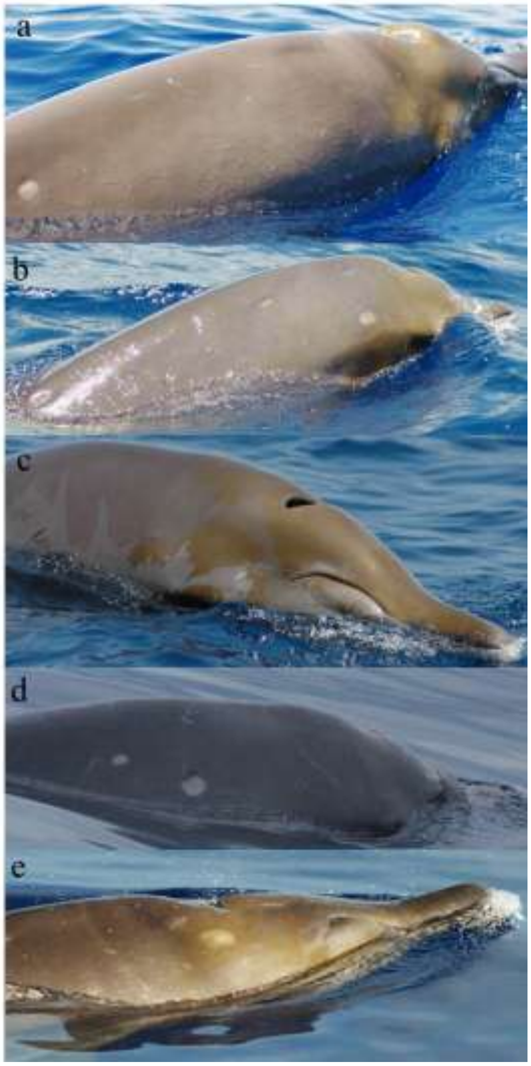

Figure 4.5. Five sub-adult whales of varying ages and both sexes: (a) Md197 at age 5 years, (b) Md190 at age 6 years, and (c) Md134 at age 7 years. These three were later determined to be females based on re-sightings when they were more than 8 years old. If they had not been re-sighted, their designation would have remained sub-adult of unknown sex. The other two photographs are of sub-adult males: (d) at age 6, Md143 has some intraspecific scarring on his head, and (e) at age 8, Md115 is beginning to show development of the mandibular arch, although he is lacking intraspecific scarring. Field notes from these encounters designated both as probable males at the time these photographs were taken. For sub-adults with either of these characteristics that were not later re-sighted, their designation would have been sub-adult male with certainty rating *C* = 2.

4.3.4.2.2 Sub-adult male: Individuals were designated as sub-adult males if evidence of sexual dimorphism was noted (Figure 4.6). Characteristics included expansion of the posterior region of the mandible, sometimes resulting in extreme elevation of the ramus, but with no evidence of erupted teeth. Intra-specific scarring concentrated in the antero-dorsal region could range from none to a dense network of overlapping scars, but even when scarring was extensive, tooth rakes appeared to have penetrated to a shallower depth than in adult males. The sex was also assigned retrospectively if an individual was re-sighted at a later date with either these characteristics or those of an adult male.

4.3.4.2.3 Sub-adult unknown: Individuals lacking adult characteristics that were never re-sighted so sex could not be assigned retrospectively.

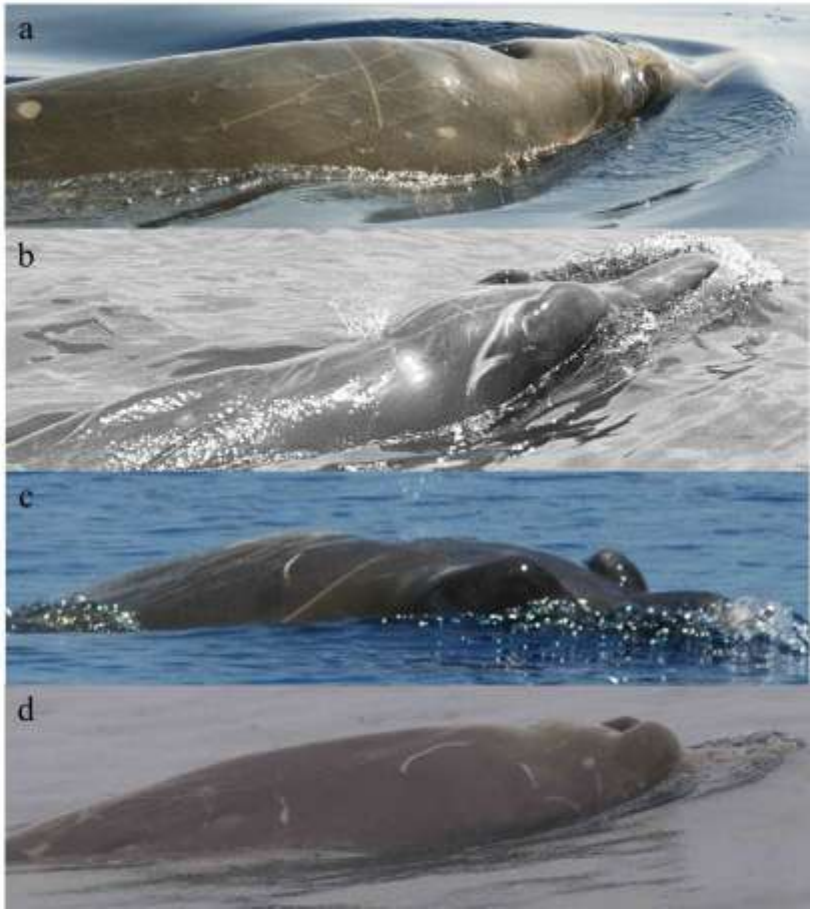

Figure 4.6. Four sub-adult males at varying stages of expansion in the posterior region of the mandible. Even before morphological changes were obvious, intraspecific scarring on the head and dorsum (a) was used to assign individuals to this class. Scarring from male-male combat increased as the elevation of the ramus continued but still seemed to consist of scars inflicted by one tooth only (b – d). The whale in (b) shows development of the dorsal ridge posterior to the blowhole. The right tooth of the whale in (c) erupted 2 years after this photograph was taken, but not the left tooth, although the area of tooth eruption looks abraded here. Photograph (d) is of Md191 at age 10 years and not yet sexually mature.

4.3.4.3 Adults

<u>4.3.4.3.1 Adult female:</u> An individual was automatically assigned to this class if it was seen with a neonate or small calf in echelon position. Assignment was also made if an individual's size was larger than young sub-adults, had numerous cookie cutter shark scars and was seen in close association with a calf. Based on the known age for onset of sexual maturity, adult females were considered to be at least 9 years old. Therefore, if an individual's age was known to be more than 9 years, its class was re-assigned to an adult female if it had the features described above, even if it was not seen with a calf. Additionally, if a calf was not present at all, individuals were assigned to the adult female class if they had extensive cookie cutter shark scarring but no evidence of heavy intraspecific scarring anterodorsally (Figure 4.7). Based on minimum ages at sexual maturity, eight adult females first documented with calves in the first years of the study had minimum ages ranging from 18 – 23 when re-sighted in the later years of the study.

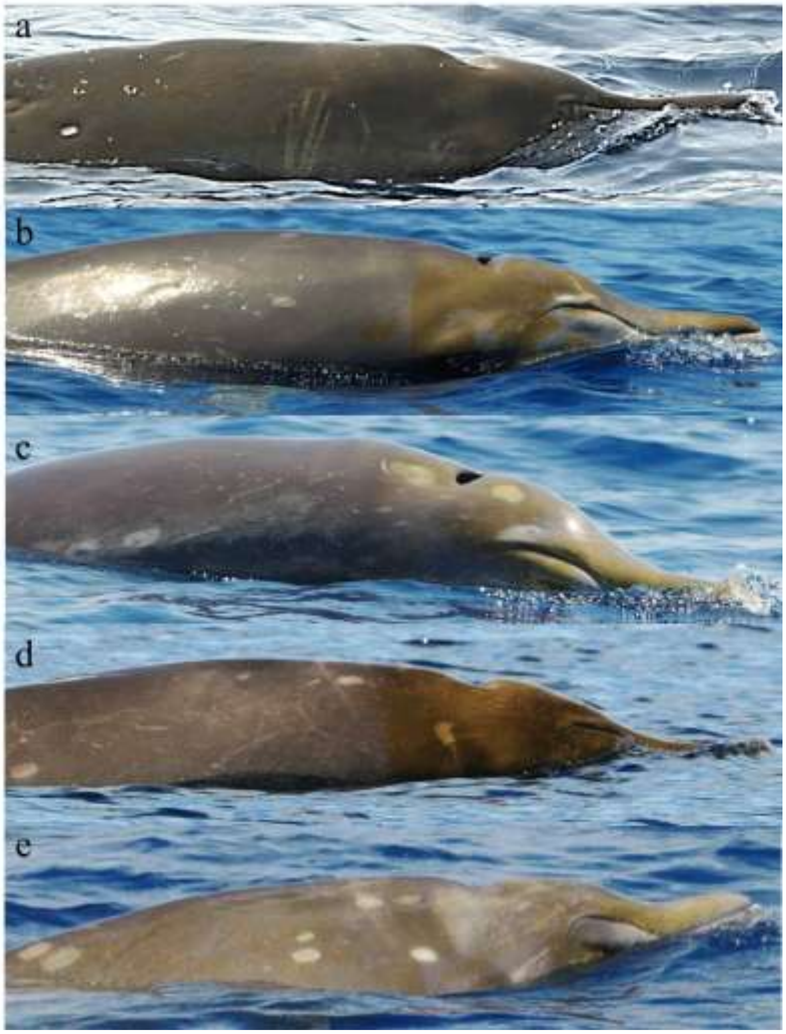

Figure 4.7. Adult females of known and minimum ages: (a) 10 years old, (b) 11 years old, (c) 13 years old, (d) at least 18 years old, and (e) at least 21 years old. Although all of these were sexually mature when photographed, without previous knowledge of the age of individuals or unless they were seen with a calf, based on the amount of cookie cutter shark (and intraspecific) scarring, only the individuals in (c) – (e) would be designated as adult females with certainty $C > 1$.

4.3.4.3.1 Adult male: An individual was automatically designated as an adult male if the teeth had erupted above the mandible, or if the teeth themselves were not visible but stalked barnacles (*Conchoderma auritum*) were present because this commensal species is unable to attach directly to the skin and must rely upon exposed hard substances such as teeth (Mead *et al.* 1982). Additionally, both teeth did not have to be visible because teeth did not necessarily erupt at the same time and erupted teeth sometimes broke off (*pers. obs.*), presumably during intense male-male combat. If photographs of the teeth were not obtained, individuals could still be reliably classed as adult males based on other characteristics (Figure 4.8), including (1) all adult males had massive development of the ramus; and (2) intraspecific scarring consisted of accumulation of deep lacerations on the head and dorsum, and concentrated on a ridge on the dorsum immediately posterior to the blowhole, although scarring could be found anywhere on the body. Adult males were also larger in size than adult females but this characteristic was not used independently of those described above. Adult males were considered to be a minimum age of 9 years. There was one adult male documented in the first year of the study which was re-sighted in the last year at a minimum age of 23 years, based on minimum ages at sexual maturity.

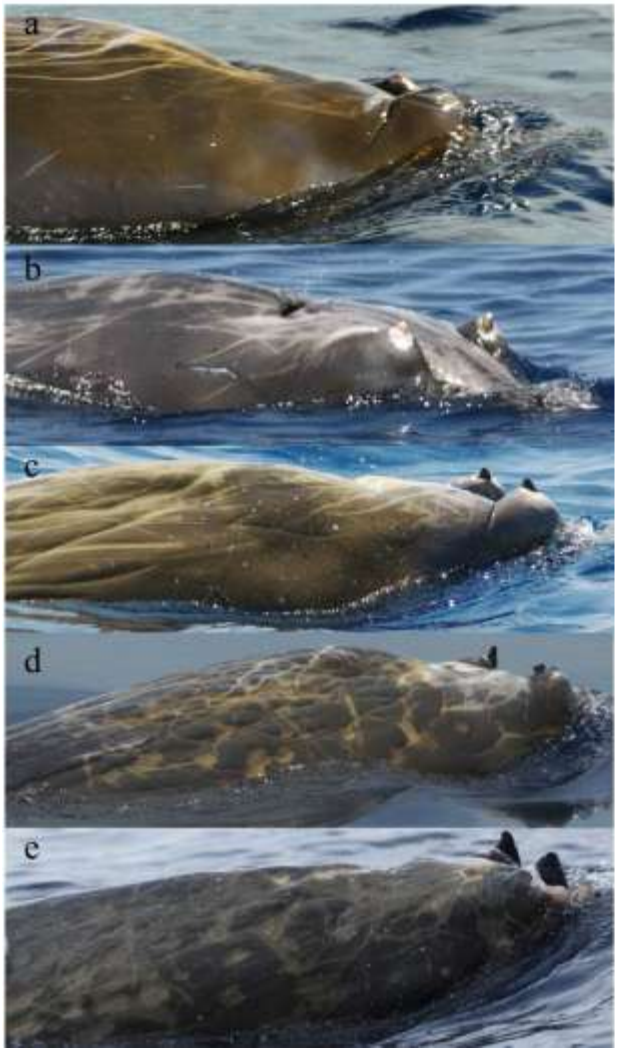

Figure 4.8. Antero-dorsal photographs of five adult males. The youngest adult is shown in (a); only the left tooth has erupted and this has occurred recently evident by the discoloured tissue near the tooth and the small size of the tooth. The individuals in (b) and (c) had teeth of a similar size and thus may have been of a similar age, but the animal in (c) had more extensive intraspecific scarring and the dorsal ridge (posterior to the blowhole) appeared larger. The tooth/teeth were visible in (a – b) but in (c – e), the teeth are covered by the stalked barnacle (*Conchoderma auritum*) giving them the dark colouration. The right tooth of the whale in (d) had broken off. Based on relative tooth size, the animal in (e) is probably the oldest whale in the series of photographs, but both (d) and (e) demonstrate the accumulation of intraspecific scarring through repetitive aggressive social interactions.

4.3.5 Population age structure

Using the characteristics described above, classes were assigned to 153 whales which were identified from high-quality photographs ($Q > 1$). Of these, only five individuals had a low certainty rating ($C < 2$). The population age structure analyses were based only on data from those individuals that were re-sighted at least once during the study, which resulted in 647 observations of 81 individuals (Table 4.5).

The median number of sightings by encounter-day was four (range 2 – 41 sightings) with lag times between re-sightings ranging from 1 day to 14 years (median 3.75 years). Based on these data, the average annual proportion of the study population represented by each class was summarised (Table 4.6). On average, the adult female class represented the greatest fraction of the population annually (mean 0.44, SD 0.10), while dependent calves, sub-adults and adult males were represented equally. In all, the fraction of mature animals found in the study population was greater than immatures (mean 0.63, SD 0.9). Moreover, there were more than twice as many adult females as adult males (ratio 2.42:1), and almost three times as many adult males as sub-adult males (ratio 2.89:1). Dependent calves primarily comprised non-neonate calves with only a few neonates observed annually (mean 0.2, SD = 0.1).

Table 4.5. Summary data for individuals assigned to a specific age, and when possible sex class during the study. Classes are: N = neonate, C = calf, SU = Sub-adult unknown sex, SF = subadult female, SM = subadult male, AF = adult female, and AM = adult male. Span time is the time in years between the first and last sighting record, and the number of sightings were counted by encounter-day. The six individuals first seen as a calf and monitored through or near to maturity are highlighted in grey.

IDs	**Calf**		**Sub-adult**			**Adult**		**Enc-**	**Span**
	N	C	SU	SF	SM	AF	AM	**days**	**(years)**
Md067							X	5	5.30
Md068							X	2	3.15
Md069							X	6	14.07
Md070						X		29	11.00
Md071						X		9	4.15
Md072		X						2	0.90
Md073	X	X	X					10	3.06
Md075							X	25	8.80
Md076						X		41	12.82
Md078						X		14	5.51
Md079						X		14	7.05
Md091						X		9	12.94
Md094						X		39	13.09
Md106						X		29	8.38
Md107		X		X		X		11	11.83
Md111						X		2	2.60
Md112						X		4	9.85
Md115	X	X			X			13	8.01
Md121				X		X		10	12.43
Md129				X		X		4	3.22
Md130					X		X	5	12.00
Md132							X	2	1.49
Md133							X	14	2.29
Md134		X		X		X		20	12.04
Md135		X		X		X		19	12.03
Md138							X	4	3.06
Md139						X		8	11.88
Md141						X		36	11.46
Md142		X						22	2.34
Md143		X			X		X	22	11.44
Md144						X		2	7.72
Md150							X	9	2.89
Md151		X						18	1.54
Md152					X			3	4.29
Md155				X		X		4	4.03
Md156						X		2	7.22
Md160						X		2	7.22
Md163						X		2	10.76
Md167		X						8	1.38
Md170					X			3	6.16
Md171					X			2	0.01

IDs	**Calf**		**Sub-adult**			**Adult**		**Enc-**	**Span**
	N	C	SU	SF	SM	AF	AM	**days**	**(years)**
Md173				X				2	0.01
Md179							X	3	0.83
Md180					X			4	1.88
Md181						X		3	2.52
Md183		X		X				4	6.15
Md184						X		2	4.04
Md185						X		3	3.07
Md190		X		X				14	8.43
Md191		X			X			10	6.25
Md193						X		3	4.76
Md194				X		X		2	4.04
Md196				X		X		9	7.99
Md197		X		X				8	4.77
Md198		X		X				12	3.87
Md200							X	2	0.32
Md201						X		3	0.64
Md202		X						2	0.12
Md203							X	2	0.12
Md208					X		X	3	3.75
Md209							X	8	5.82
Md211							X	6	3.99
Md213							X	2	1.01
Md214	X	X		X				4	4.96
Md215		X						2	2E-03
Md217		X		X				4	2.48
Md219					X			3	2.04
Md221							X	2	0.40
Md238						X		2	2.18
Md241		X						1	3E-03
Md242							X	4	1.15
Md243						X		1	3E-03
Md244		X						1	3E-03
Md245	X	X						3	1.01
Md246		X						4	1.02
Md248		X						5	0.79
Md249		X						3	0.26
Md250		X						4	0.48
Md297	X							3	0.05
Md298	X							4	0.05
Md299				X				4	0.01

Table 4.6. Summary statistics for the average annual proportions represented by each class in the study population for individuals seen more than once, identified in high quality photographs and with high class certainty ratings (SD = standard deviation).

Age / sex class	**Mean**	**SD**	**Median**	**Min.**	**Max.**
Calf - all	0.18	0.10	0.20	0.00	0.35
Neonate	0.02	0.01	0.00	0.00	0.09
Calf	0.16	0.09	0.18	0.00	0.29
Sub-adult - all	0.19	0.14	0.17	0.00	0.50
Sub-adult unknown	2.6E-03	9.9E-03	0.00	0.00	0.04
Sub-adult female	0.11	0.10	0.09	0.00	0.30
Sub-adult male	0.07	0.07	0.05	0.00	0.20
Adult female	0.44	0.10	0.45	0.20	0.67
Adult male	0.19	0.07	0.18	0.08	0.36

Variation in the annual proportion represented by each class is shown in Figure 4.9. There were no sub-adults identified in 1997 and 1998, and no dependent calves in 2008 and 2009, while adult females and adult males were seen in all years.

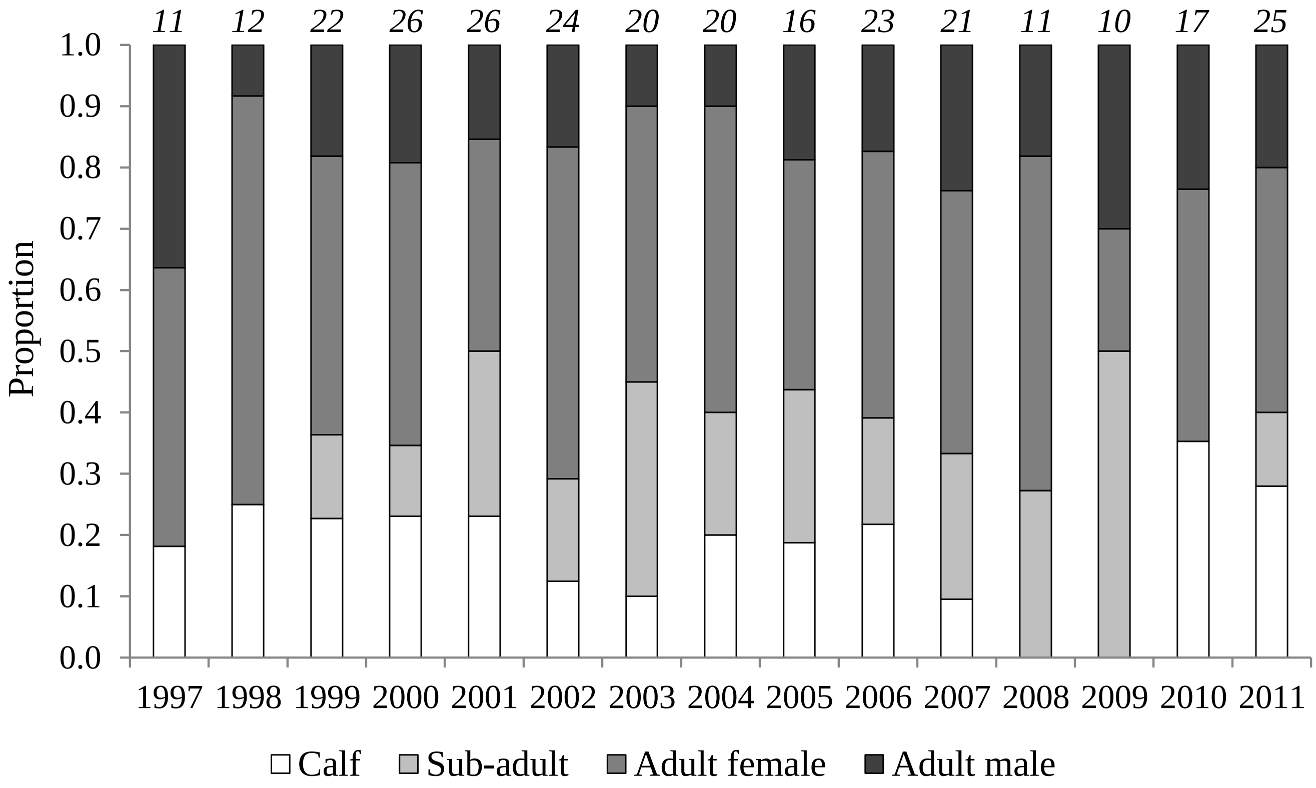

Figure 4.9. Annual proportion of each age/sex class. The italicised numbers at the top of each bar represent the total number of individuals in each year.

