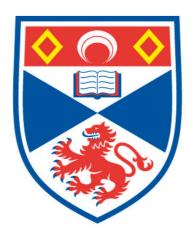
THE SEASONAL MOVEMENTS AND DYNAMICS OF MIGRATING HUMPBACK WHALES OFF THE EAST COAST OF AFRICA

Aaron M. Banks

A Thesis Submitted for the Degree of PhD at the University of St Andrews



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The seasonal movements and dynamics of migrating humpback whales off the east coast of Africa

Aaron M. Banks



This thesis is submitted in partial fulfilment for the degree of

Doctor of Philosophy

School of Biology, University of St Andrews

Date of Submission
January 2013

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I, **Aaron Banks**, hereby certify that this thesis, which is approximately **59,000** words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

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Abstract

Data collected during boat-based and aerial surveys were used to describe population structure, movements, temporal patterns of migration and skin condition of humpback whales in breeding sub-stock C1-S off southern Africa. Results confirmed that the migration route along the south coast of South Africa is linked to the winter ground off Mozambique. A lack of exchange between breeding sub-stocks C1-N and C1-S was found, suggesting that these are independent of each other. Molecular analysis revealed unexpected levels of population structure between the migration route and the winter ground of C1-S, as well as the possibility that this migration route is also utilised by some individuals from breeding sub-stock C3. A skin condition of unknown aetiology that primarily affects humpback whale mother-calf pairs was identified. The first assessment of its prevalence and severity was made, providing a baseline for future monitoring. Humpback whale abundance in an inshore region of Bazaruto Archipelago, Mozambique was estimated and attempts were also made to use the limited information off Plettenberg Bay/Knysna, South Africa. In addition to improving our understanding of humpback whales from Breeding Stock C, knowledge about another baleen whale species utilising the southwest Indian Ocean was extended. The first evidence of southern right whale presence off the coast of Mozambique since the cessation of whaling was documented. It remains unknown whether this is a remnant sub-stock or the recovering South African sub-stock reoccupying its historical range.

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This PhD consists of many words, graphs tables and pictures. Each and every one of these is a result of the blood (from cuts and bruises, scorpion stings and spider bites), sweat (Africa in general) and tears (some of joy, some of frustration) during some of the best but most challenging times of my life. Completing this thesis was quite simply the biggest challenge I have ever undertaken. Had it have not been for the help from an exhaustive list of people, this thesis may never have existed. To those of you who are not mentioned, you are by no means forgotten.

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1. Chapter 1: General Introduction

The intensity of the whaling industry in the Southern Hemisphere led to the near extirpation of many baleen whale species (Clapham & Baker, 2002; Jackson et al., 2008b; Perry et al., 1999). Two species have partially recovered in some areas: the humpback whale and the southern right whale (IWC, 2001; IWC, 2010; IWC, 2011c; IUCN, 2012). As these species recover, their conservation and any management of human activities require that current population status be evaluated. Evaluating the status of whale stocks requires examination of current stock size, recent population trends, carrying capacity and productivity, all of which requires knowledge of population structure and population dynamics (IWC, 2011c). Classifying the extent to which species or populations are at risk of extinction using criteria developed by the IUCN requires knowledge of geographic range, population size and trends, habitat and ecology and past, recent and ongoing threats (IUCN, 2012). This thesis aims to improve such knowledge of populations of these two migratory species of baleen whale, humpback and southern right whales that over-winter along the east coast of Africa. It investigates the movements and population structure of humpback whales along the coast of South Africa and Mozambique. Historically, the coast of Mozambique was also a known winter ground for southern right whales; this study investigates whether southern right whales continue to use this region.

Part of the International Whaling Commission's decision to pause all commercial whaling in 1986, was that the Scientific Committee should undertake "Comprehensive Assessments" for all whale stocks – an in depth evaluation of stock status, including the examination of current stock size, population trends, carrying capacity and productivity (IWC, 2011c). This was because the effective conservation of whale stocks, through robust management of human activities, can only be accomplished through a good understanding of population structure and abundance. Understanding of population structure can only be obtained through knowledge of spatial and temporal distribution, population dynamics (values of demographic parameters), and levels of exchange between stocks (and any sub-stocks). For stocks or sub-stocks that are data deficient, the collection of baseline data is critical to begin the process of effective management and conservation.

The term "stock" is frequently used in marine mammal management and conservation to define population units or "units to conserve". The scale or boundaries of these units are dependent upon the objectives of the conservation or management plan. A stock can be defined as either a biological stock, whereby its boundaries are based on genetic separation, or spatially as a management stock in terms of a population unit that can be successfully managed (Donovan, 1991). This can result in a management unit not necessarily being synonymous with a biological population (Clapham et al., 2008). The U.S. Marine Mammal Protection Act (MMPA 1972) defines a biological population as: "A group of marine mammals of the same species or smaller taxa in a common spatial arrangement which interbreed when mature".

A population or stock can be difficult to define in practice. Clapham *et al.* (2008) recommended that information from a variety of data collection techniques, such as behavioural, marking, tagging and acoustics should be combined with genetic analyses when defining ecologically meaningful management units. Failure to establish the correct spatial boundaries of a biological stock or sub-stock has implications for estimating its abundance and consequently the accuracy of status assessments. Similarly, it will also reduce the effectiveness of conservation efforts to mitigate against human impacts.

Gender-specific dispersal and site fidelity may yield different levels of population structure (Greenwood, 1980; Prugnolle & de Meeus, 2002); understanding how a population is structured is therefore an important requirement when defining units to conserve. The propensity of migratory marine mammals to move long distances between feeding and reproductive habitats may confound any assumptions of stock structure based simply on geographic proximity (Bowen, 1997). Individuals from different breeding grounds can mix when at feeding grounds, for example breeding stocks of humpback whales off east and west Africa show a degree of mixing on their Antarctic feeding grounds (IWC, 2011c). In other cases, individuals on a single breeding ground can also disperse to multiple feeding grounds, for example humpback whales in the North Pacific and North Atlantic (Calambokidis *et al.*, 2008). This complex structure must be understood to examine fully the extent to which a

population may have recovered from past exploitation and/or how it may be affected by current anthropogenic impacts.

Knowledge of movements of both sexes is extremely important when defining stock boundaries. Populations of cetaceans are often strongly structured, most obviously by sex and age, but also frequently by geography (Whitehead *et al.*, 1998). Behavioural barriers to gene flow may be as important as geographical barriers in defining the population structure of migratory marine mammals (Bowen, 1997). Sex-biased dispersal, which in mammalian species generally involves female phylopatry and male dispersal (Prugnolle & de Meeus, 2002), can lead to different degrees of population structure according to sex. Whilst male-mediated gene flow may occur between reproductive populations that are isolated in terms of mtDNA lineages, females ultimately govern the reproductive output of a population (Bowen, 1997).

Throughout the animal kingdom, a wide range of taxa are considered to be in some way "*migratory*", travelling in a variety of media and using numerous types of locomotion (flying, swimming, walking, drifting) (Dingle & Drake, 2007), for example, birds (Bruderer, 1997; Egevang *et al.*, 2010), insects (Drake & Gatehouse, 1995) and fish (Leggett, 1977). The Convention on the Conservation of Migratory Species of Wild Animals (also known as CMS or the Bonn Convention) defines a migratory species as:

"The entire population or any geographically separate part of the population of any species or lower taxon of wild animals, a significant proportion of whose members cyclically and predictably cross one or more national jurisdictional boundaries."

The term "migration" can be considered from different perspectives and this variability in what constitutes migration, arises as a result of the migration phenomenon broadly involving a mechanism and a function, conceptualised on two levels (Dingle & Drake, 2007):

- i) A behavioural/physiological/genetic aspect, applying to individuals.
- ii) An ecological/evolutionary aspect, applying to populations.

The outcomes of migration, which can be viewed as a population process, rely upon the underlying behavior of individuals, which ultimately affects reproductive success through natural selection (Clapham, 2001; Dingle, 2006; Dingle & Drake, 2007). Therefore to understand the function of migration, its underlying mechanisms must also be understood. Similarly, in order to understand and conserve a migratory population, one must also understand its migratory element.

Most species of baleen whale are migratory with predictable, seasonal movements between productive high-latitude summer feeding grounds and low-latitude winter breeding grounds (Corkeron & Connor, 1999); for example, humpback whales (*Megaptera novaeangliae*) (Gabriele *et al.*, 1996; Rasmussen *et al.*, 2007; Robbins *et al.*, 2011; Zerbini *et al.*, 2006), gray whales (*Eschrichtius robustus*) (Rugh *et al.*, 2001; Swartz *et al.*, 2006) and southern right whales (*Eubaleaena australis*) (Best *et al.*, 1993). Exceptions to this general rule include the migration of the western Arctic bowhead whale (*Balaena mysticetus*) stock whose movements are predominantly longitudinal rather than latitudinal (Mate *et al.*, 2000; Quakenbush *et al.*, 2010) and a non-migrating humpback whale population in the Arabian Sea (IWC, 2011c).

1.1 Humpback whale movements and population structure

Documenting movements of individuals can provide valuable information on migration routes, distribution and population structure, which is required for assessments such as those undertaken by the IUCN and IWC. Historically, whaling records and Discovery tag return data from the years of modern whaling have been used to indicate the migration routes and distributions of baleen whales (Allen, 1916; Mackintosh, 1942; Matthews, 1937). In more recent years, a shift towards the use of non-lethal techniques to collect data on marine mammal populations has led to the wide use of photo identification and molecular analysis of skin samples (for example - Arnason *et al.*, 1991; Baird & Gorgone, 2005; Barlow *et al.*, 2011; Carvalho *et al.*, 2009; Palsboll *et al.*, 1995; Patenaude *et al.*, 2007; Robbins *et al.*, 2011; Wilson *et al.*, 1997). Their use in the study of humpback whale biology is extensive but is notable for identifying rates of interchange between stocks and sub-stocks (Garrigue *et al.*, 2011; Pomilla *et al.*, 2005; Stevick *et al.*, 2010), intra-regional stock structure (Calambokidis *et al.*, 1997; Craig & Herman, 2000; Pomilla *et al.*, 2005), linkage between feeding and breeding grounds (Stevick *et al.*, 2004) and estimating levels of

site fidelity (Barendse *et al.*, 2011a; Weinrich *et al.*, 1993), and abundance (Barlow *et al.*, 2011; Cerchio *et al.*, 2008b).

The variable and uniquely pigmented ventral tail fluke surfaces and variation in the profile of the fluke trailing edge have made humpbacks particularly suitable subjects for photo-identification in mark-recapture studies (for example - Baracho-Neto *et al.*, 2012; Chaloupka *et al.*, 1999; Darling *et al.*, 1996; Salden *et al.*, 1999; Smith *et al.*, 1999). Changes in naturally occurring marks, such as pigmentation and scarring, over time may introduce bias in mark-recapture studies (Carlson *et al.*, 1990; IWC, 1990; Gowans & Whitehead, 2001; Hammond, 1986; Hammond, 1990; Hammond, 2009; Hammond, 2010). In humpback whales, morphological features such as fin shape, edges and fluke trailing edges were found to exhibit less temporal variability than features such as scarring, scratching and pigmentation (Blackmer *et al.*, 2000). Young individuals, especially those less than one year old, also have the potential to undergo substantial change to fluke colouration and markings (Blackmer *et al.*, 2000; Carlson *et al.*, 1990). Blackmer *et al.*, (2000) also found that dorsal fin edges and fluke serration peaks in humpback whales were more likely to undergo change in males than in females, with most changes occurring after sexual maturation.

The migration of humpback whales is extensive, with seasonal movements of up to 8300 km each way (Rasmussen *et al.*, 2007). Within the Southern Hemisphere, summer feeding grounds are located south of 55°S around the continent of Antarctica, whilst wintering grounds are found at approximately 20°S (Clapham & Mead, 1999) or where water temperatures range from 21.1 to 28.3°C (Rasmussen *et al.*, 2007). An exception to general wintering ground distributions is off the west coast of Central America where a winter mating and calving ground is located around the equator (Rasmussen *et al.*, 2007). Opposing seasons between hemispheres, means that Northern and Southern Hemisphere populations remain temporally separated. However, the global distribution of mtDNA haplotypes seems to suggest some historical hemispherical interchange (Baker *et al.*, 1993). Gene flow between hemispheres has been suggested to occur in the western region of Central America, which has shown to have spatial overlap of whales wintering from both hemispheres (Calambokidis *et al.*, 2000; Rasmussen *et al.*, 2007).

Population structure in humpback whales is known to be complex and features high levels of site fidelity to feeding and breeding grounds (Baker et al., 1990; Baker et al., 1993; Calambokidis et al., 2008). Rates of exchange have been found to be low between different breeding populations (Darling & Cerchio, 1993; Rosenbaum et al., 2009; Stevick et al., 2010) but this low rate of exchange may be a significant aspect of humpback whale population dynamics and gene flow (Baker et al., 1990). Regional and temporal movement patterns on feeding grounds have been shown to be in response to varying patterns of prey availability (Stevick et al., 2006; Weinrich et al., 1997). The extent of mixing will likely be influenced by factors such as population density (stage of recovery), environmental variability and the relative density and recovery of other krill predators (IWC, 2011c). In the North Pacific photographic mark-recapture studies revealed high rates of site fidelity to breeding areas although some interchange was observed and these rates were dependent upon the distances between them (Calambokidis et al., 2008; Calambokidis et al., 2001). Similarly, variation in the mtDNA of humpback whales on different feeding and breeding grounds of the North Pacific and western North Atlantic oceans shows marked segregation of mtDNA haplotypes among subpopulations as well as between the two oceans (Baker et al., 1990). Varying degrees of fidelity to specific foraging areas has also been found for humpback whales feeding in the North Pacific (Barlow et al., 2011; Calambokidis et al., 2008; Calambokidis et al., 1996; Calambokidis et al., 1997; Weinrich, 1998; Weinrich et al., 1993) and North Atlantic (Stevick et al., 2006).

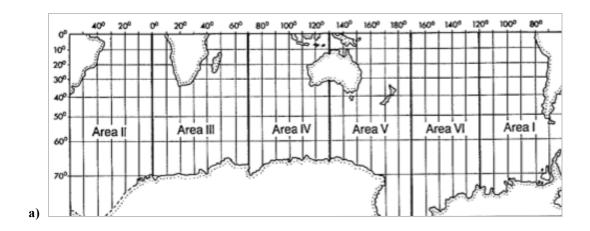
In the Southern Hemisphere, photographic mark-recapture and molecular studies have revealed complex population structure in breeding stocks in the southeast Atlantic (West Africa) and the southwest Indian Ocean (East Africa) (Carvalho *et al.*, 2010; Carvalho *et al.*, 2009; Cerchio *et al.*, 2008b; Dulau-Drouot *et al.*, 2011; Ersts *et al.*, 2011; Pomilla *et al.*, 2005; Pomilla & Rosenbaum, 2006; Rosenbaum *et al.*, 2009) and in the South Pacific (East Australia and Oceania) (Garrigue *et al.*, 2011; Hauser *et al.*, 2000; Olavarria *et al.*, 2007) resulting in the description of a number of sub-stocks and varying degrees of mixing within and between stocks. In contrast, the population structure of breeding stocks off the west and east coast of southern and Central America and the west coast of Australia appear to be much simpler in structure with no sub-stocks currently identified (IWC, 2011c). The complexity of some Southern

Hemisphere breeding stocks has proven to be of concern when estimating abundance and population trends to evaluate the recovery of these stocks (IWC, 2011c).

Sex ratio is a basic population parameter that is of importance to conservation management (Clapham et al., 1995). Failure to account for sex-biased population structure on wintering grounds can lead to underestimates of abundance (Calambokidis et al., 2008). Sex ratios have been found to be equal on feeding grounds (for example - Smith et al., 1999) but become male biased during migration (Brown & Corkeron, 1995; Brown et al., 1995) and on winter grounds (Carvalho et al., 2010; Carvalho et al., 2009; Craig & Herman, 1997; Pomilla & Rosenbaum, 2006). Similarly, male humpbacks identified by photographs on Californian feeding grounds were 2.2 times more likely to be identified on a wintering ground than were females from the same area (Calambokidis et al., 2000). This suggests that some females do not undertake the migration to the breeding grounds. Instead, females may remain at the feeding grounds throughout winter (Clapham et al., 1993) or becoming pregnant en route to the breeding grounds and returning to the feeding areas before arriving at the terminal winter destination (Craig & Herman, 1997). Matthews (1937) suggested that the sex ratio as a whole was equal, but varied in different places due to the "...whales' habits of breeding and migration".

1.1.1 Humpback whales in the Southern Hemisphere

Historically, the Antarctic region was divided into six management areas (Areas I-VI) (Figure 1.1a) (Donovan, 1991). Current assessments are focussed on seven subtropical, geographically separated breeding stocks that use these feeding areas. The breeding stocks are: (A) coastal waters of South America, (B) west coast of Southern Africa, (C) east coast of Africa, (D) east coast of Australia and the western pacific Island, (E) central south Pacific Islands, (F) Fiji, (G) west coast of South America (IWC, 1998). In addition, there is an eighth population in the northern Indian Ocean, previously named Breeding Stock X, now referred to as the "Arabian Sea Population" and considered to be a non-migratory population with a clear lack of gene flow to any of the feeding areas (IWC, 2011a).



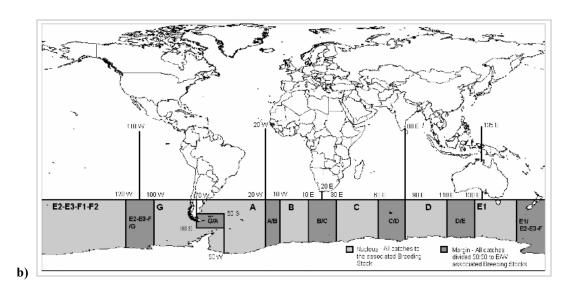


Figure 1.1a-b. a) IWC Southern Hemisphere management areas (excluding Bryde's whales) (Donovan, 1991). B) Humpback whale catch allocation reference case showing Nucleus and Margin Areas in the feeding grounds associated with breeding stocks A-G (IWC, 2010).

Over-exploitation by the modern whaling industry throughout the last century led to the depletion of humpback whale stocks with over 210,000 individuals being removed from the Southern Hemisphere alone (Clapham & Baker, 2002; Findlay, 2001). In the period 1947-1973, the USSR conducted substantial illegal whaling in the Southern and Indian Ocean as well as the North Pacific (Clapham *et al.*, 2005; Clapham & Baker, 2002). The USSR reported catches of just over 2,700 humpback whales compared to actual catches of over 48,700 humpback whales in the Southern Hemisphere. In 1963, the IWC declared a ban on humpback whale catches and by 1986 (the start of the International Whaling Commissions moratorium to end all commercial whaling), humpback whales were listed as 'Endangered' on the IUCN 1996 Red List of Threatened Species (Reilly *et al.*, 2008). As a result of recent global

stock recoveries, humpback whales are currently listed as "Least Concern". However, some sub-stocks, show little recovery. The Fiji breeding population (substock E2), is increasing very slowly compared to the East Australian Stock (E1) (Jackson *et al.*, 2008a), which is increasing at $10.6\% \pm 0.5\%$ (95% CI) per year (Noad *et al.*, 2008a). This lack of recovery may be a result of lack of immigration from adjacent sub-stocks and/or the loss of "cultural memory" about the existence of a particular habitat, extirpated together with the whales during the years of whaling (Clapham *et al.*, 2008).

1.1.2 Humpback whales around southern Africa

Substantial catches of humpback whales were taken off both the west and east coasts of southern Africa between 1908 and 1963. A total of 47,134 individuals were reportedly taken from the coastal waters of Africa between Gabon on the west coast and Mozambique and Madagascar on the east coast (Findlay, 2001), highlighting the presence of historical southern African wintering grounds. Off the African coast between 1908 and 1913, nearly 21,000 humpback whales were caught, two-thirds of the total Southern Hemisphere catch of that species between 1908 and 1930 (Best, 1994). For the southwest Indian Ocean, Winn and Reichley (1985, in Findlay and Best, 2006) suggested a post-exploitation stock size of 340 whales. The temporal distributions of humpback whale catches off the East African mainland during modern whaling are summarised in Chapter 2, Section 2.4.4.

As described above, the IWC recognises two breeding populations of Southern Hemisphere humpback whales around Africa: breeding stock B along the west coast of southern Africa; and breeding stock C along the east coast of Africa.

Breeding Stock B

The west coast of Africa is divided into two breeding sub-stocks B1 and B2 (IWC, 2001) (Figure 1.2). The breeding region encompassing sub-stock B1 extends north of 18° S. South of this is a region which is considered to be a migratory route and feeding ground, as well as containing sub-stock B2, which has been genetically

identified as different to B1 but the exact breeding location of which is unknown (IWC, 2011c). Connectivity between Breeding Stock B and the Antarctic feeding grounds is known through two individuals that were satellite tagged off Gabon and tracked to relatively low Antarctic latitudes of 56° S in Areas II and 54° S in Area III (Rosenbaum & Mate, 2006) and two genotypic matches: B1 to 55°S, 0°W (Area II) and B2 to 57°S, 1°E (Area III) (Annex H - IWC, 2010)

Breeding Stock C

Breeding stock C comprises whales that breed in the southwest Indian Ocean (IWC, 1998) (Figure 1.2). Based primarily on modern whaling catch history and distribution data, this breeding stock was initially divided into three sub-regions by Best *et al.* (1998), representing three breeding sub-stocks (C1, C2 and C3) each with their own migration streams. More recently, it has been proposed that sub-region C1 be split into C1 North (C1-N) and C1 South (C1-S); however, for management purposes, the IWC Scientific Committee has agreed that C1-N and C1-S should be considered as one breeding sub-stock (IWC, 2011c). A fourth sub-region, C4 has also been proposed (Figure 1.2).

Sub-stock C1 (C1-N and C1-S) breeds along the coastal regions of Mozambique, and its migration stream extends along the eastern coast of South Africa, at least as far west as Knysna (23°E) on the south coast of South Africa. C1 North (C1-N) extends northwards from Mozambique Island (15°S) to the northern limit of the range (southern Tanzania and possibly into Kenya). C1 South (C1-S) includes eastern South Africa and Mozambique as far north as Mozambique Island.

Sub-stock C2 breeds around the Mozambique Channel islands of Aldabra, Mayotte and the Comoros Archipelago with a speculated migration stream through the centre of the Mozambique Channel.

Sub-stock C3 breeds around the coastal waters of Madagascar with its migration stream thought to flow along the Madagascan Ridge.

Sub-stock C4 extends across the Mascarene group of islands including Mauritius and Reunion.

For the purposes of referring to data collection sites within breeding sub-stock C1 and its migration route, Cerchio *et al.*, (2008b) delineated the area used by breeding stock C1 into six coastal areas (Figure 1.3): South Coast of South Africa (SC), South Eastern South Africa (ES), North Eastern South Africa (EN), South Mozambique (MS), Central Mozambique (MC), and North Mozambique (MN). The North Eastern South Africa-Mozambique South (EN-MS) division is described as occurring at Cabo Inaca, Mozambique. Although this study's field site at Ponta Mamoli is <100km south of this division (Figure 1.3), it should be considered as Mozambique South (MS) due to its location being inside Mozambique.

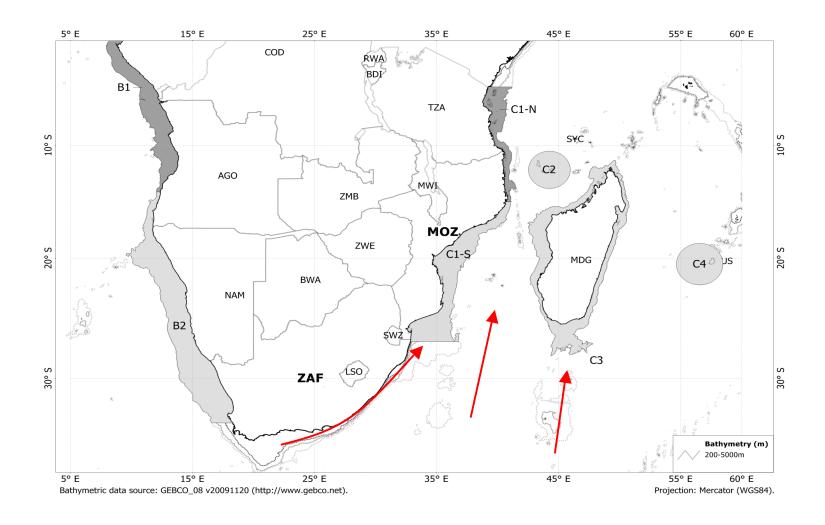


Figure 1.2 Breeding Stocks B and C and the approximate locations of their proposed sub-stocks: B1, B2, C1 (delineated into C1-N and C1-S), C2, C3, C4 (IWC, 2011c). Arrows indicate proposed migration routes into the South West Indian Ocean (Best *et al.*, 1998). Figure adapted from IWC (2010) and Best *et al.* (1998).

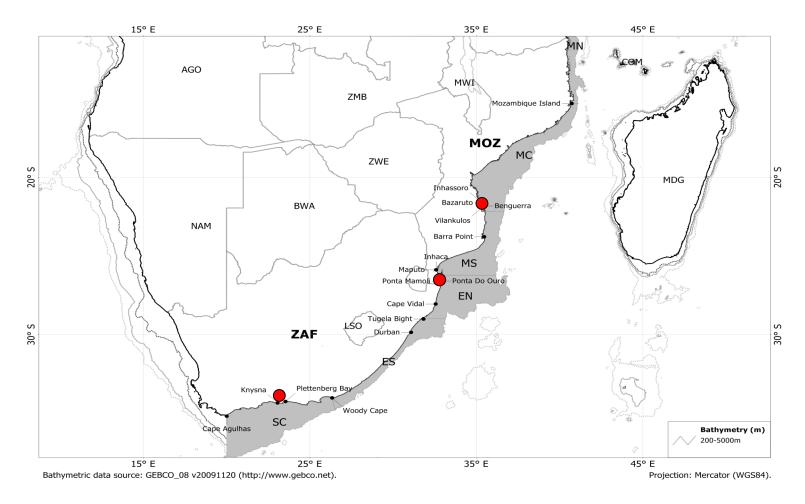


Figure 1.3 Delineation of breeding stock C1 and its migration into six data collection regions (Cerchio *et al.*, 2008b): South Coast of South Africa (SC), South Eastern South Africa (ES), North Eastern South Africa (EN), South Mozambique (MS), Central Mozambique (MC), and North Mozambique (MN). Red circles = This studies field site locations: Bottom) Plettenberg Bay/Knysna, South Africa, Middle) Bazaruto Archipelago, Mozambique, Top) Ponta Mamoli, Mozambique. (Figure adapted from Cerchio *et al.*, 2008b).

Breeding Stock C animals are considered to have a Nucleus feeding range in the Antarctic between 30°E-60°E, which extends to 10°E-80°E when including Margin Areas (Figure 1.1b) (Annex H - IWC, 2010). This corresponds to Breeding Stock C humpback whales being distributed within Antarctic Areas III and IV during summer (IWC, 1998). Connectivity between Breeding Stock C and the Antarctic feeding grounds is known through the recovery of two Discovery marks and two genotypic matches (Table 1.1-2).

Table 1.1 Summary of the migratory connections between Area C and the Antarctic from Discovery marks fired and recovered between 10°-60°E. Table adapted from IWC, 1998 (noting an error in the IWC table which lists Discovery mark 9326 twice).

Discovery mark number	Fired (Lat/Long)	Recovered (Lat/Long)
2779	64°S, 54°E	25°S, 47°E
9326	62°S, 11°E	26°S, 45°E

Table 1.2 Summary of migratory connections between breeding stock C and the Antarctic from matches of genotypes from biopsy samples. Table adapted from IWC, 2010.

Breeding sub-stock	Approx. feeding ground location	_
C1	~61°S, 5°W	_
C3	~63°S, 59°E	

An International Symposium and workshop on Southern Hemisphere humpback whales was held in Hobart, Tasmania 2006, to review the current status of humpback whales in the Southern Hemisphere and advance the comprehensive assessments for these stocks (IWC, 2011c). However, the complexities of the stock structures in breeding stocks B and C, and the lack of available data meant that further information was required before assessments for these stocks could be attempted. Comprehensive Assessments for breeding stocks B and C were completed in 2009 and 2011, respectively, with designations of two sub-stocks in Area B and four sub-stocks in Area C. However, the assessments were confounded by limited movement and mixing data and incomplete sampling coverage (IWC, 2011c). A limited understanding of interchange and distribution overlap between sub regions meant that the Breeding Stock B assessment was conducted using both a single and two-stock

model. The relationship both within and between Breeding Stocks B and C, and their subdivisions (B1, B2 and C1, C2, C3 and C4), including the extent of subdivisions, remains unclear. For Breeding Stock C, data were only available to complete assessments for sub-stocks C1 and C3, utilising four models based on different rates of exchange between the two regions.

Following the completion of Breeding Stock C's comprehensive assessment, a number of future recommendations were made by the Scientific Committee to enhance knowledge for this stock (IWC 2011). Included in these recommendations, were additional surveys to gain information on estimates of abundance and life history, with the continuation of genetic sampling to further strengthen the understanding of exchange between sub-stocks and enhance abundance estimation. The information used in the assessment of sub-stock C1, was based on a shore-based monitoring programme conducted at Cape Vidal, on the north east coast of South Africa between 1988 and 1991 (Findlay and Best 1996), two line-transect surveys off the coast of Mozambique during August and September in 1991 (Findlay *et al.*, 1994) and 2003 (Findlay *et al.*, 2011) and additional data (tail fluke images) collected by commercial whale-watching operators of the north east coast of South Africa (- See Cerchio *et al.*, 2008b and Chapter 3).

Findlay (2001) noted that differences between the CPUE indices between Mozambique and Madagascar whaling grounds during modern whaling suggested some stock segregation within the southwest Indian Ocean. Photographic and genotypic recaptures of individuals indicate potentially substantial connectivity between C2 and C3 (Ersts *et al.*, 2011) and between C3 and C4 (Dulau-Drouot *et al.*, 2011), which questions the independence between these sub-stocks. Limited movement (one individual) has been identified between C1 and C3 (Cerchio *et al.*, 2008b; IWC, 2011c). This is described in detail in Chapter 3. Molecular comparisons between the sub-stocks of Breeding Stock C suggest little gene flow with the exception of between C2 and C3 (Rosenbaum *et al.*, 2009). This is described in detail in Chapter 4.

Information regarding humpback whale migration along the south coast of South Africa is poor. Currently, there is no direct evidence to link humpback whales observed migrating past Plettenberg Bay/Knysna, South Africa with the wintering grounds off the southern coast of Mozambique. Knowledge of temporal usage patterns for the Mozambique wintering grounds is based on two line transect surveys off the coast of Mozambique in 1991(Findlay *et al.*, 1994) and 2003 (Findlay *et al.*, 2011) in August and September. Information relating to the migration route of breeding sub-stock C1 exists only for the northern section of the migration route as a result of the Cape Vidal shore-based survey (1988-1991) (Findlay & Best, 1996). With the exception of shore-based observations made by harbour pilots between 1903 and 1906 from the Knysna Heads, south coast of South Africa (Best & Ross, 1996), no information on the sub-stock C1 migration route exists south of Durban (East South Africa). A large degree of uncertainty still remains regarding the role of sub-stock C1 to the function of breeding stock C as a whole. The complex population structure of Breeding Stock C highlights the need for additional data to inform future assessments of population status.