4.4 Discussion

4.4.1 Assignment of age / sex class

4.4.1.1 Dependent calves

Some of the features used here to classify individuals as neonates confirmed previously published descriptions but there were also some discrepancies. Pigmentation patterns described by Ross *et al.* (1988) for dead stranded calves were confirmed for free-swimming individuals. These included a blaze of lighter pigmentation on the dorsal fin and light colouring ventrally, including under the lower jaw. However, pigmentation was found to change in one individual by 3 months of age. Ross *et al.* (1988) also described a dark cap on the head of immature animals that was not evident in any individuals in this study.

Here, although data were limited and quantitative photogrammetry methods were not applied, calf size appeared smaller than previously reported by Mead (1984), based on the size of neonates relative to their mothers and the total length measurements for the stranded female (estimated to be 6 months old). The estimated length of neonates was smaller than the size Mead (1984) reported for the longest foetus, and the length of the stranded female in this study was smaller than previously published size for a *M. densirostris* calf. Efforts are underway to estimate length using photogrammetry methods developed by Durban and Parsons (2006), but multiple photographs of each animal will be needed to incorporate errors associated with varying photograph-whale angles (see Webster *et al.* (2010) for details). Aerial photogrammetry (e.g., Perryman and Lynn 1993, Fearnbach *et al.* 2011) or photographs taken from a vessel's mast showing the horizon (e.g., Gordon 1990) may be better approaches. This work could also lead to development of age-length curves for *M. densirostris* which would be extremely valuable in monitoring future population health through individual growth rates (e.g. Fearnbach *et al*. 2011).

Odontocetes are generally thought to be income breeders (Perrin and Reilly 1984, Huang *et al.* 2009), yet Huang *et al.* (2010) predicted relatively large birth size and high prenatal growth rates for beaked whales, and therefore classed them as capital breeders. Huang *et al.* (2010) suggested that beaked whale foraging behaviour could be the primary reason for beaked whale calf size at birth to be larger than expected. Beaked whales exhibit extreme diving behaviour (Hooker and Baird 1999, Tyack *et al*. 2006, Baird *et al*. 2006) and, as such, may be unable to enhance food intake much further during lactation. Long post-dive recovery periods are required and therefore the number of dives is limited (Arranz *et al.* 2012). Dive duration in calves, including neonates, is the same as their mothers (*pers. obs.*). Therefore, beaked whale calves may need to be larger in order to be more advanced behaviourally and energetically to develop this diving capability. However, calves in the Abaco population do not appear to be quite as large as previously reported from strandings.

4.4.1.2 Sub-adults

The sub-adult class was the most difficult to assign, partly because some of the published descriptive features for individuals in this age class were not observed in the Abaco population and were thus of no use. Ross *et al.* (1988) described pigmentation differences in sub-adults and adults which included a dark cap over the dorsal surface of the head; this was not evident in the Abaco whales and is likely the result of colour change due to decomposition of dead stranded animals. No difference at all in pigmentation was found between sub-adults and adults.

There was a discrepancy found in the way in which sub-adult males were designated here and by McSweeney *et al.* (2007). Sub-adult males in the Abaco population had undergone development of the ramus at least two years before the teeth erupted and, by the time the teeth were visible, were considered to be adult males with a massive elevated step in jawline. Berharse (1971) described males as sexually mature when the teeth had erupted above the alveoli in the mandible which would have occurred at an earlier age than when visible above the epidermis of the mandible, the characteristic used in this study. So males were still immature when the jawline was relatively straight and no longer sub-adults when the teeth had erupted which is contrary to descriptions of sub-adult males by McSweeney *et al.* (2007).

Correlation between the amount of scarring from cookie cutter sharks and age reported by Walker and Hanson (1999) was validated in this study, although its utility in the field appears somewhat limited. Although the number of *Isistius* sp. scars was useful in distinguishing young animals from very old ones, it was insufficiently definitive to be used to differentiate mature and immature females around the age of onset of sexual maturity because there was overlap in the range of counts for adults and sub-adults. Furthermore, counts were inconsistent between very experienced observers using photographs of the highest quality. This was despite standardisation of counts from only within the ID area, which eliminated the need to prorate counts to compare scarring between individuals, as done in a similar study by McSweeney *et al.* (2007) in which a larger but inconsistent area on the whale’s body was used. *Isistius* sp. densities vary geographically, so counts used by McSweeney *et al*. (2007) to distinguish age classes in Hawaii may not be appropriate for the Abaco population. Density differences may even apply on a smaller scale, such as between whales at the Atlantic Undersea Test and Evaluation Center (AUTEC) off Andros Island (see Chapter 2) and Abaco, which deserves further investigation. Finally, it is unknown how individual health affects the level of success or failure of attacks by cookie cutter sharks.

Similarly, for young sub-adults intraspecific scarring could not be used alone as an indication of sex unless scars were found on the head and dorsum, which occurred in males at a very young age. Intraspecific scarring on females was not uncommon suggesting these resulted from intentional attacks by males and not because a female happened to be in the way during male-male interactions as suggested by McCann (1974).

4.4.2 Age at sexual maturity

The new information on age at sexual maturity for Blainville's beaked whale from this study adds substantially to previous knowledge, despite the small sample size. One adult female followed from a dependent calf through maturity was 9 years old at the onset of sexual maturity. A minimum age at sexual maturity of 8 – 9 years was estimated for a second individual. These findings provide support for a minimum age of 9 years old for a female examined post-mortem by Ross (1979), until now the only information for this species, and is also similar to ages reported from whaling data for female Baird's beaked whale (Kasuya 1977) and northern bottlenose whale (Christensen 1973). Unlike Baird's beaked whale but similar to the northern bottlenose whale, male

Blainville's beaked whales appeared to mature at a similar age to females. One male first seen as a dependent calf matured when 9 years old but another male had not yet reached sexual maturity by age 10, suggesting some individual variation and demonstrating the need for larger sample sizes. However, using similar methods as here, Gowans *et al.* (2000) showed that free-ranging northern bottlenose whale males mature at a similar age to those reported here. Combined, these studies support the reported ages of sexual maturity using both stranding and whaling data.

However, age reported here should not be considered absolute because it was based on a timeline beginning from an estimated age when a calf was first sighted and none of the whales that matured during the study were first seen as neonates. Assigned age could be wrong by +/- 1 year depending on individual differences in length at birth, growth rates, and scarring patterns. If this population continues to be monitored, age at sexual maturity will be able to be determined with greater accuracy as more known-age individuals become mature. Continued monitoring of this population will also allow maximum ages of known individuals to be updated. Although the minimum ages reported here are similar to that reported for the oldest stranded *Mesoplodon* (Perrin and Myrick 1980), they likely do not represent Blainville's beaked whale longevity which may be closer to 50 – 80 years as reported for Baird's beaked whale by Kasuya (1977).

4.4.3 Age / sex structure of the population

Population age / sex structure has not been previously described for a *Mesoplodon* species, thus the work presented in this chapter for the Abaco population provides a baseline from which to begin understanding the mechanisms underlying this structure. Age structure is a function of differential survival and reproductive rates and age at sexual maturity as well as sampling relative to dispersal (permanent emigration and immigration). Age structure within a population or between populations can vary geographically if there are age- and/or sex-specific differences in prey or habitat preferences (e.g., Robbins 2007, Herman *et al.* 2008), or temporally as a result of environmental changes which may disproportionately affect one age class, typically juveniles (e.g., Gannon and Willig 1994). As such, even when knowledge of age structure is extensive, it can be used only to make limited inference about these key parameters. However, if baseline information is available, age /sex structure can be extremely valuable in detecting changes in demography as a result of environmental change or perturbations. For example, the difference found in the age composition between whales at Abaco and AUTEC (Chapter 2), has highlighted a need for future monitoring.

In this study, exact age could be estimated for those individuals first seen as calves, but other whales had to be assigned to a class characterised by a range of ages. Despite this limitation, results generated seem consistent with what is known about this species' social structure. For example, one would expect there to be a higher proportion of adult females than adult males annually in a polygynous resource/female defence harem-type mating system (Claridge 2006). However, it should be noted that in this study the sampling area was limited to the south-western coast of Abaco Island, an area regularly used by adult females (Chapter 3). As such, the age structure described here may be that of a part of the population, rather than full sampling of a stock.

For beaked whales, sound associated with naval exercises is thought to impact immature whales to a greater extent than adults (Cox *et al.* 2006), possibly because they are more naïve. Therefore, information on age structure may be an important component of mitigation and monitoring for populations exposed to sonar use on a regular basis, such as Blainville's beaked whales at AUTEC (Chapter 2). In the Abaco study, temporal variation in age / sex structure or in the proportion of calves to non-calves did not exist, perhaps providing a valuable baseline on which to compare aspects of the population dynamics to those of the whales found at AUTEC.

4.4.4 Conclusions

In this study, sighting history data were used to investigate characteristics which can be used to categorise the age and sex of individual Blainville's beaked whales in the Abaco study population. This allowed inference to be made about the age at sexual maturity, minimum longevity for adults and the population's age / sex structure. When high quality photographs were available, class assignment was possible for 97% of the study population. Furthermore, accuracy in sexing from photographs increased to near 100% for individuals of approximately 6 years old and greater, i.e., older sub-adults. This work has validated some characteristics that have been used previously to assign age class and sex to Blainville's beaked whales, much of which was based on stranded individuals, provided new information, and found some contrary descriptions. Of equal importance is that the information gathered here on the age / sex structure of the Abaco population can be applied to mark-recapture models to incorporate individual age and sex to remove some aspects of heterogeneity and improve model estimates (Chapter 5).

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CHAPTER 5

AGE AND SEX SPECIFIC POPULATION DEMOGRAPHICS OF BLAINVILLE'S BEAKED WHALES (*MESOPLODON DENSIROSTRIS*)

5.1 Introduction

Accurate estimates of demographics are important for understanding population dynamics and implementing effective wildlife management. However, estimating abundance and survival of wild, free-ranging populations is inherently difficult. Statistical models using mark-recapture data can provide a reliable way of estimating abundance and survival but conventional mark-recapture models are built on the assumption that all individuals have equal probability of capture and survival between captures (Seber 1982, see Chapter 2 for details). If individual heterogeneity exists but is ignored, abundance estimates can be negatively biased because a biased sample of individuals are re-sighted repeatedly (Cormack 1972, Pollock *et al.* 1990) and this bias in abundance can be substantial (Hammond 1990). Thus, decreasing bias associated with individual heterogeneity in mark-recapture models is an on-going challenge. This task is difficult even when mark-recapture samples can be carefully controlled through experimental design (e.g., Larrucea *et al.* 2007, Cubaynes *et al.* 2010, Oliver *et al.* 2011, Smout *et al.* 2011, Chambert *et al.* 2012).

Individual heterogeneity in behaviour is inherent in any animal population (Lebreton *et al.* 1992). Heterogeneity of capture and survival probabilities can be caused by extrinsic factors related to study design (Mizroch *et al.* 2004, Cubaynes *et al.* 2010), and intrinsic differences among individuals, such as differences in behaviour due to age differences (Lebreton *et al.* 1992, Tavecchia *et al.* 2001), sex (Pradel *et al.* 1997, Kraus *et al.* 2008) and social status (Summerlin and Wolfe 1973, Otugu *et al.* 2006). To reduce individual heterogeneity, Seber (1982) suggested placing individuals into homogenous groups classified by age and sex, based on the assumption that individuals from the same age and/or sex may exhibit similar behaviours and therefore share similar capture and survival probabilities. An alternative approach, described by Pledger *et al.* (2003), allows for individual heterogeneity of both capture and survival by using a finite mixture model but when capture probabilities are low, very large datasets are needed which may not be available in some cetacean studies.

In mark-recapture studies of cetaceans, addressing heterogeneity is challenging and has been the focus of much attention (Wilson *et al.* 1999, Friday *et al.* 2000, Gowans and Whitehead 2000, Stevick *et al.* 2001, Whitehead 2001, Corkrey *et al.* 2008, Barlow *et al.* 2011, Fearnbach *et al.* 2012a). In their study of survival in western grey whales (*Eschrichtius robustus*), Bradford *et al.* (2006) found that models which incorporated individual heterogeneity in residency and temporary emigration of younger whales best fit the data. Similarly, Ramp *et al.* (2010) reported model selection which included heterogeneity of survival by sex for humpback whale (*Megaptera novaeangliae*).Yet, despite its importance, with the exception of a few well-studied populations (e.g., Olesiuk *et al.* 1990, Olesiuk *et al.* 2005, Ford *et al.* 2007, Ward *et al.*

2009), including stratification across multiple age classes and by sex in mark-recapture assessments is rarely possible for cetaceans.

In long-lived species, survival rates are typically lowest for the youngest individuals, then increase with age, remaining constant for adults during an extended prime period until senescence when survival begins declining (Caughley 1966, Loison *et al.* 1999, Tavecchia *et al.* 2001, Beauplet *et al.* 2006). Heterogeneity in survival can also be strongly influenced by sex in a variety of ways, depending on the biology of the species. In marine mammals, adult male mortality can be higher because males have higher concentrations of lipophilic contaminants in their blubber and other tissues than females due to the maternal transfer from females to their young (Muir *et al.* 1996, Aguilar and Borrell 1988, Ross *et al.* 2000, Metcalfe *et al.* 2004). Sex-related differences in survival may also correspond with asymmetric costs of reproduction; in many species males have to compete for access to mates while females have to invest resources in gestation and lactation.

For some sexually dimorphic species, males may engage in dangerous combat for mates and/or territories and injuries can make them more susceptible to disease (Loison *et al.* 1999). Dominant males may have to forgo foraging to defend their hierarchal ranking (Deutsch *et al.* 1989). In some animal societies adult females occur in large social units often consisting of kin (Douglas-Hamilton 1972), which may decrease predation risk through reciprocal altruism but also provide co-operative feeding opportunities (Whitehead *et al.* 1991). Group size not only contributes to increased survival of individuals but will also increase predator detection probabilities as well (e.g., Ogutu *et al.* 2006). Dominant males will have greater access to matrilineal groups which are more likely to occupy productive feeding habitat, whereas lower ranking males may be forced to wander between areas which can lead to declined health [e.g., non-resident nomadic cheetahs (*Acinonyx jubatus*) have higher cortisol levels (Caro *et al.* 1989)]. Age-related differences in survival may also depend on aspects of the biology of a species, such as sexual size dimorphism. For example, Ford *et al.* (2007) found that the added costs of growth in sub-adult male killer whales (*Orcinus orca*) resulted in higher mortality of this age / sex class.

Based on what is known about beaked whale biology, individual heterogeneity in survival and capture probability is predicted to be strongly influenced by both age and sex. Sexual dimorphism exists in all ziphiid species but is most pronounced in Blainville's beaked whale (*Mesoplodon densirostris*) and Hubb's beaked whale (*M. carlhubbsi*) (Heyning 1989, Mead 1989). Males undergo massive development of the mandible posterior to the mandibular symphysis (Besharse, 1971) and mesorostral ossification consisting of dense pachyostoteic bone (McCann 1965, Heyning 1984, Allen *et al.* 2011). At the onset of sexual maturity the teeth erupt from the alveoli in males only (Besharse, 1971) and appear to be primarily used in male-male aggression and may be better described as "tusks" (Mead *et al.* 1982, Heyning 1984).

The social structure of Blainville's beaked whale is likely to further influence heterogeneity based on age and sex for this species. Blainville's beaked whale has a defence-polygyny harem-like social structure (Claridge 2006, McSweeney *et al.* 2007) in which adult males engage in competition for dominance. Based on the extreme intra-specific scarring (see Figure 4.8), combat between adult males appears to be fierce and frequent, rendering them more susceptible to infection and disease from injuries, potentially leading to high mortality of adult males. Adult females exhibit long-term site fidelity (McSweeney *et al.* 2007, also Chapter 3) and so may be more available for capture in local study areas than other classes. Dominant males may affect residency patterns of other males as well as immature animals, some of which may permanently emigrate, constraining the ability to monitor their fates and thus further biasing survival estimates.

Despite the difficulties in studying beaked whales, it was shown in Chapter 4 that individual Blainville's beaked whales can be assigned to specific age and sex classes, thus providing an opportunity to allow for age- and sex-structured heterogeneity in mark-recapture models. In this chapter, intrinsic aspects of individual heterogeneity are addressed by placing individuals into groups classified by age and sex to potentially reduce heterogeneity (Seber 1982). Inference could then be made based on age- and sex-specific survival and recruitment, as well as temporary emigration, re-immigration, and probability of capture when in the study area, thereby incorporating the individual-based age and sex structured data in the population model and improving estimates of abundance and population dynamics.

The specific objectives of this chapter were:

(1) To compare annual rates of capture, movement, survival, recruitment, and abundance by age / sex class.

(2) To examine aspects of the population dynamics of Blainville's beaked whales using a model with age and sex-structured heterogeneity.

(3) To estimate abundance of Blainville's beaked whales off southwest Abaco Island using a mark-recapture model that accounts for heterogeneity by age and/or sex.

5.2 Methods

5.2.1 Mark-recapture model

As in Chapter 3, an open population model that parameterises emigration from and re-immigration back into the study area, along with capture probability when in the area, in addition to survival and recruitment (e.g., Whitehead 1990, Ford *et al.* 2007, Matkin *et al.* 2012) was fitted to sighting history data compiled for each individual i, starting from the time of first capture (i.e. photo-identification) through each annual interval t. These data were inputted into three different matrices based on whether the whale was captured ($Y_{it} = 1$) or not captured ($Y_{it} = 0$), whether the whale was known to be alive ($X_{it} = 1$) or not alive ($X_{it} = 0$), and whether the whale was in the study area and available for capture ($F_{it} = 1$) or outside the study area and unavailable for capture ($F_{it} = 0$) (e.g. Schofield *et al.* 2009). Whales were inputted as alive ($X = 1$) whenever they were seen ($Y = 1$) and in years between repeated sightings. Additionally, out of sample sightings were used to inform whether or not a whale was alive in years following the last interval of sighting. After its last sighting, and prior to its first sighting, the whale's status was unknown and the X_{it} were treated as missing data about which inference could be made. Similarly, when a whale was not observed in the study area ($Y = 0$), its availability state was unknown and the F_{it} were treated as missing data to be estimated.

Model parameters included the annual probabilities of survival φ_{it}, emigration λ_{it}, re-immigration κ_{it}, and capture π_{it}. However, in addition to estimating survival and movement of beaked whales, trends in recruitment were also of interest. Recruitment here represented additions of new animals in each age class, either due to influx into the area or lagged effects of birth additions into older age classes. Using the approach of Pradel (1996), the same identification histories (all three matrices) were also read backwards to estimate seniority (γ), in place of survival, conditioning on the time of last observation (e.g. Ford *et al.* 2007). The probability of seniority (or the inverse of recruitment, $1-\gamma$) is the probability that individual i present at interval t was already present in the population at time $t-1$.

To explore age and sex structured heterogeneity in Blainville's beaked whales, the re-immigration model with recruitment was fitted to photo-identification data with separate parameter vectors for four different age / sex classes through an additional data matrix C, which assigned the class c_{it} for individual i in year t, where c_1 = sub-adult female, c_2 = sub-adult male, c_3 = adult female, and c_4 = adult male. Parameter estimates thus became:

$$\varphi_{it} = \varphi_{c,t},\ \lambda_{it} = \lambda_{c,t},\ \text{etc.}$$

The photo-identification dataset consisted of high-quality photographs of individual Blainville's beaked whales which were collected off Abaco Island during an annual sampling interval from May – August, 1997 – 2011. Age / sex classes were assigned using the methods developed in Chapter 4. As in Chapter 3, data were filtered to include only those individuals with distinctive markings, but did not include calves regardless of how distinctive.

If the age of a sub-adult changed during the study, the class matrix *C* was updated with the new age of that individual for that year. In years when a sub-adult was not seen, its age class was unknown and c_{it} was treated as a missing value and inference was made about whether the individual had remained in the same class or had become an adult. These annual transitions between age classes were modelled as a Markovian process, with equal [Uniform(0,1)] prior probability distributions assigned to the probability of changing to an older age class or remaining in the same class. Transition was only allowed from a younger class to an older one and individuals could never change sex.

5.2.1.1 Priors

A flexible hierarchical approach was adopted to specific prior distributions for the vectors of annual parameters, with an overall mean μ_c for each parameter, for each class, modified by annual additive effects $b_{c,t}$. Using this formulation, annual estimates for parameters for each class could borrow strength from information over all years, drawing estimates more towards the class mean in data-poor years, whilst allowing real departures from the mean to be detected if supported by the data. For example, for parameter φ (survival),

$$\text{logit}\ (\varphi_{c,t}) = \text{logit}\ (\mu_c^{\varphi}) + b_{c,t}^{\varphi}$$

where μ_c^{φ} represents mean survival for each class (c = 1:4). Class means for each parameter were given a Uniform prior between 0 and 1 and differences between class means were evaluated.

To investigate the covariance between the classes, $c = 1,...,4$ and see how class parameters varied over time, the prior distributions for the annual effects b for each parameter were set as a multivariate Normal distributions, stratified into $q = 4$ dimensions, with a zero mean and covariance matrix $\sum$ of the order $q*q$ (Fienberg *et al.* 1999, Durban *et al.* 2010). For example, for survival, φ:

$$b_{c,t}^{\varphi} \sim N_4\ (0,\textstyle\sum^{\varphi}).$$

The left to right diagonal components of each covariance matrix were the estimates of parameter variance for each of the four classes across years, while the off-diagonal components represented covariance between pairs of classes in terms of how their parameter values varied across years. A Wishart prior distribution was set for the inverse covariance matrix $\sum^{-1}$ (Fienberg *et al.* 1999) with a scale matrix B and degrees of freedom parameter v. The value of v was set as $v = q = 4$ representing a vague prior and to allow non-negative covariance values to emerge. Prior variances were set for diagonal values of $B = 1$ for each class and for off-diagonals of $B = 0$ for a prior of no covariance between pairs of classes.

Estimates of annual capture probabilities (for each class), $\pi_{c,t}$, were used to derive average annual estimates of abundance for distinctive animals ($N_{c,t}$), through the binomial relationship:

$$n_{c,t} \sim \mathrm{Bin}\left(\pi_{c,t}, N_{c,t}\right)$$

where $n_{c,t}$ is the number of whales observed to be in each class in each year. A hierarchal prior distribution was set for $N_{c,t}$, specified in terms of a mean abundance for each class (μ_c^N) and annual additive effects ($b_{c,t}^N$) to allow departures from the mean:

$$\log(N_{c,t}) = \log\left(\mu_c^N\right) + b_{c,t}^N.$$

The prior distribution for these departure effects ($b_{c,t}^N$) was again specified as a multivariate Normal in the same way as the other parameters to allow borrowing of strength across years within classes and investigate covariance between the four classes. The average annual abundance of each class was assigned a Uniform prior between 1 and 50. The abundance of all distinctive whales was then derived as the sum of each class ($N_{c,t}$), where:

$$N_{tot,t} = \sum_{c=1}^{n} N_{c,t}.$$

To estimate the total annual abundance for the study area which included distinctive and non-distinctive whales ($A_{c,t}$), each class abundance ($N_{c,t}$) needed to be rescaled to include non-distinctive individuals. Using an approach similar to that described in Chapters 2 and 3, the distinctive proportion of the population was estimated each year, $m_{c,t}$. However, in this chapter the variance in the distinctive proportion in the different classes could be accounted for. To do this, the number of distinctive whales in each class was counted by encounter-day ($USE_{c,t,d}$), and was treated as a binomial proportion relative to all whales assigned to that class ($ALL_{c,t,d}$) on that day (d). A common proportion was assumed across encounter days thus representing the overall average proportion of the class populations that were estimated to be distinctive in each year.

$$USE_{c,t,d} \sim \mathrm{Bin}\left(m_{c,t}, ALL_{c,t,d}\right)$$

A hierarchical prior distribution was set for $m_{c,t}$ using a logit link function and annual additive effects $b^m_{c,t}$ to borrow strength across years, where:

$$\text{logit}\ (m_{c,t}) = \text{logit}\ (\mu^m_c) + b^m_{c,t}$$

Priors were set as $\mu^m_c \sim U\,(0,1)$ for the mean, but in this case, $b^m_{c,t}$ was specified by a N(0,σ) distribution (rather than multivariate), where $\sigma^m_c \sim U\,(0,20)$ was set for the standard deviation to allow non-zero departures from the mean to emerge. Abundance for each class ($N_{c,t}$) was then rescaled by the distinctive proportion for each class ($m_{c,t}$) to provide abundance estimates for distinctive and non-distinctive whales for each class, $A_{c,t} = N_{c,t} / m_{c,t}$.

To include calves in the estimate of total abundance, rescaling for adult females (as above) was expanded to include dependent calves in the number of non-distinctive "adult females". The estimates of female abundance were rescaled to account for both dependent calves and non-distinctive adult females, assuming both had similar capture probabilities. Abundance was then tallied for sub-adult female ($A_{SF,t}$), sub-adult male ($A_{SM,t}$), and adult male ($A_{AM,t}$) classes and the new class which combined adult females with calves ($A_{AF+CA,t}$). In this way total abundance was estimated ($A_{tot,t}$), accounting for age- and sex-structured heterogeneity, for differences in the distinctive proportion in each class, and including calves.

5.2.1.2 Inference and model fitting

The program WinBUGS (Lunn *et al.* 2000) was used to update the prior distributions conditional on the observed data using three Markov Chain Monte Carlo

(MCMC) chains to sample the posterior distributions of each parameter of interest. The model was run until convergence of the three chains was achieved (as determined using the method of Brooks and Gelman 1998). Inference was then based on a further 20,000 samples, after discarding the initial burn-in. A posterior predictive approach for goodness of fit testing (Gelman *et al.* 1996) as described in Chapter 2 was used to assess model fit using the discrepancy function, resulting in a Bayesian *p*-value as an indicator of model fit (Gelman *et al.* 1996, Brooks *et al.* 2000). Model fit was assessed for each class individually as well as for all classes combined.

Monitoring parameter values across MCMC iterations allowed probabilistic statements about parameter differences to be made. For example, the probability that the average survival rates for adult females exceeded that for adult males was estimated from the proportion of the post burn-in MCMC iterations for which $\mu^{\varphi}{}_{AF} > \mu^{\varphi}{}_{AM}$. Over the full MCMC sequence this proportion equated to a probability that the parameter estimates from the two classes were different, while accounting for the full uncertainty encompassed by the posterior distribution for each estimate. If the two distributions completely overlapped (i.e. there was no difference in a parameter estimate between classes), then *p* would equal 0.50. This is a two-tailed test, so if the probability is high that the average survival rate (for example) for adult females is greater than that for adult males, *p* will be close to one, and *vice versa* for *p* values close to zero if the statement is reversed. Similarly, the probability that an annual probability for a particular parameter was greater than the average for that class was estimated from the proportion of iterations for which the annual additive effect did not equal zero ($b_{c,t} <> 0$). If this probability was high, *p* would be close to 1, or contrarily, close to 0 if the estimated parameter in that particular year was less than the average, while if there was no deviation from the overall average, i.e., $b_{c,t} = 0$, p would equal 0.5.

5.3 Results

5.3.1 Mark-recapture sample

Photo-identification data were used to construct the matrices used as input to the open population model. Specifically, the mark-recapture sample consisted of $n = 75$ individuals, representing 171 non-zero entries that were included as individual captures in the sightings history matrix ($y_{it} = 1$). Age / sex classes were also known for these entries and were included as $c_{it} = 1{:}4$. An additional 121 entries were included as alive ($x_{it} = 1$) for years when whales were not seen between years of repeated identifications. Finally, from the out-of-sample identifications, there were 47 records of individuals that occurred after the annual interval of their last capture or outside the boundaries of the study area that provided additional information on an individual's survival status for a specific year. These were also included as $x_{it} = 1$ (alive) beyond the time the whale was actually last seen within the annual interval. Likewise, there were 22 records before their first captures which were included to inform on recruitment. Table 5.1 summarises the photo-identification data by class for each year of the study.

Table 5.1. Summary of the number of distinctive whales from each of the four classes that were captured during each annual interval.

Year	**Number of distinctive whales captured**			
	Sub-adult females (c = 1)	*Sub-adult males (c = 2)*	*Adult females (c = 3)*	*Adult males (c = 4)*
1997	0	0	3	3
1998	1	0	4	3
1999	1	1	8	5
2000	1	0	12	4
2001	2	1	5	2
2002	1	3	7	5
2003	3	1	3	0
2004	1	2	7	3
2005	0	2	4	5
2006	0	1	7	3
2007	1	2	5	4
2008	3	1	5	4
2009	3	1	1	2
2010	0	0	5	3
2011	3	0	8	6
Totals	20	15	84	52
Annual Median	1	1	5	3

Of the 75 distinctive whales, the majority of individuals were adults when first captured (adult females, $n = 26$; adult males, $n = 25$). [Note that this does not represent the true sex ratio of the adult population but only the ratio of distinctive adults, which differed by sex (see section 5.3.6.3 below)]. Despite a relatively even sex ratio of distinctive adults, more distinctive adult females were captured annually than distinctive adult males ($t = 3.81$, df = 28, $p < 0.001$), as well as than distinctive sub-adults (with sub-adult females: $t = 6.96$, df = 28, $p < 0.001$; and with sub-adult males: $t = 9.98$, df = 28, $p < 0.001$).The median proportion of all distinctive individuals per annual interval that were adult females was 0.50, range 0.14 – 0.71; unlike the other classes, adult females were seen in every year (Figure 5.1). Four of the six sub-adult females and three of the nine sub-adult males were dependent calves when first seen in the study area. Furthermore, five of the sub-adult females and two of the sub-adult males were later re-sighted as adults, including two sub-adult females and one sub-adult male first seen as a dependent calf.

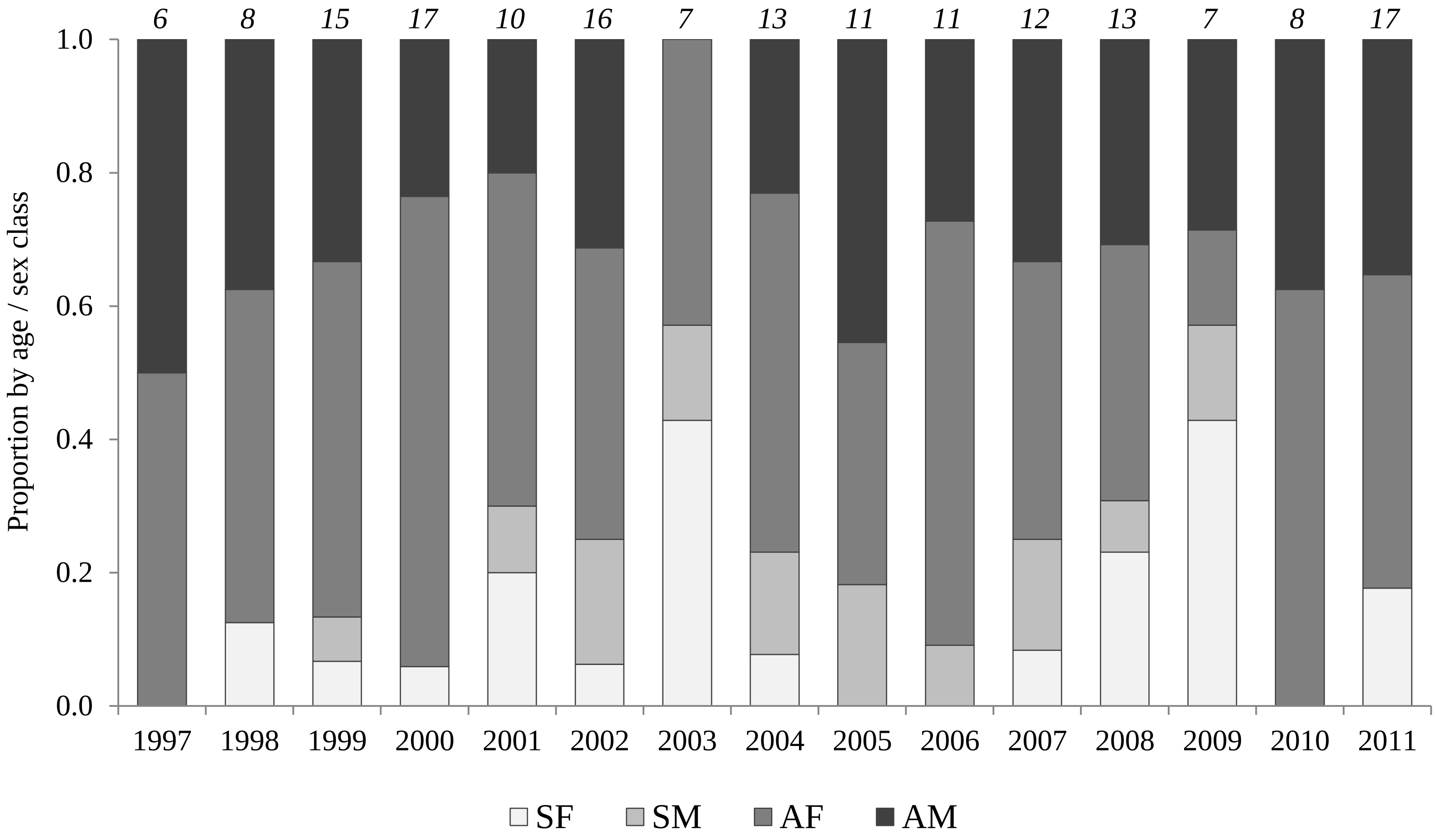


Figure 5.1. The proportion of distinctive Blainville's beaked whales observed from each of the four classes for each annual interval, 1997 - 2011. SF = sub-adult females (c = 1), SM = sub-adult males (c = 2), AF = adult females (c = 3), and AM = adult males (c = 4). The total number of distinctive whales observed from each annual sampling interval (y_{it} = 1) is shown at the top of each bar.

5.3.2 Age- and sex-stratified model fit

A re-immigration model which allowed age- and sex-structured heterogeneity provided good fit to the photo-identification data which included all classes combined. The result of the goodness-of-fit test was a Bayesian *p*-value of 0.44 which is indicative of good model fit (Brooks *et al.* 2000, King and Brooks 2002). This was derived by comparing the distribution of the discrepancy function between observed data and data simulated by the model (Figure 5.2).

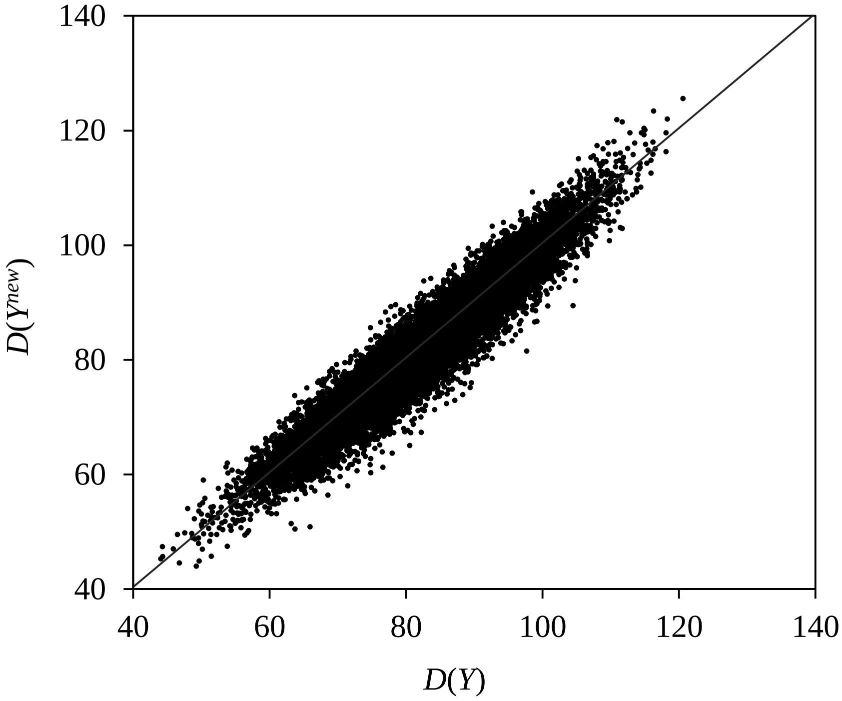
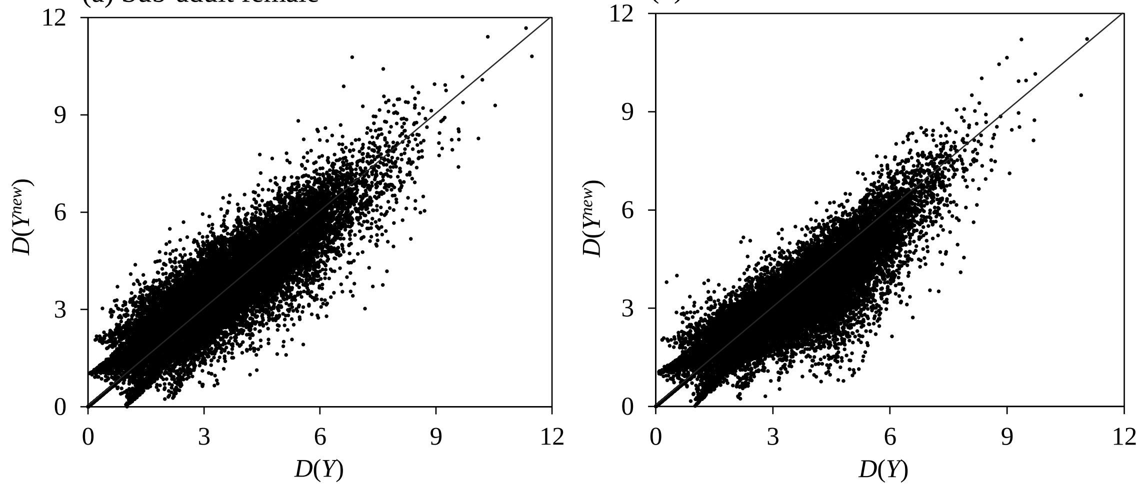


Figure 5.2. Discrepancy plot for the age- and sex-stratified re-immigration model fitted to the photo-identification data for all classes combined. Points are the 20,000 MCMC samples of a discrepancy function (*D*, Durban and Elston 2005) calculated for both observed data and data simulated by the model. The diagonal line represents the line $y = x$ and the posterior predictive value is the proportion of points that lie below the line, corresponding to Bayesian *p*-value of 0.44.

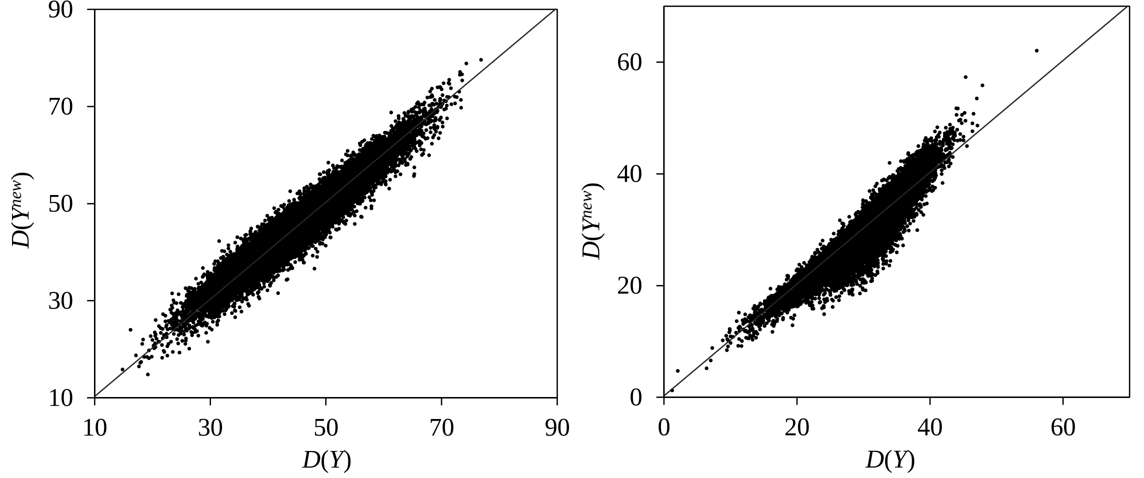
When model fit was assessed for the data from each of the four classes separately, differences in fit between classes were apparent. The Bayesian *p*-value for sub-adult females was 0.61, for sub-adult males 0.42, for adult females 0.57, and for adult males 0.36. The discrepancy plots for each class (Figure 5.3) show that the model fit the adult female class data better than the other classes.

5.3.3 Heterogeneity in capture probabilities by age / sex class

The probability of capture for each class reflects the chance of capturing whales when they were "in" the area during an annual interval, which may also be a function of temporary emigration beyond the study area within a year. Posterior estimates for adult females were more precise than any other class with a larger sample size of individuals (Figure 5.4). Sub-adult females had the highest annual probability of capture [posterior median μ^{π}_{SF} = 0.70 (95% Highest Posterior Density Intervals (HPDI) = 0.35 – 0.95)], while annual capture rates for adult females and sub-adult males were similar [posterior median μ^{π}_{AF} = 0.54 (95% HPDI = 0.37 – 0.72); posterior median μ^{π}_{SM} = 0.54 (95% HPDI = 0.23 – 0.88)]. For adult males, the annual probability of capture posterior median μ^{π}_{AM} was 0.33 (95% HPDI = 0.19 – 0.56)]. The average annual capture rate for adult males was lower than that for sub-adult females (p = 0.93), sub-adult males (p = 0.81), and adult females (p = 0.91).


(a) Sub-adult female

(b) Sub-adult male


(c) Adult female

(d) Adult male

Figure 5.3. Discrepancy plots for the age- and sex-stratified re-immigration model fit to the photo-identification data for each class separately. For each plot, points are the 20,000 MCMC samples of a discrepancy function (D, Durban and Elston 2005) calculated for both observed data and data simulated by the model. The diagonal line represents the line y = x and the posterior predictive value is the proportion of points that lie below the line, corresponding to Bayesian p-values for each class. Plots include: (a) sub-adult females, Bayesian p-value of 0.61; (b) sub-adult males, Bayesian p-value of 0.42; (c) adult females, Bayesian p-value of 0.57; and (d) adult males, Bayesian p-value of 0.36.