1.2 Southern right whales

The genus Eubalaena (right whales) in the family Balaenidae consists of three species: E. glacialis, the North Atlantic right whale; E. australis, the southern right whale; and E. japonica, the North Pacific right whale (IWC, 2001). Right whales were hunted intensively throughout the 18th, 19th and 20th century and all three species were near to extirpation (Clapham et al., 2004; Perry et al., 1999; Townsend, 1935; Wray & Martin, 1983). In the Southern Hemisphere, assessment modelling indicated that by 1920 the entire population of southern right whales declined to about 300 individuals, or roughly 60 mature females (IWC 2001). The IWC recommended that there was value in identifying past and present wintering grounds as the basic "management units", which, where possible, should be the identity of true biological populations (IWC, 2001). Based principally on the distribution of current or historical sightings and catches, 11 management units based on breeding stocks in the Southern Hemisphere were identified: sub-Antarctic New Zealand, Australia, Central Indian Ocean, Mozambique, South Africa, Namibia, Tristan da Cunha, Brazil, Argentina, Chile/Peru and mainland New Zealand/Kermadec Islands. Although the Argentina, South Africa, Australia and sub-Antarctic New Zealand populations are recovering in abundance, several of the other stocks have shown little evidence of recovery and some might have been extirpated (Jackson et al., 2008a).

Whaling records for Southern Africa show that catches occurred primarily between Walvis Bay, Namibia and Delagoa Bay, Mozambique (Best & Ross, 1986; Du Pasquier, 1986; Richards & Du Pasquier, 1989; Townsend, 1935; Wray & Martin, 1983). Right whales were also known to range as far north as Gabon (Budker & Collignon, 1952) on the west coast of Africa to Antongil Bay, Madagascar (Richards and Du Pasquier, 1989), on the east coast. However, intense open-boat and pelagic whaling in the late eighteenth/early nineteenth centuries either extirpated or reduced these sub-stocks to extremely low numbers. Richards and Du Pasquier (1989) described how, by 1800, the right whale fishery around the Cape of Good Hope (1785-1809) was so severely depleted that whalers had begun to move elsewhere. Similarly, right whale catches at Walvis Bay (1788-1803) were also in decline by 1796. However, a decline in the availability of whales on the south coast to the east of the Cape (Mossel and Plettenberg Bay) did not appear to occur until at least 1843 (Best and Ross, 1986). Richards and Du Pasquier (1989) noted further how the selective takes of mother and calf pairs prevented the already depleted stocks from recovering after 1805. Open-boat whaling in the latter part of the 19th century and modern whaling in the 20th century along the southern coast of Africa may have been sufficient to prevent stock recovery until these operations ceased (Best & Ross (1986).

Modern whaling in southern Africa began at Durban in 1908 and quickly expanded to 11 floating factories and 17 land stations operating at various locations between the French Congo (Gabon) and central Mozambique (Best, 1994; Findlay, 2001). However, these operations were fairly heavily based on catches of humpback whales and with the decline of this species only four land stations remained by 1918. In 1935, the League of Nations introduced an international ban on right whale catches, although this was not incorporated into South African legislation until 1940. At least 13 whales were taken illegally after that date, until modern whaling finally ceased in South Africa in 1975 with the closure of the Durban whaling station (Best & Ross, 1986). Illegal Soviet whaling in the south east Atlantic (20°W-32°E) and south west Indian Ocean (32-73°E) between 1960/1961 and 1970/1971 took 704 and 309 southern right whales, respectively, with catches peaking in November and December

(Tormosov *et al.*, 1998). Although the illegal Soviet fleets operated from 1948, no location data were available for catches prior to 1960/1961 (Tormosov *et al.*, 1998).

During the years of modern whaling very few right whale catches (105-106 individuals between 1908 and 1975) were recorded in southern Africa, despite this species being of greater value than all other species except large male sperm whales (Best & Ross 1986). Given their value and relative ease of capture, it is likely that right whale numbers had already been severely depleted prior to the modern whaling period. There are no recorded right whale catches in modern whaling operations in other coastal regions of East Africa (although catches in some years are unspecified). The summer Crozet whaling grounds (40°-52°E) provided the majority of the 74 right whale catches (1835-1850) by American open-boat whalers analyzed by Wray & Martin (1983), and Soviet whalers took 309 right whales, mostly north and west of the Crozets in the early 1960s (Tormosov et al., 1998). There is little evidence of any large-scale catches of right whales around Madagascar, although coastal-based whaling began here in the mid-1750s (Rosenbaum *et al.*, 2001; Wray & Martin, 1983).

Currently, the only right whale sub-stock around southern Africa to have shown strong signs of recovery is that of South Africa (IWC, 2001), where sightings are common during the breeding season (June-October) (Best, 1994) when right whales frequent sheltered, sandy bays along the South African coast between Muizenberg and Woody Cape (18°30'E to 26°30'E) (Elwen & Best, 2004). The most recent (2008) abundance estimate of 4,600 individuals and a sustained annual recovery rate of *ca* 7% (Brandão *et al.*, 2011) suggest this is arguably the largest breeding stock in the Southern Hemisphere (IWC, 2001; NMFS, 2007). Based on the assumption that right whales from Namibia, South Africa and Mozambique were of the same stock, the pre-exploitation population size of Southern African right whales was estimated to be 20,000 individuals (Richards & Du Pasquier, 1989). Under this assumption, the current population was estimated in 2008 to be 23% of its original abundance (Brandão *et al.*, 2011). However, the pre-exploitation population estimate of 20,000 individuals may be an over-estimate, which would under-estimate the degree of recovery (Best *et al.*, 1995; Brandão *et al.*, 2011).

Data relating to the existence or post-whaling recovery of other populations on the west or east coasts of southern Africa are extremely sparse. Roux et al. (2001) reported only 36 sightings in Namibian waters for the period 1971-1999 as incidental sightings or from aerial surveys. Calves have been recorded on 12 occasions since 1990 of which 10 occurred between 1996 and 1999. Since then, the frequency of right whale sightings in Namibian waters has continued to increase although sightings of calves have remained low (J.P. Roux, pers. comm.). Recently, a comparison of photographic catalogues from Namibia and South Africa revealed 16 matches, suggesting connectivity between these two sub-stocks (Roux et al., 2011). Rosenbaum et al. (2001) reported two sightings of southern right whales (a male singleton and a mother-calf pair) off the northeastern and southeastern Madagascar coast in 1997 and 1999, respectively, and an additional sighting of a single whale off the southwest coast was reported in 2006 (S. Cerchio, pers. comm.). In 2007, two juveniles were photographed in Antongil Bay (15°S – 50°E) and in 2008 at Ile Sainte Marie (16°S – 49°E) a mother-calf pair was also photographed (M. Perri, pers. comm.). A sighting was also made at Reunion in September 1993 (Le Journal de l'Île de la Reunion Nr 13 460, Dimanche 26 Septembre 1993) and a cow-calf pair was seen in July 2009 (V. Dulau, pers. comm.).

The sighting in Antongil Bay (15°31'S; 49°56'E) Madagascar reported by Rosenbaum *et al.* (2001) is currently the northernmost published sighting for right whales in the western Indian Ocean.

Recent sightings in Mozambique are rare. In the absence of any cow-calf sightings in Mozambique, the IWC suggested a population size of zero for this sub-stock (IWC, 2001). However, in light of six sightings of 10 individuals made in Northern Kwa-Zulu Natal, South Africa (Findlay & Best, 1996) of whales heading towards Mozambique, the Mozambique population is actually considered to be less than 10 individuals. If right whales utilise the waters of Mozambique, either as a small remnant population or through the reoccupation of former habitat, the first step towards their conservation and management is the need for direct evidence of right whales off the coast of Mozambique.

1.3 Long-term human impacts

The impact of human activities can pose a significant risk to marine mammal populations and, despite protective legislation in many countries, conservation efforts for marine mammals have achieved mixed results to date (Reynolds *et al.*, 2009). Climate change (Learmonth *et al.*, 2006; Moore & Huntington, 2008), degraded water quality (Jarman *et al.*, 1996; Ross *et al.*, 1996; Van Bressem, *et al.*, 2009) fisheries bycatch (Moore, 2009; Read, 2005), habitat destruction (Ragen, 2005) and anthropogenic noise (Hildebrand, 2005; Nowacek *et al.*, 2007) are some of the many factors which threaten marine mammals and their long-term conservation (Reynolds *et al.*, 2009.

The impact of climate change on marine ecosystems has received particular attention in recent years and has become an important conservation issue (Barber *et al.*, 2012; Burek *et al.*, 2008; Moore & Huntington, 2008; Sundqvist *et al.*, 2012; Tynan & DeMaster, 1997). The effects of climate change are difficult to predict in part because of uncertainties about how physical changes will manifest in diverse environments, as well as how individual species and communities might respond (Baker *et al.*, 2006). It is widely anticipated that impacts on marine mammals will be mediated primarily via changes in prey distribution and abundance and that the more mobile (or otherwise adaptable) species may be able to respond to this to some extent (Simmonds & Isaac, 2007).

Some ice-associated marine mammals are already showing distribution shifts, compromised body condition and declines in production/abundance in response to sea-ice declines (Kovacs *et al.*, 2010). Migration has been suggested to be a function of food availability on the feeding grounds and the relationship between ocean-climate effects and sea-ice extent (Chaloupka *et al.*, 1999; Friedlaender *et al.*, 2006; Loeb *et al.*, 1997). Shifts in the temporal and spatial distribution of prey due to climate change have been suggested to affect the migration timings of Eastern Pacific grey whales (Rugh *et al.*, 2001; Shelden *et al.*, 2004; Swartz *et al.*, 2006). However, the interpretation of the response of baleen whale populations to climate change will, to some extent, be confounded by the fact that nearly all populations are recovering from overexploitation (Nicol *et al.*, 2008).

Amongst the many human induced threats to marine mammals, degradation in water quality as a result of anthropogenic activity is consistently considered to be a cause for concern and has been linked to an increase in the prevalence and severity of skin disease in cetaceans, especially in populations occupying or utilizing coastal habitats (for example -Bearzi *et al.*, 2009; Van Bressem *et al.*, 2008a; Wilson *et al.*, 1999). In addition, infectious diseases may increase with changes in ocean properties as a result of climate change (Gulland & Hall, 2007). The lack of long term data on health, diseases, and toxic effects in marine mammals severely limits the ability to predict the effects of climate change on marine mammal health (Burek *et al.*, 2008). Baseline data on marine mammal health parameters along with matched data on the population and climate change trends are needed to document these changes.

1.4 Thesis Structure

This thesis utilises data collected from Plettenberg Bay/Knysna, South Africa in the period 2005-2008, Bazaruto Archipelago, Mozambique during 2007 and Ponta Mamoli, Mozambique during 2009. Chapter 3 also utilises humpback whale tail fluke catalogues from southwest South Africa (Breeding Stock B2), Zanzibar (breeding Stock C1-N), and the Antarctic (Areas II, III and IV).

Using observations of migration patterns, mark-recaptures from photo-identification and genetic analysis of mtDNA, it aims to increase knowledge of migration and population structure and determine the role of breeding sub-stock C1-S within Breeding Stock C. It also describes southern right whale presence off the coast of Mozambique.

Chapter 2 combines sighting data collected from boat-based surveys off Plettenberg Bay/Knysna, South Africa in 2005-2008, Bazaruto Archipelago, Mozambique during 2007 and Ponta Mamoli, Mozambique during 2009, and line transect aerial surveys conducted off Bazaruto Archipelago, Mozambique in 2007. It describes the migration patterns and temporal trends of humpback whales along the migration route (South Africa/Mozambique) and breeding grounds off Mozambique. The northbound and southbound migration occurred from May to August and September to February,

respectively off Plettenberg Bay/Knysna, South Africa. Humpback whales were present on winter grounds off Bazaruto Archipelago, Mozambique between July and October. A shift in migration timing was also identified.

Chapter 3 investigates the movements of humpback whales within Breeding Stock C1 and investigates the level of exchange between Breeding Stock C1 and Breeding Stock B2 and Feeding Areas II, III and IV. Humpback whale tail fluke catalogues from Plettenberg Bay/Knysna are compared with those from Bazaruto Archipelago/Ponta Mamoli, Mozambique. These catalogues are then combined and compared against tail fluke catalogues from West Africa, Zanzibar and the Antarctic. Two photographic recaptures were made between the migration route off Plettenberg Bay/Knysna, South Africa and Ponta Mamoli, Mozambique confirming that the migration route on the south coast of South Africa is linked to winter grounds off the coast of Mozambique.

Chapter 4 uses molecular techniques to estimate levels of population structure of humpback whales sampled between Plettenberg Bay/Knysna, South Africa and Bazaruto Archipelago/Ponta Mamoli, Mozambique and Madagascar. The levels of genetic differentiation found in this study suggests that the migration route along the south coast of South Africa may also be utilised by humpback whales from Madagascar (breeding sub-stock C3).

Chapter 5 provides the first description for a previously undescribed skin lesion of unknown etiology observed on humpback whales off Plettenberg Bay/Knysna, South Africa and Bazaruto Archipelago/Ponta Mamoli, Mozambique. This lesion primarily affected mother-calf pairs, with the highest levels of prevalence and severity occurring during the southbound migration.

Chapter 6 documents the first sightings of southern right whales observed off the coast of Mozambique since the cessation of whaling.

Chapter 7 (General Discussion) provides an overview of the findings from each chapter and discusses the relevance of these findings in the context of conservation and management.

2. Chapter 2: South Africa to Mozambique: Seasonal patterns of humpback whales on their migration route and within the breeding ground of the mainland east coast of Southern Africa.

2.1 Introduction

Humpback whales undertake extensive seasonal migrations between their polar, high latitude summer feeding grounds and tropical, low latitude winter mating and calving grounds (Chittleborough, 1965; Dawbin, 1966). Within the Southern Hemisphere, summer feeding grounds are located south of 55°S around the continent of Antarctica, whilst wintering grounds are found at approximately 20°S (Clapham & Mead, 1999).

In the Southern Hemisphere, seven migratory and geographically separated humpback whale Breeding Stocks (labeled A to G) are recognised by the International Whaling Commission (IWC) (IWC, 1998). These breeding stocks correspond to six management units (Areas I-VI) in the Antarctic (Mackintosh, 1942) (Chapter 1, Figure 1.1). Extensive catches of humpback whales by modern whaling operations caused the near extirpation of this species in the Southern Hemisphere (Clapham *et al.*, 2005; Clapham & Baker, 2002; Findlay, 2001). A total of 47,134 individuals were reportedly taken from the coastal waters of Africa between Gabon on the west coast to Mozambique and Madagascar on the east coast, highlighting the presence of historical Southern African wintering grounds. Off the African coast between 1908 and 1913, nearly 21,000 humpback whales were caught; two-thirds of the total Southern Hemisphere catch of that species between 1908 and 1930 (Best, 1994). For the southwest Indian Ocean, Winn and Reichley (1985, in Findlay and Best, 2006) suggested a post-exploitation stock size of 340 whales.

Analyses of line transect data from the IDCR/SOWER cruises carried out in the Southern Ocean between 1978 and 2005, estimated that humpback whale abundance south of 60°S has increased from 9,701 (CV=0.36) (1980/81) to 41,648 (CV=0.11) (1997/98) individuals with an estimated rate of annual increase of 9.6% (95% CI 5.8-13.4%) (Branch, 2006). This rate of population increase is consistent with other

estimated annual rates from finer scale wintering ground surveys within the Southern Hemisphere (Bannister & Hedley, 2001; Bryden *et al.*, 1996; Findlay & Best, 2006; Noad *et al.*, 2008b; Paterson *et al.*, 2001). Zerbini *et al.* (2010) proposed a maximum rate of increase (ROI) for population growth of this species to be 11.8% per year. In light of this, Southern Hemisphere humpback whale populations appear to be recovering at near maximal rates from previous years of exploitation.

2.1.1 Breeding stock C

Breeding stock C comprises whales that breed in the Southwest Indian Ocean (IWC, 1998) and is divided into five sub-regions representing five breeding sub-stocks (C1-N, C1-S, C2, C3 and C4) (IWC, 2011c) (Chapter 1, Figure 1.2-3). Breeding Stock C1 breeds along the coastal regions of Mozambique, and its migration stream is thought to extend along the eastern coast of South Africa, at least as far west as Knysna (23°E) on the south coast of South Africa. At Mozambique Island (15°S) breeding stock C1 is divided into C1 North (C1-N) and C1 South (C1-S) although for management purposes the IWC recommended that C1-N and C1-S be included as one breeding stock (IWC, 2011c).

Understanding the temporal patterns of humpback whales during migration and on winter grounds can reveal aspects of population structure such as age, class and reproductive status (Brown & Corkeron, 1995; Craig *et al.*, 2003; Dawbin, 1997). This is important when managing stock recovery. Information relating to humpback whale temporal usage patterns in sub region C1-S and its migration route is limited to a small number of shore and boat-based surveys (described below). Shore-based monitoring of the humpback whale migration from Cape Vidal, South Africa (the presumed migration route of breeding stock C1) (Chapter 1, Figure 1.3) between 1988 and 1991 found the northbound migration to occur from June, peaking in late July, with some northbound whales seen as late as October (Findlay & Best, 1996). A change in migration direction from north to south occurred in August with incidental sightings of southbound whales as late as December. In 1990, the number of humpback whales passing Cape Vidal was estimated to be approximately 1,700 (Findlay & Best, 1996).

A distribution and abundance survey off the coast of Mozambique in 1991 (Findlay *et al.*, 1994) estimated the abundance to be 1,954 individuals (CV 0.38), comparable to the estimate from Cape Vidal (Findlay & Best, 1996). A 2003 survey, which extended some 300 nautical miles north of the 1991 survey, was assumed to be sampling animals from the same stock and resulted in an abundance estimate of 5,965 (CV 0.17). However, the authors noted that although the estimate is considerably higher than the 1991 survey and the Cape Vidal estimate, marked differences in survey procedures, design and area prevented increase rates being calculated (Findlay *et al.*, 2011).

At the western margin of this migration route, Best and Ross (1996) described records kept by harbour pilots of humpback whales passing the Knysna Heads, South Africa between 1903 and 1906. An estimated 250-450 humpback whales were seen between April and December and, in all four years, a reversal in migration direction from east to west occurred in August.

The most current abundance estimate for Breeding Stock C1 is 7,035 (90% Probability Interval 5,742 - 8824) (IWC, 2010). Population dynamics modelling suggests that this sub-stock has recovered to 77-84% of pre-exploitation levels (Annex H - IWC, 2010). However, given the imprecise abundance estimate for C1, caution should be used when considering the level of stock recovery.

2.1.2 Seasonality of temporal and spatial distribution

The factors that influence the temporal and spatial distribution of humpback whales vary seasonally. Migratory timing can be seen as a response to different selection pressures faced by sex and age classes of whales (mature females; mature males; juvenile males and females) as well as the reproductive cycle of the mature female (Craig *et al.*, 2003). Reproductive status may affect habitat preference with, for example, extensive shallow areas being favoured more by mothers with calves (Craig & Herman, 2000). This is reflected in a study of humpback whales in Antongil Bay, Madagascar in which mother-calf pairs showed strong preference for shallow water (<20 m deep) with competitive groups consistently being found in deeper water (Ersts

& Rosenbaum, 2003). Comparison by group type indicated that mother-calf pairs, mother-calf-escort trios and singletons maintained a relatively stable distribution with respect to depth and distance from shore while other pairs and competitive groups were the most variable.

The migration of humpback whales has been shown to be temporally segregated by age class, sex and reproductive status, although the pattern of segregation has been found to be different between Southern Hemisphere and North Atlantic populations. Dawbin (1997) found that the first whales to arrive at Southern Hemisphere wintering grounds were lactating females, followed by immature males and females, then mature males and resting females, and finally pregnant females. However, in the North Atlantic, Stevick *et al.* (2003) reported that males arrived earliest at wintering grounds in the West Indies, and suggested differing selection pressures between different populations being responsible for the dissimilar migratory schedules.

Few observations of humpback whales feeding in relatively low latitude waters (Baraff *et al.*, 1991; Best *et al.*, 1995; de Sá Alves *et al.*, 2009; Stockin & Burgess, 2005; Swingle *et al.*, 1993) suggests that migration to and from low-latitude winter grounds will exert an energetic cost to individuals, influenced by differing energy requirements of different age, sex and reproductive classes (Craig *et al.*, 2003). It has been suggested that the dynamics of the migration could be a function of food availability on the feeding grounds and also the relationship between ocean-climate effects and sea-ice extent (Chaloupka *et al.*, 1999; Friedlaender *et al.*, 2006; Loeb *et al.*, 1997). The distribution of humpback whales on the Southern Hemisphere feeding grounds is consistently and predictably associated with distance from the ice-edge and bathymetry, which influence the distribution of zooplankton (Friedlaender *et al.*, 2006). Therefore, changes in sea-ice extent and prey distribution will likely affect the feeding ground distribution of humpback whales. This is likely to affect migration timings because the distance between food source and wintering destination may vary according to changes in the spatial distribution of prey.

2.1.3 Agulhas Current and Mozambique Channel currents

The degree of utilisation or avoidance of currents by humpback whales during migration for energetic advantages is largely unknown but, if it does occur, it is likely to depend on spatial scale as well as current velocities and direction.

On a fine scale, the distribution of humpback whales within a migration route may be attributed in part to current regimes. Findlay and Best (1996) noted that the northbound flow of humpback whales off Cape Vidal, was closer inshore than its southbound counterpart. They proposed that this was due to the avoidance of the southward flowing Agulhas Current further offshore and utilisation of an inshore northward flowing counter current, and use of the southward flowing current in the southward migration. Similarly, off the west coast of Australia, observations showed humpback whales to remain offshore until they reached Camden Sound – Jenner *et. al.*, (2001) hypothesised that aggregations of northbound humpbacks at Frost and Tasmanian Shoals were staging areas whilst waiting for favourable tidal conditions on their way to Camden Sound through an area of strong currents. The presence and strength of the Agulhas Current system off east Africa, suggests that it may have an influence on the migration of breeding stock C1.

However, on a wide-scale, humpback whale migration routes within the Southern Hemisphere have been suggested to not be linked to ocean currents (Dawbin, 1966). Similarly, differences such as discontinuities between the Benguela Current in the South Atlantic and Agulhas Current in the southwest Indian Ocean are thought to have little effect on humpback whale inter-ocean exchange (Rosenbaum *et al.*, 2009). Water temperature may influence the distribution of humpback whale breeding grounds at the basin scale, with a preference for water temperatures greater than 24°C, irrespective of latitude (Rasmussen *et al.*, 2007). For example, the cooler Humbolt/Peru Current system in the eastern equatorial Pacific and the Benguela Current system in the eastern South Atlantic might result in a more northerly location of Central American (Breeding Stock G) and West African (Breeding Stock B) breeding grounds (Rosenbaum *et al.*, 2009).

The Agulhas Current is the western boundary current of the Indian Ocean and is divided at Port Elizabeth into the Northern Agulhas and Southern Agulhas Current (Lutjeharms, 2007). It is fed by three precursors in the southwest Indian Ocean: flows from east Madagascar; southward flowing eddies in the Mozambique Channel; and flows from the Southwest Indian Ocean subgyre (Lutjeharms, 2007; Schouten *et al.*, 2002). The existence of a western boundary current flowing down through the Mozambique Channel has now largely been discounted (Ridderinkhof *et al.*, 2001; Schouten *et al.*, 2003; Swart *et al.*, 2010). Instead, a flow of approximately 300 km wide anticyclonic eddies propagate southwards through the channel, resulting in a rectified southward current on its western side and a rectified northward current in the centre of the channel (Swart *et al.*, 2010). The velocity of this southward current in the west of the channel has been recorded to exceed 50 cm s⁻¹, whereas the weaker northerly current in the Channel's centre exceeded 15 cm s⁻¹ (Ridderinkhof *et al.*, 2010). Along the Mozambique coast, landward of the southward current, a northward flowing inshore counter-current may exist (Lutjeharms & Jorge da Silva, 1988).

The Northern Agulhas Current flows southwards following the continental shelf (its core lies over the 200m isobath) from its northern limits of Southern Mozambique. Downstream of Port Elizabeth, the continental shelf widens forming the Agulhas Bank. There, the Southern Agulhas Current moves offshore following the eastern edge of the bank (Rouault *et al.*, 2010); (Lutjeharms, 2007). At 38°S, it reaches a zone of eastward retroflection known as the Agulhas retroflection (Gordon, 1985) making an anticyclonic turn and forming the Agulhas Return Current, flowing eastwards along the sub-tropical convergence (Lutjeharms, 2007). The retroflection zone of the current creates large anticyclonic eddies called Agulhas rings – enclosed bodies of warm Indian Ocean water which are shed from the Agulhas Current into the South Atlantic – an important factor in inter-oceanic exchange processes (Gordon, 1985; Gordon *et al.*, 1992).

Irregular anomalies in the flow of the Agulhas Current, known as Natal pulses, have been frequently described (de Ruijter *et al.*, 1999; Lutjeharms & Roberts, 1988) (Bryden *et al.*, 2005; Tsugawa & Hasumi, 2010). Originating in the Natal Bight north of Durban, Natal pulses are large solitary meanders moving downstream in the otherwise largely laterally stable Agulhas Current. Moving downstream at 10-20

km/day and growing up to 200 km in diameter, the number of meanders increases west of East London (de Ruijter et al., 1999). This can have a substantial effect on the structure of the Southern Agulhas Current regime west of Port Elizabeth (Bryden et al., 2005; Rouault et al., 2010). Furthermore, Natal pulses control the shedding of the Agulhas rings with each ring shedding preceded by the appearance of a Natal pulse close to Durban, with a time lag of 165 days (van Leeuwen et al., 2000). Associated with the Agulhas Current, are inshore counter-currents, which are known to vary in strength, substantially increasing in the presence of a Natal pulse (Lutjeharms & deRuijter, 1996). Lutjeharms and deRuijter, (1996) noted that it was also possible to predict the advent of strong inshore currents further downstream according to the presence of a Natal Pulse. Roberts and van den Berg (2005) describe the occurrence of an along-shore current on the Tsitsikamma coast (adjacent to Plettenberg Bay), which is variable, but flows predominately eastwards reaching surface velocities of 115 cm s⁻¹. If migrating East African humpback whales utilise or avoid the Agulhas Current for an energetic advantage, changes in the Agulhas Current structure may influence the offshore distribution of the migration stream.

2.1.4 Aims

The aim of this Chapter is to clarify the temporal usage patterns of humpback whales along the coast of East Africa and to consider the role of the Agulhas Current system in relation to humpback whale migration. Seasonal occurrence patterns of humpback whales are described from three locations along the mainland east coast of Southern Africa: the migration route off Plettenberg Bay/Knysna, South Africa; an area of transition between migration route and breeding ground habitat off Ponta Mamoli, Mozambique; and breeding ground habitat off the Bazaruto Archipelago, Mozambique.

2.2 Methods

2.2.1 Data collection

Three field sites (Chapter 1, Figure 1.3) were used for data collection between 2006 and 2009. These were Plettenberg Bay and Knysna, South Africa (19 June - 27 December, 2006 and 23 June – 10 December, 2008), Ponta Mamoli, Mozambique (4 August – 13 October, 2009) and Bazaruto Archipelago, Mozambique (14 June – 13 November, 2007). Observation data were collected from either commercial whalewatching vessels or research vessels on an *ad hoc* basis. In addition, aerial surveys were also conducted at the Bazaruto Archipelago in 2007. Skin samples were collected using standard biopsy sampling procedures from free-swimming and dead stranded animals.

2.2.2 Boat-based surveys

Trip duration was calculated according to the launch and beaching time for each trip (with the exception of Bazaruto research trips – see section 2.2.1). In Knysna, launch and beaching was considered to be the time the boat passed through the "Knysna Heads" - the entrance to the Knysna Lagoon. For Bazaruto, research trips were launched from Inhassoro and operated eastwards of Bazaruto Island in relatively deep water. A total of 60 minutes travel time (30 minutes after launching and 30 minutes prior to beaching) covered an area of shallow water, sand bars and reefs. Commercial whale-watching trips launched from Vilankoulos in the southwest corner of Bazaruto Bay, operated outside the Archipelago eastwards of southern Bazaruto Island, Benguerra and Margaruque. The vessels navigated out of the archipelago through narrow channels between shallow reefs that separated the open ocean from the Archipelago. Launch and beach time was considered to be the point at which the vessels passed through the channels.

Commercial whale-watching trips operated in sea conditions indicated by Beaufort scale 5 or less; biopsy sampling was prohibited from these vessels. In Plettenberg Bay/Knysna whale-watching vessels were restricted to a maximum of 20 minutes

with each group of whales. Research trips operated in sea conditions of Beaufort 4 or less. Commercial whale-watching or research trips did not follow a standard transect survey design; instead, whales were located on an *ad-hoc* basis according to the most favourable local sea conditions.

On all trips (whale-watching and research), humpback whales were located by searching for any visual cues such as blows, breaches, dorsal fins, and splashes. Sightings data (start/end time of encounter, date, GPS location, species, group size, group composition, direction of travel and weather conditions) were recorded for every group (one or more individuals) encountered during a trip. The minimum requirement for a humpback whale sighting to be recorded was for the group size to be adequately determined or estimated. A humpback whale whose body length was less than one third the length of its mother was considered to be a calf born within that season. An individual was considered to be a lactating female when accompanied by a calf. Commercial whale-watching vessels aimed to keep vessel impact to a minimum by avoiding encounters with mother-calf pairs and continuing to search for other groups. However, an initial period was spent observing the animal(s) to check for the presence or absence of a calf so such occasions were recorded as sightings. If a calf were observed, the whale-watching vessel would end the encounter and continue searching.

2.2.3 Aerial surveys

Between 9 June and 17 November 2007, 13 aerial line-transect surveys were flown over the Bazaruto Archipelago region. These surveys were designed to estimate dugong (*Dugong dugon*) abundance and as a result some areas within the survey area were unsuitable habitat for humpback whales (shallow areas, primarily south of the northern point of Bazaruto Island). Although incidental sightings are made from these shallow areas (pers comm. Martin Oosthuizen), they are believed to result from navigational errors by the whales. The only two humpback whales recorded in this area during the period of data collection were individuals stranded on sand banks, seemingly trapped by a falling tide. These areas of unsuitable habitat and the corresponding transect effort were excluded from analysis.

Survey flights were only conducted in wind speeds of less than 20 knots. The survey area suitable for humpback whales was 1,355 km² and was covered by 18 east-west line-transects between the 10 m and 20 m bathymetry contours, to the west and east, respectively. Transects had an equal north-south spacing of four nautical miles. Opportunistic sightings were recorded on north-south off-effort transits between transects. The region covered during the aerial surveys was a shallower water habitat (<20 meters) than that covered by the boat-based surveys, which occurred in deeper water.