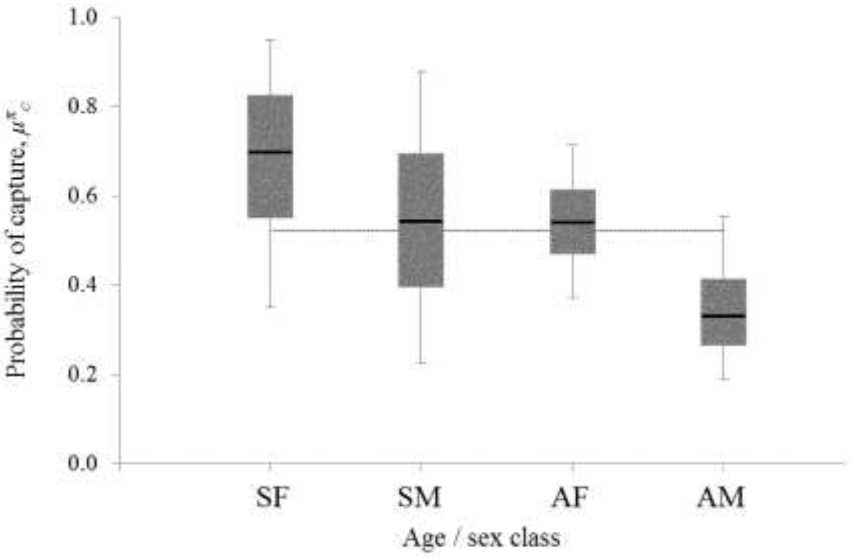


Figure 5.4. Average annual capture probability by class (μ^{π}_{c}) where SF = sub-adult females, SM = sub-adult males, AF = adult females and AM = adult males. Estimates are presented as posterior medians (solid black line within bars), with 75% (grey bars) and 95% (vertical whiskers) HPDI. The dashed line represents the mean probability of capture for all classes combined.

Annual probability of capture varied temporally for each class (Figure 5.5), although the wide spread in posterior estimates for sub-adults makes it difficult to distinguish trends. However, there is an apparent synchronicity in deviations from the average for the adult classes (Figures 5.5c and 5.5d). Specifically, for both adult females and males there was an initial increase in capture probabilities in the early years of the study, then capture rates remain just above the average until 2003 when there was a high probability of departure from the annual class means (p = 0.98 and 0.95, respectively), which corresponded with a decline. Thereafter, estimates were close to the mean until there is another decrease in 2009 (p = 0.99 and 0.83, respectively). It is noteworthy that the synchronous fluctuations noted for adults appear to be have been mirrored by inverse changes in capture probabilities of sub-adult females. For example, in 2003 and 2009 when capture rates were below the average for adults, there was a high probability of a departure from the average for sub-adult females (in 2003, $p = 0.80$, and in 2009, $p = 0.76$; Figure 5.5a), both corresponding to increases.

The estimated covariance for the classes indicated which classes had capture probabilities that were positively or negatively associated across years. Of the 12 different pair-wise combinations, all had associations where the 95% HPDI of the posterior distribution for the covariance ∑ overlapped zero, but the 75% HPDI for ∑ did not overlap zero for two combinations: for the association between adult female and sub-adult female classes, the correlation was negative, with a posterior median estimate for ∑ of -0.44 (75% HPDI = -0.720 to -0.005), while the correlation was positive between adult female and adult male classes (posterior median ∑ = 0.37, 75% HPDI = 0.116 – 0.524).

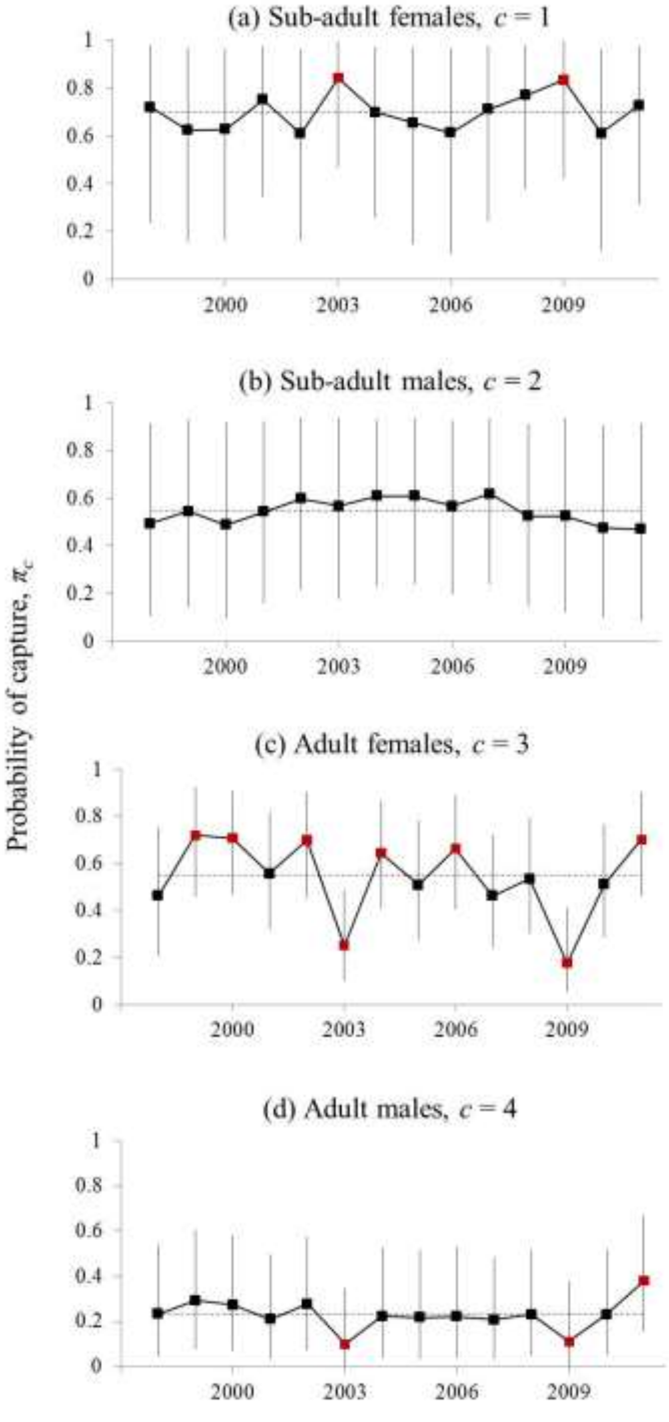


Figure 5.5. Annual capture probabilities for each class, $\pi_{c,t}$: (a) sub-adult females, (b) sub-adult males, (c) adult females, and (d) adult males. Annual median posterior estimates are shown by the square symbols with red squares representing years in which the estimate showed a departure from the overall mean which corresponded to a *p* value > 0.75). Vertical lines represent the 95% HPDI, and the dashed horizontal lines represent the median posterior estimate for all years combined, μ^{π}_{c}.

5.3.4 Comparing movement rates by age / sex class

5.3.4.1 Temporary emigration rates

Of the four classes, the annual probability of temporary emigration was lowest for adult females [posterior median μ^{λ}_{AF} = 0.25 (95% HPDI 0.13 – 0.40)] and adult males [posterior median μ^{λ}_{AM} = 0.36 (95% HPDI 0.10 – 0.67)] (Figure 5.6). Sub-adults had similar annual rates of emigration; for sub-adult females, posterior median μ^{λ}_{SF} = 0.45 (95% HPDI 0.16 – 0.75), and for sub-adult males, posterior median μ^{λ}_{SM} = 0.42 (95% HPDI 0.10 – 0.78)]. Emigration rates for sub-adult females and sub-adult males were higher than that for adult females (p = 0.84 and 0.77, respectively). The failure to see any further differences may have been because of the high variability of estimates for all classes except adult females.

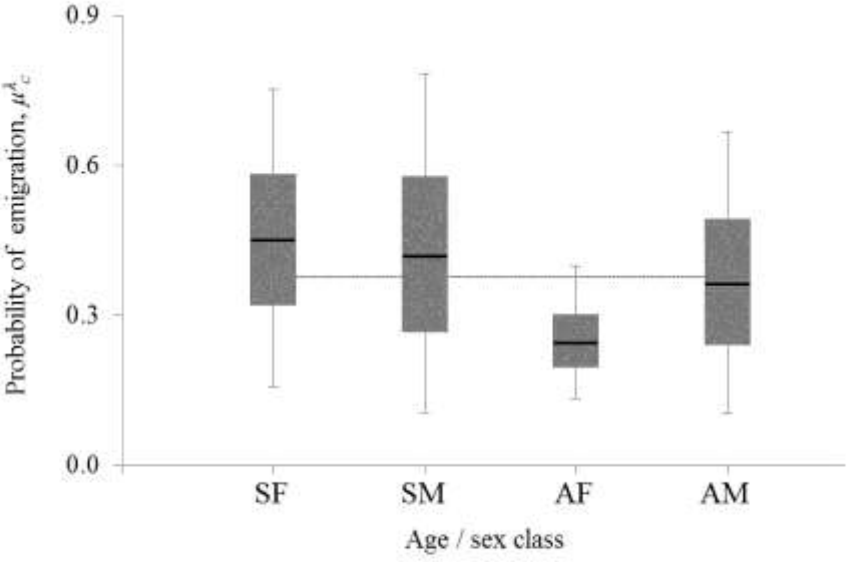


Figure 5.6. Average annual probability of temporary emigration by class (μ^{λ}_{c}) where SF = sub-adult females, SM = sub-adult males, AF = adult females and AM = adult males. Estimates are presented as posterior medians (solid black line within bars), with 75% (grey bars) and 95% (vertical whiskers) HPDI. The dashed horizontal line represents the mean probability of emigration for all classes combined.

5.3.4.2 Re-immigration rates

The annual probability of re-immigration was low for adult females [posterior median μ^{κ}_{AF} = 0.09 (95% HPDI 0.04 – 0.20); Figure 5.7], while higher rates were found for all other classes [posterior medians were μ^{κ}_{SF} = 0.53 (95% HPDI 0.09 – 0.95), μ^{κ}_{SM} = 0.60 (95% HPDI 0.15 – 0.95), μ^{κ}_{AM} = 0.55 (95% HPDI 0.24 – 0.87)]. Although posterior estimates for adult females were precise, quantitative comparisons could not be made with the other classes because the model was not able to estimate annual re-immigration rates for these, and thus the posteriors did not differ much from the Uniform priors.

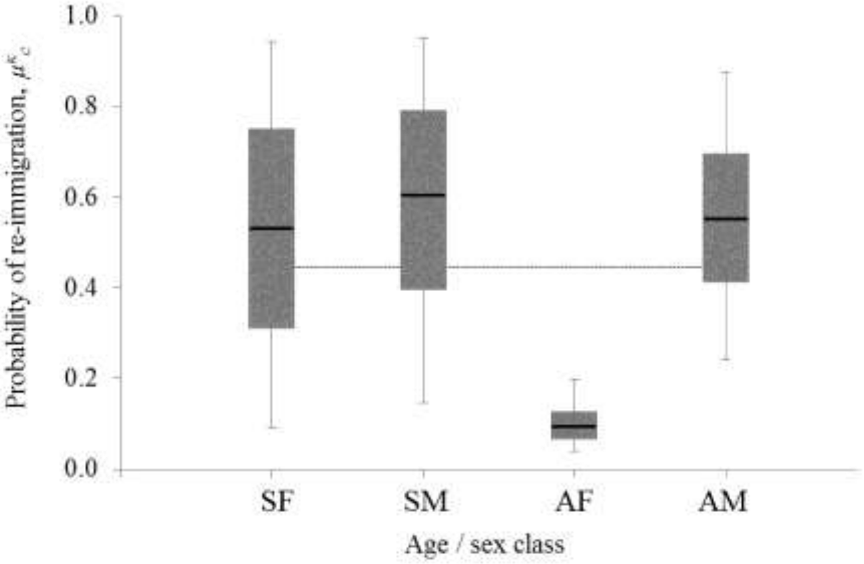
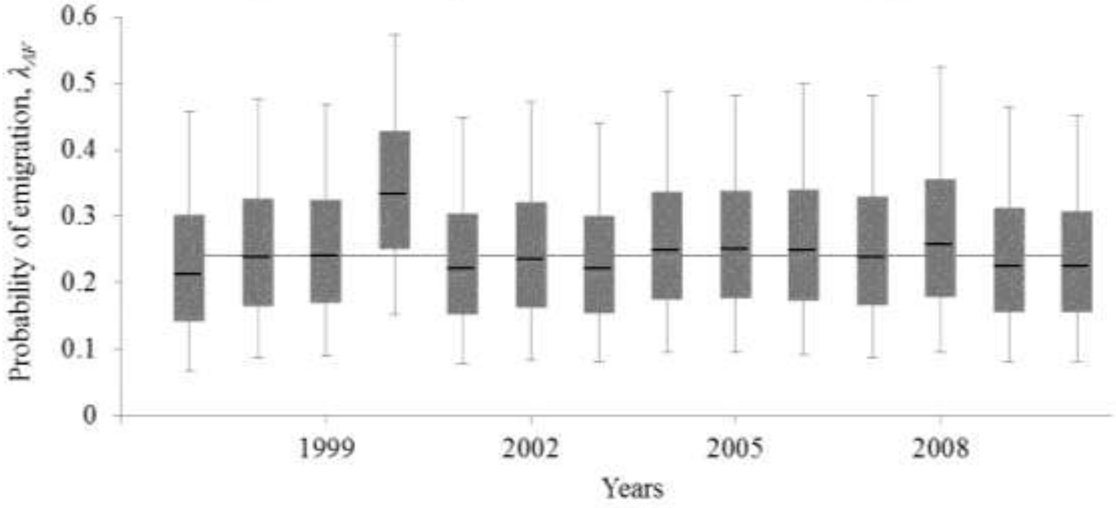


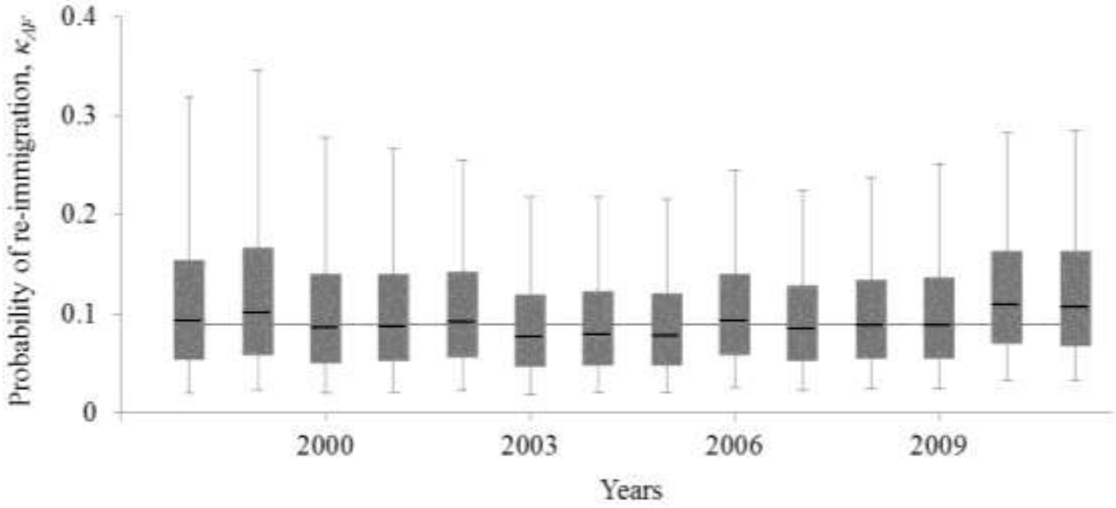
Figure 5.7. Average annual probability of re-immigration by class (μ^{κ}_{c}) where SF = sub-adult females, SM = sub-adult males, AF = adult females and AM = adult males. Estimates are presented as posterior medians (solid black line within bars), with 75% (grey bars) and 95% (vertical whiskers) highest posterior density intervals. The dashed horizontal line represents the mean probability of re-immigration for all classes combined.

5.3.4.3 Trends in movement rates of adult females

Trends in the annual rates of temporary emigration and re-immigration of adult females were examined over the 15-year time period (Figure 5.8).



(a) Annual emigration rates for adult females, $\lambda_{AF,t}$



(b) Annual re-immigration rates for adult females, $\kappa_{AF,t}$

Figure 5.8. Annual probability of (a) temporary emigration, $\lambda_{AF,t}$ and (b) re-immigration, $\kappa_{AF,t}$ for adult females. Estimates are presented as posterior medians (solid black line within bars), with 75% (grey bars) and 95% (vertical whiskers) HPDI. The dashed horizontal line represents the mean for each parameter, μ^{λ}_{AF} and μ^{κ}_{AF}.

Throughout the study, annual emigration rates appeared stable, with the exception of a single year (2000) in which an increase in the rate of temporary emigration out of the study area is apparent (Figure 5.8a). This difference represented a departure from the overall mean estimate (p = 0.78). Rates of annual re-immigration remained low for adult females throughout the time series (Figure 5.8b).

5.3.5 Annual survival and recruitment

5.3.5.1 Survival rates

The annual probability of survival was estimated for each age / sex class (Figure 5.9) and the differences between classes were assessed. Average annual survival rates differed by sex; sub-adult females and adult females exhibited higher annual survival rates than sub-adult males (p = 0.90 and 0.98, respectively) and adult males (p = 0.90 and 0.99, respectively). Annual survival estimates were high for both female classes, but highest for adult females [posterior median μ^{φ}_{AF} = 0.984 (95% HPDI 0.949 – 0.998)], while for sub-adult females, posterior median μ^{φ}_{SF} = 0.962 (95% HPDI 0.835 – 0.997). Annual survival rates for males were similar; for sub-adult males, posterior median μ^{φ}_{SM} = 0.807 (95% HPDI 0.555 – 0.883), and for adult males, posterior median μ^{φ}_{AM} = 0.859 (95% HPDI 0.759 – 0.891).

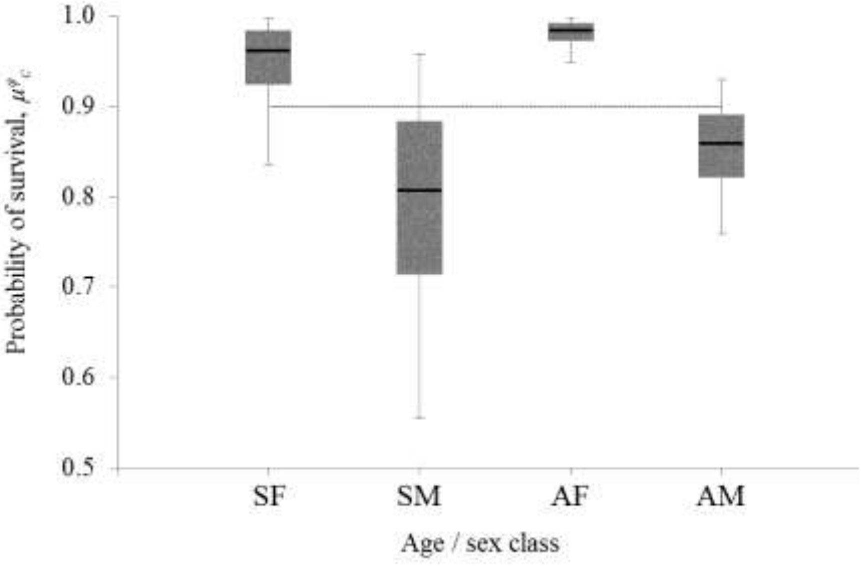
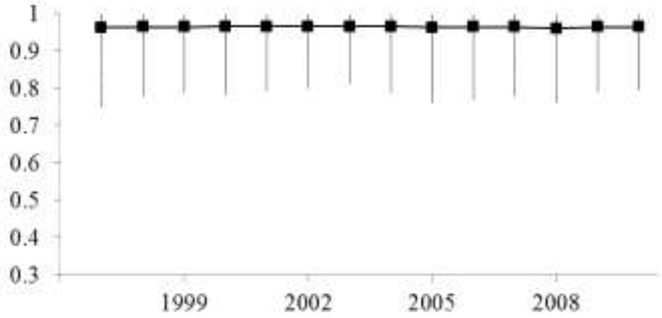


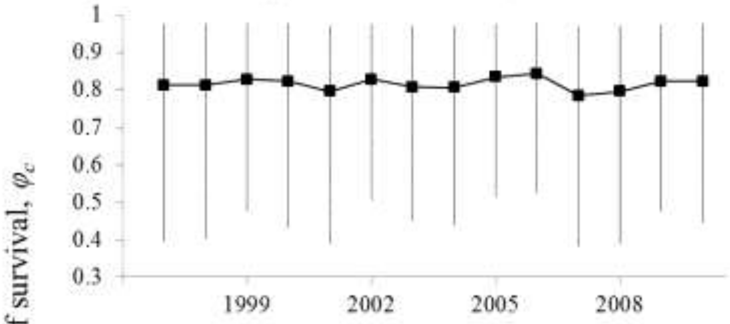
Figure 5.9. Average annual probability of survival by class (μ^{φ}_{c}) where SF = sub-adult females, SM = sub-adult males, AF = adult females and AM = adult males. Estimates are presented as posterior medians (solid black line within bars), with 75% (grey bars) and 95% (vertical whiskers) highest posterior density intervals. The dashed horizontal line represents the mean probability of survival for all classes combined.

Trends in survival were explored for each class over the time period 1997 – 2010 (Figure 5.10). Annual survival rate remained stable throughout the study with no departures from the mean for any of the classes found.