Surveys were carried out in a Cessna 182 fixed-wing aircraft flying at an altitude of 500 feet (152 meters) and a speed-over-ground of 90 knots, flown by pilots experienced in marine mammal surveys. The aircraft was fitted with four seats with the pilot and data recorder in the front seats and two observers in the rear seats. All four occupants were in continuous communication with each other throughout the survey via intercom headsets. Observers wearing polarized sunglasses visually searched an area of water perpendicular to the aircraft's flight path from as directly below the aircraft as possible to the horizon through flat Perspex windows. On-effort surveying began and ended with the start and end of each transect line. If a sighting required confirmation, the aircraft "broke-off" the transect line and circled the sighting. This period between leaving and rejoining the transect line was recorded as "confirmation mode" and "off effort".

When either observer made a sighting, the data recorder was immediately informed so that a GPS position could be taken using a handheld Garmin GPS when the sighting was abeam of the aircraft. The observer, using a handheld clinometer, measured the vertical angle to the sighting. The species and group size for each sighting were also recorded as well as the name of the observer who made the sighting.

2.2.4 Data Analysis

2.2.4.1 Vessel-based data analysis

The total vessel trip time, from launching to beaching, consisted of two components, "search time" and "handling time". In Plettenberg Bay, Knysna, Ponta Mamoli and commercial whale-watching trips in Bazaruto, trip time commenced and ended with

the launch and beach times recorded for each trip. For Bazaruto research trips, 60 minutes of travel time was required to pass through an area considered unsuitable habitat for humpback whales. This was excluded from the trip time.

The handling time associated with each sighting was determined by the start and end time of a humpback whale encounter. For a small number of sightings (<20 in total) that did not have handling times recorded, the mean handling time for that year and trip type (commercial whale watching or research trip) was used. The handling time for a sighting began as the vessel started its approach to the animal(s) and ended once the boat departed from the encounter. Total handling time on each trip was subtracted from total trip time to give search time, which was used as the measure of effort. Mean encounter rates (sightings per unit effort) for each month were then calculated with standard errors relating to the variability of encounter rates among trips within each month. Encounter rates for sightings, individuals and mother-calf pairs per hour were plotted for each year and field site.

Mean group size was calculated by month. The frequency of each group size was calculated for each field season. For Plettenberg Bay/Knysna, group size data were pooled for the two seasons (2006 and 2008) and stratified into the northbound and southbound migration. The northbound section included all sightings up to and inclusive of 31 August. The southbound section included all sightings from 1 September onwards. This division was based on changes in encounter rates, travel direction and group composition data (see sections 2.3.1.1 to 2.3.1.3).

Travel direction according to the eight cardinal compass points was determined for all sightings. This was determined at the first opportunity during the approach in order to minimise any impact of the vessel on the direction of the animals(s). If a direction could not be determined due to a lack of suitable observation, the direction of travel was recorded as "Undetermined". Sightings in which the animals were not travelling (e.g. logging or milling) were recorded as "No direction".

Potential Bias due to southern right whale sightings

During August and September, southern right whales (Eubalaena australis) are

present within Plettenberg Bay and are also targeted by the commercial whale watching vessels. Fewer sightings of southern right whales occur along the more exposed coastline of Knysna and their commercial whale watching vessels continue to target humpback whales preferentially. However, humpback whale encounter rates between Plettenberg Bay and Knysna showed no evidence of an encounter rate bias due to the presence of southern right whales in Plettenberg Bay. Therefore data from Plettenberg Bay and Knysna were combined for 2006 and 2008.

2.2.4.2 Aerial survey data analysis

The aerial survey data were analysed using software DISTANCE version 6.0 release 2 (Thomas *et al.*, 2009) to estimate abundance by fitting a detection function to the perpendicular distance data.

The areas of shallows, reefs and shifting sand bars considered unsuitable habitat for humpback whales were excluded from analysis by restricting it to areas greater than 10 meters in depth. There was no single bathymetry dataset that adequately covered the entire survey area so a combination of bathymetry datasets - GEBCO one minute global grid (www.gebco.net), GEBCO 30 second global grid (www.gebco.net; www.gebco.net, 2010), STRM30 Plus (Becker et al., 2009; Smith & Sandwell, 1997), ETOPO1 (Amante & Eakins, 2009; Becker et al., 2009) and high resolution satellite imagery (<u>www.bing.com/maps/</u>, 2011) - were used to create an estimated 10 m depth contour along the coastline of the Bazaruto Archipelago region using the GSHHS Coastlines dataset (Wessel & Smith, 1996). The shallow region inside the Archipelago often included "pools" equal to, or deeper than 10 m (although these varied greatly with each bathymetry dataset); these were not included because of the shallow (<10 m) surroundings. The shifting nature of the sand banks within the Archipelago means that over time, any bathymetry dataset for this region will inevitably become inaccurate over certain areas. The estimated 10 m bathymetry aimed to account for numerous and large variations between the different bathymetry sets. All transect lengths were calculated using the estimated 10 m bathymetry contour as the western limit.

Multiple flights along the same transect lines were treated as a single sampling unit. This was to avoid treating the 18 transects which were repeated on up to 13 occasions as 220 separate sampling units, which would violate the assumption of independence among transects leading to a bias in the variance estimate (Buckland *et al.*, 2001).

The distance of the sighting from the track line was calculated using the equation:

$$d = \frac{h}{90 - (TAN\theta)}$$

Where d = perpendicular distance, h = altitude of aircraft, θ = angle of declination.

2.2.4.2.1 Abundance estimation

Because of the low sample size of humpback whales recorded during the aerial surveys the detection function was modelled using humpback whale sightings made during both on-effort (along transect lines) and off-effort (the flight path between transect lines) periods ('all-effort' dataset). Non-bubble windows limited the ability to observe the trackline directly below the aircraft, and, thus, g(0) < 1, therefore the perpendicular distance from the transect line was left truncated at 175 metres. General methodology is available for left-truncation (Alldredge and Gates 1985). The perpendicular distance from the transect line was right truncated at 1116 meters. Humpback whale abundance, \hat{N} , was estimated using 'on-effort' sighting data only, using the equation:

$$\hat{N} = \hat{D} \cdot A$$

where,

$$\hat{D} = \frac{n \cdot \overline{s}}{2wL \cdot \hat{P}a}$$

Where \hat{D} =estimated density of individuals, A= area of survey (km²), \bar{s} = mean group size, n = number of groups detected, w= right truncation width, L = total combined lengths of all transects, $\hat{P}a$ = estimated average probability of detection derived from

the detection function fitted to both on-effort and off-effort sighting data. Bias in mean group size was assessed by regressing group size on perpendicular distance.

Because different parameters were estimated from different datasets, the different components of the abundance estimate variance, $\hat{var}(\hat{N})$, were combined using the Delta method (Buckland *et al.*, 2001). The detection probability variance $\hat{var}(\hat{P}a)$ and cluster size variance $\hat{var}(\bar{s})$ were derived from the detection function using the 'all-effort' dataset. The variance of n, $\hat{var}(n)$, was derived from variability in encounter rate among transects in the 'on-effort only' dataset (Buckland *et al.*, 2001).

$$\operatorname{var}(\hat{N}) = \hat{N}^{2} \cdot \left\{ \frac{\operatorname{var}(n)}{n^{2}} + \frac{\operatorname{var}(\overline{s})}{(\overline{s})^{2}} + \frac{\operatorname{var}(\hat{P}_{a})}{(\hat{P}_{a})^{2}} \right\}$$

2.2.4.2.2 Detection function/model selection

Half-normal and hazard rate key functions were used to model the detection function g(y). Series expansions to the key functions in the form of cosine, Hermite and simple polynomial functions were added to try to improve the fit of each model to the data. Model selection was based on Akaike's Information Criterion corrected for small sample size (AICc). Goodness of fit diagnostics - Chi-square test, Kolmogorov-Smirnov test and QQ-plots - were used to assess the model fit to the data.

2.3 Results

2.3.1 Plettenberg Bay/Knysna, South Africa

In 2006, 141 boat trips were conducted (Table 2.1) (mean monthly trip frequency 20.1 trips, SE=3.1). Of these, 133 trips were carried out onboard commercial whale watching vessels (mean trip length 123 minutes, SE=1.8) and 8 trips were carried out onboard a research vessel (mean trip length 208 minutes, SE=6.8). In 2008, a further 140 trips were made (mean monthly trip frequency 20 trips, SE=4.2). Of these, 135 trips were carried out onboard commercial whale watching vessels (mean trip length

109 minutes, SE=2.3) and 5 trips were from a research vessel (mean trip length 250 minutes, SE=52.8).

Table 2.1 Number of trips and hours of sea time conducted from commercial whale watching and research vessels, from June to December 2006 and May to December 2008.

	Number of	Trips	Number of	Hours
	2006	2008	2006	2008
Commercial	133	135	272	246
Research	8	5	28	21
Total	141	140	300	267

Humpback whale encounters were made up to 11.5 km offshore from Robberg Peninsula (the most southerly point of the study area), limited only by the offshore range of the vessel. Beyond this, blows were still regularly seen out on the southern horizon. Based on the observer's height above sea level on the vessel, the horizon distance is approximately 5 km. Therefore, the width of the migration stream extends a minimum of 16.5 km offshore. Anecdotal evidence from skippers of sailing and fishing vessels suggests that the width of the migration stream off Plettenberg Bay/Knysna extends much further offshore, with unconfirmed reports of humpback whales being sighted 40 km from the coast. An unknown number of whales are likely passing Plettenberg Bay/Knysna undetected and the width of the stream beyond 16.5 km and its density distribution is also unknown.

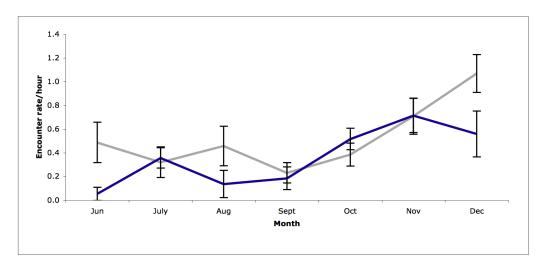
2.3.1.1 Encounter rates

Mean monthly encounter rates of sightings (Figure 2.1a), individuals (Figure 2.1b) and mother-calf pairs (Figure 2.1c) in 2006 and 2008 followed a similar trend. However, encounter rates of sightings and individuals during 2008 were higher for June, August and December. In June 2006 only one sighting consisting of two individuals was made. This sighting occurred at the very end of the month on 30 June, 11 days after fieldwork commenced, compared to 2008 when five sightings totalling 20 animals were made from 23 June. Mean monthly encounter rates of sightings decreased in August 2006 but increased in August 2008. In 2006, no

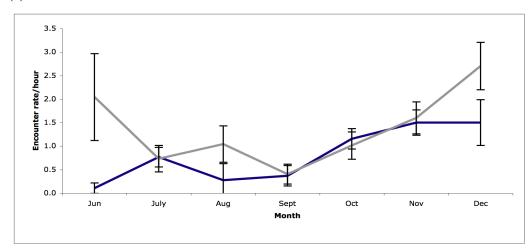
humpback whale sightings occurred between 13 August and 23 September (41-day break in sightings), whilst during the same period in 2008, humpback whales continued to be sighted, with 10 sightings of 20 individuals being recorded over the equivalent time frame, with no obvious break in sightings.

Mean monthly encounter rates were higher in 2008 than in 2006 but in 2008, data were only collected until 10 December, compared to 27 December in 2006. Excluding sightings after 10 December 2006 did not increase the mean monthly sighting encounter rate for December 2006 to those observed in December 2008. Therefore, the mean monthly encounter rate for sightings in December 2008 compared to December 2006 did not suffer from an upwards bias by only having data from the first half of the month.

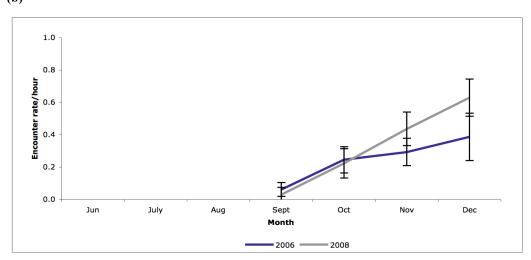
Mother-calf pairs were first observed on 24 September 2006 and 22 September 2008 with an increasing trend to the end of the study period in December (Figure 2.1c). On breeding grounds, mother-calf pairs are known to utilize shallow, inshore waters more than other cohorts of the population (Ersts & Rosenbaum, 2003). If this habitat preference continues through the migration, it would likely cause a degree of sampling heterogeneity, as the whole width of the migration stream (possibly as wide as 40 Km) could not be sampled.



(a)



(b)



(c)

Figure 2.1 (a-c). Mean encounter rates per hour for each month in Plettenberg Bay and Knysna, from June to December 2006 and 2008 for (a) all sightings, (b) individuals and (c) mother-calf pairs. Standard error for each monthly mean is shown as a vertical bar.

2.3.1.2 Direction of travel

The direction of travel data (Figure 2.2) clearly show a distinction between the northbound and southbound migration, as represented by an eastbound (June to August) and westbound (September-December) flow along the approximately southfacing coastline of Plettenberg Bay and Knysna.

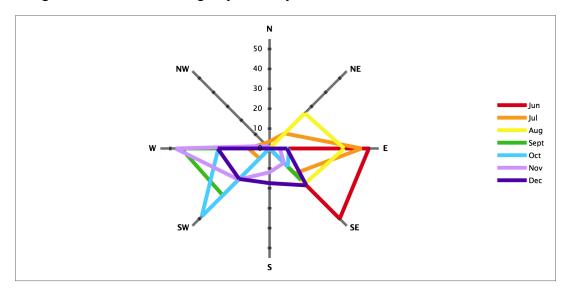


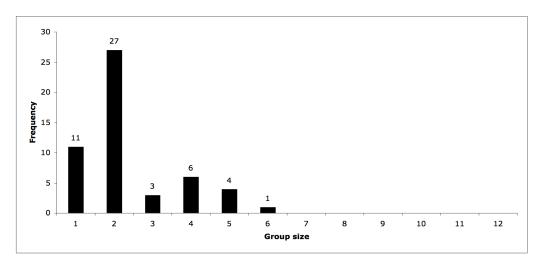
Figure 2.2 Proportional travel direction relative to cardinal compass points for each month (June to December) in Plettenberg Bay and Knysna during 2006 and 2008. Each cardinal point displays the percentage of sightings travelling in that direction within each month displayed as a different colour.

2.3.1.3 Group size and composition

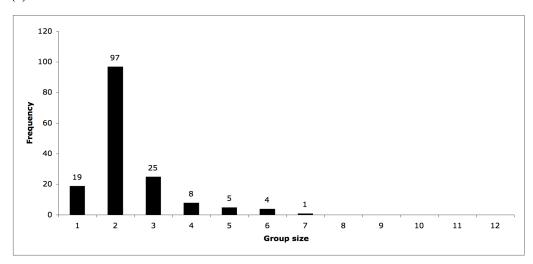
Group size frequency data were pooled for 2006 and 2008 (N=209) and then divided into the northbound migration (Figure 2.3a) and southbound migration (Figure 2.3b) – based on the first sightings of mother-calf pairs, increasing mean monthly encounter rates for sightings and individuals in September, direction of travel data and a 41-day absence of sightings between 13 August and 23 September 2006. Pairs (52%) and singletons (21%) made up the main proportion of the northbound migration followed by groups of 4 (12%) and 5 (8%) individuals. For the southbound migration, the majority of sightings consisted of pairs (61%) followed by trios (15%) and singletons (11%). This increase in the number of pairs and trios during the southbound migration was partly due to mother-calf pairs and mother-calf-escort trios. The proportion of sightings that contained one or more mother-calf pair for each month

during the southbound migration (September to December) in Plettenberg Bay and Knysna during 2006 and 2008 increased from 23% in September (n=13) to 62% in December (n=29).

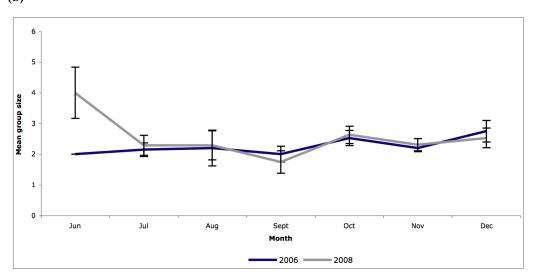
Mean monthly group size (Figure 2.3c) was consistent between 2006 and 2008. Pooling over 2006 and 2008 resulted in a mean group size of 2.4 individuals for both the northbound and southbound migration (northbound SE=0.2, southbound SE=0.1).



(a)



(b)



(c)

Figure 2.3 (a-c). Group size frequency during (a) the northbound migration (June to August) n=50 and (b) the southbound migration (September to December) n=159 and (c) mean group size for each month from June to December in Plettenberg Bay and Knysna during 2006 and 2008. Standard error for each monthly mean is shown as a vertical bar.

2.3.1.4 Feeding event

On 16 November 2008, an atypical behavioural observation was made from a stationary vessel with its engines turned off during an encounter of two adult humpback whales off Knysna in sea conditions of Beaufort 1. The observed behaviour strongly suggests that these two humpback whales were feeding on shoals of baitfish during their southbound migration. The two whales remained in an area for more than 45 minutes where large, dense shoals of baitfish (most likely sardine) could clearly be seen below the surface and as dark patches covering several thousand square meters on the surface. The whales remained parallel during synchronous surface intervals, generally maintaining a distance of 10-50 meters from each other. Fluke-up dives were always very steep combined with very irregular dive intervals and ventilation frequency. Rapid directional changes within the location of the shoals of fish were evident upon each surfacing. No lunge feeding was observed at the surface but it was apparent that the whales were diving only within or along the edge of the baitfish shoals. Moving at a fast pace within the area, ventilations were markedly more powerful than observed during other behavioural states, indicative of high intensity behaviour. No competitive or sexual interactions such as "chasing" or "avoidance" of one animal by another was seen to occur at any point to indicate this to have been a social interaction rather than a feeding event. Cape gannets (Morus capensis) were also observed feeding in the vicinity of the whales.

2.3.2 Bazaruto Archipelago, Mozambique

During 2007, 29 trips (144 hours) were conducted (Table 2.2) (mean monthly trip frequency 4.8 trips per month, SE=1.1). Of these, six were carried out onboard commercial whale watching vessels (mean trip length 189 minutes, SE=14.4) and 23 trips were carried out onboard a research vessel (mean trip length of 327 minutes, SE=31.4). Compared to previously described trips in Plettenberg Bay/Knysna, trips were much fewer in frequency per month but more than 50% longer. Mean monthly encounter rates were therefore more susceptible to daily variability in humpback whale occurrence and in some months, represent an unequal spread of effort within a given month. Whales were encountered up to 13 km eastwards of Bazaruto, the most easterly point of the study area, (43 km from the launch site of Inhassoro) and limited

only by the offshore range of the vessel. Beyond this, blows were still regularly seen out on the eastern horizon, which when based on the observer's height above sea level, equates to surfacing whales being seen approximately 18 km offshore from Bazaruto Island. However, blows and breaches would have been visible at much greater distances.

Table 2.2 Number of trips and hours of sea time conducted from commercial whale watching and research vessels at Bazaruto Archipelago, from June to November 2007.

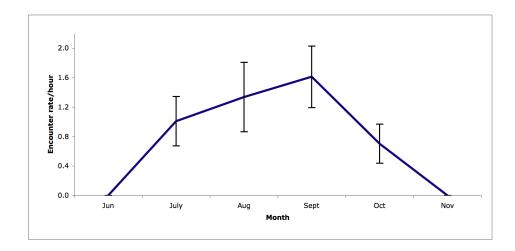
	Number of Trips	Number of Hours
	2007	2007
Commercial	6	19
Research	23	125
Total	29	144

2.3.2.1 Encounter rates

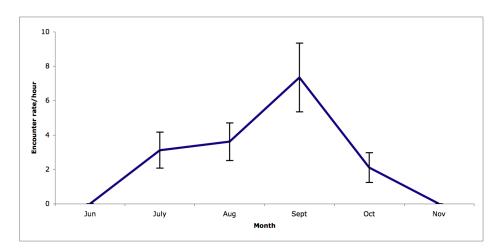
Whales were encountered between 1 July and 18 October (Figure 2.4a) but no subsequent trips were conducted until 8 November. A 28-day gap in the data occurred from 12 September to 10 October, which may have biased September encounter rates if they were different during the rest of the month. The mean number of sightings (Figure 2.4a) and individuals (Figure 2.4b) encountered per hour within each month are represented by a unimodal peak in September. Encounter rates of sightings and individuals per hour increased from 1.3 and 5.1, respectively, at the start of September to 2.8 and 13.3, respectively, by 12 September. This suggests that mid-September may represent peak densities for humpback whales off Bazaruto Archipelago.

Mother-calf pairs were only encountered between 2 September and 18 October (Figure 2.4c). Direction of travel data (Figure 2.5) and three descriptions recorded in the field also strongly support the assumption that the southbound migration begins no later than the first few days of September. On 4 September, a mother-calf-escort trio was observed heading eastwards around the northern tip of Bazaruto before veering southwards on a steady course. A second mother-calf pair was also recorded later that day as travelling directly southwards. On the same day, a visual scan of the

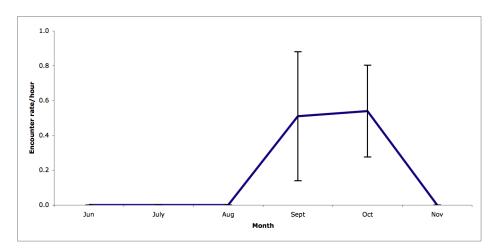
eastern horizon estimated 8-10 groups of humpback whales to be visible with each scan (the highest rate recorded in the field notes), all of which appeared to be moving southwards.



(a)



(b)



(c)

Figure 2.4 (a-c). Mean encounter rates for (a) sightings (b) individuals and (c) mother-calf pairs per hour for each month in Bazaruto Archipelago, from June to November 2007. Standard error for each monthly mean is shown as a vertical bar.

2.3.2.2 Direction of travel

Data collection primarily occurred on the eastern side of Bazaruto Island. As a result, humpback whale sightings were rarely observed to be heading southwest, west or northwest due to the physical barrier of Bazaruto Island (Figure 2.5). A steep shelf edge running north-south on the eastern side of Bazaruto then veers to the northeast of Bazaruto Archipelago forming the Sofala Bank. In July, all travelling whales were seen to be heading either north or northeast, following this topographic feature. This suggests that animals observed in the early part of the breeding season were animals migrating to a location north or north east of Bazaruto. During August, there was no clear directional movement of travelling humpback whales with only 11 sightings recorded as travelling. The southbound migration becomes apparent during September, increasing into October (Figure 2.5).

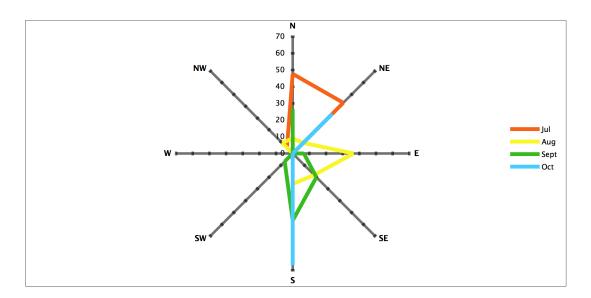
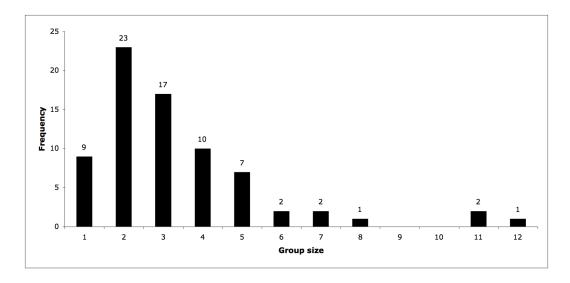


Figure 2.5 Proportional travel direction relative to cardinal compass points for each month (July to October) in Bazaruto Archipelago during 2007. Each cardinal point displays the percentage of sightings travelling in that direction within each month, with each month displayed as a different colour.

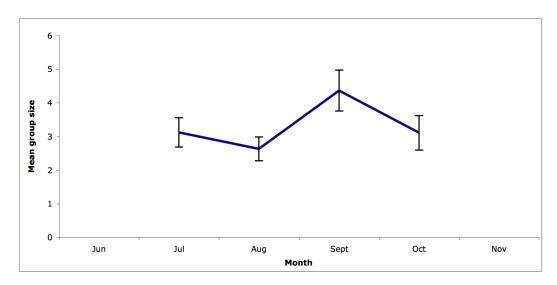
2.3.2.3 Group size and composition

Group size ranged from 1 to 12 animals (n=74) (Figure 2.6a). Pairs (31%) and trios (23%) were most frequently sighted, followed by quartets (13.5%), singletons (12%) and groups of 5 (9.5%). The proportion of sightings that contained one or more

mother-calf pair, for each month in Bazaruto Archipelago from July to October during 2007, increased from 37.5% in September (n=24) to 79% in October (n=9). Mean group size was 3.36 (SE=0.26) across the survey period. Mean monthly group size (Figure 2.6b) was highest during September (4.36 individuals, SE=0.61).



(a)



(b)

Figure 2.6 (a) group size frequency n=74 and (b) mean group size for each month in Bazaruto Archipelago from June to November during 2007. Standard error for each monthly mean is shown as a vertical bar.

2.3.2.4 Aerial surveys

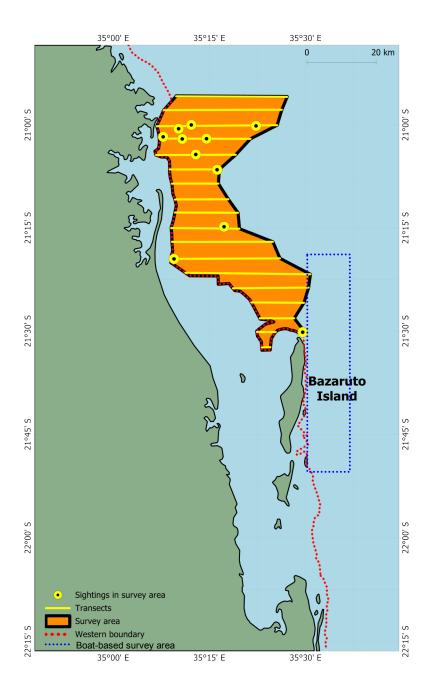


Figure 2.7 Map of the Bazaruto Archipelago region, Mozambique, showing the line-transect aerial survey area (the western boundary restricted by depth >10m using an estimated 10m-bathymetry contour), flown transect lines and on-effort humpback whale sightings. Boat-based survey area is indicated by blue dots.

2.3.2.4.1 Survey area

With the exception of 17 September when only the four most southerly transects were completed, all 18 transects were flown on each aerial survey where the most northern

and southern transects in Figure 2.7 correspond to transect numbers 3 and 20, respectively, in Table 2.3. Individual transect lengths ranged from 2.35 to 30.01 km with 359.81km on-effort distance flown per survey (with the exception of 17 September which covered a distance of 32.79 km). A combined total on-effort distance of 4350 km was flown during the 13 aerial surveys.

Table 2.3 Aerial survey effort for all surveys flown between 9 June and 17 November 2007, Bazaruto Archipelago region, Mozambique. Transect lengths are restricted to habitat suitable for humpback whales. * = Transect flown. X = Transect not flown.

			Combined]	Date						
Transect No.	Length (Km)	Frequency flown	length (Km)	09 Jun	19 Jun	26 Jun	08 Jul	17 Jul	04 Aug	20 Aug	17 Sept	20 Sept	06 Oct	14 Oct	29 Oct	17 Nov
3	30.01	12	360.10	*	*	*	*	*	*	*	X	*	*	*	*	*
4	31.90	12	382.75	*	*	*	*	*	*	*	X	*	*	*	*	*
5	32.53	12	390.75	*	*	*	*	*	*	*	X	*	*	*	*	*
6	24.62	12	295.45	*	*	*	*	*	*	*	X	*	*	*	*	*
7	21.52	12	258.24	*	*	*	*	*	*	*	X	*	*	*	*	*
8	13.40	12	160.81	*	*	*	*	*	*	*	X	*	*	*	*	*
9	12.55	12	150.63	*	*	*	*	*	*	*	X	*	*	*	*	*
10	14.40	12	172.76	*	*	*	*	*	*	*	X	*	*	*	*	*
11	17.03	12	204.36	*	*	*	*	*	*	*	X	*	*	*	*	*
12	18.42	12	221.02	*	*	*	*	*	*	*	X	*	*	*	*	*
13	27.20	12	326.46	*	*	*	*	*	*	*	X	*	*	*	*	*
14	29.36	12	352.32	*	*	*	*	*	*	*	X	*	*	*	*	*
15	33.69	12	404.32	*	*	*	*	*	*	*	X	*	*	*	*	*
16	20.39	12	244.74	*	*	*	*	*	*	*	X	*	*	*	*	*
17	14.19	13	184.43	*	*	*	*	*	*	*	*	*	*	*	*	*
18	9.29	13	120.80	*	*	*	*	*	*	*	*	*	*	*	*	*
19	6.95	13	90.39	*	*	*	*	*	*	*	*	*	*	*	*	*
20	2.35	13	30.60	*	*	*	*	*	*	*	*	*	*	*	*	*
Total (Km)	359.81		4350.52													

2.3.2.4.2 Sightings

Humpback whales were sighted inside the survey area between 4 August and 29 October, occurring on 4 (31%) of the 13 surveys. A total of 13 on-effort sightings (Table 2.4) were made during the 13 aerial surveys, comprising 23 adults and three

calves. A peak in sightings occurred on 20 August with no sightings made during September or November. Group size ranged from 1-3 individuals. Mother-calf pairs were sighted between 20 August and 6 October. Sightings were also recorded outside (eastwards) of the survey area during off-effort periods, of which four were utilized in the fitting of the detection function, to estimate the abundance of humpback whales within the survey area (see 2.2.5.1-2.2.5.2). The earliest of these off-effort sightings occurred on 26 July - five days earlier than the earliest boat-based sighting of humpback whales in the region of Bazaruto Archipelago during the 2007 field season.

Table 2.4 On-effort humpback whale sightings made during 13 aerial surveys from 9 Jun to 17 Nov 2007

Date	Transect No.	Group Size	Adults	Calves	
4 Aug	6	2	2	0	
4 Aug	7	1	1	0	
20 Aug	5	2	2	0	
20 Aug	5	2	2	0	
20 Aug	6	3	3	0	
20 Aug	8	1	1	0	
20 Aug	15	1	1	0	
20 Aug	19	2	1	1	
6 Oct	5	3	2	1	
6 Oct	14	2	1	1	
29 Oct	5	1	1	0	
29 Oct	12	3	3	0	
29 Oct	18	3	3	0	

2.3.2.4.3 Detection function

The lack of bubble windows meant that the visibility beneath the aircraft was restricted. After inspection of the data, they were left truncated at 175 m from the transect line. One sighting at 1959 m was categorised as an outlier and the data were right truncated at 1116 m, the perpendicular distance of the next most distant sighting (Figure 2.8). This discarded 12% (n=2) of sightings at 53 m and 1959 m, which, although it was a high proportion of the data because of the very low overall sample size, was necessary to achieve a good fit of the detection function to the data. The

remaining fifteen sightings were used to model the 'all-effort' detection function, which included four off-effort sightings.

For the 'all-effort' dataset, the half-normal model performed best with the least number of parameters; the addition of series expansions or covariates did not improve model performance (Table 2.5).

Table 2.5 Model outputs for half-normal and hazard rate key functions using the 'all-effort' dataset. P-values are given for Chi-square goodness of fit test and Kolmogorov-Smirnov test.

Model	AICc	# Parameters	GOF Chi-p	K-S p
Half-normal	202.49	1	0.648	0.909
Hazard rate	204.70	2	0.369	0.978

The average probability of detection, $\hat{P}a$, was 0.400 (CV=0.25). This gives an estimated effective strip half-width of 444.41 m for the fitted detection function (Figure 2.8).

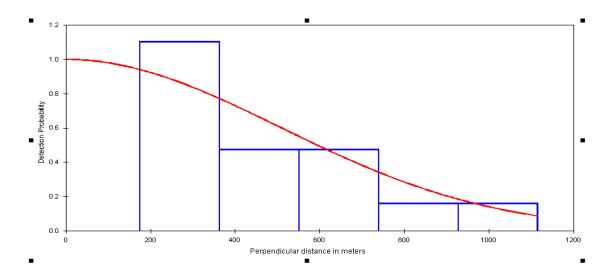


Figure 2.8 Probability of detection g(y) for 'all-effort' with data left-truncated at 175 m and right-truncated at 1116 m (n=15).

2.3.2.4.4 Group size

Expected group size was estimated as 2.16 (SE=0.28), which was not significantly different (p = 0.58) from the mean observed group size of 2.0 (SE=0.19). Therefore, mean observed group size and its variance were used to estimate abundance.

2.3.2.4.5 Abundance estimate

Abundance was estimated using the on-effort sightings (n=11) resulting in an estimate of 8 individuals (Table 2.6) and upper and lower 95% confidence intervals of (3, 19).

Table 2.6 Summary of values for estimated abundance, density and their associated parameters and variance. * Indicates values derived from 'on-effort-only' dataset. CVs are shown in brackets. esw=Effective strip width.

L (Km)	esw (m)	Р̂а	n*	\overline{S}	<i>Ô</i> (Km ⁻²)	A (Km 2)	Ñ
4350.5	444.41	0.40	11	2	0.0056		8
		(0.25)	(0.37)	(0.10)			(0.46)

2.3.3 Ponta Mamoli, Mozambique

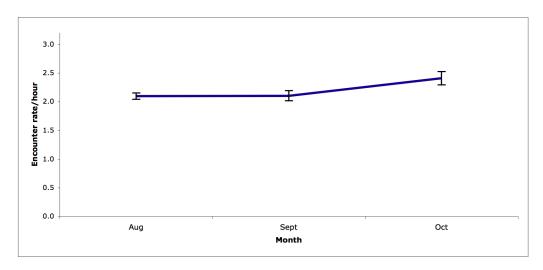
During 2009, 13 trips (34 hours) were conducted (Table 2.7) from a research vessel (mean monthly trip frequency 4.3 trips per month, SE=1.3), with a mean trip length of 156 minutes, (SE=15.9). Seven trips were conducted in August. Only three trips were conducted during 4-10 September and three trips during 3-13 October. This unequal sampling across the months of September and October means that these data may not be representative. Furthermore, data collection was conducted at least 7 nautical miles offshore, seaward of a Marine Protected Area (MPA) offshore boundary. A number of sightings, many of which were known to be mother-calf pairs, were seen but not recorded during transit across the MPA. Land-based observations also indicated that humpback whales primarily occurred offshore.

Table 2.7 Number of trips and hours of sea time conducted from commercial whale watching and research vessels at Ponta Mamoli, Mozambique, from August to October 2009.

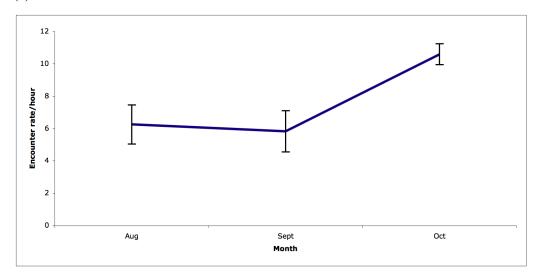
	Number of Trips	Number of Hours
	2009	2009
Commercial	0	0
Research	13	34
Total	13	34

2.3.3.1 Encounter rates

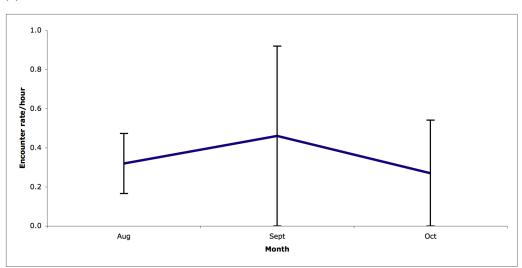
Encounter rates at Ponta Mamoli were higher than those recorded in both Plettenberg Bay/Knysna and Bazaruto. Humpback whales were encountered on all 13 trips. The mean monthly encounter rate of sightings (Figure 2.9a) remained constant between August and October (2.1 sightings per hour August-September, August SE=0.3; September SE=0.4; 2.4 sightings per hour October, SE=0.5). Within months, the lowest encounter rate of sightings occurred on 4 August (0.6 sightings per hour) whilst the highest occurred on 6 October (3.4 sightings per hour). Mean monthly encounter rates of individuals (Figure 2.9b) remained constant during August and September (August 6.2 individuals per hour, SE=1.2; September 5.8 individuals per hour, SE=1.3). Subsequently, the encounter rate of individuals almost doubled during October (10.6 individuals per hour (SE=0.6)). Mother-calf pairs were only recorded on six occasions – three pairs in August, two pairs in September and one pair in October. However, the three mother-calf pairs recorded at Ponta Mamoli during August were all still travelling in a north easterly direction. The first mother-calf pairs travelling southwards were recorded on 4 September. Although the sample size is small and the encounter rates likely biased, the overall trend in these results is consistent with those from Bazaruto.



(a)



(b)



(c)

Figure 2.9 (a-c) Mean encounter rates for sightings (a) individuals (b) and mother-calf pairs (c) per hour for each month in Ponta Mamoli, from August to October 2009. Standard error for each monthly mean is shown as a vertical bar.

2.3.3.2 Direction of travel

Humpback whales were recorded to be travelling primarily northeast during August at Ponta Mamoli (Figure 2.10). In contrast, in Bazaruto, this northerly flow appeared to have stopped during the same period, occurring only in July. A clear change to a southerly direction occurred from 31 August. Prior to this date, 86% (6 sightings) of sightings recorded as travelling were heading northeast. From 31 August onwards, 86% (12 sightings) were recorded travelling in an approximate southbound direction. This change to a southward flow from 31 August is consistent with Bazaruto, which indicated the start of the southbound migration from 4 September.

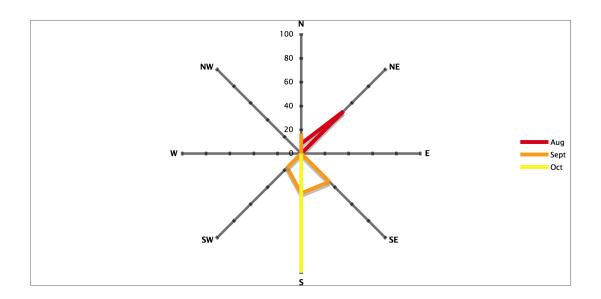
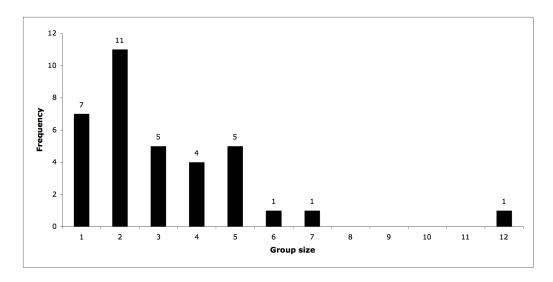


Figure 2.10 Proportional travel direction relative to cardinal compass points for each month (August to October) in Ponta Mamoli during 2009. Each cardinal point displays the percentage of sightings travelling in that direction within each month, with each month displayed as a different colour.

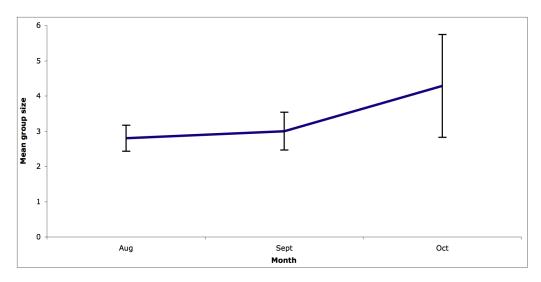
2.3.3.3 Group size and composition

Group size ranged from 1 to 12 animals (n=35) (Figure 2.11a). Pairs (31.5%), singletons (20%), Trios (14%) and groups of 5 (14%) were most frequently sighted. Mean group size (Figure 2.11b) remained constant during August to October (August 2.8 individuals, SE=0.37; September 3.0 individuals, SE=0.53; October 4.2 individuals, SE=1.46). The higher variation in mean group size during October was

solely due to a single encounter of 12 individuals. Overall mean group size was 3.14 (SE=0.38).



(a)



(b)

Figure 2.11 (a-b). Group size frequency N=35 (a) and mean group size for each month (b) in Ponta Mamoli from August to October 2009. Standard error for each monthly mean is shown as a vertical bar. Y axis = Group size frequency (a); Mean group size (b).

2.4 Discussion

2.4.1 Plettenberg Bay/Knysna

The field seasons in 2006 and 2008 did not commence until 19 and 23 June, respectively; therefore data for June represents an incomplete month of effort. In 2008 one trip made by the Centre for Dolphin Studies, prior to the start of the field season for this research project, sighted three singleton humpback whales on 29 May. Similarly, photo identification data also collected by the Centre for Dolphin Studies after the end of this project's field season in December, show humpback whales still to be migrating southwards as late as 26 February. These sightings and photo identification records show that the start of the northbound and end of the southbound migration occurred outside of this study's field season and also show that humpback whales occur off the coast of Plettenberg Bay/Knysna between May and February. The northbound migration at this latitude occurs from late May to August whilst the southbound migration occurs from September to late February. Determining when the migration switched direction was based on a number of factors: sightings of mother-calf pairs and increasing mean monthly encounter rates for sightings and individuals in September; a 41-day absence of sightings between 13 August and 23 September 2006, combined with a distinct difference in the directional flow of animals between August and September (Figure 2.2). The seasonal bimodality, with well defined directions of travel according to a northbound and southbound migration of whales off Plettenberg Bay/Knysna is partially consistent with Best and Ross (1996) who describe observations made by the pilot(s) at the Knysna Heads between 1903 and 1906. These authors noted that humpback whales were present between April and December with a switch in migration direction from east to west, during August. The data presented here suggests a possible shift in seasonality by one month for the start of the northbound migration and by two months for the end of the southbound migration (- see section 2.4.4).

Incidental sightings and strandings (pers. comm. Ryan Johnason and Stephan Swanson, Oceans Research) at Mossel Bay (22° 07' E) and Wilderness (22° 33' E) (pers. obs.) plus direction of travel data recorded off Plettenberg Bay/Knysna provides evidence that the migration extends westward of Knysna (23° E). Best *et al* (1998)

suggested that a sighting of a mother-calf pair on 2 January 1997 made from the 'Shonan Maru 2' at 35° 22' S, 20° 11' E could either represent the western extent of southbound migrating East African humpback whales or alternatively be animals from the West African breeding population.

A mean group size of 2.4 was recorded for both the north and south bound migration. Whales migrating northbound (Figure 2.3a) and southbound (Figure 2.3b) were dominated by groups of two animals with a maximum group size of seven individuals. In June 2006, despite 9 sea trips being made from 19 June, only one sighting of two individuals was made compared to the same month in 2008 where five sightings were made during seven trips from 23 June. In Bazaruto Archipelago and Ponta Mamoli, however, a much higher frequency of groups larger than two were recorded. Brown and Corkeron (1995) found a similar trend in migrating whales off eastern Australia to that off Plettenberg Bay/Kynsna although the group size was largely singletons as well as pairs. Findlay and Best (1996) showed group size for migrating whales off Cape Vidal also to be dominated by pairs of animals. However, the distribution of group sizes from Cape Vidal falls between Plettenberg Bay/Knysna and Bazaruto Archipelago, which is logical considering its location between the two regions.

It thus appears that larger groups (>2) become much less frequent with distance from the breeding ground. This is likely to be due to a reduction of large competitive group activity as competition between males for female access declines away from the wintering grounds as the balance between the desire to breed or feed shifts. Brown and Corkeron (1995) suggested that for migrating whales off eastern Australia it was likely that the determinants of group size were social rather than ecological because neither foraging strategies nor responses to predation appeared to be major factors. Craig *et al.* (2003) suggested that a complex interaction between photoperiod, hormonal state, body condition and food availability will likely determine when or if individual whales migrate. Animals were detected as far as 16.5km from the coast, with anecdotal reports of humpback whales up to 40km. Chittleborough (1965) noted that migrating humpback whales along the Australian coast passed mainly within 18.5 km of the coast, with few being seen more than 37 km from the coast. As the fast southward flowing Agulhas Current exists further offshore and largely out of visual

range, any animals utilizing this for an energetic advantage during migration would also likely pass un-detected.

If the assumption that the southbound migration at Plettenberg Bay/Knysna begins in September is correct, then August would be considered as the end of the northbound migration where encounter rates of sightings would likely decrease to zero (assuming no overlap between the north and southbound migration at this latitude). In 2006, a 41-day absence of sightings occurred between 13 August and 23 September. Yet in August 2008 an increase in mean monthly encounter rates for sightings and individuals was observed with relatively continuous sightings through August and September.

Differences between 2006 and 2008 in encounter rates during August and September may have been due to the presence of a Natal pulse. Using a time series of ASAR and AVISO range-directed surface velocities, Rouault *et al* (2010) described an anomaly in the Agulhas Current, which was observed around 12 and 13 August 2008 offshore of Port Elizabeth for a period of approximately one month. This 150 km diameter Natal pulse, (Rouault *et al.*, 2010) and its cyclonic circulation was followed by an early Agulhas Current retroflection in September (M.Rouault, pers. comm.). As a result of the interruption of this warm Agulhas input, changes to inshore countercurrents and colder water would have also been expected on the coastal and shelf regions (Bryden *et al.*, 2005) (M.Rouault, pers. comm.).

This could have affected migrating humpback whales and their detection in two ways:

- 1) Migrating whales that typically pass undetected offshore of Plettenberg Bay/Knysna could have been pushed closer inshore by this pulse in 2008 making them available for detection.
- 2) A faster flowing or an additional temporary inshore counter-current in 2008 could have resulted in whales passing at a faster rate leading to an increase in encounter rates.

The first scenario seems the most likely cause for the increase in encounter rates observed during August 2008, although the second scenario or a combination of both cannot be ruled out. The first scenario is consistent with Lutjeharms and deRuijter

(1996) who suggested that any substantial change in the flow behaviour of the Agulhas Current might force a change of unknown magnitude in the distribution and behaviour of both inshore and offshore organisms. With relatively high flow rates in the southern Agulhas Current of up to 2 m s⁻¹ (7.2km/h) (Lutjeharms, 2007), temporal variability in the flow and structure of the Agulhas Current may present a significant influence on the direct route of migrating humpback whales. Findlay and Best (1996) proposed that the northbound migration of humpback whales off Cape Vidal, South Africa in 1990 occurring closer inshore than its southbound counterpart could be a result of whales utilising an inshore, northwardly-flowing counter-current, avoiding the southwardly-flowing Agulhas Current.

Although it is not possible to quantify the influence of the Agulhas Current on humpback whale migration using the data presented here, it is hard to disregard any influence of the Natal Pulse on encounter rates. The location, timing and effects of such a large Natal Pulse, combined with its close proximity to Plettenberg Bay/Knysna appear to correlate closely to differences in encounter rates observed off Plettenberg Bay/Knysna between 2006 and 2008. If so, the migration route of humpback whales would appear to have been somewhat influenced by the Agulhas Current. An energetic advantage could be gained by migrating closer inshore to avoid swimming against high velocity water masses further offshore driven by a Natal Pulse. Alternatively, increased flow rates of either existing or temporary inshore counter-currents induced by the Natal Pulse could also provide more energetically advantageous conditions for northbound migrating whales than in the absence of a Natal Pulse. Either of these scenarios would result in an increase in encounter rates such as those observed off Plettenberg Bay/Knysna in 2008.

Records of feeding events in low-latitude waters range from the opportunistic (Danilewicz *et al.*, 2008; de Sá Alves *et al.*, 2009; Stockin & Burgess, 2005; Swingle *et al.*, 1993) to more regular and pronounced occurrences. Barendse *et al.* (2010b) and Best *et al.* (1995) describe numerous and regular feeding events off the west coast of South Africa during the migration of the West African humpback whale population. This caused a temporary suspension of the migration (Best *et al.*, 1995) for a number of these whales where the Benguela upwelling region off the west coast of South Africa may function as an important feeding area (Barendse *et al.*, 2010b).

The feeding behaviour observed off the coast of Knysna is the first description of any feeding activity by east African humpback whales during their migration. However, as this record was the only example of this behaviour observed during the entire study period, it is likely that this simply represents an opportunistic foraging opportunity, unlike the more pronounced activity observed by Barendse *et al.* (2010b) and Best *et al.* (1995).

2.4.2 Bazaruto Archipelago and Ponta Mamoli

Although differences in methodologies and survey platforms between the shallow water aerial surveys and deeper water boat-based surveys prevent a direct comparison between the two areas, some clear differences and similarities are evident. No humpback whales were sighted by either boat-based or aerial surveys after the end of October.

Boat-based encounter rates and frequent observations of numerous groups of whales indicated by sets of blows occurring in multiple locations across the survey area indicate that the deeper waters outside the Archipelago support a much higher density of humpback whales than the shallower areas covered by the aerial surveys. The line-transect aerial surveys over the region north and westward of Bazaruto Archipelago estimated 3 – 19 individuals, density 0.0056 km², utilised the inshore, shallow areas between late June to the end of October. However, due to such a low sample size, the abundance estimate is imprecise and without correction for the number of animals missed along the transect line. Nonetheless, occasional boat-based exploratory trips across the aerial survey area also resulted in minimal sightings, which also suggest a low density of humpback whales in that area.

Findlay *et al.* (2011) calculated mean group sizes and densities of humpback whales to the north and south of Bazaruto Archipelago between 20-200 metre isobaths. Group sizes of 1.63 (SE=0.67) and 2.50 (SE=0.22) and densities of individuals (n.miles²) of 0.41 (SE=0.10 and 0.56 (SE=0.18), for north and south respectively, were found. Group sizes recorded during the aerial surveys ranged between 1-3 individuals with a mean of 2 individuals, which was lower than a mean group size of 3.36 (SE=0.26) individuals recorded off Bazaruto Archipelago and 3.14 (SE=0.37) off

Ponta Mamoli during boat-based surveys in comparatively deeper waters. A potential bias in recorded group sizes may exist due to the visual detection of animals favouring larger groups, however during data collection, groups of all sizes were searched for and larger groups were not targeted preferentially over smaller groups. The aerial and boat-based survey mean group sizes are consistent with Ersts and Rosenbaum (2003) who found social organisation to be a function of depth, where mother-calf pairs and escorted mother-calf pairs show a preference for shallow waters.

Mother-calf pairs accounted for 30% of the aerial survey sightings within this shallow water in Bazaruto Bay, with the first mother-calf pair being sighted on 20 August. This was 10 days earlier than the records from boat-based surveys, where the first sightings were of mother-calf pairs seemingly migrating south. Those boat-based records described mother-calf pairs to be navigating eastwards into deeper water to pass the physical barrier of the Bazaruto Archipelago islands before veering southwards whilst staying close to the coast. This suggests that these whales were moving from the shallower waters covered by the aerial surveys to the north and west of Bazaruto Island, which is consistent with early mother-calf pair sightings associated with the shallow waters and with an absence of deep-water sightings. It is therefore likely that mother-calf pairs utilise the coastal waters immediately north of the Archipelago, either as a nursing area or as part of their southward migration route from areas further north, whilst other cohorts favour the deeper water regions beyond the shelf of the Sofala Banks.

This is consistent with a 20m yacht survey of the coastal regions of southern and central Mozambique between 18° and 26° S during August/September in 1991 (Findlay *et al.*, 1994). The authors found humpback whales to be distributed throughout the region where densities of groups with calves were higher over the Sofala Bank region than the rest of the survey area. Conversely, a ship based survey in 2003 reported a relatively even distribution of such groups across the survey (Findlay *et al.*, 2004). Furthermore, Findlay *et al* (2004) also reported lower than expected sighting frequencies in areas of low salinity - the lowest being on the Sofala Banks where the Save, Zambezi and Pengue Rivers discharge. These authors suggested the avoidance of turbid waters by humpback whales might have influenced their distribution over the Sofala Banks. During an exploration flight north of the

aerial survey area, a substantial increase in turbidity associated with the proximity of the Save River (the most southerly river input on the Sofala Banks and closest to the survey area) was evident. If humpback whales avoid turbid waters as suggested by Findlay *et al* (2004), then the low abundance estimate for Bazaruto Bay, derived from aerial surveys in this study, is consistent with the observed turbidity in shallow waters north of the aerial survey area relative to the proximity and discharge of the Save River.

Although the abundance estimate derived from the aerial surveys is imprecise and negatively biased, it does provide further information on humpback whales in the Bazaruto Archipelago region, which is consistent with patterns seen during the boat-based surveys and of those described elsewhere (Ersts & Rosenbaum, 2003; Findlay *et al.*, 2004; Findlay *et al.*, 1994). For the aerial survey area (shallow water), 20 August had the highest density of sightings whereas during the boat-based surveys (deep-water), encounter rates peaked in mid-September. Group size frequencies from Bazaruto (Figure 2.6a) and Ponta Mamoli (Figure 2.11a) showed pairs to be the most frequently sighted groups although larger groups of up to 12 individuals were also common. This is different from that recorded by Findlay *et al* (2004) where singletons and pairs made up the large majority of sightings with a maximum group size of only five individuals being recorded.

Seasonal catch data of humpback whales from Inhambanne (formerly Linga Linga) 23° 47′ S, 35° 32′ E during 1912 and 1913 indicated unimodal seasonality and, consequently, the suggestion of this being the northern limit of the migration (Best *et al.*, 1998). The author also noted a difference in the timing of these peaks, which occurred during the first 10 day period of August in 1912 and in July in 1913. Encounter rates from Bazaruto Archipelago follow this unimodal seasonality although its peak did not occur until late August (aerial sightings) or September (boat-based encounter rates) – which are quite different considering the proximity of Inhambanne to the Bazaruto Archipelago (~250km). Ponta Mamoli seems to be an area of transition between migration route and breeding ground habitat.

At Cape Vidal, between 1988 and 1991, the peak of the northward migration occurred in late July, switching from a north to southward migration between 5 and 25 August

– although northwardly migrating groups still occurred as late as October in 1990 (Findlay & Best, 1996). This is somewhat different to the patterns observed at Ponta Mamoli and Bazaruto Archipelago. At Ponta Mamoli, prior to 31 August, only one out of seven sightings recorded travelling were heading south, the remainder were heading north or northeast. From 31 August onwards only 3 of the 16 sightings recorded travelling had any northerly heading. Although the sample size is small for Ponta Mamoli, the switch from north to south migration on 31 August is similar to that found at Bazaruto Archipelago, where a southbound movement was evident from the start of September.

What is strikingly different is the occurrence of northwardly migrating groups observed by Findlay and Best (1996) at Cape Vidal as late as October. At Bazaruto there was very little northerly movement after the end of July. More importantly, the last known sightings (which were recorded during aerial surveys) on 29 October signified the end of the seasonal occurrence of humpback whales at Bazaruto. An aerial survey over shallow water and boat-based surveys in deeper water were made after this date, but no further sightings were made. It could be that a number of whale sightings were missed during this period; however, boat-based encounter rates were already decreasing throughout early October and were at their lowest point by mid-October. In light of this and combined with the direction of travel data from Bazaruto Archipelago and Ponta Mamoli, it seems unlikely that the northbound migration in October observed by Findlay and Best (1996) continued much further north. It is possible that some males occasionally head north for short periods whilst on the southbound migration in search of reproductive females (pers comm. Ken Findlay). This could account for the northbound migration animals observed in October by Findlay and Best (1996). Alternatively, those whales travelling north did so at a distance offshore greater than the range of detection available during this study.

2.4.3 Migration route and breeding ground links

The historic records of one lost and recovered harpoon links the whaling grounds of Durban, South Africa, and Ling-linga, Mozambique (Olsen, 1914). Two individual humpback whales have been re-sighted through photo identification between

Plettenberg Bay/Knysna and Ponta Mamoli (approximately 650 km south of Bazaruto Archipelago) (see Chapter 3, Section 3.3.2.). This links whales observed on the migration route off the coast of Plettenberg Bay/Knysna to the breeding grounds off Mozambique (Area C1S).

Using theodolite tracking, Findlay (1994 in Best *et al.*, 1995) estimated average net swim speeds to be 3.6 - 5.4 km/h during the northbound migration and 5.3km/h during the southbound migration off Cape Vidal. Findlay and Best (2006) noted that such instantaneous swim speeds should be regarded with caution when integrating them into migration rates. However, as these are the only swim speeds estimated for the east African humpback migration, they were used to estimate expected timings of whales between Plettenberg Bay/Knysna and Bazaruto Archipelago. The distance from Plettenberg Bay/Knysna to Bazaruto Archipelago is approximately 2000 km. Using the speeds estimated by Findlay (1994 in Best *et al.*, 1995) and assuming a continuous swim speed, northbound migrating whales observed in Plettenberg Bay/Knysna could be expected to take between 15.4 and 23.1 days to reach the Bazaruto Archipelago. Similarly, southbound migrating whales observed in Bazaruto could be expected to take 15.7 days to reach Plettenberg Bay/Knysna.

Sighting records show that humpback whales were present in Plettenberg Bay/Knysna as early as 29 May in 2006 and, in 2008, whales were recorded from 23 June. Assuming a continuous swim speed equal to the estimates made by Findlay (1994 in Best *et al.*, 1995), whales observed in Plettenberg Bay/Knysna in late May should be present off Bazaruto Archipelago between 12-20 June. The first humpback whales to be seen at Bazaruto were on 26 June, which is slightly later than expected using the northbound swimming speeds from Cape Vidal. This may have been a result of an overall slower swim speed due to resting activities (Chittleborough, 1965), slower movement during the night and under poor weather conditions when Findlay and Best could not track the animals or earlier animals at Bazaruto being missed. Observations of frequent blows far out on the eastern horizon off Bazaruto Archipelago suggest that whales were distributed much further offshore than was accessible during data collection. Furthermore, direction of travel data from Bazaruto also shows that animal movements appeared to still be travelling northwards in July. Findlay and Best (1996) noted that the peak of the northbound migration did not occur until late

July off Cape Vidal during 1991. Therefore not all whales observed in Plettenberg Bay/Knysna would necessarily have been encountered at Bazaruto – an unknown portion may have passed undetected or offshore on route to areas further north. Alternatively, some whales may have remained south of Bazaruto.

Applying the same swimming speed estimates, the first mother-calf pairs recorded to be travelling south from Bazaruto on 4 September would be expected to pass Plettenberg Bay/Knysna on 19 September. This is consistent with the first sightings of mother-calf pairs in Plettenberg Bay/Knysna occurring on 22 September in 2006 and 24 September 2008. Swimming speed estimates made by Noad and Cato (2007) during the southbound migration off southeast Queensland, Australia varied according to group composition; groups containing calves were 15% slower (3.6 km/h) than non-calf groups (4.2 km/h). This was a result of stop-start swimming activity likely due to the nursing and resting of young. Therefore mother-calf pairs would be expected to travel at speeds slightly slower than the average speed estimated by Findlay (1994 in Best et al., 1995) for the southbound migration as a whole, which is also consistent with the slightly later than predicted arrival of mother-calf pairs at Plettenberg Bay/Knysna. The Agulhas Current is also fast flowing off Cape Vidal and so the short instantaneous measurements made by Findlay et al (1994) could overestimate the speed of migration. The speed of migration could also be further affected according to spatial and velocity variability in the Agulhas Current such as the previously discussed presence of the Natal pulse.

Findlay and Best (1996) noted that southwardly migrating groups were observed as late as December off Cape Vidal. This is fairly consistent with the sighting and photo identification records from Plettenberg Bay/Knysna, which show humpback whales, including mother-calf pairs, to be present as late as February. However, the last observed sightings from Bazaruto Archipelago occurred at the end of October, considerably earlier than at Cape Vidal and Plettenberg Bay/Knysna. If whales were not present at Bazaruto after the end of October but are known to still be heading south as late as December off Cape Vidal (with an estimated 95% of whales passing Cape Vidal within the visibility limits of the land based survey (Findlay and Best, 2006)) and February off Plettenberg Bay/Knysna, why were these later whales not observed off Bazaruto? One possible explanation is that although humpback whales

may not be present off Bazaruto after October, the continuation of breeding ground habitat to the south of Bazaruto, may mean that some whales continue their association with the breeding ground south of Bazaruto.

The yacht survey conducted throughout southern and central Mozambique during August/September in 1991 (Findlay et al., 1994) found whales to be distributed throughout the region with no overwhelming evidence that the distribution of whales was influenced by water depth. This is in contrast to the 2003 line transect survey off the coast of Mozambique (Findlay et al., 2004) which found higher than expected frequencies of humpback whales in the 100-200 metre depth interval. Bazaruto Archipelago is located at the southern point of the Sofala Bank region where the continental shelf breaks away from the coast in a northeasterly direction. Therefore, if whales were moving south from more northerly regions, humpback whales could be expected to pass outside the range of detection from the coast of Bazaruto as a result of some bypassing the lower salinity waters found on the shallow Sofala Bank to the north. This partial avoidance of the Sofala Bank was also suggestive in the northbound movements of travelling whales off Bazaruto in July, whose movements featured a north easterly direction in line with where the edge of the bank falls from a depth of 20m as they passed Bazaruto.

Large numbers of blows regularly seen out on the eastern horizon off Bazaruto Island suggests that the offshore distribution extends a minimum of 18 km offshore and in a water depth of up to 500m from Bazaruto Island. Therefore an unknown number of whales may utilise more distant waters, which may also include whales travelling southward from areas further north of the Bazaruto Archipelago after October. Findlay and Best (1996) found humpback whales to be visible at up to 18 km offshore from the Cape Vidal shore-based observation platform. Findlay and Best (2006) noted that two offshore-onshore transects carried out from the FRS *Algoa* off Cape Vidal during 2002 found that 95% of humpback whale sightings occurred within this visibility limit. The region off Bazaruto also coincides with the energetically advantageous southerly current resulting from the southward moving anticyclonic eddies in the western side of Mozambique Channel (Swart *et al.*, 2010), which soon after become absorbed into the Northern Agulhas Current south of Southern Mozambique. This scenario could then account for those later whales observed as

late as December at Cape Vidal by Findlay and Best (1996) and in February at Plettenberg Bay/Knysna, and the relatively early cessation of sightings at Bazaruto Archipelago. The depth of water in which humpback whales were observed offshore from Bazaruto is deeper than generally reported elsewhere for humpback whales distributed on wintering grounds for example Felix & Hasse (2005). However, humpback whales are known to use deeper waters on wintering grounds (Frankel *et al.*, 1995).