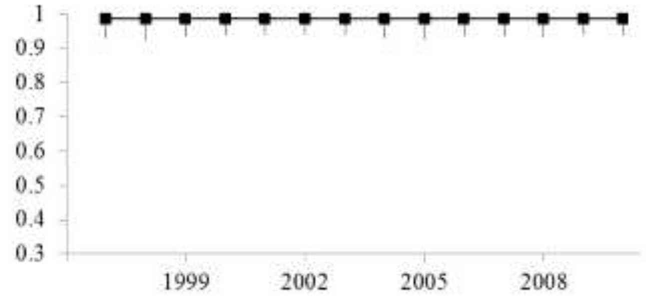
(a) Sub-adult females, $c = 1$



(b) Sub-adult males, $c = 2$



(c) Adult females, $c = 3$



(d) Adult males, $c = 4$

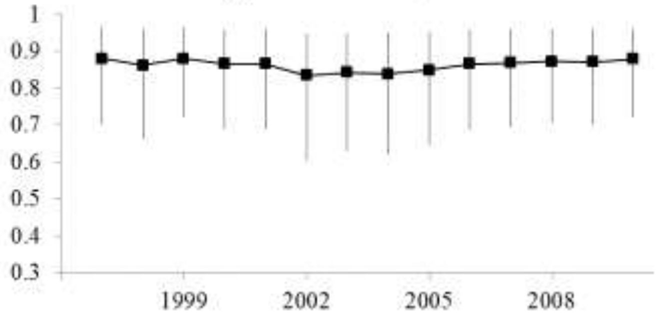


Figure 5.10. Annual survival probabilities for each class, $\varphi_{c,t}$. Annual median posterior estimates are shown by the square symbols and vertical lines represent the 95% HPDI.

5.3.5.2 Recruitment

Annual probability of recruitment was higher for sub-adults than adults (Figure 5.11), reflecting births with lag times.

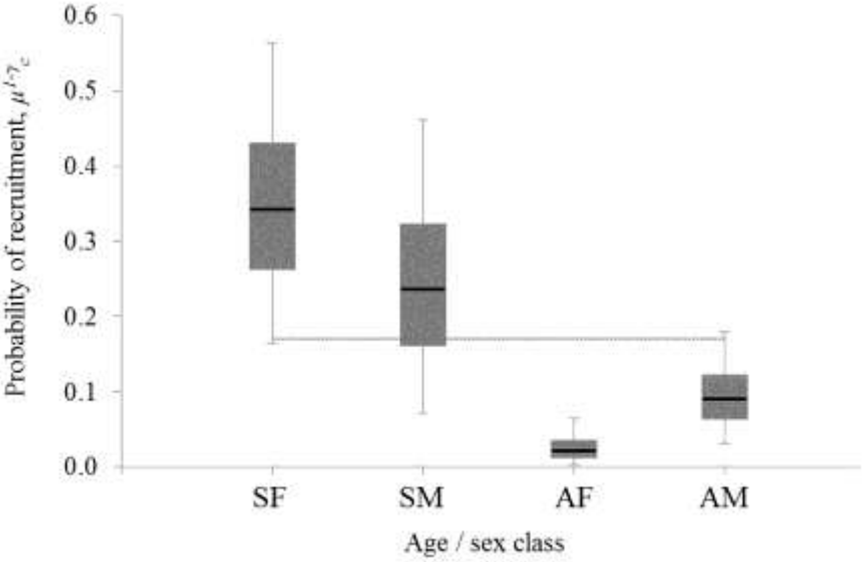
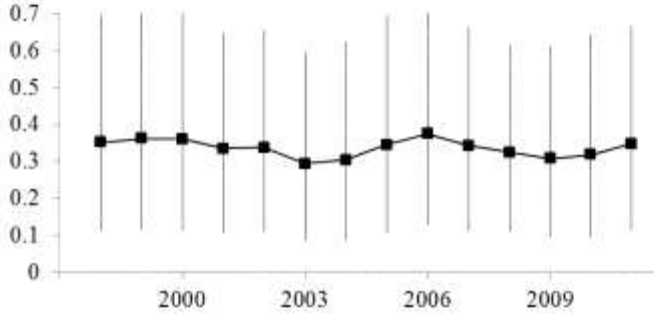


Figure 5.11. Average annual recruitment probability by class ($\mu^{1-\gamma}_{c}$) where SF = sub-adult females, SM = sub-adult males, AF = adult females and AM = adult males. Estimates are presented as posterior medians (solid black line within bars), with 75% (grey bars) and 95% (vertical whiskers) HPDI. The dashed horizontal line represents the mean probability of recruitment for all classes combined.

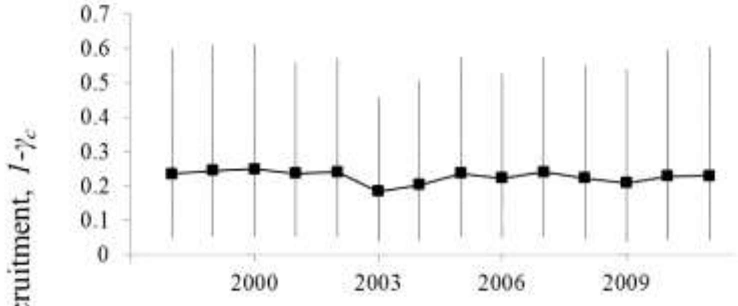
Annual recruitment rates were similar for sub-adult females [posterior median $\mu^{1-\gamma}_{SF}$ = 0.343 (95% HPDI = 0.165 – 0.563)] and sub-adult males [posterior median $\mu^{1-\gamma}_{SM}$ = 0.237 (95% HPDI = 0.160 – 0.462)]. However, annual recruitment of sub-adult females was higher than that of adult females and adult males, p = 0.99 and 0.98, respectively; similarly recruitment of sub-adult males was higher than adult females and adult males, p = 0.99 and 0.89, respectively. Of the adult classes, posterior estimates of annual recruitment rates were lowest for adult females [posterior median $\mu^{1-\gamma}_{AF}$ = 0.022 (95% HPDI = 0.003 – 0.065)], and although average annual recruitment rate of adult males was also low [posterior median $\mu^{1-\gamma}_{AM}$ = 0.091 (95% HPDI = 0.063 – 0.179)], annual recruitment of adult females was lower than that of adult males (p = 0.93).

Trends in annual rates of recruitment ($1-\gamma_{c,t}$) were examined for each class separately. For adults, annual rates of recruitment remained stable throughout the study period (Figure 5.12a). However, for sub-adults, recruitment rates appeared to vary and changes in the trend seemed to be synchronous between males and females (Figure 5.12b), but estimated covariance for the classes did not indicate associations (i.e., $\sum$ overlapped zero).

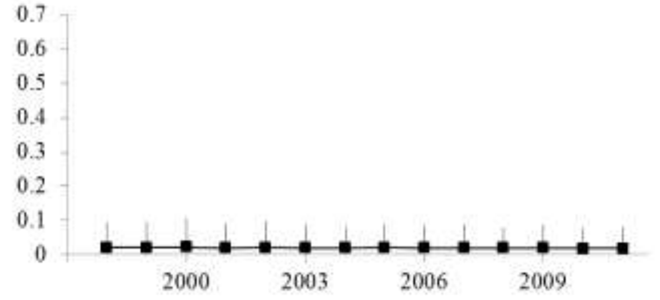
(a) Sub-adult females, $c = 1$



(b) Sub-adult males, $c = 2$



(c) Adult females, $c = 3$



(d) Adult males, $c = 4$

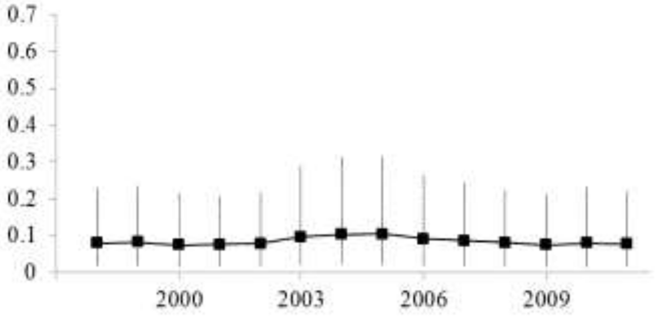


Figure 5.12. Trends in annual recruitment rates by class ($1\text{-}\gamma_{c,t}$). Black circles and squares represent females and males, respectively, with 95% HPDI shown by the vertical lines.

5.3.6 Estimates of abundance

5.3.6.1 Abundance of distinctive whales by class

Annual abundance of distinctive whales was estimated for each age / sex class (Figure 5.13) and differences between classes were assessed. Annual abundance of distinctive adults was considerably higher than abundance of sub-adults ($p = 0.99$ for each comparison of adult classes to sub-adult classes). For females, the posterior median for the annual abundance of distinctive whales μ^N_{AF} was 10 whales (95% HPDI = 7 – 15); and for males, posterior median μ^N_{AM} = 10 whales (95% HPDI = 6 – 18). For sub-adult females, posterior median μ^N_{SF} = 2 whales (95% HPDI = 1 – 4); and for sub-adult males, posterior median μ^N_{SM} = 2 whales (95% HPDI = 1 – 5).

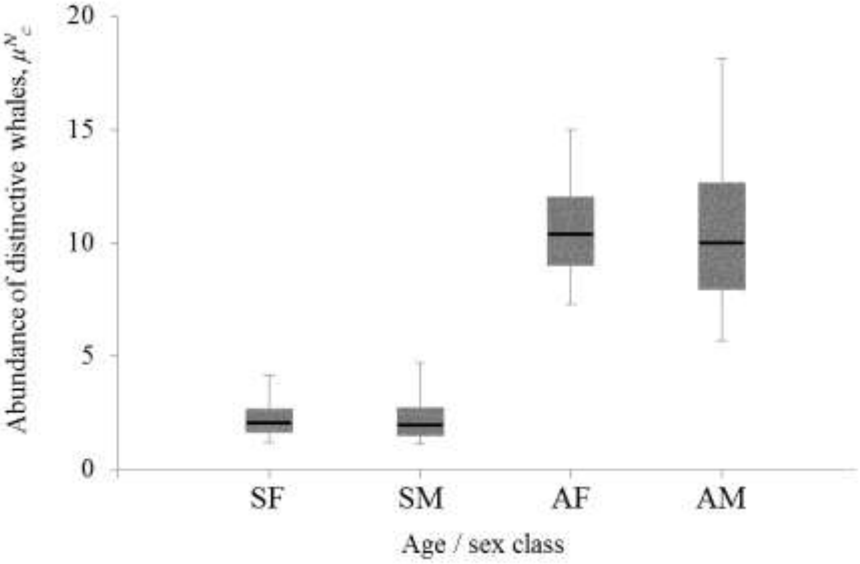


Figure 5.13. Average annual abundance of distinctive whales by class (μ^N_c) where SF = sub-adult females, SM = sub-adult males, AF = adult females and AM = adult males. Estimates are presented as posterior medians (solid black line within bars), with 75% (grey bars) and 95% (vertical whiskers) HPDI.

Assessment of trends in abundance of distinctive whales by class ($N_{c,t}$) showed little variation over the study period (Figure 5.14). There were three years in which annual class estimates deviated from the average for a particular class. The strongest departure effect was noted in 2000 when the estimated abundance of adult females was higher than the class mean (p = 0.85). Additional departures occurred in 2002 when abundance of sub-adult males was higher than the class mean (p = 0.77), and in 2003 when abundance of adult males was lower than the class mean (p = 0.76).

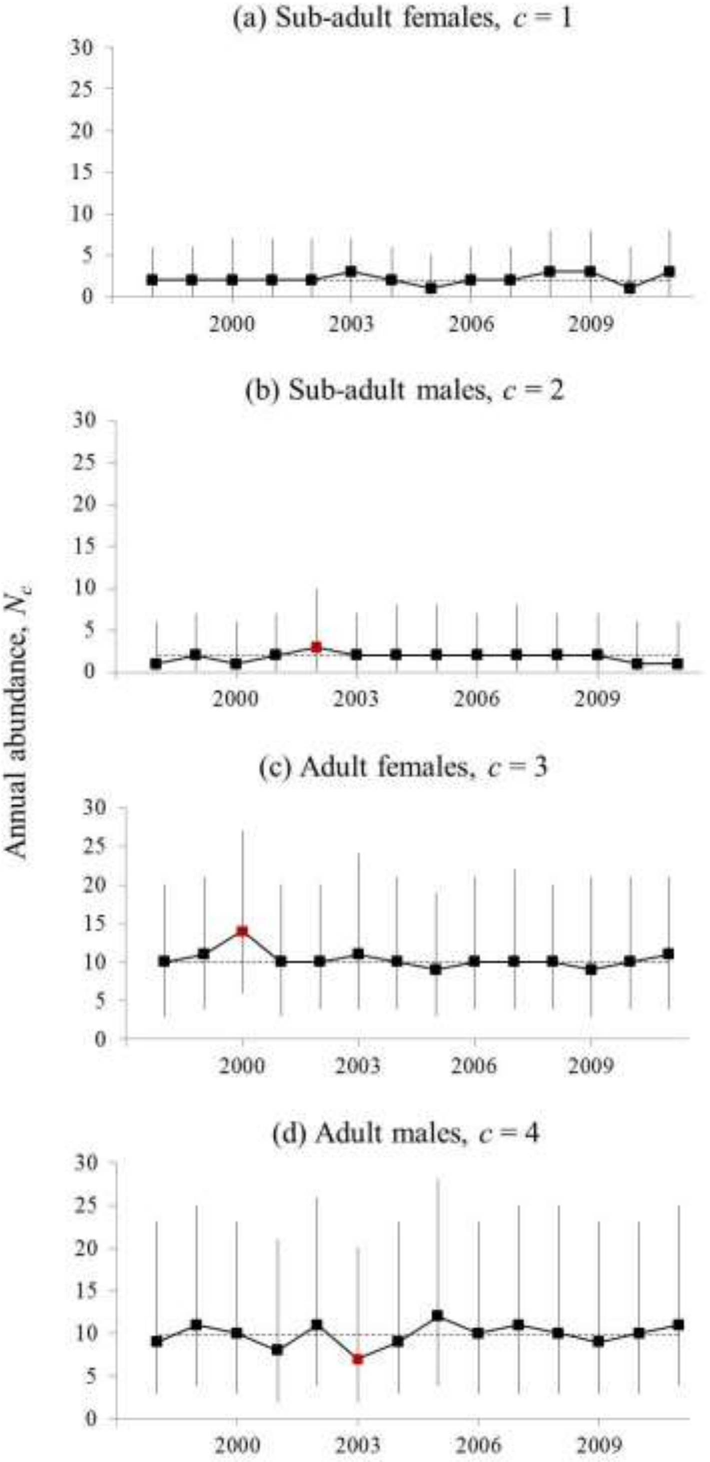


Figure 5.14. Trends in annual abundance by class ($N_{c,t}$) for distinctive whales over the time series 1998 – 2011. Annual median posterior estimates are shown by the black symbols; the symbols coloured red represent estimates with a high probability of deviation from the mean. Vertical lines represent the 95% HPDI, and the dashed horizontal lines represent the median posterior estimate for all years combined, μ^{N}_{c}.

5.3.6.2 Total annual abundance of distinctive whales

To obtain an estimate of annual abundance for all distinctive whales ($N_{tot,t}$), abundance estimates of distinctive whales for each class ($N_{c,t}$), were summed to give a total estimate of abundance for each year. The posterior median for total annual abundance of distinctive whales, μ^{N}_{tot} was 27 whales (95% HPDI = 20 – 36). There was no clear trend in abundance of all distinctive whales during the study (Figure 5.15), with little variation from the average annual abundance.

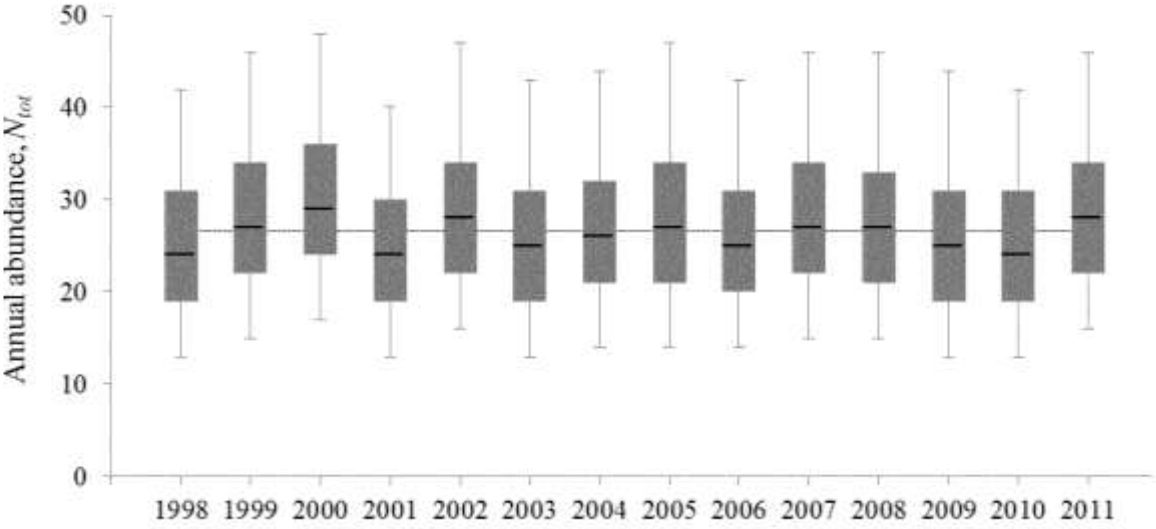


Figure 5.15. Annual abundance of all distinctive Blainville's beaked whales ($N_{tot,t}$). Estimates are presented as posterior medians (solid black line within bars), with 75% (grey bars) and 95% (vertical whiskers) highest posterior density intervals. The horizontal dashed line represents the average annual abundance of distinctive whales, μ^{N}_{tot}.

5.3.6.3 Proportion of population distinctive

To estimate total abundance for the population, the estimate for distinctive whales only (N_{tot}) was rescaled to include sub-adults and adults using the study area that were not distinctive, including calves. For sub-adults, there were insufficient encounter-days to estimate the proportion for each class separately, so both sub-adult classes were grouped to generate a single annual proportion distinctive for all sub-adults [posterior median $\mu^{m}_{SF,SM}$ = 0.63 (95% HPDI = 0.50 – 0.75)]. The posterior median for the proportion of adult females that were distinctive, μ^{m}_{AF} was 0.84 (95% HPDI = 0.75 – 0.91), and for the combined group which included adult females and calves, posterior median μ^{m}_{AF+CA} was 0.48 (95% HPDI = 0.42 – 0.55). Adult males were all distinctive (i.e. μ^{m}_{AM} = 1.00), so no rescaling was needed for this class because all adult males identified from high-quality photographs were included in the mark-recapture component of the model.

5.3.6.4 Total non-calf abundance by class

After rescaling abundance estimates to include both distinctive and non-distinctive whales for each class, the posterior median for total annual non-calf abundance, μ^{A}_{c} was 33 (95% HPDI = 25 – 45). Trends in non-calf abundance revealed that the estimated number of adults using the study area annually exceeded that of sub-adults (Figure 5.16).

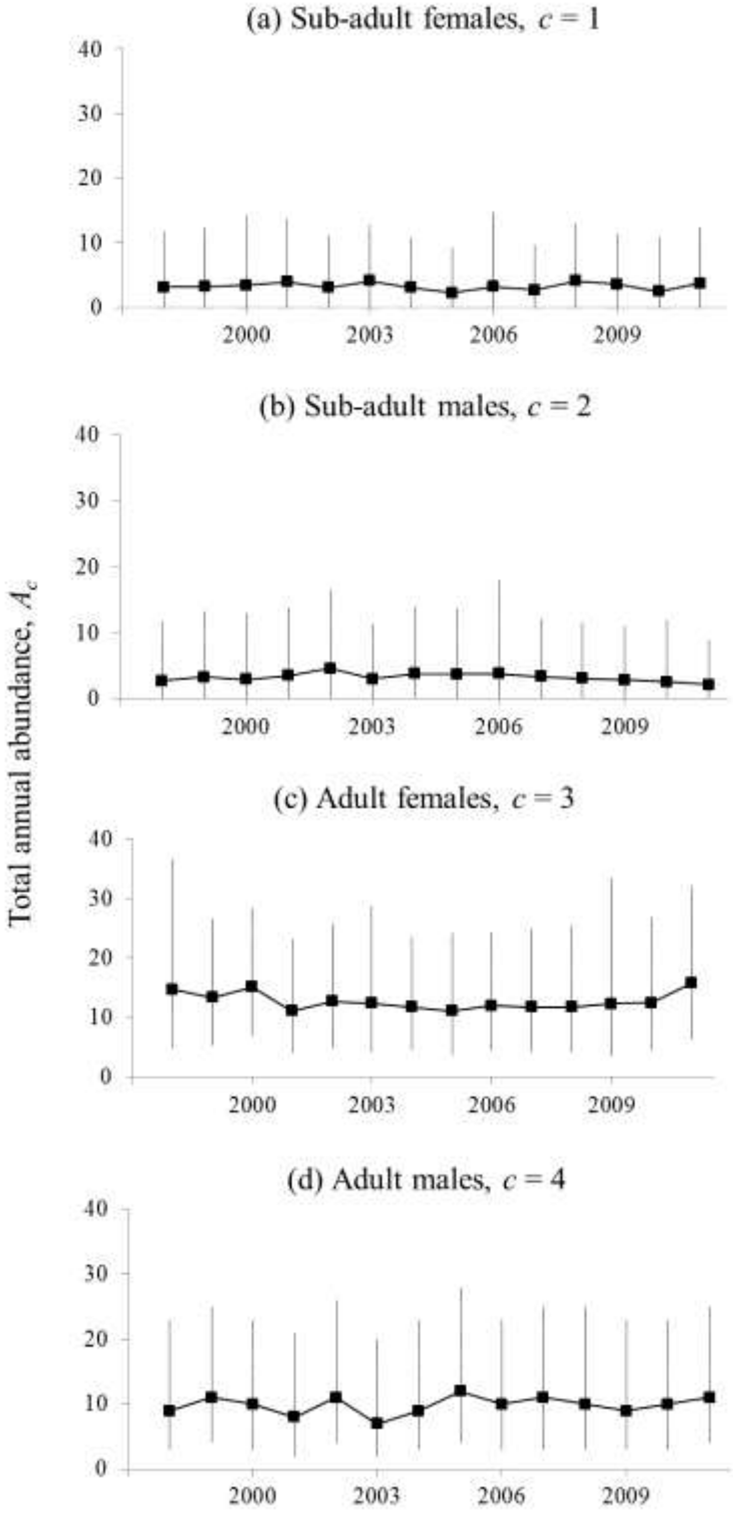


Figure 5.16. Trends in non-calf abundance by class ($A_{c,t}$) from 1998 – 2011. Annual median posterior estimates are shown by the black symbols. Vertical lines represent the 95% HPDI.

5.3.6.5 Total annual abundance (including calves)

The posterior median for the total abundance, including calves, μ^{A}_{tot} was 43 whales using the study area annually (95% HPDI = 32 – 57). Total annual abundance $A_{tot,t}$ remained stable throughout the study period (Figure 5.17) with 2000 representing the greatest deviation, although still slight, from the mean estimate for all years.

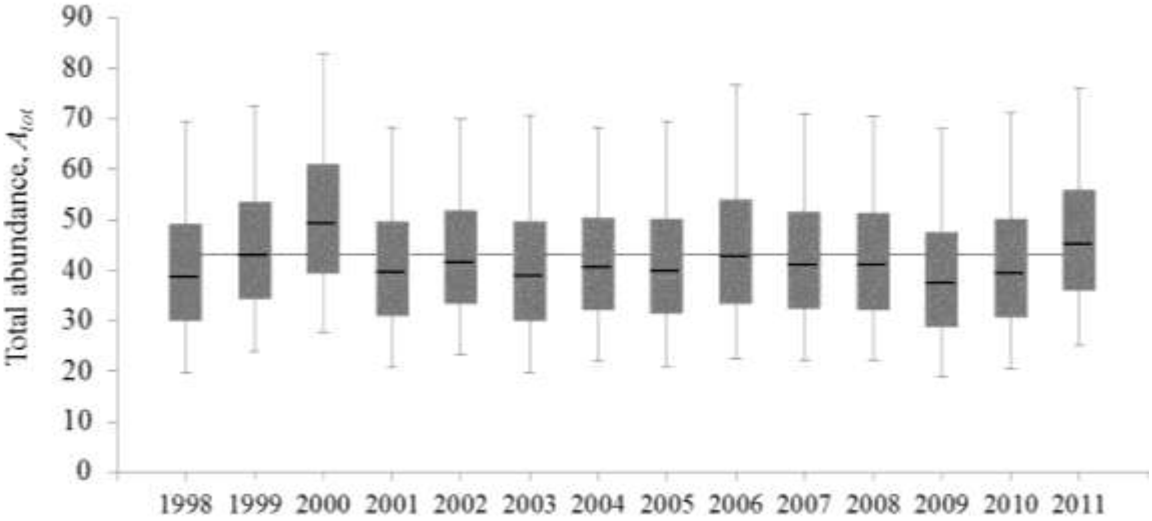


Figure 5.17. Trends in annual total abundance of Blainville's beaked whales for all four classes combined, and including calves, $A_{tot,t}$. Estimates are presented as posterior medians (solid black line within bars), with 75% (grey bars) and 95% (vertical whiskers) highest posterior density intervals. The dashed horizontal line represents mean abundance, μ^{A}_{tot}.

5.4 Discussion

5.4.1 Age- and sex-structured heterogeneity in capture probabilities

Individual heterogeneity in capture probabilities introduces biases in abundance estimates (Seber 1982) but is difficult to account for. This bias can be considerable; for example, Cubaynes *et al.* (2010) found abundance of wolves (*Canis lupus*) underestimated by 27% when individual variation in capture probabilities was ignored. Using the method of Pledger *et al.* (2003), Whitehead and Wimmer (2005) found abundance estimates for a population northern bottlenose whales off the Scotian Shelf which appears to be poorly-mixed due to differences in individual ranging patterns that were 20% higher than those reported previously using a homogeneous model (Gowans *et al* 2000).

By using the same dataset as in Chapter 3, this study provided an opportunity to compare estimates of abundance using a model which accounted for heterogeneity in the population and one that did not, i.e. Chapter 3. Here, heterogeneity in capture probabilities was evident, with substantial differences found both between age classes and between sexes (Figure 5.4). Despite this, differences in abundance estimates using these two models were minimal; estimates of average annual abundance of both distinctive whales and all whales (distinctive and non-distinctive whales, including calves) were just slightly underestimated by the model without heterogeneity. However, model fit was greatly improved when heterogeneity was addressed by stratifying parameters by age and sex; see Figures 3.7 and 5.2, corresponding to Bayesian *p*-values of 0.82 for the model which was not stratified and 0.44 for the stratified model. This was particularly true for adult females for which model fit was most improved (Figure

5.3c). For this reason, the mark-recapture model which accounted for heterogeneity was considered the best fit for these data.

5.4.2 Heterogeneity in "apparent" survival

Blainville's beaked whales in this study also exhibited age- and sex-structured heterogeneity in survival rates (Figure 5.9). However, the models applied here estimated "apparent" survival rate, which is a product of true survival and permanent emigration. As found elsewhere (e.g., McSweeney *et al.* 2007), adult females in Abaco exhibit high long-term site fidelity (Chapter 3), such that permanent emigration occurs at a low rate, so survival estimates for this class are presumed to be close to true survival. While a small percentage of adult females temporarily emigrated annually, almost half of which re-immigrated, the majority showed no movement, exhibiting residency to the study area. This does not seem to be the case with the other classes (or poorer precision affected the ability to draw conclusions), so it was not surprising then to find that adult female annual survival rates were the highest of the four classes. However, survival rates of both female classes exceeded those of males, which provided insight into differences in occupancy patterns by sex, and changes that may occur as males mature in either survival or permanent movement out of the study area.

Some, as yet, unknown component of this difference in apparent survival between sexes may well represent a difference in true survival rates. Sexual differences in survival rates are not uncommon in mammalian species with polygynous mating systems (Trivers 1985), although some causes known for other species can be eliminated here. For example, sexual size dimorphism is not evident in this species

(MacLeod 2006). Nor can differences be readily explained by elevated contaminant levels in males because lipophilic pollutants appear to be low in this population (Claridge *et al.* 2012). A reasonable explanation for differences in survival in female and male Blainville's beaked whales is a greater cost of reproduction for males.

Given the sexual dimorphism and dominance-ranked social structure of this species, male-male aggression may be the most important factor in higher mortality rates for adult males. In their study of five ungulate populations, Loison *et al.* (1999) found that differences in social behaviour and the level of aggression between males rather than the level of polygyny contributed to sexual differences in survival. Agonistic interactions between males and associated injuries lead to increased susceptibility to disease (Moore and Wilson 2002) and result in a decline in the health of adult males. Ramp *et al.* (2010) hypothesised that mate competition in humpback whales (Tyack and Whitehead 1981) may be an important cause of elevated male mortality for this species. In a dominance hierarchal social system, maintaining dominance ranking has additional costs; Deutsch *et al.* (1989) reported rate of mass loss in northern elephant seals (*Mirounga angustirostris*) increased with increase in dominance ranking during the breeding season. However, sub-ordinate males may bear the highest reproductive cost if forced to roam (e.g., Caro *et al.* 1989).

Despite the lack of sexual size dimorphism in Blainville's beaked whales (MacLeod 2006), costs of developing pronounced secondary sexual characteristics may be a contributing factor for sub-adult males having the lowest survival rates. Ford *et al.* (2007) found that of all age- and sex- classes examined, survival estimates were lowest for sub-adult male killer whales (*Orcinus orca*) and attributed this partially to the added costs of growth and encumbrance of a larger dorsal and pectoral fins as well as maintenance of a larger body. It is unknown what the energetics costs of developing an enlarged mandibular arch, larger teeth, and increased rostral ossification may be to a young Blainville's beaked whale, but this is a cost incurred by males only. Additionally, like subordinate males, younger animals may be forced to feed in areas where predation risks or human-induced impacts may be higher (e.g., Claridge 2006).

Lower capture probabilities for adult males suggest that short-term occupancy patterns for adult males differ from those of adult females, and perhaps sub-adults as well. However, the probability of capture is affected by not just presence or absence of an individual in the study area, but lower capture rates of adult males could also be related to behaviour; for example, adult males may roam singly between female groups making their detection more difficult. Whatever the cause, it is probable that the low estimate of apparent survival rate for adult males incorporates some significant component of permanent emigration, presumably of non-dominant males.

Differences in annual recruitment rates by age / sex classes were also evident and may provide further support for permanent emigration of adult males. As expected, annual probability of recruitment was higher for sub-adults than adults resulting from births with lag times, as a young animal would be recruited to a sub-adult class first (unless it were not seen until it was an adult). Variation temporally in recruitment of sub-adults simply reflected birth pulses, with a time lag. However, annual recruitment rates were higher for adult males than adult females, yet average annual abundance of adult males appeared to remain stable throughout the study (Figure 5.16). Assuming maturing sub-adults are recruited to adult classes at the same rate, the remaining difference in recruitment between adult classes must result from immigration of "new" males (but not “new” females). New arrivals will challenge the social hierarchy, thereby replacing subordinate males that have permanently emigrated.

The emerging knowledge of this particular population suggests that long range movements are rare (e.g., lack of movement between Abaco and AUTEC, Chapter 2), and that localised foraging is apparent from both analyses of chemical tracers and satellite telemetry data (Claridge *et al.* 2012). Only one adult male has been satellite tagged in Abaco to date, and location data received during the 14-day deployment supported site fidelity to an area approximately twice the size of the study area. Further study is needed to investigate occupancy patterns of adult males and improve estimates of survival rates based on adapting survey methodologies and the extent of the study area. Studies will need to include photographic sampling from a wider area to improve capture probabilities for males which may have ranged outside the study area, biopsy sampling to increase sample sizes for chemical marker studies, and telemetry studies to further explore temporal aspects of site fidelity in males.

5.4.3 Biological factors affecting heterogeneity

The underlying causes of heterogeneity are of interest because they can provide valuable information about the biology of the species (Corkrey *et al.* 2008). A degree of social separation exists between adult and sub-adult age classes in Blainville’s beaked whales (Claridge 2006), thus heterogeneity may be partially driven by social constraints. In this chapter, synchronous trends in capture probabilities for adults and, in some years, for sub-adults provide further insight into possible age-specific segregation. Moreover, in years when fewer adults were captured in the study area, more sub-adults were captured (Figure 5.5). Yet there were no obvious differences in coverage of the study area in those years, which may have influenced capture of one age class over another and, in fact, in one of the years (2003), survey effort was one of the highest of all during the study (Table 3.1). Age-specific behavioural response to capture could change during the study as whales repeatedly approached by the research vessel matured, but neither a linear temporal increase nor decrease was observed for either age class. Age class separation was further corroborated by a negative association in covariance for annual capture rates of adult females and sub-adult females, while covariance of adult females and adult males was positively associated.

Although somewhat speculative, it is possible that social constraints can help explain inverse capture probabilities by age classes found in this study. In other species in which sexual selection has resulted in males being heavily weaponised, males compete aggressively for mates and/or exhibit extreme territoriality, subordinate individuals such as sub-adults typically avoid conflict and injury by avoiding areas occupied by adult males [e.g., Clinton and Le Boeuf (1993), Loison *et al.* (1999), Pierce *et al.* (2000)]. In Blainville's beaked whales, a resource-defence social hierarchy may be limiting sexually immature females and males from entering areas usually occupied by adults. Reasons why adults would temporarily leave an area that presumably represented preferred habitat could include temporal changes in prey availability or disturbance, to which older more experienced individuals respond by moving (e.g., elephants). In the absence of adult presence, immature animals may move into the area.

5.4.4 Demographic change following the March 2000 stranding

Demographic changes occurred after the March 2000 atypical stranding of beaked whales in Abaco caused by the use of navy sonars (Balcomb and Claridge 2001, Evans and England 2001), which suggest a possible population-level effect of this event. This change was not detected in the analysis presented in Chapter 3 (although alluded to through an account of empirical data) but became evident once individual heterogeneity was accounted for in the mark-recapture model. However, the effect was contrary to what one might expect from an event which resulted in mortalities (Balcomb and Claridge 2001) linked to acoustic trauma-related injuries (Evans and England 2001).

Rather than a decrease in estimated abundance, an increase in abundance occurred in 2000 in the sampling interval immediately following the stranding but was only evident for the adult female class (Figure 5.14c). The increase was temporary because it was followed by an increase in the rate of temporary emigration in adult females between 2000 and 2001 (Figure 5.8a). Thereafter, both abundance estimates and temporary emigration rates returned to pre-2000 levels and remained stable for the remainder of the study. There was no discernible change in adult female survival, nor was there evidence of higher re-immigration before or after 2000, suggesting that abundance increased due to the arrival of new whales, although no change in recruitment was noted. Recruitment is difficult to separate from discovery, particularly with small sample sizes and at the start of a time series, and thus is difficult to estimate (as noted in Chapter 3), so it is possible that a change may have gone undetected. Empirical data presented in Chapter 3 supported temporary immigration of “new” adults in 2000, suggesting recruitment did occur. It is important to note that increases in temporary emigration rate and abundance in 2000 were shown for distinctive adult females only, and it has been assumed that distinctive and non-distinctive individuals had equal probability of capture and responded to changes in their environment in the same way behaviourally. However, the proportion of adult females that were distinctive was high, so biases associated with this assumption should be low. So if new adult females were recruited to the population, where did they come from? Where did they go when they emigrated? And perhaps more importantly, why did this happen?

Limitations in our knowledge of biological, oceanographic or anthropogenic factors that drive distribution make it difficult to understand why temporal changes in ranging patterns may occur (Wilson *et al.* 2004). Perhaps a shift in prey availability was the cause for the temporary immigration of adult females in 2000 but one can only speculate. The time period is coincident with a weak La Niña event which ended in early 2001[1]. The La Niña cool-phase of the El Niño-Southern Oscillation (ENSO) has been linked to increased hurricane activity in the northwest Atlantic (Goldenberg *et al.* 2001), and although no cyclones occurred in the study area in 2000, three occurred in 1999. Such major weather events can cause mass biological and oceanographic disruption but impacts of cyclones on ocean productivity are as yet unstudied in The Bahamas. ENSO events have been linked to changes in squid biomass in the Californian Current (Jackson and Domeier 2003), but intense cyclones are also linked to increased mortality in cetaceans (Mignucci-Giannoni *et al.* 1999, Fearnbach *et al.* 2012b). But what would be the implications if there was an increase in prey available to beaked whales in 2000?

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[1] See: http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml

Lack of knowledge about beaked whale feeding ecology and population structure hampers all but a hypothetical response. If habitat selection of Blainville's beaked whale is density dependent as suggested for sperm whales (Whitehead *et al.* 1997, Whitehead 2000), competition and social hierarchy may cause exclusion of some individuals when resources are less abundant, but sharing resources with reproductive females during more productive years, may be a mating strategy of choice for dominant males. Whether or not this would be a good strategy is unknown. Would a male benefit by sharing resources with females which do not remain in "his" territory rather than protecting resources for his harem and presumed offspring? Breeding with transient females may occur but, without knowing what role males play in protecting their offspring, it is unknown whether or not this may be successful. There is anecdotal evidence that adult males present a threat to calves as intraspecific scarring on calves has been observed (*pers. obs.*). If males do choose to share resources to increase breeding opportunities, this may explain why the increase in abundance in 2000 was only noted for adult females; however, it is likely that there were not enough data to detect changes in the other classes. Research is needed into Blainville's beaked whale social organisation, group relatedness and paternal investment as well as studies of prey densities to begin to understand the relationship between demographic changes and prey biomass.

Another hypothesis is that anthropogenic factors were the driving force behind a temporal change in ranging patterns. During the naval exercise on 15 March 2000, surface ships using tactical sonars transited through the middle of Northwest Providence Channel (see Figure 3.1). No such event had occurred previously or has since. Sound propagation models showed cumulative ping levels in the mid-channel waters (Evans and England 2001) which exceeded those known to cause behavioural responses in beaked whales (Tyack *et al.* 2011). Avoidance response would reduce exposure to sonar in a similar way to an anti-predator response but in this case because animals moved away from the sound sources they could be at risk of stranding as they approached coastal areas. Live stranded beaked whales were observed in Abaco's shallow coastal areas within hours after the ships' passage (Balcomb and Claridge 2001). Mature females may have had previous experience with disturbances, and exhibited a response which avoided navigating into shallow waters, thus preventing stranding, but could nonetheless have been displaced by the event, although the "new" females seen in 2000 were not observed until August. There are numerous examples of cetaceans being displaced by noise disturbance (Richardson *et al.* 1995, Morton and Symonds 2002), including beaked whales (McCarthy *et al.* 2011, Tyack *et al.* 2011). Some displacement has been shown to be temporary; for example, when shipping traffic increased, grey whales abandoned a calving lagoon in Baja California and then returned after traffic diminished (Bryant *et al.* 1984). Similarly, beaked whales moved off a navy testing range during training exercises involving the use of sonars, but later returned when exercises ceased (McCarthy *et al.* 2011, Tyack *et al.* 2011).

However, a potential caveat in this study is that the heterogeneity model used here is heavily parameterised (5 parameters for each of 4 classes over 14 sampling intervals), with very little data in some years. As such, these results should be interpreted with some caution.

5.4.5 Conclusions

Heterogeneity in capture probabilities between individuals from different age / sex classes resulted in only a slight negative bias in the estimate of abundance when not accounted for, but model fit was greatly improved when heterogeneity was addressed by stratifying parameters by age and sex. Annual survival was highest for adult females, but permanent emigration of adult males inhibited estimating true survival for this class. Social hierarchy in Blainville's beaked whales may be a driving factor contributing to individual heterogeneity as dominant males limit access to resources and/or territories from sub-adults and other males. The added energetics costs of growth of sexually dimorphic features in males may contribute to survival rates being lowest in sub-adult males. Heterogeneity in movement patterns of adult females appeared to be associated with the temporary immigration or displacement of some individuals in 2000, resulting in an apparent increase in adult female abundance in that year. This was coincident with (1) an ENSO event which may have influenced prey available but also increased cyclone activity, and (2) an anti-submarine warfare exercise which caused behavioural responses in the local population. Interpreting the potential effects of either of these events is hampered without more knowledge about the ecology of Blainville's beaked whale. Much like cetacean life cycles, global weather patterns are complex and span decades but, based on the findings here which include no apparent change in population dynamics in years with more severe cyclones and previously documented displacement of cetaceans caused by anthropogenic noise, the noise displacement hypothesis may have more support. Regardless of the cause, the effect appeared to be temporary as both abundance estimates and temporary emigration rates returned to pre-2000 levels and remained stable for the remainder of the study, although this result may need to be interpreted with some caution. This work may provide the first evidence of a population-level effect of a single anti-submarine warfare exercise, emphasising the valuable role that longitudinal studies will have in monitoring impacts of future events.

5.5 References

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CHAPTER 6

RE-SIGHTINGS OF BEAKED WHALES RE-FLOATED DURING AN ATYPICAL MASS STRANDING COINCIDENT WITH NAVAL SONAR

6.1 Introduction

During mass strandings of cetaceans, although some individuals within the group may be ill, the majority of animals are alive and considered to be healthy (Wiley *et al.* 2001). However, without human intervention, many, if not all, of the animals will perish. Response protocols at mass strandings therefore call for dealing with the live animals first with the goal of returning to the sea (re-floating) as many individuals as quickly as possible, prioritising the healthiest and strongest animals (Geraci and Lounsbury 2005). Yet the fate of re-floated individuals is rarely documented. An exception can occur if an individual has been taken into captivity, successfully rehabilitated, and been freeze-branded or instrumented with a telemetry tag to allow monitoring post-release (e.g., Mate 1989, Mate *et al.* 1994, Wells *et al.* 2009). However, most animals are simply re-floated without instrumentation, with no opportunity to monitor their long-term survival. The only known account is given by Visser and Fertl (2000) in which a sub-adult male killer whale (*Orcinus orca*) stranded, was re-floated 21 hours later and subsequently re-sighted over a 28-month period.

Although this individual’s dorsal fin was severely damaged by a vessel’s propeller 16 months after re-floating, the vessel strike was not considered to be related to stranding, and the re-floating was deemed successful.

Although reasons for mass strandings of cetaceans are not always understood (Geraci and Lounsbury 2005), mass strandings of beaked whales have been correlated with Navy sonar and seismic exploration (Simmonds and Lopez-Jurado 1991, Frantzis 1998, Jepson *et al.* 2003, Peterson 2003, Cox *et al*. 2006). Post-mortem observations from whales that died during these events included bleeding in the inner ear and brain (Evans and England 2001), and acute gas bubble lesions (Jepson *et al.* 2003, Fernandez *et al.* 2005). During these atypical strandings, first responders have driven some of the live-stranded whales back out to sea, but no follow-up has been reported nor have any re-floated whales been re-sighted.

Here post-re-floating survival of beaked whales following an atypical stranding coincident with a naval sonar exercise in the northern Bahamas is reported on. On 15 March 2000, an antisubmarine warfare exercise involving four surface ships using high-powered mid-frequency active sonars transited Northwest Providence Channel causing the stranding of at least 14 beaked whales (Balcomb and Claridge 2001, Evans and England 2001; Figure 6.1). Two beaked whale species were involved in the stranding: Cuvier’s beaked whale (*Ziphius cavirostris*, *n* = 11) and Blainville’s beaked whale (*Mesoplodon densirostris*, *n* = 3). Details of the re-floating of four animals are provided here and re-sightings of two of these whales post-stranding are reported.