The direction of travel data from Ponta Mamoli during October, show that all travelling whales were moving in a southbound direction. However, this represented only 33% of the sightings, the remainder were observed to be milling with an undetermined direction. Mother-calf pairs were first seen at Ponta Mamoli on 8 August – almost two weeks earlier than at Bazaruto Archipelago (20 August). These earlier mother-calf pair sightings at Ponta Mamoli were recorded to still be heading northwards during August. This tentatively suggests that they were born at some point along the migration route, south of Ponta Mamoli but continued heading north into the breeding grounds. It also indicates that some calves were being born in late July/early August, which is consistent with Matthews (1937), which shows birth frequencies to peak in August. The first movements of mother-calf pairs heading south from 4 September is consistent with Bazaruto Archipelago.

Studies from other humpback whale populations have shown that the timing of the migration is segregated by age class and reproductive status and that mothers with calves are the last cohort of the population to leave their breeding grounds (Craig *et al.*, 2003; Dawbin, 1966; Dawbin, 1997). However, data from all three sites for this study have shown that the first recorded departure of mother-calf pairs occurred in conjunction with the start of the southerly movement away from the breeding grounds in early September. Nevertheless, mother-calf pairs made up the majority of sightings observed at the end of the breeding season off Bazaruto Archipelago. Similarly, some of the first recorded sightings of the southbound migration off Plettenberg Bay/Knysna consisted of mother-calf pairs where the proportion of sightings containing mother-calf pairs increased to 62% by December. This shows that although mother-calf pairs may be the last cohort to be present on the breeding grounds or migration route, the first departure, certainly for this population, occurs in

line with the start of the southbound movement. As a result, their time of departure appears to be spread across the entire period of the southbound movement but favours a delayed departure from the breeding ground, which is consequently reflected in the occurrence trend in the southbound migration off Plettenberg Bay/Knysna. It must be noted that the time of first departure has been taken from travel direction only.

Although mother-calf pairs were photographed as late as February, primary data collection in Plettenberg Bay/Knysna ended in December and so exactly how this trend continued into January and February is largely unknown.

2.4.4 Seasonal shift in presence of humpback whales in East African waters during the last 100 years.

Table 2.8 Timing of catches and sightings of humpback whales shown as presence, stratified by three approximate areas based on latitude and sub-ordered by year in east African waters. Peaks in catches or encounter rates are also shown where known. Table adapted from Findlay *et al.* (2004).

Location	Lat	Year	Apr	May	Jun	Jul	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Source
Linga-linga	23°S	1912													Olsen (1914)
Linga-linga	23°S	1913													Lea (1919)
Bazaruto	21°S	2007													Banks et al
Durban	30°S	1918-1928													Mathews (1937)
Durban	30°S	1948-1954													Dawbin (1997)
Cape Vidal	27°S	1988-1991													Findlay and Best (1996)
Knysna	34°S	1903-1906													Best and Ross (1996)
Plett/Knysna 34°S 2006-2008 Banks et al								Banks et al							
Occurence Peak															

During the early part of the century, whales were present off Knysna between April and December (Table 2.8) with a switch in migration direction in August (Best & Ross, 1996). However, the current data from Plettenberg Bay/Knysna show that the northbound migration did not start until the end of May (over one month later) whilst the southbound migration did not end until February (two months later). In 2006, the start of the southbound migration occurred in the third week of September. This was preceded by a 41-day break in sightings after the end of the northbound migration, whilst in 2008, no break was observed possibly as a result of the previously discussed

Natal Pulse. Seasonal catch rates from Linga-linga (23°S) in 1913 show a unimodal peak in the first 10 day period of August in 1912 and July in 1913 (Best et al., 1998). At the Bazaruto Archipelago in 2007, the peak in encounter rates did not occur until late August (aerial surveys) or September (boat-based surveys) – again, at least three weeks later than Linga Linga (23°S) in 1912/1913. Catches of humpback whales at Durban, Natal (30°S), 1918-1928, show that whales were present from the first half of May until the end of November, with bimodal peaks in July and September (Matthews, 1937). This is consistent with the timings described for Knysna, 1903-1906, by Best and Ross (1996). Catches of humpback whales off Durban, Natal (30°S) between 1948 and 1954, occurred from mid-May until the end of October (Dawbin, 1997) with an estimated mid-August switch in migration direction. Assuming that the whales caught off Durban, Natal passed Plettenberg Bay/Knysna, the earliest and latest catches in early-May and late-November (1918-1928) and mid-May and late-October (1948-1954) at Durban would indicate whales to have been present from late-April to early-December (1918-1928) and early-May to mid-November (1948-1954) off Plettenberg Bay/Knysna.

Dawbin (1997) noted that during 1948-1954, humpback whales were probably caught as opportunity arose between catches of more valuable species. Thus the humpback whale catch data for that period are probably not a consistent sample of the locally migrating population, which had crashed to very low levels by this stage. Potentially therefore, a number of whales could have been passing Durban before and after the earliest and latest documented catches in mid-May and the end of October respectively. The timing of a switch in migration direction is much harder to infer from the data due to north and southbound migration timings overlapping closer to the breeding grounds and lack of exact dates in the whaling catch data. It is also possible that humpback whales were present at Linga-linga and Durban earlier and later than the catch timings suggest, as a result of a much lower abundance of humpback whales during the 'tail-end' periods and catch effort focused towards other species during this time. At the Knysna Heads (1903-1906) it is unknown if observer effort continued after December.

Comparing the data collected in this study with previous data it appears that there may have been a shift in seasonality by one to two months from 100 years ago to that of

today. This is clearest in Plettenberg Bay/Knysna shifting from April/December to May/February, whilst the breeding ground peak at Linga-linga and Bazaruto also appears to have shifted, the degree of shift depends on which peaks are compared. Alternatively, a large section from the start of the northbound migration past Plettenberg Bay/Knysna could have been missed during this study's data collection. However, if the present migration does start in April, then by the start of May, a relatively large number of humpback whales would be expected to be passing Plettenberg Bay/Knysna. Three very active whale watching companies operate year-round in Plettenberg Bay/Knysna (as well as a research boat being used to study Bryde's whales (*Balaenoptera edeni*) throughout 2005-2008). Therefore, if humpback whales were present, sightings would have almost certainly been made. In absence of these sightings, it seems very unlikely that the current northbound migration starts as early as April.

Furthermore, if the earliest and latest known dates of humpback whale sightings along the migration route throughout the century are compared, it would imply humpback whales to be present in relatively low-latitude waters for approximately 10.5 months of the year (from April (1903-1906) heading northbound, until mid-February (present day) heading southbound)). The timing of catches off Durban (1918-1928) (Matthews, 1937) also shows that humpback whales were not caught after November (even though catches of other species are noted to have occurred into January (Best, 1994) unlike the recent observations of humpback whales present until mid-February off Plettenberg Bay/Knysna. This represents a difference of approximately 11 weeks. This does not suggest that the residency time of individuals at the breeding grounds has changed over time; only that whales are present in the waters off east Africa over a longer period of time. As humpback whales stocks are recovering from the previous century's exploitation (Branch, 2006; Findlay et al., 2004), a degree of temporal expansion in the presence of the humpback whales could be expected. However, as the requirement to feed is likely to be a strong driving force of humpback whale seasonality, synchronising their timing at the feeding grounds with the abundance of their food source will undoubtedly influence their migratory timings to and from their breeding grounds. A temporal change in presence on their breeding ground and migration route over the century could be influenced by or be in response to an ecosystem change at the feeding grounds, which may be affecting the populations'

food resources. Peak abundances of blue whales (*Balaenoptera musculus*), fin whales (*B. physalus*), sei whales (*B. borealis*) and humpback whales off the Azores Archipelago were found to be related to the onset of the spring bloom in that region (Visser *et al.*, 2011). The timing of their presence tracked the onset of the spring bloom with mean time lags of 13, 15, 15 and 16 wk, respectively, and was more strongly related to the onset of the spring bloom than to the actual time of year, suggesting that these whales synchronize their migration according to prey distribution and availability.

The effect of changes in the sea-ice ecosystem of Antarctica and its potential effect on krill and baleen whales were reviewed by Nicol *et al* (2008). The authors noted that although the abundance of krill can vary considerably over short periods of time, if climate change causes monotonic shifts in either krill distribution and/or abundance, this could lead to decreases in reproductive success of dependent whale species. However, they also highlighted that interpretation of the response of baleen whale populations to climate change will, to some extent, be confounded by the fact that nearly all populations are recovering from overexploitation. It has also been suggested that the overall range of Antarctic krill off the Antarctic Peninsula has contracted and that the centre of abundance is now further south than earlier last century (Atkinson *et al.*, 2008). However, it is not fully understood if this contraction in krill range observed by Atkinson *et al.* (2008) extends further than their study area between 0° and 90° W.

Friedlaender *et al* (2008) found a significant relationship between the relative abundance of humpback whales and the size-distribution of krill targeted by Adelie penguins around Anvers Island, Antarctica. In the North Atlantic, Stevick *et al*. (2003) showed that feeding ground origin influenced the temporal presence of humpback whales on their West Indian breeding grounds where whales from different feeding origins arrived at different times. In the southern Gulf of Maine in the North Atlantic, Weinrich *et al* (1997) described a shift in humpback whale distribution from Stellwagen Bank to Jeffrey's Ledge between 1988-1994, returning to a distribution similar to that documented until the late 1970s. The authors attributed this to be related to a shift in the abundance of primary prey resulting from either the over-fishing of herring in the mid to late 1970s or natural fluctuations in its abundance. The

mean arrival date of humpback whales at their feeding grounds in the Gulf of St Lawrence, Canada, has also shown a temporal shift, becoming on average one day earlier each year over the last 30 years (pers. comms. Christian Ramp). This suggests a temporal or geographic change in their prey distribution. It is currently unknown if these earlier arrival times observed in the feeding grounds in the Gulf of St Lawrence are reflected by similar changes in wintering ground departure times.

A one-week shift in migration timing is known to have occurred in the gray whale (*Eschrichtius robustus*) population of the eastern North Pacific after 1980 (Rugh *et al.*, 2001). Rugh *et al.* (2001) hypothesised this to be due to an oceanographic regime shift in the 1970s influencing food availability, which caused a redistribution of whales on the feeding ground or by competition for food resources of an increasing population. Consequently, whales would be distributed over a wider area or further north in search for food therefore increasing the distance of their southbound migration (Rugh *et al.*, 2001). Swartz *et al.* (2006) also noted that the timing of the southbound migration by eastern North Pacific gray whales, may be affected by how widely the population is distributed for foraging, and this is affected in part by the onset of winter and the extent of ice coverage in the Arctic. In the same population, Shelden *et al.* (2004) found that one-quarter to one-half of pregnant gray whales gave birth north of the Mexican breeding grounds. The authors attributed this to the same migration delay, whereby a one-week delay in the migration, without a change in calving dates, would mean that calving would occur 1000km further north.

If this is a real shift in seasonal occurrence rather than simply due to an expanding population or an artefact resulting from differences in sampling effort or methods, this is the first documented shift in migration timing for Southern Hemisphere humpback whales. Perhaps more importantly, this may also represent a large scale effect on a population of Southern Hemisphere baleen whales as a result of climate change and by its nature, is unlikely to be restricted to just this population or species.

3. Chapter 3: Photographic evidence for humpback whale population structure off Southern Africa.

3.1 Introduction

Populations of cetaceans are often strongly structured, most obviously by sex and age, but also frequently by geography (Whitehead *et al.*, 1998). Selection of the appropriate management unit is critical to the conservation of animal populations and defining such units should be based on both genetic and non-genetic evidence of population sub-structure (Clapham *et al.*, 2008). Knowledge of population structure or sub-structure is thus a prerequisite when evaluating the status of whale stocks (IWC, 2011c).

Humpback whales occur throughout the Southern Hemisphere. Seven winter breeding stocks, termed Breeding Stocks A-G are associated with six summer high latitude feeding areas, termed Area I-VI (IWC, 1998). Some sub-structuring may occur within these feeding areas (K. Findlay pers. comm.). Of the seven breeding stocks, knowledge of population structure for stocks A, D and G has enabled their status to be successfully evaluated (IWC, 2011c). These stocks have been found to have a relatively simple stock structure, with a single winter breeding region being linked by one migration route to the feeding areas. However, the structures of Breeding Stocks B, C, E and F have been found to be more complex involving multiple migration routes to and from sub-stocks in multiple winter breeding areas.

Heavy exploitation by the modern whaling industry throughout the majority of the 20th century led to a global collapse of humpback whale stocks. Humpback whales were hunted on both the feeding and breeding grounds as well as on migration routes (Findlay, 2001). Since the cessation of all commercial whaling in 1986, Southern Hemisphere humpback whale stocks have shown differential recovery trajectories (IWC, 2011c). Increasing knowledge of humpback whale biology and population structure will help to improve the accuracy of the data utilised in assessments of the recovery and, therefore, conservation status of this species.

The west and east coast of Southern Africa are known winter grounds for two stocks of Southern Hemisphere humpback whales, termed Breeding Stock B and C, respectively, (IWC, 1998).

Current knowledge of population structure for these Breeding Stocks is based largely on differential catch histories (IWC, 1998) and on information gained through comparisons of photographic and genotypic data (Barendse *et al.*, 2011a; Barendse *et al.*, 2010b; Barendse *et al.*, 2011b; Carvalho *et al.*, 2010; Carvalho *et al.*, 2009; Cerchio *et al.*, 2008a; Cerchio *et al.*, 2008b; Collins *et al.*, 2010a; Dulau-Drouot *et al.*, 2011; Ersts *et al.*, 2011; Pomilla *et al.*, 2005; Rosenbaum *et al.*, 2009). The work presented in this chapter considers population structure based on photographic matching data; genetic aspects are considered in depth in Chapter 4.

Off the east coast of Africa, five potential sub-stocks associated with particular areas have been identified: C1 South (C1-S), including Mozambique as far north as Mozambique Island (15°S); C1-North (C1-N), extending northwards from Mozambique Island to the northern limit of the species range (Southern Tanzania and possibly into Kenya); C2, including Mayotte, the Comoros Islands and the Mozambique Channel; C3, Madagascar; and C4, extending across the Mascarene islands, including Mauritius and Reunion (IWC, 2011c). C1-North is data deficient and the IWC has linked C1-S and C1-N as one breeding sub-stock, C1, for management purposes (IWC, 2011c).

Information regarding mixing between sub-stocks C1 and C3 is poor. Comparisons of tail fluke catalogues from sub-stocks C1 and C3 revealed only two recaptures, one of which involved a photograph of very poor quality which could not be utilised in analyses. Both recaptures were from the same year and movement direction: captured in C1 in 2003 and recaptured in C3 in 2006 (Cerchio *et al.*, 2008b). In that study, catalogued images from C1 were contributed by commercial whale-watching operators off the east coast of South Africa and from three research cruises off the southern portion of Mozambique and eastern South Africa between 2002-2005 (C1-S and its postulated migration route). The majority (93%) of C1 images used to investigate levels of exchange between C1 and C3 were collected off northern KwaZulu Natal and the Eastern Cape, South Africa. Both identified recaptures

originated from the migration route off SA rather than from the Mozambique breeding grounds.

Movements of individuals have recently been found between sub-region C3 and C4. Preliminary comparisons of tail fluke catalogues from Madagascar (C3) (2000-2006) and Reunion (C4) (2001-2010) revealed three inter-regional recaptures, suggesting a degree of connectivity between these regions (Dulau-Drouot *et al.*, 2011). The three individuals were captured in Madagascar in 2000, 2001 and 2002 and recaptured in Reunion in either 2008 or 2010; a time interval of 7-8 years. Recent increases in whale numbers observed off Reunion suggest a range expansion by C3 animals and, because of the relatively small sample size of Reunion animals, exchange between C3 and C4 may be greater than between C1 and C3 (Dulau-Drouot *et al.*, 2011).

There is also evidence of exchange between C2 (Mayotte and Geyser-Zélée Complex) and C3 with nine between-year recaptures found between regions (four via tail fluke, four via genotype, and one via dorsal fin), which questions the independence of C2 and C3 as separate breeding sub-stocks and the significance of the delineation of these southwest Indian Ocean stock boundaries (Ersts *et al.*, 2011). Movements of animals between C2 and C3 have also been found through satellite telemetry; two humpback whales tagged off Mohéli Island (12°24' S, 43°45' E) in the Comoros Archipelago visited Western Madagascar during their southbound migration (Fossette *et al.*, 2012). This is the first report of within-year movements of individuals between sub-stocks C2 and C3.

The west coast of Africa is divided into two breeding sub-stocks B1 and B2 (IWC, 2001). The breeding region encompassing sub-stock B1 extends north of 18° S. South of this is a region which is considered to be a migratory route and feeding ground, as well as containing sub-stock B2 (which has been genetically identified as different to B1) and the exact breeding location of which is unknown (IWC, 2011c). The occurrence of humpback whales off west South Africa (south of 18° S) has been found to extend through the summer months, accompanied by observations of feeding whales (Barendse *et al.*, 2011a; Barendse *et al.*, 2010b). A high between-year recapture rate (15.65%), with more than 11% of whales also seen within the same year indicates high site fidelity for this region, which appears to serve as a feeding

ground for a number of individuals during summer months as well as a migratory stream to B1 and/or B2 (Barendse *et al.*, 2011a; Barendse *et al.*, 2010b). A preliminary comparison of tail fluke images from west South Africa and Namibia revealed no matches (Barendse *et al.*, 2011b). However, the movements of 11 individuals between the west coast of South Africa and Gabon are known through genotypic (Carvalho *et al.*, 2009) and photo-identification (Collins *et al.*, 2010b) matches.

There is some evidence of exchange between breeding grounds in the southeast Atlantic (Breeding Stock B) and the southwest Indian Ocean (Breeding Stock C); a single inter-oceanic genetic match between Gabon on the west coast (sub-stock B1) and Madagascar on the east coast of Africa (sub-stock C3) (Pomilla & Rosenbaum, 2005). An individual humpback whale has also been documented in two non-adjacent wintering grounds. A female, first photographed on Abrolhos Bank, Brazil (Breeding Stock A) in 1999, was recaptured off the east coast of Madagascar (C3) in 2001, representing a minimum distance travelled of over 9,800 km (Stevick *et al.*, 2010).

The management-based boundaries used by the IWC to define stocks are not necessarily synonymous with biological populations; rather they are often spatial groupings of whales that are convenient for the purpose of management (Clapham *et al.*, 2008). Although seven Breeding Stocks are recognised by the IWC, substantial population structure is known to occur within them. For example, in the South Pacific (Breeding Stocks E and F) up to seven sub-stocks may exist (IWC, 2011c). Similarly, evidence of exchange between breeding stocks (described above) indicates that gene flow can and does occur between them. Increasing understanding of how populations are connected is an important step to improve our knowledge of this apparently complex system.

Breeding Stock C animals are considered to have a Nucleus feeding range in the Antarctic between 30°E-60°E, which extends to 10°E-80°E when including Margin Areas (Annex H, Figure 1 - IWC, 2010). This corresponds to Breeding Stock C humpback whales being distributed within Antarctic management Areas III and IV during summer (IWC, 1998). Connectivity between Breeding Stock C and the

Antarctic feeding grounds is known through the recovery of two Discovery marks and two genotypic matches (- See Chapter 1, Table 1.1-2 and Figure 1.1).

Connectivity between Breeding Stock B and the Antarctic feeding grounds is known through two individuals that were satellite tagged off Gabon and tracked to relatively low Antarctic latitudes of 56° S in Areas II and 54° S in Area III (Rosenbaum & Mate, 2006) and two genotypic matches: B1 to 55°S, 0°W (Area II) and B2 to 57°S, 1°E (Area III) (Annex H - IWC, 2010).

Evaluating the status of whale stocks requires examination of current stock size, recent population trends, carrying capacity and productivity, all of which requires knowledge of population structure and population dynamics (IWC, 2011c). Recent assessments for Breeding Stock C, conducted by the Scientific Committee of the International Whaling Commission (IWC), considered four stock assessment models for sub-stocks C1 and C3 – the so-called Sabbatical, Tourist, Migrant and Resident models. These models allowed for varying degrees of interchange on the wintering grounds as well as mixing on the feeding grounds (IWC, 2010). The Sabbatical model assumes that there is a probability that an individual will visit another winter ground in one year but will return to its home winter ground in the following year. The Tourist model assumes that there is a probability that in any one year an individual may visit both wintering grounds. The Migrant model assumes that if an individual travels to a wintering ground as a visitor in one year, it will continue to do so in all future years. The Resident model assumes no interchange among winter grounds. The need to consider all these models reflects the lack of knowledge about stock structure in this area.

Of the four models considered, the Sabbatical model was favoured, which gave estimates of current abundance of 7,035 (90% Probability Interval 5,742 - 8824) for sub-stock C1 and 7,389 (90% PI 5,642 - 9,855) for sub-stock C3 (IWC, 2010). Posterior median population estimates relative to pre-exploitation levels ranged from 77-84% for sub-stock C1 and 69-87% for sub-stock C3 (Annex H - IWC, 2010). The Committee highlighted that uncertainty associated with the parameter describing interchange between sub-stocks C1 and C3 remained one of the largest sources of uncertainty in the assessment. However, despite its poor precision, the degree of

interchange was considered to be low between sub-stocks C1 and C3. Too little information was available from C2 or C4 to include these regions in the Breeding Stock C assessment. Therefore the abundance of Breeding Stock C is likely to have been under estimated. In addition, the abundance estimate for sub-stock C3 assumes that all Madagascar animals visit Antongil Bay and so some components of the C3 stock may not be included here. The abundance estimate for sub-stock C1 will also be an under estimate as this only included survey data from a section of C1-S.

Knowledge of occupancy rates, which describe the minimum time that an individual remains in a certain area, has been used to infer habitat usage and levels of mixing between individuals on winter grounds (Craig & Herman, 2000). Occupancy rates on humpback whale wintering grounds, such as Brazil, (mean = 15.4 days) (Wedekin *et al.*, 2010), Caribbean (mean = 6 days) (Mattila *et al.*, 1994), Antongil Bay, Madagascar (3-5 days, median= 2 days) (Cerchio *et al.*, 2008a) and Gabon (within-year recapture intervals between 9.4 to 15 days) (Collins *et al.*, 2010a) show that on average, humpback whales may spend a relatively short time in a given area. There is no information on occupancy rates for sub-region C1, although habitat usage is described in Chapter 2.

Satellite tagging of humpback whales on wintering grounds off the coast of Brazil revealed that within-region movements varied substantially but, whilst differences in movement patterns may be related to sex, age-class and reproductive status, movement patterns and residency patterns also vary substantially among individuals, resulting in unequal recapture probability (Zerbini *et al.*, 2006). Daily movement rates off the coast of Brazil varied from 1 km to more than 60 km and varied greatly according to the individual - with some individuals known to remain in an area over many weeks whilst others moved over 100km in just a few days (Wedekin *et al.*, 2010). Similarly, satellite tags deployed on two mothers accompanied by calves and a third individual of unknown sex in October (late-breeding season) off the Comoros Archipelago (C2) showed wide variability in their movements as well as providing evidence of within-year inter-regional exchange (Fossette *et al.*, 2012).

Matches of tail fluke images at a single location between years have also increased knowledge of migration structure, revealing remarkably consistent between-year synchrony in their migratory timing of some individuals. For 21 individuals that were sighted in more than one year migrating off the east coast of Australia, the mean interval between the day of the year sighted from one year to the next was 6.5 days (S.D =5.21) (Burns et al., 2012). Similarly, three individuals showed consistent between-year timings on wintering grounds off the coast of Ecuador, with intervals of 0, 7 and 21 days, respectively (Felix & Haase, 2001). Strong consistencies were found in humpback whale sighting dates between years in Antongil Bay, Madagascar (C3), where 76% of between-year recaptures occurred within 10 Julian days (Cerchio et al., 2008a). In 21 cases of pair-wise recaptures, 16 (76%) occurred within 10 Julian days of the date of the initial year's capture, 13 (62%) within 5 days and 7 (33%) within 2 days. This suggests that migration structure is complex with consistent differences among individuals as well as being structured by sex, age-class and reproductive status (Dawbin, 1966; Dawbin, 1997) where the timing of females has been shown to vary according to their reproductive status (Craig et al., 2003).

Using photographic individual recognition data, this study aimed to investigate the level of exchange between sub-region C1-S and C1-N, B2 and Feeding Areas II, III, IV and estimate the abundance of humpback whales migrating past Plettenberg Bay/Knysna, South Africa in order to strengthen the current knowledge of population structure for Breeding Stock C and its sub-stock C1-S. I present new results, which confirm connectivity between the southern South Africa migration route and breeding grounds off Mozambique and possible non-mixing of individuals between C1-N and C1-S. This new information will help increase the accuracy of future conservation and management assessments and guide future revisions of stock boundaries for this complex and highly structured population of humpback whales.

There were insufficient data to conduct mark-recapture analyses to estimate useful abundance estimates but some information on abundance is presented in Appendix 2.

3.2 Methods

Photographs of humpback whales were collected during sea trips described in Chapter 2, section 2.2.2. All approaches to whales in South African waters were made under a permit issued to the Centre for Dolphin Studies by Marine and Coastal Management, reference number V1/1/5/1. In addition to the data recorded for each humpback whale sighting (see Chapter 2, section 2.2.2) during each encounter, an attempt was made to allocate an 'individual number' to each individual based on distinguishing marks, scars, or skin pigmentation observed on the body, dorsal fin or tail fluke. This helped to identify which individuals remained to be photographed, allowed the correct assignment of sex and age class to an individual (when known) and aided in assigning the correct skin biopsy sample to an individual when a biopsy sample was taken. During image cataloguing, these notes also aided the assignment of dorsal fin images to tail flukes in order to produce a complete photographic record for an individual in each sighting. Attempts were made to obtain photographs of the tail fluke, left-side dorsal fin and right-side dorsal fin for all individuals. Whales were mostly photographed using a hand held Canon 350D or 40D with a 70-300 mm lens.

A photographic catalogue for Southern South Africa and Mozambique (C1-S) was created which contained every individual photographed in each encounter during each trip on each day. Whenever possible, each individual was represented by three images: a tail fluke, a left-side dorsal fin and a right-side dorsal fin. Each of these three images was chosen based on image exposure, focus, lighting aspect and orientation to the animal. This resulted in an individual being represented by the best quality image for each identification feature from that encounter.

3.2.1 Image Catalogues

The catalogue created during this study (Southern South Africa and Mozambique C1-S), was matched to three additional photographic catalogues for inter-regional comparisons (see section 3.2.2). Each catalogue is described below.

3.2.1.1 Southern South Africa and Mozambique (C1-S, n=309)

This catalogue contained digital images of tail flukes collected from three localities (see Chapter 1, Figure 1.3 and Chapter 2, section 2.2.1). All data were pooled into one catalogue, which was sub-divided according to sampling location. In addition, scanned slides taken between 2000 and 2004 by the Centre for Dolphin Studies and a small number of incidental digital photographs taken by the Centre for Dolphin Studies and Ocean Safaris whale-watching company in Plettenberg Bay/Knysna between 2005 and 2008 were included.

One site was located on the south coast of South Africa (SC - See Cerchio *et al.*, 2008a) and sampled during 2005-2008: Knysna/Plettenberg Bay (34°S-23°E). Two sites were located in Southern Mozambique (MS - See Cerchio *et al.*, 2008a): Bazaruto Archipelago (21°S-35°E), sampled during 2007, and Ponta Mamoli (26°S-32°E), sampled during 2009. The first site sampled the migration stream (Best & Ross, 1996), while the central and southern Mozambique sites sampled the Mozambique breeding ground (Findlay & Best, 1996; Findlay *et al.*, 1994). Images were taken from dedicated small-boat surveys and commercial whale-watching vessels over sampling seasons shown in Table 3.1 and Figure 3.1.

Each photographed humpback whale was assigned a sighting number and an individual number from each trip. To allow effective searching within the catalogue, IPTC and EXIF metadata fields were used to add information such as location and photographer, whilst keywords were assigned to each image based on trip number, individual number, vessel type, sex, age class, biopsy sample number, fluke type and quality grades.

This catalogue is independent of a larger 'East African Mainland' catalogue held by Oceans and Coasts (formerly MCM), Department of Environmental Affairs, Cape Town, South Africa which includes eight between-year recaptures off the north east coast of South Africa (Cerchio *et al.*, 2008b). A request to Oceans and Coasts for the use of their catalogue in this study was declined and so no comparison to the Oceans and Coast catalogue has been made.

3.2.1.2 West South Africa (Breeding Stock B2, n=195)

This catalogue contained scanned film (1983-2004) and digital images (2004-2008) of tail flukes collected from multiple sources: two dedicated humpback whale studies conducted at Cape Columbine (1993) and Saldanha Bay (2001-2003); and incidental sightings during other cetacean research work and routine multi-disciplinary scientific cruises (1983-2008). This catalogue is described in detail in Barendse *et al.* (2010a) and the results of the B2 – C1 catalogue comparison is described in Banks *et al.* (2010).

3.2.1.3 Zanzibar, Tanzania (Breeding Stock C1-N, n=180)

This catalogue contained digital images of humpback whale flukes collected during boat-based humpback whale studies in 2006 and 2008-2009 conducted off Zanzibar, Tanzania (pers. comm. F. Christiansen).

3.2.1.4 Antarctica: Area II (n=20), Area III (n=106), Area IV (n=68)

The Antarctic Humpback Whale Catalogue (AHWC) is an online catalogue, curated by the College of the Atlantic's marine mammal research group, Allied Whale. Images are contributed by scientists, naturalists and tourists as part of an international collaborative project investigating the movements of humpback whales in the Southern Ocean. Images are organised into collections according to fluke type and can be further sub-categorised according to geographic region. For this study, all tail flukes, of all qualities and orientations within Area II, III and IV (Figure 1.1) were used (http://www.flickr.com/photos/ahwc/collections/72157623423919294/).

3.2.2 Photographic matching procedure

Largely following the procedure and format described in Minton *et al.* (2010), images (digital and scanned) from west South Africa were catalogued into a Microsoft *Access* database. Images from the East African mainland (Southern South Africa, Mozambique and Tanzania) were catalogued using Apple Mac *Aperture* image cataloguing software. All catalogues had previously undergone separate intraregional, within-year and between-year comparisons by the curators of each catalogue, selecting the best quality image for each individual. Each image was

assigned a 'Fluke Type' number based on fluke pigmentation patterns, on a 1-5, all-white to all-black scale (as described by Minton *et al.*, 2010). The AHWC had additional fluke type sub-categories for Type-1 flukes (all white flukes); however, for the purpose of this study, these additional fluke types were not used. Each image was also assigned a rating for photographic quality, orientation of subject and individual distinctiveness based on a 5-point scale: Not Useable, Poor, Fair, Good and Excellent.