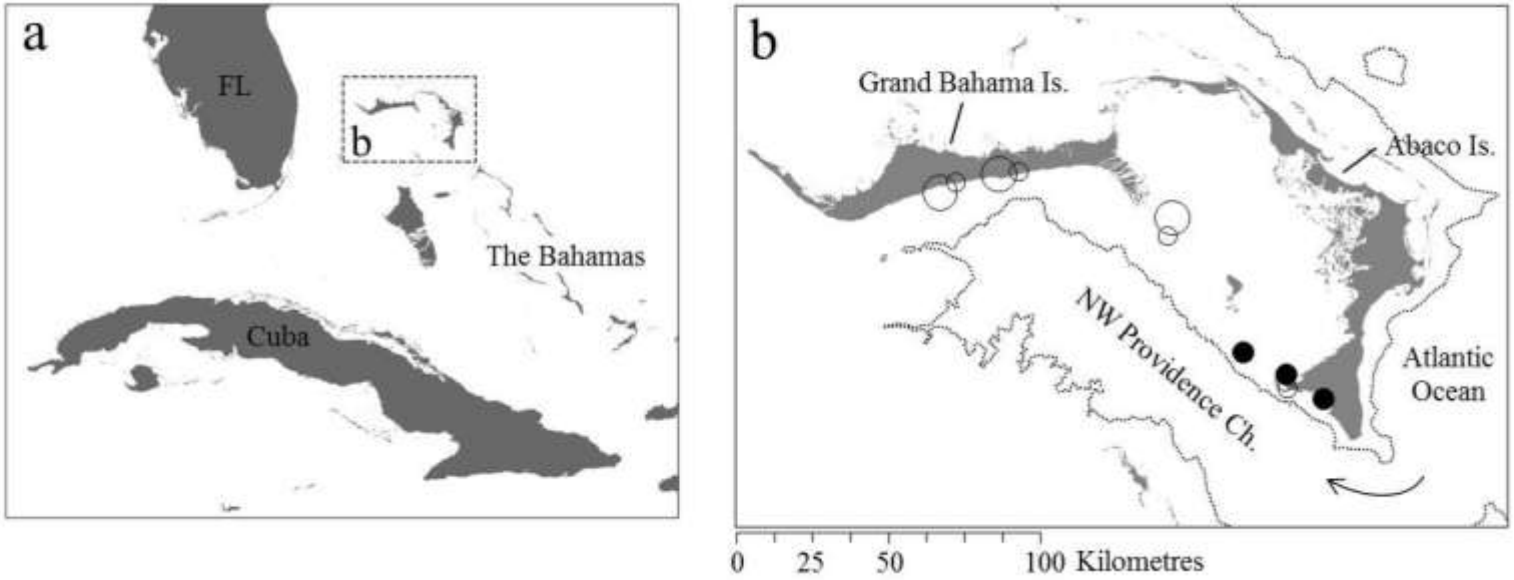

Figure 6.1. Map of The Bahamas showing the area where 14 beaked whales stranded on 15 March 2000 on Abaco and Grand Bahama Islands as navy ships transited from the Atlantic Ocean through Northwest Providence Channel (as indicated by the arrow) conducting an antisubmarine warfare exercise. The circles represent stranding locations of a single whale (small circle) and two whales (large circle). Blainville's beaked whales ($n = 3$) are shown in black and Cuvier's beaked whales in white ($n = 11$). The 1000 m isobath is shown by the dotted line.

6.2 Methods

6.2.1. Stranding response

Four live-stranded whales were found along the southwest coast of Abaco Island (Figure 6.1). No rehabilitation facilities existed and euthanasia was not possible, so the response consisted only of attempts to re-float the animals as quickly as possible. Two methods were employed: animals were either re-floated at the site of stranding (n = 2) or transported to another site and re-floated there (n = 2). As far as possible, standard measurements were collected following Geraci and Lounsbury (1993). Tissue samples were collected opportunistically and stored in a preservation solution [20% dimethyl sulphoxide (DMSO), supersaturated in NaCl] immediately after collection. Samples were later transported to the Southwest Fisheries Science Center, La Jolla, California, USA for molecular sexing (Morin *et al.* 2005).

6.2.2 Post stranding

6.2.2.1 Vessel surveys

From 1997 to 2011, randomly placed line transect surveys and opportunistic sightings surveys for beaked whales were conducted using small boats (< 9 m) off the south-western coast of Abaco Island, in the northern Bahamas (26.0N, 77.3W), resulting in more than 40,000 km of vessel track line (see Figure 3.1). From 2007 to 2011, visual and acoustic ship-based surveys were conducted more widely throughout Great Bahama Canyon using standardised search methods (Buckland *et al.* 2001; Zerbini *et al.* 2007), covering an additional 8,885 km. When beaked whales were encountered, attempts were made to photo-identify all individuals within a group on both right and left sides (see Chapter 2 for details). Each identification image was later visually examined either using a light table and magnifying eyepiece (for the black and white negatives) or a high-resolution computer monitor (for the digital images), and individual beaked whales were identified using the unique pattern of scarring on the body and nicks in the dorsal fin or at the base of the fin.

6.2.2.2 Tagging

On 9 May 2009, during a ship-based survey of Great Bahama Canyon, a “dart” tag (Andrews *et al*. 2008) with a satellite transmitter (SPOT5 model, Wildlife Computers, Redmond, WA; http://www.wildlifecomputers.com) was deployed on an adult female Cuvier’s beaked whale (Zc027). This small (49 g) tag was attached with two barbed titanium posts which penetrated 4.5 cm into the dorsal fin. The tag was deployed using a black powder gun to fire a delivery bolt from a range from 10 m (e.g., Tyack *et al*. 2011); the bolt fell away on contact with the whale, leaving only the tag attached. The tag was scheduled to transmit up to 400 times during 12 hours each day (John Durban, *pers. comm.*), timed to coincide with passes of satellites from the ARGOS satellite system (CLS America, Largo, MD; http://www.argos-system.org/). Received transmissions were used to calculate locations and estimated error radii, using a positioning algorithm implemented by the Argos satellite system that employs Kalman filtering of the received frequency measurements (Lopez and Malardé 2011).

6.3 Results

6.3.1 Re-floating accounts

Of the 14 whales that stranded on 15 March 2000, eleven were alive when first observed but re-floating was only attempted or possible for six individuals (Table 6.1).

6.3.1.1 Animal ID BMMS 00-02

At 0730 EST on 15 March 2000 a large calf/juvenile Cuvier's beaked whale was found by local residents completely grounded on a rocky shoreline approximately 20 m from the water's edge. Volunteers kept the whale wet until responders arrived at 0840. Due to the rugged terrain, current distance of the whale from the water, and an ebbing tide (high tide was at 0347, low at 1018), the decision was made to keep the whale moist and as comfortable as possible until the tide was high enough to move it. Towels were placed on its back and a team of volunteers used buckets to keep the towels wet. Standard length measurement was taken (length 366 cm) and a skin sample was collected for genetic analysis. The whale was bleeding ventrally from abrasions caused by the sharp rocks, attracting two black-tipped sharks (*Carcharhinus limbatus*) which circled just offshore throughout the rescue. At 0940, the animal was carefully rolled onto a tarp to provide some protection against the rocks. At 1212, the tide was high enough and sufficient volunteers were available to lift/re-float the whale in the tarp which was then held in place alongside a 6 m rigid-hulled inflatable boat (RHIB). The two sharks approached repeatedly and had to be repelled using sticks. The RHIB was slowly manoeuvred around the rocky promontory towards the edge of the canyon wall, a distance of 0.4 km, and the whale was released from the tarp. Its condition was

Table 6.1. Summary information for 11 beaked whales first observed alive during the Bahamas stranding on 15 March 2000. (For a complete summary of all animals that stranded during this event, see Balcomb and Claridge 2001. To allow cross-reference, the same animal IDs were used here). Zc = Cuvier's beaked whale and Md = Blainville's beaked whale. Note: Castaway Cay was formerly known as Gorda Cay.

Animal ID	Species	Age class and sex	Location	Response	Fate
BMMS 00-02	Zc	Calf/juvenile, unk. sex	Rocky Point, Abaco	Kept moist, re-floated in tarp, released offshore	Unknown
BMMS 00-03	Zc	Adult female	Sandy Point, Abaco	Pushed off beach, guided offshore by RHIB	Re-sighted
BMMS 00-04	Md	Adult female	Sandy Point, Abaco	Pushed off beach, guided offshore by 2 kayaks	Unknown
BMMS 00-05	Md	Adult female	Castaway Cay, Abaco	Not kept moist, re-floated in tarp, released offshore	Re-sighted
BMMS 00-06	Zc	Sub-adult female	High Rock, Grand Bahama	None	Died at site
BMMS 00-08	Zc	Adult female	Peterson Cay, Grand Bahama	Pushed off beach/rocks	Unknown
BMMS 00-09	Zc	Calf, unk. sex	Peterson Cay, Grand Bahama	Pushed off beach/rocks	Unknown
BMMS 00-10	Zc	Adult male	Red Shank Cay, Grand Bahama	None	Unknown
BMMS 00-11	Zc	Adult or sub-adult, unk. sex	Red Shank Cay, Grand Bahama	None	Unknown
BMMS 00-13	Zc	Adult female	Gold Rock Creek, Grand Bahama	None	Died at site
BMMS 00-14	Zc	Sub-adult male	Gold Rock Creek, Grand Bahama	None	Died at site

considered to be poor at the time of release. It kept circling back towards the rocks but kayakers were able to prevent re-stranding by physically blocking its path on the surface. At 1258 the whale began moving into deeper water (6.5 m) and at 1303 it was last seen swimming down and away from the edge of the carbonate bank to the south. This whale did not match to any individuals previously photographed and was given the new catalogue number Zc037.

6.3.1.2 Animal ID BMMS 00-03

At 0815 an adult female Cuvier’s beaked whale was found live stranded in the shallows at the beach 2 km from BMMS 00-02 (above). Its body condition was good and, as there was a direct route to deep water to the southwest and only 3 km away, the whale was immediately turned away from the shore and pushed off the sandy bottom. Its progress was monitored by observers in the RHIB; when it moved towards shallow water, the RHIB itself was used as a physical barrier, but with limited success. The whale re-grounded three times and had to be pushed off the bottom and re-directed offshore. Small ventral lacerations presumably from the rocky substrate were observed by a snorkeler. At 0916, the whale continued swimming southwest off the edge of the carbonate bank and into the Great Bahama Canyon, remaining at the surface as it swam away from the RHIB. It was later determined that this individual matched to a whale photo-identified previously in Abaco (identification number Zc027). On 26 February 1999, Zc027 had been sighted 23 km to the southeast of the stranding location (Figure 6.2a) and was accompanied by a dependent calf, and had been re-sighted on 1 March 2000 25 km horizontal distance southeast of the stranding location (Figure 6.2b) with a large calf/juvenile, presumably the same calf as in 1999, although there were no markings on the calf that could be used to confirm this. However, the calf/juvenile with Zc027 on 1 March 2000 did not match BMMS 00-02 above, i.e. it was not Zc037.

6.3.1.3 Animal ID BMMS 00-04

An adult female Blainville's beaked whale was found in the shallows 0.5 km from ID BMMS 00-03 at approximately 0830. The first responders immediately turned it around, pushed it offshore, and followed/directed it towards deep water (3 km away) by paddling a kayak on either side of the whale. This method proved remarkably useful; when the RHIB joined the two kayakers at 0930, they had travelled more than half the distance to the edge of the bank and the whale was swimming in a directed path towards the bank's edge. Field notes state that this animal appeared in good condition. At 1033, this animal was last observed in approximately 30 m depth swimming south into the canyon, remaining at the surface as it swam away. This whale did not match to any individuals previously photographed and was given the catalogue number Md148.

6.3.1.4 Animal ID BMMS 00-05

An adult female Blainville's beaked whale was found at Castaway Cay, some 16 km from the other three stranded whales, live stranded in the shallows of a mangrove lagoon. The whale was in poor body condition (it had not been kept moist) but lacking other options it was decided to re-float it (Figure 6.4a and c). A sloughed skin sample was collected for genetic analysis. The whale was then manoeuvred onto a tarp which was held alongside the RHIB and towed in this way out of the lagoon and 1.5 km west of the stranding location. It was released from the tarp at 1715 at the edge of the carbonate bank in approximately 10 m depth and was observed swimming towards the west into the canyon. This whale did not match to any individuals previously photo-identified and was given the catalogue number Md149.

6.3.2 Re-sightings

During field efforts conducted in the northern Bahamas after the stranding, the whales recorded as BMMS 00-03 (Zc027) and BMMS 00-05 (Md149) were re-sighted (Table 6.2).

6.3.2.1 Zc027

During a ship-based survey on 6 May 2009, individual Zc027 was photographed (Figure 6.2d, e) off north Eleuthera Island, 77 km horizontal distance south of the stranding location (Figure 6.3). There were three whales in the group, including an individual thought to be either a large juvenile (dependent calf) or a sub-adult that was closely associated with Zc027. Biopsy samples were collected from both individuals but genetic analyses have not been completed at this time so their relationship cannot be confirmed.

There were 22 locations estimated from the transmitter on Zc027 during the 12-day transmission period (10 – 21 May 2009), with estimated error radii ranging from 940 m to 25,000 m (median 4,300 m). During this time Zc027 ranged from eastern New Providence Island to the Atlantic side of Eleuthera Island (Figure 6.3).

Table 6.2. Sighting histories for Zc027 and Md149. AF = one adult female, AM = one adult male, C = one dependent calf/juvenile. The number in parentheses is the number of individuals in the group from each age / sex class if there were more than one. C/SA represents an individual recorded as a dependent calf in the field but photographs show the size and markings are indicative of a sub-adult.

Whale ID	Date	Group size	Group composition	Location	Notes
Zc027	26-Feb-99	5	AM, AF (2), C (2)	SW Abaco	
	01-Mar-00	3	AM, AF, C	SW Abaco	
	15-Mar-00	1	AF	SW Abaco	Live stranded; re-floated
	06-May-09	3	AF, C/SA, unk. adult/sub-adult	N Eleuthera	Dart tag deployed; biopsy sample collected
Md149	15-Mar-00	1	AF	SW Abaco	Live stranded; re-floated
	09-Jun-03	3	AF (3)	SW Abaco	

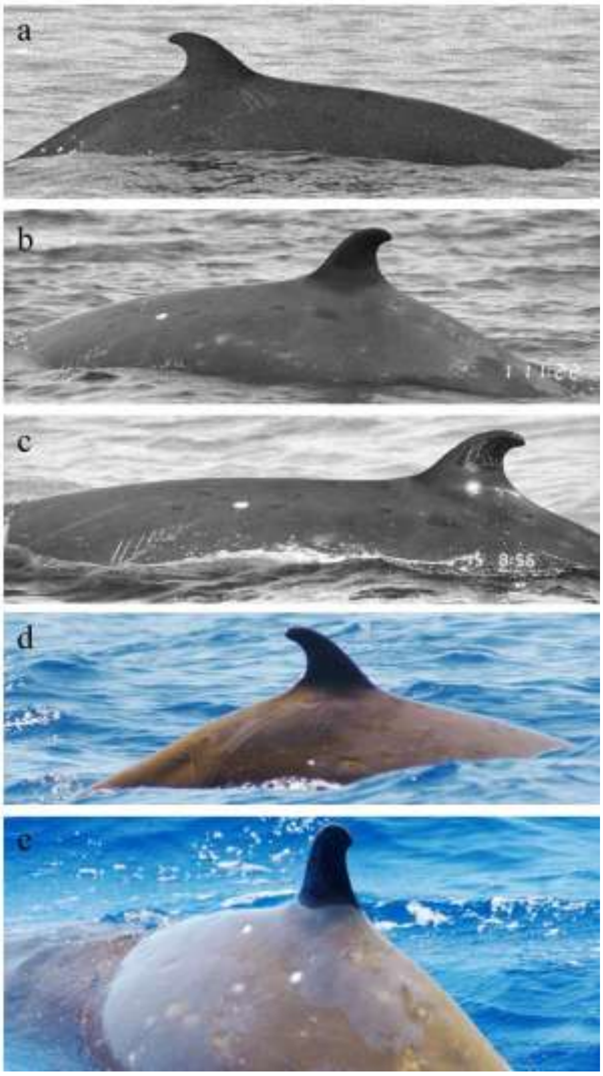

Figure 6.2. Photographs of an adult female Cuvier's beaked whale, Zc027 taken pre-, during and post-stranding. Pre-stranding sightings include (a) the first sighting on 26 February 1999 off southwest Abaco, and (b) re-sighted on 1 March 2000 in the same area. (c) Zc027 live stranded on the beach at Sandy Point, southwest Abaco, on 15 March 2000, was re-floated and followed as it returned to deep water. (d) Zc027 was re-sighted post-stranding off north Eleuthera on 6 May 2009. The unique pattern of oval scars from cookie cutter sharks (*Isistius* sp.), dorsal fin shape and two small indentations in the leading edge of the fin were used to confirm the photographic matches. Note that this photograph is not taken perpendicular to the dorsal fin as in (a), and new marks have been acquired in the 10-year period between photographs. (e) This photograph was taken of Zc027 on the surfacing series just prior to deploying a satellite transmitter tag on the dorsal fin.

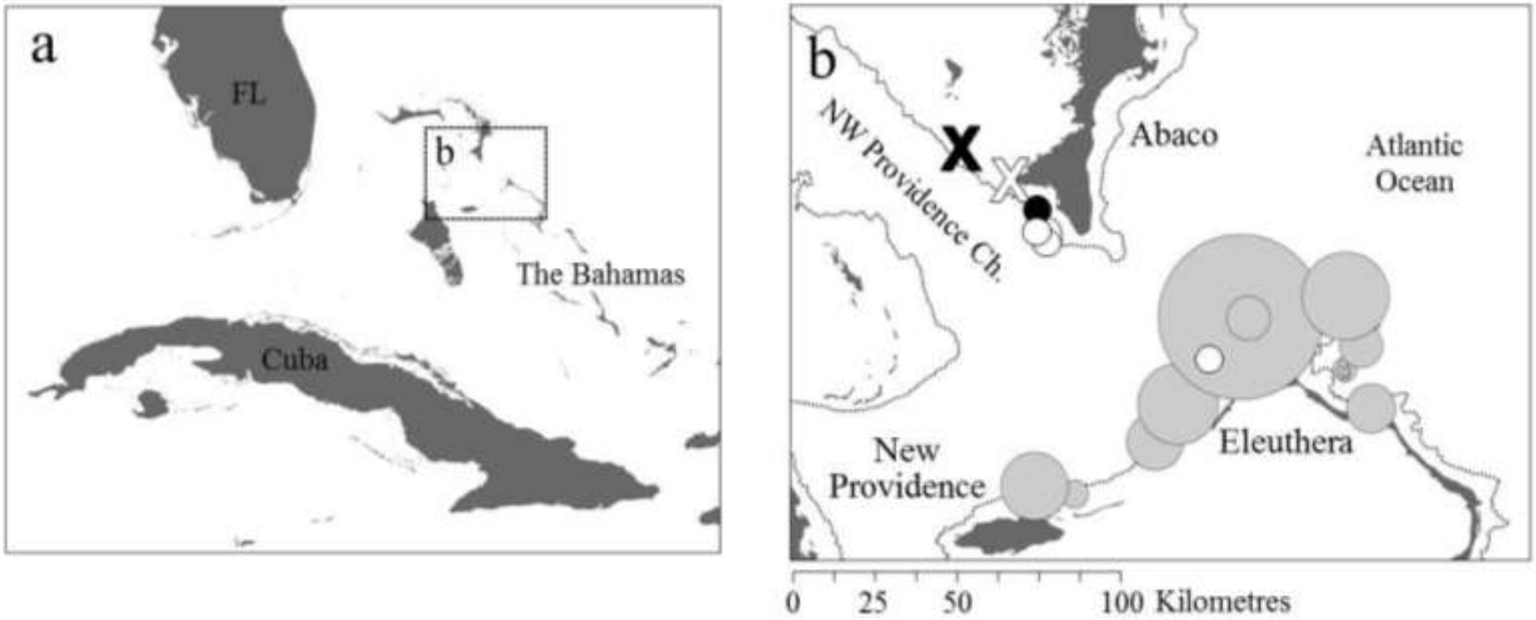

Figure 6.3. Map of The Bahamas showing the area in which stranding/re-floating, pre- and post- re-floating sightings and tagging occurred. Stranding/re-floating locations are marked with a black "X" for the Blainville's beaked whale, Md149, and the post-stranding sighting location off southwest Abaco Island by the black circle. The white "X" represents the stranding/re-floating location for the Cuvier's beaked whale, Zc027, and white circles mark the two pre-stranding sighting locations off Abaco Island and the subsequent post-stranding sighting north of Eleuthera Island, during which a satellite transmitter was deployed on Zc027. Estimates of tag location derived from the Argos Satellite System are shown as grey circles, with the size of circles being proportional to the estimated error radii. The 1,000 m isobath is shown by the dotted line.

6.3.2.2 Md149

During a line transect sightings survey off southwest Abaco on 9 June 2003, Md149 was photographed (Figure 6.4b, d and e) with two adult females known previously from the Abaco study area. The re-sighting location was 26 km southeast of the release site off Castaway Cay (Figure 6.3). Of particular note during the re-sighting was that Md149 had experienced some form of severe trauma since the stranding as shown by a healed wound measuring approximately 50 cm laterally on the left side posterior to the thoracic area. The scar's large size and evidence of healing by granulation due to its colour change, is indicative of a trauma which removed a large section of tissue below the entire skin depth in a single laceration (*pers. comm.* F. Gulland, 10 August 2012). The scar on Md149 closely resembles those caused from a ship's propeller (*pers. comm.* A. Knowlton, 10 August 2012); see photographs of the right whale RW#3503 on the New England Aquarium's right whale catalogue website: http://rwcatalog.neaq.org/Default.aspx, as this whale's injury from a ship strike progresses through the healing process. Md149 had additional new scars on the thoracic region but these were consistent those inflicted by conspecifics as described in Chapter 4.

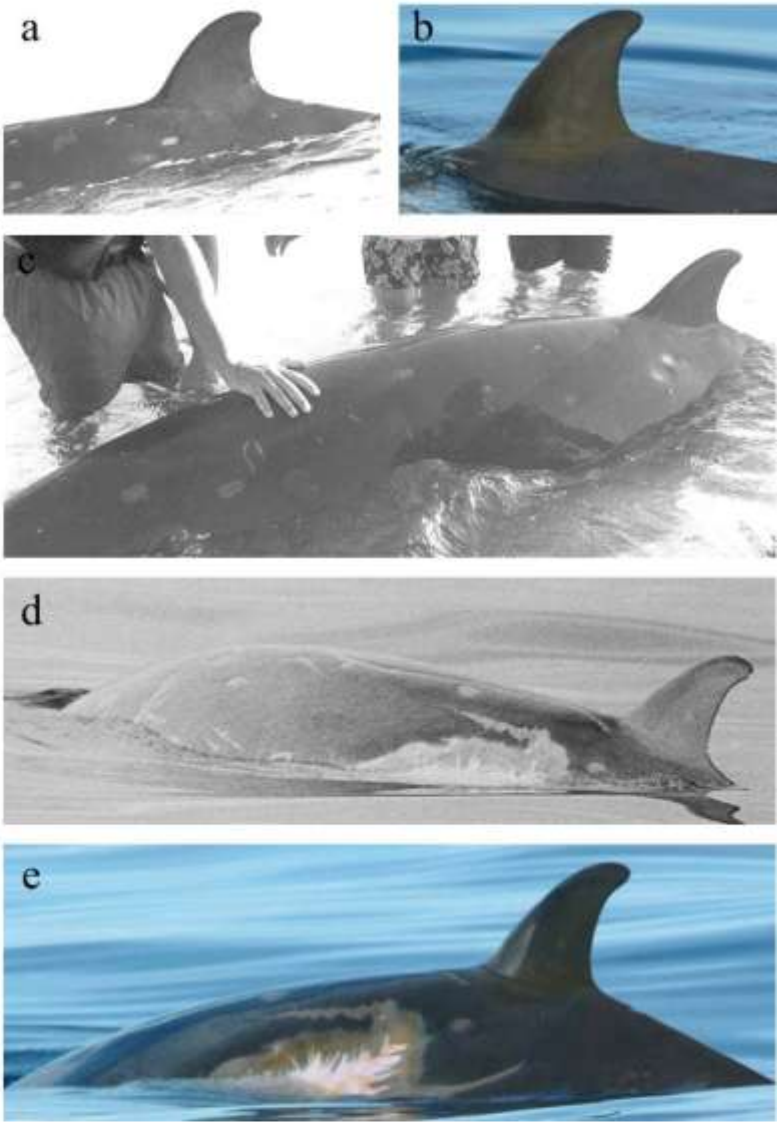

Figure 6.4. Photographs of an adult female Blainville's beaked whale, Md149, taken during and post-stranding. ID photos taken (a) during the live stranding on 15 March 2000 and (b) when Md149 was re-sighted on 9 June 2003 show a small notch in the tailstock. Additional photographs of the thoracic region taken during (c) stranding and (d) post-stranding show oval scars from cookie cutter sharks that were used to confirm the match. (e) The healed wound from a deep laceration is visible posterior to the thoracic region which occurred sometime after stranding.

6.4 Discussion

At least two beaked whales survived exposure to mid-frequency tactical sonars, the physiological stress of stranding and were re-sighted years later. Thus the re-floating of these individuals was considered a success.

Zc027 had shown multi-year site fidelity to southwest Abaco prior to stranding, and the re-sighting and location data from the satellite transmitter tag showed further site fidelity post-stranding to the same general area, i.e., the entrance to the Great Bahama Canyon. In Hawai'i, Cuvier's beaked whales have exhibited long-term site fidelity (up to 15 years), with maximum distances between re-sighting locations ranging up to 89 km (mean of maximum distances = 31.1 km, SD = 25.3 km, McSweeney *et al.* 2007). Zc027 was seen post-stranding 77 km away from pre-stranding sighting locations and in an area where *Ziphius* have been sighted previously (Claridge *et al.* 2012). Furthermore, movement of Cuvier's beaked whales between the Abaco study area and Eleuthera has been documented previously, although only once; the other individual was an adult male (BMMRO unpublished data), further suggesting Zc027's movement may represent normal behaviour. Zc027 was seen post-stranding in a typical social grouping for this species (McSweeney *et al.* 2007) but, until the genetic analyses are completed, it remains unknown if the large juvenile/sub-adult accompanying Zc027 on 6 May 2009 was her offspring.

Md149 survived at least three years post-stranding, was in a social group typical for this species (Claridge 2006, McSweeney *et al.* 2007) but appeared to have experienced acute trauma sometime post-stranding, possibly the result of a strike by a ship's propeller. As in all cetaceans, vessel strikes can be a cause of death in

Mesoplodon beaked whales (Van Waerebeek *et al.* 2007, Carrillo and Ritter 2010, Nielson *et al.* 2012), although evidence of a vessel strike has never been reported in stranding records in The Bahamas. No other individual from a catalogue of over 360 individual Blainville's beaked whales from The Bahamas shows evidence of a vessel strike. Therefore vessel strikes on this species are considered rare. This incident is similar to the account given by Visser and Fertl (2000) in which the ship strike of a killer whale occurred 16-months post-stranding but the authors considered it unlikely that the two were related because of the long interval between events. In the case of Md149, the interval between stranding and the presumed ship strike is unknown, but the time needed to recover to the state of the observed scar after such a traumatic injury is estimated to be a year to 18 months (*pers. comm.* A. Knowlton, 22 January 2013). Injuries associated with atypical strandings coincident with navy sonar include haemorrhages in the inner ear and brain (Evans and England 2001, Fernandez *et al.* 2005) which may partially explain the poor condition of Md149 when released. Until recovery from the pathophysiological stresses of sonar exposure and stranding, a whale's ability to detect and avoid an approaching vessel could be compromised (Richardson *et al.* 1995). Although inconclusive, it is possible that the stranding of Md149 and subsequent ship strike were related.

The fate of the other two whales that were re-floated (BMMS 00-02 and 00-04) remains unknown, although it is unlikely that the juvenile Cuvier's beaked whale survived because of its poor condition when released and the close presence of aggressive sharks. What happened to the juvenile sighted with Zc027 on 1 March 2000 is also unknown. The impact of the March 2000 naval exercise on Blainville's beaked whale populations is discussed in Chapters 3 and 5, but the paucity of data for Cuvier's beaked whale constrains such an assessment for this species. Claridge (2006) and Weilgart (2007) reported a decline in *Ziphius* sightings in the Abaco study area for several years after the 2000 stranding, despite increased field effort in most years. Although Cuvier's beaked whale sightings off Abaco continue to be infrequent, an adult female first photo-identified off southwest Abaco in 1997 was re-sighted in the same area in 2007, demonstrating long-term site fidelity of whales in this region, spanning a time period from before to after the stranding (BMMRO unpublished data). A thorough review of the photo-identification data for *Ziphius* in The Bahamas is currently underway which may provide new insights into whale movement and site fidelity.

6.4.1 Conclusions

Although it is unlikely that the impact of the 2000 sonar exercise on beaked whale populations in the northern Bahamas will ever be fully understood, the main finding of this work is that at least some individuals can survive exposure to mid-frequency active sonars and the physiological stresses related to stranding if re-floated and directed back into deep water.

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CHAPTER 7

GENERAL DISCUSSION

7.1 Filling key gaps

Quantifying population demographics is necessary to analyse the status of wildlife populations and to support effective conservation and management. Such a need exists for beaked whales which exhibit behavioural responses to anthropogenic noise, including navy sonar, suggesting that this group is particularly vulnerable among cetaceans (Cox *et al.* 2006). In this thesis, longitudinal photo-identification data collected over 15 years in The Bahamas has been used to advance our knowledge of the population demographics of Blainville’s beaked whales (*Mesoplodon densirostris*) and investigate the potential population-level effects of military sonars.

Mark-recapture models were fitted to photo-identification data collected from 2005 – 2010 at the Atlantic Test and Evaluation Center (AUTEC) where sonar was regularly used and 170 km away at Abaco where sonar use was limited and thus considered a control site. During the study, a mass stranding of beaked whales, including Blainville’s beaked whales, occurred in March 2000 near the Abaco site which was correlated with a navy sonar exercise (Evans and England 2001, Filadelfo *et* *al.* 2009) and population dynamics surrounding this event were explored using the full-time series of data available (1997 – 2011).

Key advances that my work has contributed to understanding the population demographics of Blainville's beaked whale include estimating population age-structure, survival and recruitment rates, movements in and out of my study areas and abundance both on and off a navy range. The population age-structure found in Abaco supported a polygynous resource/female defence harem-type mating system known for *M. densirostris* (Claridge 2006, McSweeney *et al.* 2007). However, the age structure described here may be that of a part of the population, rather than full sampling of a whole population because the sampling area was limited to the south-western coast of Abaco Island, an area regularly used by adult females. For beaked whales, sound associated with naval exercises may impact immature whales to a greater extent than adults (Cox *et al.* 2006), possibly because they are naïve. As such, information on age structure may be an important component of mitigation and monitoring for populations exposed to sonar use on a regular basis, such as at AUTEC, and the new information from Abaco provides a valuable baseline for comparison.

For *Mesoplodon* species, almost all information on age and sexual maturity has come from the examination of carcasses from stranded animals (Mead 1989, Heyning 1989) and is limited by the rarity of strandings of the majority of the species. Age at sexual maturity was only reported for a single stranded female *Mesoplodon* examined post-mortem (a Blainville's beaked whale, Ross 1979). My work here has supported this initial finding from free-ranging females and I have also contributed new information on the age at sexual maturity for males.

Survival is one of the most critical demographics needed to monitor population dynamics but, for beaked whales, information on survival has been lacking for all but one species (Gowans *et al.* 2000). I presented the first survival estimates for a *Mesoplodon* species. Adult females exhibited high long-term site fidelity, as has been reported for this species in Hawaii (McSweeney *et al.* 2007). Permanent emigration occurred at a low rate, so apparent survival estimates that I have reported should be close to true survival. For the sub-adult classes poorer precision affected the ability to draw conclusions, but estimated survival rates of both female classes exceeded those of males.

This provided insight into differences in occupancy patterns by sex and suggests that males may permanently emigrate at a higher rate than females. The added energetics costs of growth of sexually dimorphic features in males may contribute to survival rates being lowest in sub-adult males. Male-male combat and associated injuries could lead to increased susceptibility to disease (Moore and Wilson 2002) and result in a decline in the health of adult males (Ramp *et al.* 2010), or the cost of maintaining dominance (Deutsch *et al.* 1989) may be a contributing factor to increased mortality in mature males. However, the low estimate of apparent survival rate for adult males infers that it must incorporate some permanent emigration, presumably of non-dominant males. Variation temporally in recruitment of sub-adults reflected birth pulses, with a time lag. However, differences in annual recruitment rates in adults appeared to reflect differences in the rate of immigration of “new” adults that were primarily males. New arrivals will challenge the social hierarchy, thereby replacing subordinate males that have permanently emigrated.

Analyses of the data from the longer time series available revealed that Blainville's beaked whales in Abaco are part of a larger parent population providing support for turnover in the study area. The dispersion of individuals within a population depends on prey density, factors affecting dispersal, and behavioural interactions (Cain *et al.* 2008). I believe that social hierarchy in Blainville's beaked whales is a driving factor contributing to turnover as dominant males limit access to resources and/or territories from sub-adults and other males. However, it was surprising to find that individual dispersion of Blainville's beaked whale, especially of adult males, was so geographically limited in the northern Bahamas, suggesting some degree of population structuring. As shown in Hawaii (Schorr *et al.* 2009), individual movement within the Great Bahama Canyon may be on spatial scales in the range of tens of kilometres with regular home ranges that do not overlap at AUTEC and Abaco.

I have provided the first estimate of abundance for Blainville's beaked whales (or any mesoplodont) using mark-recapture methods, and compared abundance on and off a navy range. Average annual abundance of Blainville's beaked whales was lower at AUTEC when compared to an area of the same size in Abaco. Of particular concern was that, despite a similar number of adult females at both sites, a higher female:calf ratio was found on the navy range, suggesting that lower recruitment through births at AUTEC may be contributing to the lower overall abundance than at the control site. Lower reproductive rates and/or calf survival may be attributed to exposure of resident adult females to chronic stress associated with frequent use of navy sonars at AUTEC, a hypothesis that still needs to be tested.

Estimates of abundance have allowed me to determine the status of the Abaco population, which appears stable. Although changes in population dynamics were not noted during the study some demographic changes were observed. Immediately after the 2000 stranding, abundance and temporary emigration increased, suggesting displacement of individuals may have occurred. However, the following year abundance and population parameters returned to pre-2000 levels and remained stable thereafter.

Two individuals in the 2000 stranding were re-sighted years later, demonstrating that some beaked whales can survive exposure to mid-frequency active sonars and the physiological stresses related to stranding if re-floated and directed back into deep water. This implies that behavioural responses can occur that pre-empt permanent physiological damage even when exposed to multiple sonars operated at 235 dB re 1µPa or even higher (Evans and England 2001). This response appears similar to that described by Tyack *et al.* (2011) in controlled exposure experiments where Blainville's beaked whales reacted to sound pressure levels below 142 dB re 1µPa by moving away from the sound source. However, in the case of the two whales here (Zc027 and Md149), their response resulted in stranding, and without human intervention, they would likely have perished. It is important to note too that the primary species represented in the 2000 stranding was Cuvier's beaked whales and it remains unknown what the impact on this species may have been.

Monitoring of even a small number of individuals in the Abaco study site for more than a decade provided valuable life history data from free-ranging mesoplodonts. These life history data and other vital parameters will be applied to models to predict the population-level consequences of regular sonar use at AUTEC and on other navy ranges (National Research Council 2005). In addition to the estimates given here, the extensive individual-based dataset from Abaco can be used to examine other aspects of Blainville's beaked whale life history and behaviour such as estimating inter-birth intervals (e.g., Barlow and Clapham 1997), assessing trends in age structure (e.g., Fearnbach *et al.* 2012a), and examining social structure (e.g., Lusseau *et al.* 2005, Jaquet and Gendron 2009). Similar future applications of the AUTEC data, although too limited currently, would allow a more comprehensive comparison of the population ecology of Blainville's beaked whales on and off a navy range.

7.2 Potential conservation implications

The primary goal of this work was to fill some of the critical gaps in our knowledge of the population demographics and to a lesser extent population dynamics of Blainville's beaked that will have implications for the conservation of this species.

Despite its proximity to Abaco, the AUTEC "sub-population" may need to be managed as a separate unit. On-going studies to define the geographic bounds of individual movement through satellite telemetry and photo-identification work should be continued. A genetic study underway which includes tissue samples collected in The Bahamas during this study will provide information on the breeding population structuring for this species in the region (see Morin *et al.* 2012 for preliminary results). Defining the extent to which these two "sub-populations" interact is of great importance to management of human activities, particularly at AUTEC. Management strategies may need to prioritise efforts to improve precision in the population demographics presented here and conduct a thorough assessment of potential threats to the AUTEC subpopulation, which are likely not just to be limited to the impacts of sonar. Prey density studies would be extremely valuable to interpreting abundance differences found here between Abaco and AUTEC. Such management strategies are currently being employed elsewhere; for example, management of the southern resident killer whale (*Orcinus orca*) population in Washington State as a separate stock under the US Endangered Species Act which required implementation of a recovery plan to increase conservation efforts for this population and its habitat (National Marine Fisheries Service 2008).

High residency of adult females inhabiting navy ranges may put them at particular risk of exposure to stressors associated with frequent and repeated use of navy sonars which may reduce their fitness, a concern particularly for pregnant and lactating females, young calves and even foetuses (Curry 1999, Wright *et al.* 2007). Although a quantitative answer to whether frequent sonar use at AUTEC is causing stress to resident beaked whales does not exist currently, the potential implications to mitigation of navy activities on the AUTEC range (and elsewhere) are great, and testing this hypothesis is a priority. Studies of pregnancy and stress hormone (e.g., Rolland *et al.* 2005, Hunt *et al.* 2006, Kellar *et al.* 2006, 2009), and the use of satellite tags to investigate potential changes in foraging behaviour of whales displaced during sonar tests will provide a context for interpreting low recruitment at AUTEC. Aerial photogrammetry conducted at Abaco and AUTEC such as that done by Fearnbach *et al.* (2011) would provide a means of comparing fitness between the two areas.

Monitoring trends in abundance and survival in beaked whales are important for understanding future impacts of other anthropogenic activities which are known to affect ziphiids such as shipping noise (Aguilar de Soto *et al.* 2006, Pirotta *et al*. 2011) and fisheries interactions (Read and Wade 2000), although the latter is of less concern in The Bahamas where large scale commercial fishing does not currently occur. However, anthropogenic sound associated with increasing shipping traffic and its effects on cetaceans has raised concern about masking communication sounds, energetic costs of behavioural disruption and displacement, and physiological effects and stress (Payne and Webb 1971, Richardson *et al.* 1995). Ambient noise associated with shipping traffic measured off San Nicholas Island, California had increased by 10 – 12 dB (95% CI = 2.6 dB) between 1964 and 2004, or 2.5-3 dB per decade (McDonald *et al.* 2006). In 1997 the Freeport Container Port began operations in the northern Bahamas and serves as one of the major transhipment hubs for the eastern seaboard of the United States, increasing traffic of containerships in Northwest Providence Channel. Although this increase has not been quantified, and the status of beaked whales closer to the shipping lanes is unknown, information on the status of the Abaco "sub-population" located nearby and its future monitoring may provide a valuable baseline. Of perhaps equal relevance to beaked whales inhabiting tropical waters may be the effects of climate change with increasing frequency and intensity of tropical cyclones which can have direct and indirect effects on cetaceans (Mignucci-Giannoni *et al.* 1999, Miller *et al.* 2010, Fearnbach *et al.* 2012a, 2012b).

The apparent stability of the Abaco population has provided an extremely useful baseline (or control) for comparing the population demographics on a navy range. For example, AUTEC densities reported previously (Marques *et al.* 2009) were higher than anywhere else (Moore and Barlow 2013), yet abundance at AUTEC has been shown here to be low relative to a population nearby. Without the comparative approach taken here, the concerns highlighted about potential impacts to beaked whales from regular exposure to sonar would not have been evident. This work may provide the first evidence of a population-level effect of both regular sonar use at AUTEC and the 2000 stranding event (although apparently short-term), emphasising the valuable role that longitudinal studies can have in monitoring impacts of anthropogenic activities, including in areas where sonar is regularly used such as on navy ranges.

7.3 Additional considerations

7.3.1 Bayesian versus likelihood approaches

I chose to use a Bayesian approach to statistical inference which is quite different from the classical approach. In classical statistics, model parameters are considered to be fixed values that are to be estimated, typically by finding the values that maximise the likelihood. In Bayesian statistics, the data is fixed but parameters are variable and themselves have distributions. Before data collection, prior distributions describe the variability in the parameter, while after collection these priors are replaced by the posterior distributions through the application of Baye’s Theorem (Bayes 1763). Bayesian inference is based on the philosophy that knowledge cannot be built entirely through experimentation, but requires prior knowledge (Roberts 2007).

However, it is precisely the subjectivity in assigning prior distributions that has been substantially criticised by frequentist statisticians (e.g., Dennis 1996), especially when little or no information is available. Yet in ecological applications the prior provides a means of incorporating knowledge from related studies that would otherwise be excluded, and with sparse data, inference can be made that would otherwise be impossible. In the work presented in this thesis, I selected hierarchal priors which diluted the influence on the posterior of any prior assumption by essentially creating random effects of the model parameters (King *et al.* 2010). Here, I used flat priors for the means of each parameter set, and then a normally distributed prior centred on zero and bound by the standard deviation for the annual effects. To ensure that this prior was indeed vague, in all cases I checked that the posterior estimate for the standard deviation was smaller than that for the prior and thus did not influence posteriors unless there was enough data to support deviation from the parameter mean. This approach was important given the sparse data available.

Another criticism is that model selection is less formal than that of non-Bayesian approaches. For example, when using the posterior predictive loss approach to model selection (Gelfand and Ghosh 1998), there is no guidance on how different models need to be for one to be considered better than the other. In the work presented here, the re-immigration model was always selected as the better fit over the standard Cormack-Jolly-Seber but sometimes the loss difference between models was quite small. Despite this, I selected the re-immigration model but that decision was augmented by direct evidence of re-immigration through telemetry data collected from individuals in the same population. Model selection supported this choice.

There are of course advantages and disadvantages of both Bayesian and classical approaches. One of the key advantages of the Bayesian approach is that it provides interpretable answers, based on inferences that are conditional on the data and are exact, which aids managers and policy-makers in their decision-making process.

7.3.2 Individual heterogeneity of capture

Although I was able to address some aspects of heterogeneity within the study population by using a model which accounted for heterogeneity within age and sex classes, I still did not address individual heterogeneity. Instead I assumed that individuals within each class behave in a similar way. It is unlikely that this is the case. For example, within the adult female class there was some evidence of heterogeneity in ranging patterns of individuals; although some adult females appeared to be resident, a small percentage temporarily emigrated and only a few of these returned, suggesting turnover of some adult females in the study area annually. This will introduce heterogeneity of capture and perhaps, survival, which will bias the abundance estimates to some yet unknown extent as it was not accounted for sufficiently in this study.

This work could be further improved to include individual heterogeneity of capture and survival but more data would be needed and/or a different approach may be required such as using a mixture model (Pledger *et al.* 2000, 2003) which allows for individuals to be clustered according to their probability of capture and survival. This method was successfully employed by Whitehead and Wimmer (2005) using a likelihood approach, and within a Bayesian framework by Durban *et al.* (2010) and Fearnbach *et al.* (2012b).

7.4 References

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