Tail fluke images in each catalogue - from the west coast of South Africa (B2), Tanzania (C1-N) and Antarctica (Area II, III and IV) - were compared to the C1-S catalogue on two computer screens, utilising a screen loupe on each screen to aid the inspection of finer detail within the images. Initially, each image in the first catalogue was compared to all images of the same Fluke Type category in the second catalogue. If no matches were found, it was then compared to all images in adjacent Fluke Type categories (so that a Fluke Type 4 image was compared to Types 4, 3 and 5 in the second catalogue). Images of all photographic qualities were used in the comparison but a filter for photographic quality was applied so that 'Poor' and 'Not Usable' images could be excluded from calculations of recapture rates.

Same-day matches

Same-day matches were defined as one individual being identified in the same day but in different sightings. This is a result of the movement of individuals between groups or from the accidental re-approach of a group previously recorded that day.

Within-year matches

Within-year matches were defined as an individual being identified on more than one occasion within the same calendar year (Jan-Dec).

Between-year matches

Between-year matches were defined as any individual identified in different calendar years.

Using abundance estimates for Breeding Stocks C1 and B2 and Feeding Areas II, III, and IV, the expected number of intra- and inter-regional recaptures found during the

Southern South Africa and Mozambique catalogue comparisons were estimated using a derivation of the Chapman estimator:

$$\hat{m}_2 = \left(\frac{n_2}{N}\right) n_1$$

Where \hat{m}_2 = estimated number of recaptures, n_1 = number of marked individuals in the Southern South Africa and Mozambique (C1-S) catalogue, n_2 = number of marked individuals in the compared breeding or feeding stock, N = estimated population size of the compared breeding or feeding stock. This method for estimating recapture rates assumes complete mixing of individuals between stocks.

The Chapman's modification of the Petersen estimator is commonly used in studies that use mark recapture methods to estimate abundance (Hammond, 2009). It reduces small sample size bias and allows a finite estimate of variance to be estimated.

It must be noted that due to uncertainty associated with the abundance estimates used to estimate the recapture rates (See Table 3.4 & Table 3.7), the reliability of the estimated recapture rates must be treated with caution.

3.2.2.1 Use of dorsal fins

In the Southern South Africa and Mozambique (C1-S) catalogue, dorsal fin images were primarily used to establish a complete photographic description of an individual so that when possible each individual was represented by a tail fluke, left dorsal fin and right dorsal fin image. This was important when assigning information such as skin biopsy samples to individuals. An attempt was made to use dorsal fins for photo-identification. Dorsal fins were categorised according to the shape of the dorsal fin's trailing edge (forward sloping/no slope/falcate). Dorsal fins were also graded according to the presence of distinctive marks along the trailing edge, leading edge and dorsal fin base. Each image was also assigned a rating for photographic quality, orientation of subject and individual distinctiveness, based on a 5-point scale: Not Useable, Poor, Fair, Good and Excellent.

3.3 Results

3.3.1 Southern South Africa and Mozambique (C1-S)

In total, this catalogue contained 331 images comprising 323 digital images and 8 scanned slides of tail fluke images, representing 309 individuals from three sampling localities (Table 3.1). The sampling location of Plettenberg Bay/Knysna, South Africa contained 161 individuals represented by 8 scanned slides and 166 digital images. Scanned slides were taken in 2000-2004. These were pooled and classed as "<2004". Bazaruto Archipelago and Ponta Mamoli, Mozambique sampling locations were represented by digital images only, with 157 images of 109 individuals in 2007 and 42 images of 39 individuals in 2009, respectively.

Within the same sampling location, the number of individuals identified by tail fluke images varied within and between years (Figure 3.1). In 2000-2003 and 2005 in Plettenberg Bay/Knysna, only 12 individuals were identified. This was due to a lack of fieldwork and suitable photographs and sighting data from these years.

Table 3.1 The number of individuals identified by tail flukes in each year for the Southern South Africa and Mozambique (C1-S) catalogue ordered by sampling localities before (All) and after (QF) filtering for quality (excluding poor and not useable images). SC=South coast of South Africa, MS= Southern Mozambique. * = Scanned images of tail fluke slides taken by the Centre for Dolphin Studies in 2000-2004. () = Number of new individuals in that year.

Locality	Number of	Year								
	Individuals	<04	05	06	07	08	09			
Plettenberg Bay/Knysna (SC)	All	8* (8)	4 (4)	54 (52)	24 (23)	75 (74)	-			
	QF	7* (7)	4 (4)	42 (40)	24 (23)	74 (73)	-			
Bazaruto Archipelago (MS)	All	-	-	-	109 (109)	-	-			
	QF	-	-	-	104 (104)	-	-			
Ponta Mamoli (MS)	All	-	-	-	-	-	41 (39)			
	QF	-	-	-	-	-	40 (38)			

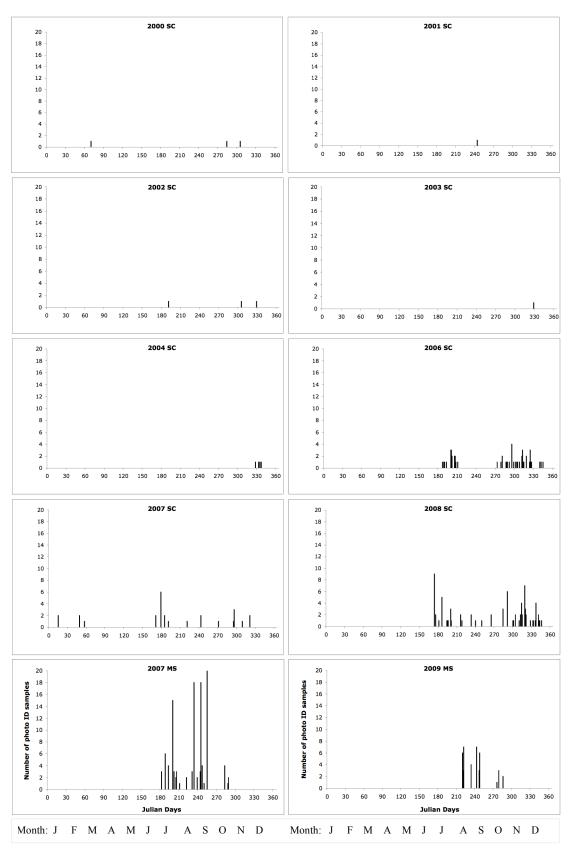


Figure 3.1 The number of tail fluke images taken within each year in sub-region C1-S and its migration route. SC = Plettenberg Bay/Knysna, South Africa. MS = Bazaruto Archipelago (2007) and Ponta Mamoli (2009), Mozambique.

3.3.2 Recaptures within Southern South Africa and Mozambique (C1-S)

All recaptures

In total there were 22 recaptures of humpback whales in the period 2003-2009. This total includes "same-day", "within-year" and "between-year" recaptures.

Same-day recaptures

There were 16 same-day recaptures, representing 16 different individuals, all of which were only recaptured once within a day.

Within-year recaptures

Excluding same-day recaptures, no within-year recaptures were found.

Between-year recaptures

Six between-year recaptures were found (Table 3.2, Table 3.3 and Plate 3.1), representing six different individuals on five capture days and five recapture days. All between-year recaptures were of adults of unknown sex. The time between mark-recapture ranged from one to four years between 2003 and 2009.

All six individuals recaptured between years were first captured off Plettenberg Bay/Knysna. Of these, four individuals were recaptured again off Plettenberg Bay/Knysna whilst two individuals were recaptured off Ponta Mamoli, Mozambique.

Of those captured-recaptured off Plettenberg Bay/Knysna, one individual was captured during the southbound migration and subsequently recaptured in the northbound migration. Three individuals were captured-recaptured during the southbound migration off Plettenberg Bay/Knysna. The capture and recapture dates for each of these three individuals differed by 5, 9 and 16 Julian days (Mean=10 days) between years (Table 3.2).

Table 3.2 All between-year tail fluke matches within the Southern South Africa and Mozambique (C1-S) catalogue. N=Northbound migration, S=Southbound migration. The difference between capture and recapture dates are given in Julian days.

ID	Capture	Capture	Recapture	Recapture	Julian Day	Year	
ID	Date	Location	Date	Location	Difference	Difference	
C1S 008	31/10/03	Plett/Knysna	30/7/06	Plett/Knysna	123	3	
C15 000	31/10/03	(S)	30/1/00	(N)	123	5	
C1S 010	29/11/05	Plett/Knysna	8/12/06	Plett/Knysna	9	1	
C18 010	29/11/03	(S)	6/12/00	(S)	9		
C1S 011	29/11/05	Plett/Knysna	22/8/09	Ponta Mamoli	99	4	
C15 011	2)/11/03	(S)	22/0/07	i onta iviamon))	,	
C1S 025	21/7/06	Plett/Knysna	22/8/09	Ponta Mamoli	32	3	
C15 025	21///00	(N)	22/0/07	i ona iviamon	32	3	
C1S 058	21/11/06	Plett/Knysna	7/12/08	Plett/Knysna	16	2	
C15 056	21/11/00	(S)	//12/00	(S)	10	2	
C1S 061	22/11/06	Plett/Knysna	17/11/07	Plett/Knysna	5	1	
	22/11/00	(S)	1 // 1 1/0 /	(S)	3	1	

Individuals C1S 010 and C1S 011 were captured together in the same sighting during the southbound migration off Plettenberg Bay Knysna on 29/11/05. Individual C1S 010 was later recaptured during the southbound migration off Plettenberg Bay/Knysna, South Africa on 8/12/06. However, individual C1S 011 was recaptured off Ponta Mamoli, Mozambique on 22/8/09 along with individual C1S 025, which had previously been captured during the northbound migration off Plettenberg Bay Knysna, South Africa on 21/7/06. The recapture of these two individuals in Mozambique occurred just two hours apart.



C1S 008 Capture date: 31/10/03



C1S 008 Recapture date: 30/7/06



C1S 010 Capture date: 29/11/05



C1S 010 Recapture date: 8/12/06



C1S 011 Capture date: 29/11/05



C1S 011 Recapture date: 22/8/09



C1S 025 Capture date: 21/7/06



C1S 025 Recapture date: 22/8/09

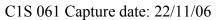


C1S 058 Capture date: 21/11/06



C1S 058 Recapture date: 7/12/08







C1S 061 Recapture date: 17/11/07

Plate 3.1 Between-year recaptured individuals within the C1S catalogue

Table 3.3 Within-region between-year recaptures in Plettenberg Bay/Knysna, South Africa (2000-2008) and Bazaruto Archipelago (2007) and Ponta Mamoli (2009), Mozambique.

Capture	Recapture Year											
Year	2000	2001	2002	2003	2005	2006	2007	2008	2009			
2000	0	0	0	0	0	0	0	0	0			
2001		0	0	0	0	0	0	0	0			
2002			0	0	0	0	0	0	0			
2003				0	0	1	0	0	0			
2005					0	1	0	0	1			
2006						0	1	1	1			
2007							0	0	0			
2008								0	0			
2009									0			

When the 16 same-day recaptures are excluded from the total number of recaptures, six recaptures were found. When the catalogue was subdivided according to migration route (Plettenberg Bay/Knysna) and breeding ground (Bazaruto Archipelago/Ponta Mamoli) sampling locations, three recaptures m_2 were expected to be found (Table 3.4), which assumes complete mixing of individuals, all with equal capture probability within a sampling occasion and unbiased sampling. This was similar in number to the two recaptures found between these locations (Table 3.2).

Table 3.4 Expected number of photographic recaptures from an intra-regional comparisons of the Southern South Africa and Mozambique (C1-S) catalogue based on quality filtered sample sizes. N=population size, n_1 = number of marked individuals in Southern South Africa (Plettenberg Bay/Knysna), n_2 = number of marked individuals in Mozambique (Bazaruto Archipelago and Ponta Mamoli), m_2 = expected number or recaptures.

Stock	N	n_1	n_2	m_2	Source of abundance estimate
Breeding Stock C1-S	7035	1.51	144	3	(IWC, 2010)
Diecung Stock C1-S	(90% PI =5742-8824)	151	144	3	(1WC, 2010)

Using theodolite tracking, Findlay (Findlay & Best, 1996) estimated average net swim speeds to be 3.6 - 5.4 km/h during the northbound migration and 5.3km/h during the southbound migration off Cape Vidal. Findlay's northbound average net swim speed was applied to the between-year sighting dates of individual C1-S 025 on 21 July 2005 off Plettenberg Bay/Knysna, South Africa and 22 August 2009 off Ponta Mamoli, Mozambique to estimate the expected date of recapture. An individual travelling at a constant speed of 3.6 - 5.4 km/h should take 13 - 21 days to travel the 1650 km distance between Plettenberg Bay/Knysna, South Africa and Ponta Mamoli, Mozambique. The earliest expected re-capture date was therefore estimated to be between 3 and 12 August (Table 3.5). Between-year recapture dates to the same location were found to vary between 5-16 days (mean =10 days) (Table 3.2). When this 5-16 day variation was applied to the expected recapture date based on the slower swim speed, individual C1-S 025 was estimated to be recaptured between 17-28 August. This is consistent with its observed recapture date.

Table 3.5 Observed capture-recapture dates and estimated recapture dates for individual C1-S 025. Estimated dates are based on net swim speed estimates (3.6 to 5.4 km/h) and a distance travelled of 1650 km. \pm 10 d = A 10-day mean difference in between-year capture-recapture dates estimated from three individuals.

-	Observed capture	Estimated recapture	Estimated recapture	Observed recapture
ID	date (Plett/Knysna	date (Ponta Mamoli)	date (Ponta Mamoli)	date (Ponta Mamoli
	2005)	(speed 3.6 km/h)	(speed 5.4 km/h)	2009)
C1-S	21 July	3 August	12 August	22 August
025	21 July	(+/- 10 days)	(+/- 10 days)	22 August

3.3.3 Inter-regional comparisons

Three independent catalogues (see sections 3.2.1.2, 3.2.1.3, 3.2.1.4) were compared to the Southern South Africa and Mozambique (C1-S) catalogue. The number of individuals in each catalogue for each year is shown in Table 3.6. Tanzania (C1-N) contained 180 individuals from 2006, 2008-2009. West South Africa (B2) contained 510 images from 1983 - 2008 representing 195 individuals. Antarctica Area II contained 24 images from 2005 - 2011 representing 20 individuals. Antarctica Area III contained 157 images from 2005 - 2010 representing 106 individuals. Antarctica Area IV contained 80 images from 2008 - 2010 representing 68 individuals.

There were no tail fluke recaptures found between the Southern South Africa and Mozambique (C1-S) catalogue and any of the three compared catalogues: Tanzania C1-N; West South Africa B2 and Antarctica (Area II, III, IV).

Table 3.6 The number of individuals identified by tail flukes in each year for each catalogue from Zanzibar, Tanzania (Breeding Stock C1-N, n=180); West South Africa (Breeding Stock B2, n=195) and Antarctica feeding grounds Area II (n=20), III (n=106) and IV (n=68) before and after filtering for quality (excluding poor and not useable images). Each catalogue was compared to the Southern South Africa and Mozambique (C1-S) catalogue.

Catalouge	Number of										Yea	ır									•	
Catalouge	Individuals	83	94	88	89	90	92	93	97	99	00	01	02	03	04	05	06	07	80	09	10	11
Tanzania	All	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	-	63	109	-	-
(C1-N)	QF	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	-	63	109	-	-
West South Africa	All	2	2	3	1	3	2	7	1	3	2	33	37	27	20	15	24	12	1	-	-	-
(B2)	QF	1	1	2	0	1	1	6	1	0	1	15	17	16	11	12	18	10	1	-	-	-
Antarctica	All	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	12	-	-	-	6	1
Area II	QF	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	12	-	-	-	6	1
Antarctica	All	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	104	-
Area III	QF	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	78	-
Antarctica	All	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	67	-
Area IV	QF	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	67	-

Table 3.7 Expected number of photographic recaptures from inter-regional photographic comparisons of tail fluke images in catalogues from Tanzania (C1-N); West South Africa (B2) and Antarctica (Area II, III, IV) with the Southern South Africa and Mozambique (C1-S) catalogue based on quality filtered sample sizes. N=population size, n_1 = number of marked individuals in the Southern South Africa and Mozambique (C1-S) catalogue, n_2 = number of marked individuals in the compared stock, m_2 = expected number or recaptures.

Stock	N	n_1	n_2	m_2	Source of abundance estimate
Breeding Stock C1-N	7035 (90% PI 5742-8824)	295	180	8	(IWC, 2010) ¹
Breeding Stock B2	510 (95% CI 230-790	295	114	66	(Barendse et al., 2011a)
Antarctic Feeding Area II	1,178 (CV 0.39)	295	20	5	(Branch, 2011) ²
Antarctic Feeding Area III	2,504 (CV 0.40)	295	80	9	(Branch, 2011) ²
Antarctic Feeding Area IV	17,938 (CV 0.18)	295	68	1	(Branch, 2011) ^{2,3}

¹ No abundance estimate exists for C1-N and so the abundance estimate for Breeding Stock C was used

,

² Abundance estimate is South of 60° only

³ Only ten degrees of Area IV feeding ground is "hypothesized" to be a C fringe feeding area.

3.3.4 Dorsal fins

Although an attempt was made to compare dorsal fins within the Southern South Africa and Mozambique (C1-S) catalogue, problems associated with subjectivity in defining dorsal fin shape and the potential for distinguishing marks to change quickly over time resulted in the assessment of dorsal fins being deemed insufficiently accurate to identify individual humpback whales with certainty over time. The orientation of the dorsal fin relative to the camera caused large variations in the apparent shape of the dorsal fin between images of the same individual.

An attempt was made to use only dorsal fin images considered to be of excellent orientation in order to reduce the potential for mis-identifications. However, the shape of the dorsal fin appeared to alter according to body position between surfacing and diving causing a large degree of subjectivity in defining or assessing dorsal fin shape. Furthermore, a large number of dorsal fin images did not show any distinguishing marks, which resulted in many comparisons being solely dependent on the subjective shape.

The use of distinguishing marks was also considered to have significant problems due to the potential variability of these marks over time. This was confirmed when reviewing dorsal fin images of a number of recaptured humpback whales from a humpback whale catalogue from the Gulf of St Lawrence, Canada, curated by C. Ramp, Mingan Island Cetacean Study Group, St Lambert, Canada (C. Ramp, pers. comm.) It was apparent that distinctive dorsal fin marks could change so significantly over a short period of time (days), that an individual photographed on two sampling occasions may be considered two different individuals. The use of humpback whale dorsal fins as identification features was combined with tail flukes and microsatellites to estimate the abundance of Breeding stock B2 (Barendse *et al.*, 2011a). Relatively high rates of false negatives (9-14%) were found when using dorsal fins alone.

3.4 Discussion

Before discussing the results of this study in a biological context, it is appropriate first to consider the limitations of the data.

3.4.1 Data limitations

A number of factors restricted the ability to provide a useful abundance estimate for Plettenberg Bay/Knysna through mark-recapture. This was largely driven by incomplete effort coverage. Continued seasonal effort is required to gain and maintain a suitably large sample size of tail fluke images in each catalogue to increase the likelihood of recaptures. This requirement was restricted by logistics and the costs involved associated with the geographic distribution of humpback whales in this study. As a result, the C1-S catalogue represents only 309 individuals of an estimated population size of 7,035 (90% PI 5,742; 8824) for C1 as a whole in 2006 (IWC, 2010).

For sampling that took place in Plettenberg Bay/Knysna, South Africa, the years 2006 and 2008 represented the most consistent coverage of photo-identification samples and effort compared to other years; these were the two years specifically covered by this project in June-December. Images and data for the remaining years were sourced from non-dedicated humpback whale surveys by the Centre for Dolphin Studies (2000-2003, 2005, 2007) and commercial whale-watching companies (2007). Chapter 2 (section 2.4.1) reported incidental sightings of southbound migrating humpback whales as late as February by the Centre for Dolphin Studies - much later than when data collection ended in December for this study. The migratory timing of individual females appears to vary across years, according to their reproductive status (Craig et al., 2003; Dawbin, 1997). Females which delay their departure from the wintering ground due to the nursing of newly born calves (mother-calf pairs) and any associating male escorts, may have passed Plettenberg Bay/Knysna after the end of the field season (December). This could have caused them to pass undetected in that year whilst being available in non-calving years resulting in a reduction in the probability of recapture.

The short (three month) field season in Ponta Mamoli also resulted in incomplete coverage for that season.

Some individuals show very consistent timings in Julian date recaptures between years. If sampling takes place in the same short period each year, those individuals that have a tendency to arrive during that period have a higher probability of recapture than others (Cerchio *et. al.*, 2008a). Conversely, for sampling periods that occur at different non-overlapping times between years, different sections of the population will be sampled (Burns *et al.*, 2012; Cerchio *et al.*, 2008a; Felix & Haase, 2001). This will negatively bias recapture rates, which leads to positively biased abundance estimates. The inconsistent, non-overlapping sampling dates between years off Plettenberg Bay/Knysna, violates the assumption that all animals have an equal capture probability, leading to heterogeneity of capture probabilities.

Trip duration and distance travelled offshore was restricted when using whale-watching vessels as platforms of opportunity in South Africa compared to using research vessels. However, both types of sampling platforms were unable to travel far enough offshore to sample the entire width of the migration stream. Thus individuals were only sampled in inshore regions whilst those travelling further offshore remained undetected. Variability in the spatial structure and velocity of the southward flowing Agulhas current could have affected the distribution of animals during the north and south bound migration (See Chapter 2, Section 2.4.1). In 2008, the presence of a Natal Pulse (See Chapter 2, section 2.4.1) could have caused "offshore" migrating individuals, who would have otherwise remained undetected, to move closer inshore making them only available for capture in that year.

3.4.2 Population structure within Breeding Stock C1-S

Six between-year recaptures of between 1 and 4 years were found (2% of individuals, N=295) within the Breeding Sub-stock C1-S and its migration route of which two recaptures were made between the migration route and winter ground. This low recapture rate suggests that the population size for this region is large; this is consistent with an estimated abundance of 7,035 (90% PI 5,742; 8824) for C1 as a

whole (IWC, 2010) and an estimated 3 expected recaptures between the migration route and winter ground of C1-S (section 3.3.2). The number of recaptures found between the migration route of Plettenberg Bay/Knysna and winter grounds of Bazaruto Archipelago and Ponta Mamoli is consistent with the estimated number of recaptures between these locations.

During this study, no within-year recaptures (excluding same-day recaptures) were found on the wintering ground regions off Mozambique (Bazaruto Archipelago, 2007 and Ponta Mamoli, 2009).

The lack of within-year recaptures on the wintering grounds off Mozambique may indicate a lack of site fidelity to the survey area, with short occupancy times. However, short occupancy times (e.g. no more than one day) could be expected on expansive winter grounds such as Mozambique (K. Findlay pers. comm.) compared to smaller island or bay winter grounds, where occupancy rates are expected to be longer (Baracho-Neto *et al.*, 2012; Cerchio *et al.*, 2008a; Mattila *et al.*, 1994; Wedekin *et al.*, 2010). The migration of individuals through a wintering ground heading to a more northern wintering ground destination could account for the lack of within-year recaptures. This is consistent with humpback whales found to be distributed at least as far north as 14°26'S off the coast of Mozambique (Findlay *et al.*, 2011) and the observation of an individual moving over 450 km in ten days through the winter ground off the coast of Mozambique in 1991 (Findlay *et al.*, 1994). Anecdotal data has also shown humpback whales to occur as far north as Kenya (02°S) during winter (pers. comm. P. Evans).

The temporal distribution of encounter rates at Bazaruto Archipelago was unimodal, peaking in August/September (Figure 2.5a-b). Either side of this peak, direction of travel data (Figure 2.6) indicated that a high proportion of animals appeared to continue moving through the area in a northerly direction in July and southerly during October and November - perhaps to or from more northerly coastal regions. However, no recaptures were found during inter-regional photographic comparisons between C1-N and C1-S (discussed further in section 3.4.3).

Alternatively or additionally, the lack of recaptures could be attributed to low sampling frequencies, which were only 4-5 days/month on average (see sections 2.3.2 and 2.3.3). This sampling frequency would have severely impacted the ability to recapture any individual occupying the area for less than several days.

In addition, variability in the daily movements of individuals on a wintering ground can impact recapture rates especially where the sampling area is relatively small compared to the daily range of an individual. The large majority of sampling off Bazaruto Archipelago occurred within a strip approximately 20-35 km offshore from the coastline, whilst at Ponta Mamoli sampling only occurred beyond 10km. In these deeper, more offshore areas, cohorts tend to be more mobile than the shallower inshore regions typically favoured by less mobile mother-calf pairs (Ersts & Rosenbaum, 2003; Martins *et al.*, 2001). The potential geographic ranges for individuals encountered during sampling (Fossette *et al.*, 2012; Wedekin *et al.*, 2010; Zerbini *et al.*, 2006) are likely to have been far greater than the area covered during surveys thus decreasing the probability of recapture.

Four capture-recaptures were made off Plettenberg Bay/Knysna, South Africa (SC-SC), whilst two were made between Plettenberg Bay/Knysna, South Africa and Ponta Mamoli, Mozambique (SC-MS). Of the four SC-SC recaptures, one individual was captured in the southbound migration and recaptured three years later during the northbound migration. This provides the first evidence of an individual using this route for both its north and southbound migration.

The temporal pattern and direction of whales passing Knysna between 1903-1906 indicated their breeding ground destination to be off East Africa, such as Central or Southern Mozambique (Best & Ross, 1996) or further north such as Tanzania or Kenya. This is now confirmed by the two SC-MS recaptures reported in this study and represent the most important recaptures from within the Southern South Africa and Mozambique (C1-S) catalogue.

These two recaptures offer a deeper understanding of population structure within Breeding Stock C by providing the first confirmed connectivity for north and

southbound migrating humpback whales off Plettenberg Bay/Knysna with the wintering grounds off southern Mozambique. This is also consistent with the comparison of temporal patterns between the south coast of South Africa and Mozambique, reported in Chapter 2 and two incidents of movement between Lingalinga, Mozambique and Durban, South Africa established from the recovery of lost harpoons (Olsen, 1914).

Although it is likely that individuals on the Mozambique wintering ground use the migration route off the south coast of South Africa for both their north and southbound migration in a single year, the fact that these were between-year recaptures cannot confirm this. However, additional results, which are discussed below, provide further support for this. Sex-specific migratory behaviour has been observed off the east coast of Australia, which suggested that the two sexes of any single matrilineal stock might select different and only partially overlapping migratory routes (Valsecchi *et al.*, 2010).

For three individuals captured and recaptured whilst travelling in the same migration direction, the mean sighting date between one year and the next was 10 days (Table 3.2). Although this is based on only three individuals of unknown sex and without considering other factors known to affect migration timing such as sex, age-class and reproductive status (Craig *et al.*, 2003; Dawbin, 1966) or feeding ground origin (Stevick *et al.*, 2003), it suggests a high degree of periodicity for some migrating C1-S individuals. Similar results in migration timing synchrony have also been observed elsewhere (Burns *et al.*, 2012; Felix & Haase, 2001). The northbound migration of humpback whales off Cape Vidal, South Africa also appears to be composed of regular "pulses" of animals each year (Findlay & Best, 1996). Strong consistencies in humpback whale sighting dates between years in Antongil Bay, Madagascar (C3) were also found, where 76% of between-year recaptures occurred within 10 Julian days (Cerchio *et al.*, 2008a).

In this regard, the estimated number of days required for an individual to migrate between Plettenberg Bay/Knysna and Ponta Mamoli was remarkably similar to the difference in sighting dates of individual C1-S 025 captured off Plettenberg Bay/Knysna in 2005 and recaptured off Ponta Mamoli in 2009. This close

correlation between sighting dates and the estimated travel time between the two capture locations, suggests that in this case, for this individual, its periodicity remained similar between 2005 and 2009. It also provides further support for the swim speeds estimated by Findlay (1994 in Best *et al.*, 1995) and for the assumption that individual C1-S 025 used the migration route passing Plettenberg Bay during its northbound migration to the Mozambique wintering grounds in the same year.

It remains unclear whether all of the individuals observed off the coast of Mozambique begin and end their coastal migration as far west as Plettenberg Bay/Knysna. Some individuals may join or depart from the coastal migration route between Plettenberg Bay/Knysna and Cape Vidal. Therefore the number of animals passing Plettenberg Bay/Knysna may only be a proportion of C1-S population thought to pass Cape Vidal in its entirety (Findlay & Best, 1996). Unfortunately, the three pairwise abundance estimates calculated for humpback whales migrating past Plettenberg Bay/Knysna are largely uninformative.

The Mozambique section of the catalogue could contain a number of 'visitors' from other sub-regions, however, these numbers would be expected to be low (Annex H - IWC, 2010). Conversely, it is also possible that the migration route contains animals that continue to Madagascar instead of following the east coast northwards to Mozambique. This potential scenario is discussed in detail in Chapter 4.

3.4.3 Levels of inter-regional exchange between Breeding Stock C1-S and C1-N, B2 and connectivity to Antarctic Feeding Areas II, III, IV

Although two sub-stocks (C1-S and C1-N) off the east coast of Africa have been suggested, the delineation between them may be a cline rather than a definite line (IWC, 2011c). Consideration of seven stock structure models by the Scientific Committee of the International Whaling Commission found the most plausible scenario was to link C1-N and C1-S together as one breeding stock sub-stock. In this study, no recaptures were found between humpback whales photographed off Plettenberg Bay/Knysna, South Africa, Bazaruto Archipelago and Ponta Mamoli, Mozambique (C1-S) and Zanzibar, Tanzania (C1-N). If these two sub-stocks were to

be treated as a single sub-stock, mixing of individuals should be expected and individuals from C1-N should be identified along the migration route off the coast of South Africa. This is inconsistent with the lack of recaptures between the photographic catalogues of C1-N and C1-S, which was estimated to produce eight recaptures if complete mixing occurred and all individuals had an equal probability of capture. One caveat to this is that the expected number of recaptures in C1-N was calculated using the abundance estimate for C1 as a whole. As mentioned previously, this abundance estimate for sub-stock C1 was only based on survey data from C1-S, which would have led to the abundance of C1 being under estimated, which in turn would have positively biased the expected number of recaptures for C1-N. No recaptures may suggest that C1-N and C1-S are in fact separate sub-stocks, which use separate migration routes. Complete mixing between individuals observed on the migration route off Plettenberg Bay/Knysna and the Mozambique winter grounds is also assumed to occur (although genetic information presented in Chapter 4 provides some partial evidence to dispute this) and this is consistent with the number of recaptures found during this study.

Alternatively, individuals from C1-N could utilise only the most eastern section of the migration route along the coast of South Africa, therefore not being available for capture off Plettenberg Bay/Knysna. Similarly, those individuals could pass through the wintering grounds off the coast of Mozambique at a greater distance offshore than was accessible by boat during data collection. Humpback whales that appeared to be moving northwards and southwards at least 18km off shore from Bazaruto Island (or 43km from the African mainland) were observed but remained un-sampled. However, although a north-south movement of animals must exist in order for the northern extents of the East African winter grounds to be reached, it seems very unlikely that individuals from C1-N could pass through the wintering grounds concurrently occupied by individuals of C1-S without any mixing between the two sub-stocks. Given no recaptures between C1-N and C1-S, a second alternative is that C1-N is an extension of C2 and C3 sub-stocks.

The lack of recaptures between Breeding Stocks C1-S and B2 found during this study is consistent with the assumed low levels of exchange between Breeding Stocks B and C. Evidence of exchange is known only through two genotypic match between C3

and B1 (Pomilla & Rosenbaum, 2005). The abundance of humpback whales off West South Africa was estimated to be 510 individuals between September and March (Barendse *et al.*, 2011a), with a high between-year recapture rate of 15.6%. This suggests that those individuals have high site fidelity to this region between years. Humpback whales have been observed feeding in the Benguela upwelling region off the west coast of South Africa throughout summer (Barendse *et al.*, 2010b; Findlay & Best, 1995). The close proximity of this area to East African humpback whales migrating past Plettenberg Bay during their southbound migration is potentially a viable alternative feeding location for Breeding Stock C1-S individuals, especially for those which were observed to be migrating westward past Plettenberg Bay/Knysna as late as February (See Chapter 2, Section 2.4.1). However, this is inconsistent with the assumed low levels of exchange between East and West Africa (Pomilla *et al.*, 2005), significant levels of differentiation between B2 and C1-S (Rosenbaum *et al.*, 2009), and a complete lack of recaptures from this study.

No matches between C1-S and the Antarctic feeding grounds (Areas II, III, IV) were found. This was consistent with the estimated expected number of recaptures for Area IV given the small sample size relative to the large population (however this did not consider that only ten degrees of longitude in Area IV is hypothesised to be used by animals from Breeding Stock C) (Table 3.7), but lower than expected for Area III (Table 3.7). Both of these Areas are considered to be feeding grounds for Breeding Stock C individuals (Annex H: IWC, 2010). In addition, a number of animals, particularly females, are also known to remain at the feeding grounds between years, without undertaking their annual migration to the breeding grounds (Brown *et al.*, 1995). Therefore if any female captured during this study failed to migrate in any of the following years, they would not be available for recapture in that year.

In light of the fact that recapture rates were generally lower than expected throughout this study possibly due to incomplete, non-overlapping effort coverage, conclusions regarding levels of exchange and population structure must be drawn with caution.

4. Chapter 4: Genetic diversity and population structure of east African humpback whales inferred from the mtDNA control region.

4.1 Introduction

4.1.1 Population structure

In widely distributed species, natural populations do not behave as a single panmictic unit, in which random mating occurs (Kimura & Weiss, 1964). Instead, they form genetically structured populations, the extent of which may be determined by several factors such as geographic isolation by distance (Wright, 1943) or barriers, social structure, mating systems and dispersal behaviours (Goncalves da Silva, 2007; Greenwood, 1980; Olivieri *et al.*, 1995; Slatkin, 1987).

Sex-biased dispersal, which in mammalian species generally involves female philopatry and male dispersal (Greenwood, 1980; Prugnolle & de Meeus, 2002), can lead to different degrees of population structure according to sex. This is believed to be the case in humpback whales in the South Atlantic and Indian Ocean with stronger population structure in females than males (Pomilla *et al.*, 2005; Rosenbaum *et al.*, 2009). Movements between winter grounds in Oceania, South Pacific was found to be low but appeared to be biased towards males (Garrigue *et al.*, 2011). In the absence of geographic barriers, maternally driven site fidelity to migratory destinations is thought to be the cause of marked population structure among subpopulations of humpback whales in the North Pacific and North Atlantic (Baker *et al.*, 1990; Palsboll *et al.*, 1995).

Humpback whales undertake seasonal latitudinal migrations between their summer high-latitude feeding grounds and low-latitude natal wintering grounds, which span several thousand kilometres. As well as these more predictable migratory movements, a small number of long-range "exploratory" or "ranging" movements to other wintering breeding or summer feeding grounds have been documented (for example - Darling & Cerchio, 1993; Salden *et al.*, 1999). These long range movements, although rare, demonstrate the flexibility in movements for a species

which is typically philopatric (Stevick *et al.*, 2010) and may be an important aspect of humpback whale population dynamics and gene flow (Darling & Cerchio, 1993; Salden *et al.*, 1999). In Southern Africa, a male humpback whale was observed on wintering grounds in two ocean basins (Pomilla & Rosenbaum, 2005), being first identified off Madagascar in the southwest Indian Ocean and then recaptured off Gabon in the southeast Atlantic Ocean. Gene flow estimates indicated that the eastern South Atlantic and the southwestern Indian Oceans are expected to exchange approximately 35 migrants per generation in each direction (Pomilla & Rosenbaum, 2005). However, the same analysis estimated that only approximately one individual per generation is expected to migrate from Madagascar to Gabon (Pomilla & Rosenbaum, 2005). In contrast to the general expectation of female philopatry, the long-range movement of a female humpback whale has also been documented. Identified by its tail fluke markings, the female was first identified off the coast of Brazil and subsequently recaptured off Madagascar, a minimum distance travelled of 9800 km (Stevick *et al.*, 2010).

Sex ratio is a basic population parameter that is of importance to conservation management (Clapham et al., 1995). Population models for humpback whales assume that all individuals undertake their winter-summer migrations (Brown et al., 1995). When monitoring the recovery of humpback populations, it is important to know whether all animals migrate each year or whether the failure to migrate is restricted to one or more segments of the population. Failure to account for sexbiased population structure on wintering grounds can lead to underestimates of abundance (Calambokidis et al., 2008). Sex ratios that differ from parity (1:1) have been reported during migration and on wintering grounds. A male biased sex-ratio of 2.4:1 was found among humpback whales during both the north and southbound migration off the eastern Australian coast (Brown et al., 1995). On wintering grounds, a male bias was found in Hawaii (1.86:1) (Craig & Herman, 1997), Northeast Madagascar (2.4:1) (Pomilla & Rosenbaum, 2006) and in two studies in Gabon (1.9:1) (Pomilla & Rosenbaum, 2006) and (2.1:1) (Carvalho et al., 2010). Off West South Africa, ratios were close to 1:1 (Carvalho et al., 2010) only deviating from near parity during mid-spring, resulting in a female-biased sex ratio (2.88:1) (Barendse et al., 2010b). Differences in haplotypic composition have been found between northbound migrating males and females in the South Pacific (Valsecchi et

al., 2010), suggesting that the two sexes of any single matrilineal stock might select different and only partially overlapping migration routes. However, observed skewed sex ratios may result from sampling biases including biases resulting from whale behaviour, group size or the timing of sampling (IWC, 2011b). Habitat preference is known to affect social organisation on wintering grounds, with mother-calf pairs preferring shallow inshore waters (Ersts & Rosenbaum, 2003). The sex-composition of surface activity groups on wintering grounds is known to be skewed towards males (Clapham et al., 1992). The relatively larger group size and activity of these types of groups gives them a higher chance of being detected and thus sampled, than for smaller groups or single individuals.

In the North Atlantic, individuals from multiple feeding grounds migrate to a shared breeding ground in the West Indies, although their migration appears to be temporally segregated according to feeding ground origin (Stevick *et al.*, 2003). Individuals from different feeding ground origins in the North Pacific have been shown to converge through a number of migratory links on shared wintering ground destinations off Japan, Hawaii and Mexico (Baker *et al.*, 1986; Barlow *et al.*, 2011; Calambokidis *et al.*, 2008; Calambokidis *et al.*, 1997).

This chapter focuses on population structure of humpback whales within the Southwest Indian Ocean, termed Breeding Stock C (IWC, 1998). Five potential sub regions used by whales in breeding stock C have been identified (IWC, 2011c). Sub region C1 includes the East African coastline, which is further delineated into C1-North and C1-South in the region of 15°S. Sub region C2 includes Mayotte, the Comores and the Mozambique Channel, whilst sub region C3 includes Madagascar. Further eastwards, the Mascarene group of island including Mauritius, Reunion and the Mascarene Group form sub region C4. More details are given in Chapter 1.

Based primarily on modern whaling catch history and distribution data, three migration routes have been proposed to be used by humpback whales into the Southwest Indian Ocean from their Antarctic feeding grounds (Best *et al.*, 1998). The southern and east coast of South Africa is thought to convey whales into sub region C1 whilst the Mozambique Channel has been proposed to feed into C2. A migration

route following the Madagascan Ridge is thought to convey whales into C3 and possibly C4 (IWC, 2011c).

Movements of individuals can provide information on population structure. Population structure of humpback whales in the Southwest Indian Ocean has been studied by investigating exchange between these sub regions (for example - Cerchio et al., 2008a; Cerchio et al., 2008b; Ersts et al., 2011; Ersts & Rosenbaum, 2003; Findlay et al., 2011; Fossette et al., 2012; Pomilla et al., 2005; Rosenbaum et al., 2009). Molecular, photographic and telemetry data have revealed limited movements of humpback whales between Mayotte (C2) and Madagascar (C3) (Ersts et al., 2011; Fossette et al., 2012), Madagascar (C3) and Reunion (C4) (Dulau-Drouot et al., 2011) and of one individual between Madagascar (C3) and East Africa (C1) (Cerchio et al., 2008b). The rate of exchange between C1 and C3 has been estimated to be lower than between C3 and either C2 or C4, resulting in higher and lower levels of differentiation respectively (IWC, 2011c). No significant genetic differentiation was found when Mozambique was compared with either East South Africa, Southern Madagascar or Northeast Madagascar (Antongil Bay) (Pomilla et al., 2005). However, significant differentiation was found when East South Africa was compared to Northeast Madagascar, except when males were tested separately, suggesting that movement is male biased between these two locations. Variation in the mitochondrial DNA control region has indicated significant population structure for all regions of breeding stock C, with the exception of C2 vs C3 (Rosenbaum et al., 2009). A higher degree of differentiation was found in females than in males, consistent with female philopatry and male dispersal; however, the authors noted that this could not be fully tested without nuclear or male-specific markers. Markedly different catch histories between whaling grounds off Mozambique and Madagascar also suggest segregation between these two stocks (Best et al., 1998; Findlay, 2001). This work has largely been driven by a requirement to provide information to the Scientific Committee of the IWC to inform ongoing assessments of Southern Hemisphere humpback whale stocks (IWC, 2011c)

Information on the migration route of Breeding Stock C1-S humpbacks, which was proposed by Best *et al.* (1998), is limited to shore-based monitoring at Cape Vidal on the northeast coast of South Africa (Findlay *et al.*, 2011; Findlay & Best, 1996) and

observations of humpback whales passing the Knysna Heads along the south coast of South Africa between 1903-1906 (Best & Ross, 1996). The migration route of humpback whales belonging to Breeding Stock C1 is not fully resolved. It is currently assumed that all whales observed migrating past Plettenberg Bay/Knysna on the south coast of South Africa are travelling to and from sub region C1 (Best *et al.*, 1998; Best & Ross, 1996). Recent support for this comes from the two photographic recaptures of individuals between Plettenberg Bay/Knysna, South Africa and Ponta Mamoli, Mozambique (See Chapter 3, Section 3.3.2.). Similarly, recent comparisons of temporal changes during migration off Plettenberg Bay/Knysna fit closely to temporal changes observed on the wintering grounds off Mozambique (Bazaruto Archipelago and Ponta Mamoli) (see Chapter 2).

However, the southbound migration off Plettenberg Bay/Knysna has been observed to continue into mid-February, several weeks later than expected, based on sighting data from Mozambique (see Chapter 2) and shore based surveys off Cape Vidal (Findlay & Best, 1996). Genetic information from these 'late' individuals off Plettenberg Bay/Knysna is lacking. Similarly, population structure in sub region C1 (East Africa) is limited to whales sampled off East South Africa and Mozambique (for example -Pomilla et al., 2005; Rosenbaum et al., 2009). Therefore, there is no information on the population structure of humpback whales along a substantial section of the coastal migration route along the south coast of South Africa. This study compares levels of genetic differentiation in humpback whales sampled in the western section of the East African migration route off the south coast of South Africa and in wintering grounds of Mozambique using the mtDNA control region. In addition, it compares these two sampling regions to existing haplotype sequences from Antongil Bay, north east Madagascar. This is the first genetic study of individuals migrating past Plettenberg Bay/Knysna on the south coast of South Africa. This will provide the first assessment of population structure between this region and winter grounds off Mozambique and northeastern Madagascar, which will enhance the current knowledge of population structure within the south west Indian Ocean.

4.1.2 Effects of biopsy sampling

Anthropogenic disturbance that is not directly lethal to individual humpback whales could still have detrimental effects on individuals from a welfare perspective. One of

the techniques employed to collect data in this study was skin biopsy sampling, which removes a sample of skin and blubber suitable for genetic analysis from live individuals. Due to the invasive nature of this method, it is important to evaluate the level of disturbance or harm inflicted upon an individual. Behavioural changes and displacement from habitat (short and long term), wound healing time and the cumulative effects to either the individual or population are all factors which need to be considered when justifying the use of skin biopsy sampling in genetic studies. However, studies analysing biopsy sampling affects and wound healing in cetaceans have found no evidence of long-term effects or physiological complications (for example - Best et al., 2005; Gimenez et al., 2011; Krutzen et al., 2002; Weller et al., 1997). Skin biopsy wounds on pilot whales (Globicephala melas) in the Strait of Gibraltar, were found to close as rapidly as four days, whilst complete repigmentation occurred within less than one year (Gimenez et al., 2011). Similarly, Indo-Pacific humpback dolphins (Sousa chinensis) sampled in the waters off Hong Kong showed wounds to be completely healed over with tissue after 21 days (Jefferson & Hung, 2008).

The behavioural response by a whale to a biopsy shot (whether hit or miss), termed "reaction" has frequently been used to indicate the level of disturbance caused by the method of biopsy sampling. Relatively high rates of reaction have been reported for some species of odontocetes. For example, a 100% reaction rate was reported for sperm whales (*Physeter macrocephalus*) (Whitehead *et al.*, 1990), 89% in northern bottlenose whales (*Hyperoodon ampullatus*) (Hooker *et al.*, 2001) and 81% in killer whales (*Orca orcinus*) (BarrettLennard *et al.*, 1996). In humpback whales, reaction rates differ according to whether they are being sampled during migration or on feeding or wintering grounds. During their migration off the east coast of Australia, 44% of individuals reacted to biopsy sampling (Brown *et al.*, 1994), compared to a response rate of 55.9% on the Silver Bank wintering grounds in the West Indies (Clapham & Mattila, 1993) and 93% on the Gulf of Maine feeding grounds (Weinrich *et al.*, 1992). In a small number of cases involving humpback whales, behaviours considered to correspond to a high-level reaction, such as tail thrashing and breaching, have been observed (Clapham & Mattila, 1993).

Differences in reaction rates between sexes have also been found. A reaction was significantly more likely to be invoked in females than males migrating along the east Australian coast, although there was no significant difference in the intensity of the reaction (Brown *et al.*, 1994). Conversely, mothers with calves on the wintering grounds of the West Indies reacted significantly less than all other classes, possibly as a result becoming desensitised to tactile stimulus through continued touching by nursing calves (Clapham & Mattila, 1993).

Photo identification was carried out prior to biopsy attempts in the studies of Clapham & Matilla (1993) and Weinrich *et. al.* (1992), which may have added a cumulative effect of disturbance from boat approaches leading to a higher response rate or intensity of reaction (Brown *et al.*, 1994).

In this study, the immediate behavioural responses of humpback whales to biopsy sampling attempts were categorised hierarchically, graded from no response to a strong response (Table 4.2). This allowed reaction rates to be determined as well as evaluating the level of disturbance caused by this technique. This information will add to existing knowledge on the effects of biopsy skin sampling on cetaceans and will allow more accurate assessments to be made when considering the use of this method in future studies.

4.2 Methods

4.2.1 Sample collection

Thirty four skin samples were obtained from humpback whales, of which thirty three samples were from free-swimming or dead stranded humpback whales off the coast of Plettenberg Bay/Knysna, South Africa (2008) and Bazaruto Archipelago (2007) and Ponta Mamoli (2009), Mozambique (Table 4.1). One sample, a piece of sloughed skin, was collected by a member of the public after a live individual temporarily stranded on a sand bar during an ebbing tide in Bazaruto Archipelago, Mozambique 2007 (Table 4.1). The sloughed skin was collected during attempts to keep the animal cool with water before a successful re-floatation occurred on a flooding tide. All

samples were subsequently accessioned into the Port Elizabeth Museum, South Africa with each sample allocated a unique museum specimen number (PEM NO).

Table 4.1 Skin samples collected and used in this study, obtained from humpback whales from Plettenberg Bay, South Africa (2008), Bazaruto Archipelago (2007) and Ponta Mamoli (2009), Mozambique. Approximate sample locations are given in latitude and longitude. PEM_No. = Port Elizabeth Museum specimen number. Location code: Plett = Plettenberg Bay, Baz = Bazaruto, P. Mam = Ponta Mamoli. Country codes: S.A. = South Africa, MZ = Mozambique. * = Sloughed skin provided by a member of the public after a live humpback whale temporally stranded on a sand bar during an ebbing tide. Sample group: Samples collected during a sighting have the same sample group number. n/a = sample not sequenced.

Sample No.	Sample Group	PEM. No.	Date	Location	Country	Lat. (S)	Long. (E)	Sample Type
SA_1	1	4567	10/10/2008	Plett	S.A.	34°10'	23°50'	Biopsy
SA_2	1	4568	10/10/2008	Plett	S.A.	34°10'	23°50'	Biopsy
SA_3	2	4569	19/10/2008	Plett	S.A.	34°10'	23°50'	Biopsy
SA_4	3	4570	11/10/2008	Plett	S.A.	34°10'	23°50'	Biopsy
SA_5	3	4571	11/10/2008	Plett	S.A.	34°10'	23°50'	Biopsy
SA_6	3	4572	11/10/2008	Plett	S.A.	34°10'	23°50'	Biopsy
SA_7	3	4573	11/10/2008	Plett	S.A.	34°10'	23°50'	Biopsy
MOZ_1	4	4552	18/10/2007	Baz	MZ	21°30'	35°35'	Biopsy
MOZ_2	5	4553	8/11/2007	Baz	MZ	21°35'	35°20'	Stranding
MOZ_3	n/a	4554	8/10/2009	P. Mam	MZ	26°35'	33°00'	Biopsy
MOZ_4	n/a	4555	8/8/2009	P. Mam	MZ	26°35'	33°00'	Biopsy
MOZ_5	6	4556	8/8/2009	P. Mam	MZ	26°35'	33°00'	Biopsy
MOZ_6	7	4557	8/8/2009	P. Mam	MZ	26°35'	33°00'	Biopsy
MOZ_7	7	4558	8/8/2009	P. Mam	MZ	26°35'	33°00'	Sloughed Skin
MOZ_8	8	4559	3/10/2009	P. Mam	MZ	26°35'	33°00'	Biopsy
MOZ_9	8	4560	3/10/2009	P. Mam	MZ	26°35'	33°00'	Biopsy
MOZ_10	8	4561	3/10/2009	P. Mam	MZ	26°35'	33°00'	Biopsy
MOZ_11	9	4562	10/8/2009	P. Mam	MZ	26°35'	33°00'	Biopsy
MOZ_12	9	4563	10/8/2009	P. Mam	MZ	26°35'	33°00'	Biopsy
MOZ_13	10	4564	10/9/2009	P. Mam	MZ	26°35'	32°54'	Stranding
MOZ_14	11	4565	9/8/2009	P. Mam	MZ	26°35'	33°00'	Biopsy

MOZ_15	11	4566	9/8/2009	P. Mam	MZ	26°35'	33°00'	Biopsy
MOZ_16	12	4574	2/9/2007	Baz	MZ	21°30'	35°35'	Biopsy
MOZ_17	13	4575	4/9/2007	Baz	MZ	21°30'	35°35'	Biopsy
MOZ_18	14	4576	12/9/2007	Baz	MZ	21°30'	35°35'	Biopsy
MOZ_19	14	4577	12/9/2007	Baz	MZ	21°30'	35°35'	Biopsy
MOZ_20	15	4578	10/10/2007	Baz	MZ	21°30'	35°35'	Biopsy
MOZ_21	16	4579	10/10/2007	Baz	MZ	21°30'	35°35'	Biopsy
MOZ_22	16	4580	10/10/2007	Baz	MZ	21°30'	35°35'	Biopsy
MOZ_23	17	4581	10/10/2007	Baz	MZ	21°30'	35°35'	Biopsy
MOZ_24	18	4582	13/10/2007	Baz	MZ	21°35'	35°20'	Stranding *Sloughed skin
MOZ_25	19	4583	6/10/2009	P. Mam	MZ	26°35'	33°00'	Biopsy
MOZ_26	20	4584	13/10/2009	P. Mam	MZ	26°35'	33°00'	Biopsy
MOZ_27	n/a	4585	12/9/2009	P. Mam	MZ	26°35'	33°00'	Biopsy

4.2.1.1 Biopsy sampling procedures

Skin biopsies were collected from whales using specially designed biopsy sampling tips attached to flotation-fitted bolts fired from a crossbow. The biopsy sampling tips were 8mm in diameter with a skin penetration depth of 30mm (Figure 4.1). Each tip was fitted with a stopper to limit penetration of the tip into the whale. To reduce the risk of infection to the whale and to avoid cross-contamination between samples, biopsy tips were sterilised by immersion in 50% hydrogen peroxide prior to a biopsy being taken. Skin samples were removed from the biopsy-sampling tip whilst still on board the research vessel and immediately stored in 50% ethanol in eppendorf tubes. Once back onshore, the eppendorf tubes were frozen and stored in a standard domestic freezer until the samples were transferred to the Port Elizabeth Museum, South Africa, and stored in their freezer facilities.

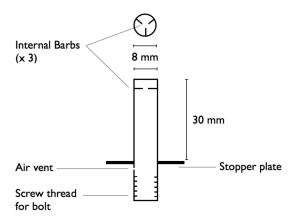


Figure 4.1 Biopsy tip design. Circle shows a vertical view of the tip barrel with three internal barbs used to retain the skin sample inside the tip.

Where possible, a photograph was taken of the tail fluke or dorsal fin of the whale being biopsied in order to assign an individual identification to the skin sample.

To reduce bias in sampling of age/sex classes, all group sizes and individuals within a group were considered for biopsy sampling regardless of group composition. Skin samples were also taken from dead stranded animals and stored as described above. All sampling in South Africa was carried out under a permit issued by the Director, Marine and Coastal Management (MCM), South Africa (Appendix 1a), and in accordance with the stipulated biopsy sampling permit conditions, skin samples were only collected during trips onboard the research vessels. In Mozambique, all samples were collected outside Marine Protected Areas where a permit to obtain skin samples through biopsy sampling was not required.

The immediate behavioural reactions by individual humpback whales to skin biopsy attempts were recorded to assess the level of disturbance attributed to skin biopsy procedures during this study. Data collected off Bazaruto Archipelago, Mozambique in 2007 was undertaken using a two-man team (skipper and data collector). This meant that with the exception of physically driving the boat, all activities were conducted by a single person (the data collector) during a sighting including data scribing, camera operation for photo-identification images, biopsy darting and sample retrieval, and directing the skipper when manoeuvring around the animals. This

limited the ability to record detailed behavioural reactions throughout the biopsy sampling procedure. Therefore, only the level of behavioural reaction immediately following a strike with the biopsy tip was recorded. These were graded on a hierarchal scale according to the severity of the reaction on a scale of 1-4 (no reaction to strong reaction) (Table 4.2), largely following the grading system and reaction descriptions defined by Clapham and Matilla (1993).

Table 4.2 Behavioural descriptions used to grade (Scale 1-4) the reactions of individual humpback whales subjected to skin biopsy attempts (after Clapham & Mattila, 1993).

Scale	Behavioural reaction description
1	None: No observable behavioural response
2	Low: A brief startle (flinch)/quick submergence or both
3	Moderate: One or two tail flicks
	Strong: Multiple tail flicks and/or lateral tail thrashes and/or high energy behaviours (e.g.)
4	breach/tail breach/lobtail/flipper slap.

4.2.2 Shipment

The transfer of skin samples between countries was done in accordance with the regulations for "Appendix I" species listed by CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora). All required Export, Reexport and Import Permits were obtained from CITES before samples were shipped (Appendix 1b-c). An Animal Health Import Licence was issued by Defra (Department for Environment, Food and Rural Affairs, UK) certifying that the import of the skin samples into the UK posed no risk to British fauna or flora (Appendix 1d). All samples were shipped to the UK in eppendorf tubes containing ethanol and frozen at -20°C upon arrival at the Centre for Evolution, Genes and Genomics, University of St Andrews, Scotland, the location for sample processing.

4.2.2.1 mtDNA extraction

Laboratory procedures:

Between 10-20 mg of finely diced tissue (skin) was added to 600 μl cell lysis buffer solution (0.1 M EDTA, 0.2 M Tris, pH 8.5, 1% SDS) in a 1.5 ml eppendorf tube and 3 μl Proteinase K (20 mg/ml) was added to the lysate and incubated at 50°C overnight with agitation. If complete digestion had not occurred, an additional 3μl of Proteinase K was added, followed by further periods of incubation at 50°C. After Proteinase K digestion, 3 μl RNAse A (10 mg/ml) was added to the lysate and the sample was inverted 25 times to mix and then incubated at 37° C for 15-60 minutes. Once cooled, 200 μl 5M KAc was added to the solution, which was then inverted, vortexed at high speed for 20 seconds and centrifuged at 13,000 rpm for 3 minutes.

The supernatant was decanted into a clean 1.5 μl eppendorf tube with 600 μl 100% isopropanol and inverted until a DNA precipitate formed and centrifuged at 13,000 rpm for 1 minute. The supernatant was removed and the pellet washed by adding 600 μl 70% ethanol, followed by 1 min centrifugation at 13,000 rpm before removing the supernatant. This was repeated a second time before a third centrifugation for 1 min at 13,000 rpm. Any remaining ethanol was removed and the eppendorf tube containing the pellet was left to dry. Once dry, the DNA pellet was resuspended overnight at room temperature in 20-100 μl Mili-Q water (depending on pellet size). Once resuspended, the concentration of DNA was measured on a Nanodrop (ND-1000 Spectrophotometer, Thermo Fisher Scientific, USA). Dilutions of 20 ng DNA/μl were made for samples measuring >20 ng DNA/μl.

In addition, a phenol-chloroform extraction was also performed for one sample (Moz-27) following the protocol for organic extraction (Sambrook *et al.*, 1989).

4.2.2.2 PCR Amplification

A 750 bp fragment of the mtDNA control region was amplified using the primers M13Dlp1.5 (5'-GTAAAACGACGGCCAGTTCACCCAAAGCTGRARTTCTA-3') and Dlp8G (5'-GGAGTACTATGTCCTGTAACCA-3') (Dalebout *et al.*, 2005). Fragments of the mtDNA control region for all samples were amplified using a 25 µl

reaction with 2.5 μl 10x PCR buffer (Bioline), 0.75 μl 50 mM MgCl₂, 0.25 μl 0.24 nM dNTP's (Bioline), 0.5 μl 50 pM of each primer, 0.3 μl 0.5 unit BioTaq (Bioline), 17.75 μl Mili-Q water, 5-20 ng genomic DNA. The polymerase chain reaction (PCR was conducted in a PTC-100 Programmable Thermal Controller (MJ Research, Inc.) with a cycling profile of 95°C for 5 minutes and 30 cycles of 30 seconds denaturing at 95°C, 30 seconds annealing at 58°C and 60 seconds extension at 72°C. This was followed by a single 5 minute denaturing step at 72°C. The amplification products were stained with 6x Orange Dye and separated by electrophoresis at 80v through a 2% Agarose gel in 0.5x TBE buffer stained with Ethidium Bromide (EtBr). The gel was viewed under UV light to confirm product length and the absence of contamination in a negative control.

4.2.2.3 Sequencing

Amplified products were cleaned using QIAquick® PCR Purification Kit before being outsourced to Genepool, Edinburgh, UK for sequencing using a Big Dye reaction in an ABI 3730 Sanger machine.

4.2.2.4 Sex determination

ZFY and ZFX nucleotide sequences were amplified in 20 μl volumes using three mysticete oligonucleotide primers ZFY0582F, ZFY0752R and ZFX0785R (as described by Berubé & Palsboll, 1996). Initially, the separation of amplified products by gel-electrophoresis was attempted using the conditions previously described, but this resulted in poor separation. Successful separation was achieved using gel-electrophoresis at 180v through a 2% Metaphore® Agarose gel in 1x TBE buffer and post-stained for 15 minutes with EtBr. For samples that had only small volumes of PCR product remaining after the initial separation attempts, a re-amplification was conducted to increase the PCR product volume.

4.2.3 Analysis

Skin biopsy samples from individual humpback whales were categorised by region (South Africa and Mozambique) (Table 4.1). Sequences were viewed and edited by

eye in *Chromas Lite v.2.1* (Technelysium Pty Ltd). Alignment of the forward and reverse sequences was performed in CLC Sequence Viewer *v.6.7.1* (CLC bio A/S) using a ClustalW plug-in *v.1.4.1*. to construct a 538 base pair consensus mtDNA Control Region fragment, containing the majority of variable nucleotide positions in the humpback whale mtDNA Control Region (Baker *et al.*, 1993).

In addition to the samples sequenced in this study, 22 haplotype sequences from north east Madagascar and three from both Mozambique and East South Africa identified by location in a study by Rosenbaum *et. al.* (2009) (Table 4.3) were also added to this study's sequences. This allowed control region variation in the neighbouring sub region of Madagascar (C3) to be compared to those covered here. These additional sequences were slightly longer at the 5' end and shorter at the 3' end than the sequences obtained during this study. Therefore, a second alignment was performed, where all sequences were aligned and truncated to equal length, to produce a consensus mtDNA control region fragment of 401 base pairs.

Statistical parameters and tests to estimate genetic diversity, differentiation and population structure were calculated in *Arlequin v.3.5* (Excoffier & Lischer, 2010). The analysis was conducted in two stages:

Stage 1: This was performed using the first alignment (538 base pair control region fragment), which were the sequences from this study only. Genetic diversity within South Africa and Mozambique was estimated by calculating the number of unique control region haplotypes, haplotype frequencies, number of polymorphic sites, number of transitions, transversions and indels, nucleotide frequency, haplotype diversity (h) and nuceliotide diversity (π). Haplotype diversity represents the probability that two randomly sampled alleles are different, while nucleotide diversity (π) is defined as the average number of nucleotide differences per site in pairwise comparisons among DNA sequences (Nei, 1987 In: de Jong et al., 2011). Differentiation between South Africa and Mozambique was quantified as a pairwise Fst score (Markov chain steps 100,000, dememorisation steps 10,000) where a value of zero implies no differentiation between populations and a value of one implies complete population differentiation.

A phylogenetic Neighbour-Joining tree was constructed in DAMBE v.5.3.9 (Xia & Xie, 2001), using the K80 parameter (Kimura, 1980) which distinguishes between transitions and transversions, to examine the phylo-geographic history of the mtDNA haplotypes.

Stage 2: This was performed using the second alignment (a shorter 401 base pair control region fragment), which combined sequences from this study with additional GenBank sequences from East South Africa, Mozambique and Madagascar (Table 4.3).

Differentiation between South Africa and Mozambique and Madagascar was quantified as pairwise Fst scores (Markov chain steps 100,000, dememorisation steps 10,000). Analysis of Molecular Variance (AMOVA) in Arlequin (Excoffier *et al.*, 1992), which uses information on nucleotide differences between haplotypes as well as haplotype frequency, was used to investigate genetic structure among and between these three regions by computation of conventional F-statistics from haplotypes with 1000 permutations. This procedure calculates variance components and an array of haplotypic correlation measures for population studies, referred to as Φ-statistics, which is analogous to Wright's F-statistics (Rosenbaum *et al.*, 2009). Regions (South Africa, Mozambique and Madagascar) were assigned into two groups, with one of these groups containing two regions as subsets, for example Group 1: South Africa and Mozambique, Group 2: Madagascar. All grouping combinations were tested.

Table 4.3 Additional GenBank haplotype sequences from Madagascar (HBA, n=22), Mozambique (HMZ, n=3) and East South Africa (HZE, n=3).

Haplotype	Region	GenBank accession number	Source
HBA048	Madagascar	GQ913738.1	Rosenbaum et. al., 2009
HBA050	Madagascar	GQ913740.1	Rosenbaum et. al., 2009
HBA052	Madagascar	GQ913742.1	Rosenbaum et. al., 2009
HBA058	Madagascar	GQ913744.1	Rosenbaum et. al., 2009
HBA063	Madagascar	GQ913746.1	Rosenbaum et. al., 2009
HBA070	Madagascar	GQ913748.1	Rosenbaum et. al., 2009
HBA072	Madagascar	GQ913750.1	Rosenbaum et. al., 2009
HBA074	Madagascar	GQ913752.1	Rosenbaum et. al., 2009
HBA076	Madagascar	GQ913754.1	Rosenbaum et. al., 2009
HBA078	Madagascar	GQ913756.1	Rosenbaum et. al., 2009
HBA080	Madagascar	GQ913758.1	Rosenbaum et. al., 2009
HBA082	Madagascar	GQ913760.1	Rosenbaum et. al., 2009
HBA084	Madagascar	GQ913762.1	Rosenbaum et. al., 2009
HBA086	Madagascar	GQ913764.1	Rosenbaum et. al., 2009
HBA088	Madagascar	GQ913766.1	Rosenbaum et. al., 2009
HBA096	Madagascar	GQ913770.1	Rosenbaum et. al., 2009
HBA098	Madagascar	GQ913772.1	Rosenbaum et. al., 2009
HBA100	Madagascar	GQ913774.1	Rosenbaum et. al., 2009
HBA102	Madagascar	GQ913776.1	Rosenbaum et. al., 2009
HBA104	Madagascar	GQ913778.1	Rosenbaum et. al., 2009
HBA111	Madagascar	GQ913780.1	Rosenbaum et. al., 2009
HBA113	Madagascar	GQ913782.1	Rosenbaum et. al., 2009
HEZ001	East South Africa	GQ913802.1	Rosenbaum et. al., 2009
HEZ002	East South Africa	GQ913803.1	Rosenbaum et. al., 2009
HEZ003	East South Africa	GQ913804.1	Rosenbaum et. al., 2009
HMZ001	Mozambique	GQ913842.1	Rosenbaum et. al., 2009
HMZ002	Mozambique	GQ913843.1	Rosenbaum et. al., 2009
HMZ005	Mozambique	GQ913844.1	Rosenbaum et. al., 2009

4.3 Results

In total, 31 of 34 samples collected during this study were successfully sequenced and analysed. One sample (MOZ-27) failed to amplify after using the described extraction method (section 4.2.2.1) as well as a Phenol-chloroform extraction (Sambrook *et al.*, 1989). Two samples (MOZ-3 and MOZ-4) amplified but did not sequence successfully. Gel-electrophoresis of the genomic DNA from the three samples showed the DNA was degraded, possibly as a result of poor sample preservation.

Sex was determined for 33 individuals, resulting in a total of 21 males and 12 females (South Africa: males=5, females=2, n=7) (Mozambique: males=16, females=10, n=26) (Figure 4.2). This gave a male:female sex-ratio in South Africa of 2.5:1 and Mozambique 1.6:1. However, these did not vary significantly from parity (South Africa: n=7, χ^2_{Yates} =0.571, df=1, p=0.450; Mozambique: n=26, χ^2_{yates} =0.962, df=1, p=0.327) (Yates corrected for one degree of freedom).

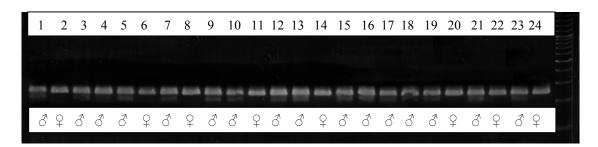


Figure 4.2 Example of the ZFX and ZFY amplification products after gel electrophoresis for sex determination of sampled individuals. Lanes 1-7 = SA1-7. Lanes 8-24 = Moz 1-17. One band = \Im . Two bands = \Im .

4.3.1 Stage 1: Genetic diversity and differentiation (sequences from this study only).

In the 538 base pair control region fragment from 31 individual humpback whales (South Africa: n=7, Mozambique: n=24), both sampling regions had equal mean nucleotide frequencies: 22.0% cytosine, 33.5% thyamine, 28.7% adenine and 15.8% guanine. The number of transitions, transversions, substitutions, indels, and

polymorphic sites found within each sampling region (South Africa and Mozambique) are shown in Table 4.4. The much higher number of indels in South Africa (n=18) compared to Mozambique (n=2) is due to a single haplotype containing a 16 base pair indel.

Levels of haplotype diversity (h) and nucleotide diversity (π) were similar between regions, both showing equally high levels of haplotype diversity and low levels of nucleotide diversity within-regions (Table 4.5).

In total, 21 haplotypes were identified (Table 4.6 and Table 4.7) resulting in a complete non-overlap in haplotype distribution between regions. The most common haplotypes (Hap_2, Hap_6 and Hap_12) were all found in Mozambique, each being shared by three individuals, whilst the majority of haplotypes (n=14) were unique to particular individuals (Table 4.6). Pairwise inter-haplotypic distances (Table 4.7) found haplotypes to differ by 1 to 29 nucleotide changes, with haplotype 18 (Hap_18) being the most distinct. The relatively large number of nucleotide differences observed in this unshared haplotype (belonging to individual SA-2) is due to the inclusion of a 16 base pair indel not present in the mtDNA control region of other individuals (Table 4.8).

Table 4.4 The frequency of transitions, transversions, substitutions, indels, and polymorphic sites found within each sampling region. Number of Samples: South Africa n=7, Mozambique n=24). *=Two single bp indels plus one 16 bp indel.

Region	Transitions	Transversions	Substitutions	Indels	Polymorphic sites
South Africa (n=7)	19	1	20	18*	36
Mozambique (n= 24)	33	2	35	2	36

Table 4.5 Number of haplotypes, haplotype diversity (h), nucleotide diversity (π) within each sampling region (South Africa n=7, Mozambique n=24). Standard deviation in parentheses.

Region	Number of haplotypes	h (SD)	π (SD)
South Africa (n=7)	5	0.905 (0.103)	0.0240 (0.0141)
Mozambique (n= 24)	16	0.960 (0.0222)	0.0191 (0.0101)

Analysis of mtDNA control region haplotypes using only the individuals sampled during this study found significant differentiation between South Africa and Mozambique ($F_{st} = 0.064$, P=0.009). In contrast, examination of the Neighbour-Joining tree (Figure 4.3) suggests that lineages of both South African and Mozambique individuals are inter-mixed. Monophyletic groups (clades) that contain haplotypes from South African individuals are also shared by those from Mozambique.

Table 4.6 The distribution, frequencies and relative frequencies (combined and within-region) of unique haplotypes (n=21) identified from all sampled individuals in both regions (South Africa n=7, Mozambique n=24). The number of individuals per haplotype is given per region. Sample group: Samples collected during a sighting have the same sample group number. n/a =sample not sequenced.

	Sample	Haplotype	frequency	Haplotype re	lative frequency		
Haplotype	Group	South Africa (n=7)	Mozambique (n=24)	Combined	Within region		
Hap_1	4, 9, 17	-	3	0.0968	0.125		
Hap_2	5	-	1	0.0323	0.0417		
Hap_3	6, 13	-	2	0.0645	0.0833		
Hap_4	7	-	1	0.0323	0.0417		
Hap_5	7	-	1	0.0323	0.0417		
Hap_6	8, 14	-	3	0.0968	0.125		
Hap_7	8	-	1	0.0323	0.0417		
Hap_8	8	-	1	0.0323	0.0417		
Hap_9	9, 15	-	2	0.0645	0.0833		
Hap_10	10	-	1	0.0323	0.0417		
Hap_11	11	-	1	0.0323	0.0417		
Hap_12	11, 16	-	3	0.0968	0.125		
Hap_13	12	-	1	0.0323	0.0417		
Hap_14	18	-	1	0.0323	0.0417		
Hap_15	19	-	1	0.0323	0.0417		
Hap_16	20	-	1	0.0323	0.0417		
Hap_17	1	1	-	0.0323	0.143		
Hap_18	1	1	-	0.0323	0.143		
Hap_19	2 1		-	0.0323	0.143		
Hap_20	_20 3 2			0.0645	0.286		
Hap_21	3	2	-	0.0645	0.286		

Table 4.7 Inter-haplotypic distance (number of nucleotide differences) matrix of pairwise differences for all identified unique haplotypes. Standard deviations are above the diagonal.

	Hap_1	Hap_2	Hap_3	Hap_4	Hap_5	Нар_6	Hap_7	Hap_8	Hap_9	Hap_10	Hap_11	Hap_12	Hap_13	Hap_14	Hap_15	Hap_16	Hap_17	Hap_18	Hap_19	Hap_20	Hap_21
Hap_1		3.314	3.314	3.314	2.597	3.187	3.254	3.254	2.723	3.254	3.254	2.937	3.029	2.835	3.314	3.187	3.029	3.537	2.723	3.314	3.254
Hap_2	16		3.029	3.112	3.029	3.029	2.937	2.937	3.254	2.723	3.112	3.367	3.413	3.314	3.029	3.029	2.835	3.565	3.254	3.029	3.112
Hap_3	16	12		2.124	3.029	1.920	2.723	1.680	3.112	2.124	2.723	3.112	3.187	3.029	1.920	2.835	3.187	3.487	2.937	1.920	2.458
Hap_4	16	13	5		3.112	2.458	2.835	1.386	3.187	2.597	2.835	3.187	3.254	3.254	0.990	2.723	3.112	3.554	3.029	1.680	2.597
Hap_5	8	12	12	13		2.835	3.112	2.937	1.680	2.723	3.112	2.124	2.301	1.920	3.029	3.029	2.835	3.570	2.124	3.029	3.112
Hap_6	14	12	4	7	10		2.723	2.124	2.937	2.124	2.458	2.937	3.029	3.029	2.301	2.597	3.187	3.314	2.723	2.301	2.124
Hap_7	15	11	9	10	13	9		2.597	3.187	2.597	1.386	3.314	3.367	3.254	2.723	1.680	2.723	3.565	3.187	2.723	2.835
Hap_8	15	11	3	2	11	5	8		3.029	2.301	2.597	3.029	3.112	3.112	0.990	2.458	2.937	3.515	2.835	0.990	2.301
Hap_9	9	15	13	14	3	11	14	12		3.029	3.187	2.301	2.458	0.990	3.112	3.112	3.112	3.570	1.386	3.112	3.187
Hap_10	15	9	5	8	9	5	8	6	12		2.835	3.187	3.254	3.112	2.458	2.937	2.723	3.515	3.029	2.458	2.597
Hap_11	15	13	9	10	13	7	2	8	14	10		3.187	3.254	3.254	2.723	0.990	2.937	3.537	3.029	2.723	2.597
Hap_12	11	17	13	14	5	11	16	12	6	14	14		0.990	2.458	3.112	3.112	3.254	3.570	2.301	3.112	3.187
Hap_13	12	18	14	15	6	12	17	13	7	15	15	1		2.597	3.187	3.187	3.314	3.565	2.458	3.187	3.254
Hap_14	10	16	12	15	4	12	15	13	1	13	15	7	8		3.187	3.187	3.187	3.570	1.680	3.187	3.254
Hap_15	16	12	4	1	12	6	9	1	13	7	9	13	14	14		2.597	3.029	3.537	2.937	1.386	2.458
Hap_16	14	12	10	9	12	8	3	7	13	11	1	13	14	14	8		2.835	3.554	2.937	2.597	2.723
Hap_17 Hap_18	12	10 27	14	13 23	10 25	14 16	9 24	11	13 25	9 21	11	15 26	16 27	14 26	12	10 23	29	3.537	3.112	3.029	3.254
нар_18 Нар_19	29 9	15	20	12	5	9	14	10	25	12	12	6	7	3	11	11	13	23	3.554	2.937	3.029
нар_19 Нар_20	16	12	4	3	12	6	9	10	13	7	9	13	14	14	2	8	12	22	11	2.93/	2.124
Hap_21	15	13	7	8	13	5	10	6	14	8	8	14	15	15	7	9	15	21	12	5	2.124
110P_21	1.0	10			10	,	10		A-4	-		44	1.0	1.0			1.0	4.1	14	,	

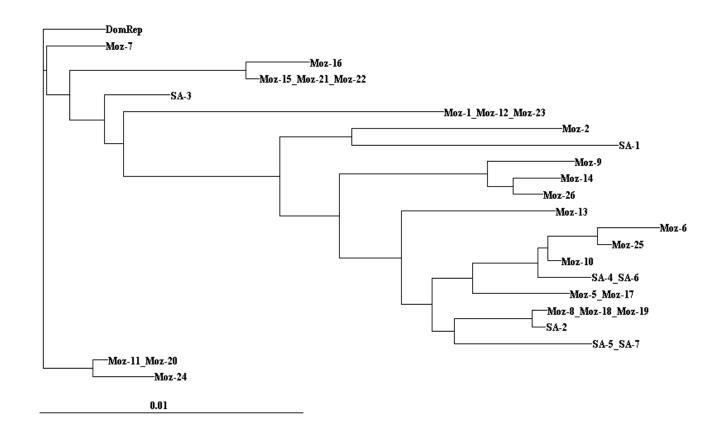


Figure 4.3 Neighbour-Joining phylogram based on the K80 parameter showing the relationship between control region haplotypes (n=21) identified from all individuals (n=31). The tree was rooted using an out-group sample from the Dominican Republic (DomRep) (GenBank accession number GQ353253.1). Moz = Mozambique individuals, n=26. SA=South Africa individuals, n=7. Scale= Phylogenetic distance (the number of nucleic acid substitutions which have taken place along a branch). Each haplotype shows the individuals that possess that particular haplotype

Table 4.8 Polymorphic sites for all unique haplotypes from South Africa and Mozambique individuals. a) Loci 1-118. b) Loci 129-392. Indel (-). Number of individuals with haplotype (#).

a)

												Polyr	norph	ic site	es																		
Haplotype	#	Individual	7	20	28	29	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	62	66	71	79	80	91	106	107	112	116	118
Hap_1	3	Moz-1,12,23	С	Т	С	Т	G	Т	Α	Т	G	Т	Α	С	Т	Α	С	С	Α	С	Α	Т	-	-	С	G	G	Т	Т	Т	Т	G	Т
Hap_2	1	Moz-2	Т	Т	Т	С	G	T	Α	Т	G	T	Α	С	Т	Α	С	C	Α	С	Α	Т	Т	-	Т	Α	G	Т	Т	Т	C	Α	С
Hap_3	2	Moz-5,17	Т	Т	Т	С	G	Т	Α	Т	G	Т	Α	Α	Т	Α	С	С	Α	С	Α	Т	-	-	Т	Α	Α	C	Т	С	С	Α	С
Hap_4	1	Moz-6	Т	Т	Т	С	G	Т	Α	Т	G	Т	Α	Α	Т	Α	С	C	Α	C	Α	Т	-	-	Т	Α	Α	C	Т	Т	С	Α	С
Hap_5	1	Moz-7	С	Т	Т	Т	G	Т	Α	Т	G	Т	Α	С	Т	Α	С	С	Α	С	Α	Т	-	-	С	Α	G	С	Т	Т	Т	Α	С
Hap_6	3	Moz-8,18,19	Т	С	Т	Т	G	Т	Α	Т	G	Т	Α	Α	Т	Α	С	С	Α	С	Α	Т	-	-	Т	Α	G	С	Т	С	С	Α	С
Hap_7	1	Moz-9	Т	Т	Т	С	G	Т	Α	Т	G	Т	Α	С	Т	Α	С	С	Α	С	Α	Т	-	-	Т	Α	G	Т	Т	С	С	Α	С
Hap_8	1	Moz-10	Т	T	Т	С	G	Т	Α	Т	G	Т	Α	Α	Т	Α	С	С	Α	С	Α	Т	-	-	Т	Α	Α	С	Т	Т	С	Α	С
Hap_9	2	Moz-11,20	С	T	Т	Т	G	Т	Α	Т	G	С	Α	С	Т	Α	С	С	Α	С	Α	Т	-	Т	С	Α	G	С	Т	Т	Т	Α	С
Hap_10	1	Moz-13	Т	T	Т	С	G	Т	Α	Т	G	Т	Α	Α	Т	Α	С	С	Α	С	Α	Т	-	-	Т	Α	G	С	Т	С	С	Α	С
Hap_11	1	Moz-14	Т	Т	Т	Т	G	Т	Α	Т	G	Т	Α	С	Т	Α	С	С	Α	С	Α	Т	-	-	Т	Α	G	Т	Т	С	С	Α	С
Hap_12	3	Moz-15,21,22	С	Т	Т	Т	G	Т	Α	Т	G	Т	Α	С	Т	Α	С	С	Α	С	Α	Т	-	-	С	Α	G	С	С	Т	Т	Α	С
Hap_13	1	Moz-16	С	Т	Т	Т	G	Т	Α	Т	G	Т	Α	С	Т	Α	С	С	Α	С	Α	Т	-	-	С	Α	G	С	С	Т	Т	Α	С
Hap_14	1	Moz-24	С	Т	Т	Т	G	Т	Α	Т	G	С	Α	С	Т	Α	С	С	Α	С	Α	Т	-	Т	С	Α	G	С	Т	Т	Т	Α	С
Hap_15	1	Moz-25	Т	T	Т	С	G	Т	Α	Т	G	Т	Α	Α	Т	Α	С	С	Α	С	Α	Т	-	-	Т	Α	Α	С	Т	Т	С	Α	С
Hap_16	1	Moz-26	Т	T	Т	Т	G	Т	Α	Т	G	Т	Α	С	Т	Α	С	С	Α	С	Α	Т	-	-	Т	Α	G	Т	Т	Т	С	Α	С
Hap_17	1	SA-1	Т	Т	Т	С	G	Т	Α	Т	G	Т	Α	С	Т	Α	С	С	Α	С	Α	Т	-	-	С	G	G	Т	Т	Т	С	Α	С
Hap_18	1	SA-2	Т	С	Т	Т	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	Т	Α	G	С	Т	С	С	Α	С
Hap_19	1	SA-3	С	Т	Т	Т	G	Т	Α	Т	G	С	Α	С	Т	Α	С	С	Α	С	Α	Т	-	Т	С	Α	G	С	Т	Т	Т	Α	С
Hap_20	2	SA-4,6	Т	Т	Т	С	G	Т	Α	Т	G	Т	Α	Α	Т	Α	С	С	Α	С	Α	Т	-	-	Т	Α	Α	С	Т	Т	С	Α	С
_Hap_21	2	SA-5,7	<u>T</u>	T_	С	T	G	T	Α	T	G	T	Α	Α	T	Α	С	С	Α	С	Α	T	T	-	T	Α	G	С	T	С	С	Α	C

										Polyn	norph	ic site	es									
Haplotype	#	Individual	129	186	190	191	193	206	208	209	210	211	214	218	229	230	231	251	261	262	325	392
Hap_1	3	Moz-1,12,23	Т	Т	G	Т	С	Α	Α	Т	Т	Т	Т	Α	Т	С	Т	Α	С	Т	С	Т
Hap_2	1	Moz-2	Т	С	G	Т	C	Α	G	Т	C	Т	Т	G	Т	C	C	Α	С	C	C	C
Hap_3	2	Moz-5,17	Т	Т	G	C	C	Α	G	Т	Т	Т	Т	G	Т	C	Т	G	С	Т	C	Т
Hap_4	1	Moz-6	Т	Т	Α	C	C	Α	C	Т	Т	C	Т	G	Т	C	Т	Α	С	Т	C	Т
Hap_5	1	Moz-7	Т	Т	G	Т	C	Α	G	Т	C	Т	Т	Α	C	C	Т	Α	С	Т	C	Т
Hap_6	3	Moz-8,18,19	Т	Т	G	С	С	Α	G	Т	Т	Т	Т	G	Т	С	Т	Α	С	Т	С	Т
Hap_7	1	Moz-9	C	Т	G	Т	С	Α	G	C	Т	C	С	G	Т	С	Т	Α	С	Т	С	Т
Hap_8	1	Moz-10	Т	Т	G	С	С	Α	G	Т	Т	C	Т	G	Т	С	Т	Α	С	Т	С	Т
Hap_9	2	Moz-11,20	Т	Т	G	Т	С	Α	G	Т	Т	Т	Т	Α	С	С	Т	Α	С	Т	С	Т
Hap_10	1	Moz-13	Т	Т	G	Т	С	Α	G	Т	С	Т	Т	G	Т	С	Т	Α	Т	Т	С	Т
Hap_11	1	Moz-14	C	Т	G	С	С	Α	G	C	Т	C	С	G	Т	С	Т	Α	С	Т	С	Т
Hap_12	3	Moz-15,21,22	Т	Т	G	С	Т	Α	G	Т	Т	Т	Т	Α	С	Т	Т	Α	С	Т	С	Т
Hap_13	1	Moz-16	Т	Т	G	С	Т	G	G	Т	Т	Т	Т	Α	С	Т	Т	Α	С	Т	С	Т
Hap_14	1	Moz-24	Т	Т	G	Т	C	Α	G	Т	Т	Т	Т	Α	С	C	Т	G	С	Т	С	Т
Hap_15	1	Moz-25	Т	Т	Α	С	C	Α	G	Т	Т	C	Т	G	Т	C	Т	Α	С	Т	С	Т
Hap_16	1	Moz-26	C	Т	G	C	C	Α	G	C	Т	C	C	G	Т	C	Т	Α	С	Т	C	Т
Hap_17	1	SA-1	Т	Т	G	Т	C	Α	G	Т	C	C	C	Α	Т	C	Т	Α	Т	C	C	Т
Hap_18	1	SA-2	Т	Т	G	C	C	Α	G	Т	Т	Т	Т	G	Т	C	Т	Α	С	Т	C	Т
Hap_19	1	SA-3	Т	Т	G	C	C	Α	G	Т	Т	Т	Т	Α	Т	C	Т	Α	C	Т	С	Т
Hap_20	2	SA-4,6	Т	Т	G	C	C	Α	G	Т	Т	С	Т	G	Т	C	Т	Α	C	Т	Т	Т
Hap21	2	SA-5,7	Т	Т	G	С	С	Α	G	Т	Т	С	Т	G	Т	С	Т	Α	С	Т	Т	T

b)

4.3.2 Stage 2: Differentiation and population structure with the additional genotypes from Genbank

A comparison of the additional sequences acquired through GenBank found no haplotype sharing between South Africa and Mozambique or South Africa and Madagascar. Similarly, there was no sharing of haplotypes between those of this study with those from GenBank. However, two haplotypes were shared between Mozambique and Madagascar - which were two of the three Mozambique GenBank haplotypes. When sequences from this study were combined with the additional GenBank sequences, significant differentiation still remained between South Africa and Mozambique (F_{st} =0.038, P=0.006) (Table 4.9), slightly lower than that found using only sequences from this study (F_{st} = 0.064, P=0.009). When comparing pairwise differences for all regions, differentiation was higher between Mozambique and South Africa than between Mozambique and Madagascar, whilst the level of differentiation between South Africa and Madagascar was non-significant (Table 4.9).

Table 4.9 Pairwise measure of genetic differentiation (Fst) between three sampling regions using the combined dataset. Below diagonal =Fst. Above diagonal = P-value <0.05. Significant results highlighted in bold.

Region	South Africa	Mozambique	Madagascar
South Africa	-	0.00551	0.320
Mozambique	0.0374	-	0.0339
Madagascar	0.0208	0.0108	-

Analysis of Molecular Variance (AMOVA) found significant population structure, whereby regardless of groupings, Φst was significant between regions (p=<0.05): South Africa and Mozambique vs Madagascar (Φst= 0.0139, p=<0.00001); South Africa and Madagascar vs Mozambique (Φst=0.0190 p=0.00196); Mozambique and Madagascar vs South Africa (Φst=0.0296, p=0.00293). However, the majority of all molecular variance (97.0-98.6%) was "within-region".

Due to the relatively small sample size for South Africa (n=10), it seemed appropriate to consider the effect of Haplotype_18 (SA2), which contained a 16 base pair indel

(Table 4.7 & Table 4.8). The observed pairwise differences between regions could have been heavily skewed by the presence of the relatively large difference in this single haplotype. To investigate this, pairwise Fst values and AMOVA were computed after excluding Haplotype_18 (SA-2) from the South African sample set (Table 4.10).

Table 4.10 Pairwise measure of genetic differentiation (Fst) between three sampling regions using the combined dataset after excluding Haplotype_18 (SA-2) from the South African sample set. Below diagonal =Fst. Above diagonal = P-value <0.05. Significant results highlighted in bold.

Region	South Africa	Mozambique	Madagascar
South Africa	-	0.00541	0.333
Mozambique	0.0423	-	-
Madagascar	0.0256	-	-

The results indicate that the removal of Haplotype_18 (SA-2) had little effect on pairwise Fst (Table 4.10) or AMOVA results: South Africa and Mozambique vs Madagascar (Φst= 0.015, p=<0.00784); South Africa and Madagascar vs Mozambique (Φst=0.02 p=0.002); Mozambique and Madagascar vs South Africa (Φst=0.034, p=0.004). The majority of molecular variation remained attributed to "within-region" variation (96.57-98.5%).

4.3.3 Behavioural responses to biopsy sampling

A total of 35 behavioural reactions by humpback whales to bolt strikes during biopsy sampling procedures were recorded (Table 4.11). Almost two-thirds of the struck individuals displayed no observable reactions.

Table 4.11 Reactions by humpback whales to bolt strikes during biopsy sampling. N=35.

	Total number of		Reactio		
	recorded reactions	None	Low	Moderate	Strong
Strikes	35	22	6	5	2
Percent	100	63	17	14	5.7

4.4 Discussion

4.4.1 Behavioural reactions to biopsy sampling

Behavioural reactions by humpback whales in this study (Table 4.11) were remarkably consistent with those found by Clapham and Mattila (1993) on the Silver Bank wintering ground in the West Indies (Dominican Republic). The percentage of individuals that showed no reaction (62.9%) was identical in both studies, whilst low, moderate and strong reactions rates were also very similar between studies. During this study, only two strong reactions were observed. Both reactions were observed as two violent lateral tail-thrashes with no additional high-energy behaviours occurring. All low and moderate reactions appeared to be "startle" responses such as shudders or slight tail flicks. Startle responses to biopsy sampling procedures have also been observed in other species for example northern bottlenose whales (Hyperoodon ampullatus) (Hooker et al., 2001), sperm whales (Physeter macrocephalus) (Whitehead et al., 1990), bottlenose dolphins (Tursiops truncatus) (Weller et al., 1997) and right whales (Eubalaena glacialis) (Brown et al., 1991). These examples also include occasions where the biopsy dart missed the individual but still invoked a startle response, possibly from an audio stimulus of the bolt striking the water or from the approach of the vessel.

The fact that a large proportion of individuals in this study showed no reaction whilst only two showed strong reactions (5.7%), strongly suggests that biopsy sampling caused little distress to these individuals, and confirms that the use of this method for obtaining skin and blubber samples from live, free-swimming animals is likely to have little impact on individuals (Best *et al.*, 2005; Brown *et al.*, 1994; Clapham & Mattila, 1993; Weller *et al.*, 1997).

4.4.2 Genetic differentiation and population structure

Levels of haplotype diversity (h) found in this study are consistent with levels found in wintering grounds within the South Atlantic, and the northern and south western Indian Ocean (Rosenbaum et al., 2009). Nucleotide diversity (π) was slightly higher

than found by Rosenbaum *et. al.* (2009) for sub region C1 (which combined samples from East South Africa and Mozambique), but similar to levels found in the remainder of their study sites.

High haplotype diversity in concurrence with low nucleotide diversity has been linked to rapid population growth after a period of low effective population size (Grant & Bowen, 1998). This results in a large number of haplotypes with few nucleotide differences. The high levels of haplotype diversity and low nucleotide diversity found for both South Africa and Mozambique are therefore consistent with the recovery of East African humpback whale stocks after exploitation from modern whaling (IWC, 2011c). However, it has been shown that the intensity and duration of modern whaling was not sufficient enough to reduce genetic variability in whale populations (Amos, 1996; Baker *et al.*, 1993). A neighbour-joining phylogram (Figure 4.3) supported the presence of many, closely related haplotypes and a lack of historical population separation between South Africa and Mozambique.

A complete non-overlap of haplotype sharing was found between South Africa and Mozambique and pairwise Fst statistics showed highly significant differentiation between these two regions, whilst no differentiation was found between South Africa and Madagascar. The inclusion of Haplotype 18 (SA-2), which contained a 16 base pair indel, in the small South African sample set (n=10) was found not to affect Fst or Φst scores for pairwise comparisons between South Africa and Mozambique or Madagascar. This was unexpected given the small sample size and the large number of nucleotide differences of this haplotype relative to all other identified haplotypes. The degree of differentiation between South Africa and Mozambique and South Africa and Madagascar was substantial, with pairwise Fst scores differing by two orders of magnitude. This is surprising given the current opinion that individuals migrating past Plettenberg Bay/Knysna in South Africa are those wintering off the coast of Mozambique (Best et al., 1998; Best & Ross, 1996; IWC, 2011c). Although the results from this study show substantial differences in levels of differentiation, the South African sample size was small (n=10) and so these results must be interpreted with some caution. Notwithstanding this, the results presented here question the assumption that the migration route off Plettenberg Bay/Knysna acts solely as a route to and from the wintering grounds of Mozambique (sub region C1). Rather, it

suggests that the southern section of this migration route may also be utilised by some individuals from Madagascar (sub region C3).

Significant differentiation between Mozambique and Madagascar was also found. This is consistent with a low number of migrants per generation (Nem) estimated to exchange between sub regions C1S and C3 in either direction (C1S to C3 = 1-2.4 Nem; C3 to C1S = 1-1.5 Nem) (Rosenbaum *et al.*, 2009).

Differentiation between South Africa and Mozambique remained significant (although at a slightly lower probability level) after the three East South African haplotypes and three Mozambique haplotypes identified by Rosenbaum et al. (2009) were added to the analysis (Table 4.3). This could be due to sampling location. This hypothesis is strengthened when considering the significant differentiation found between Mozambique and Madagascar (this study and Rosenbaum et al., 2009) and between East South Africa and northeast Madagascar (Pomilla & Rosenbaum, 2005). If some of the whales from the Madagascan wintering grounds do migrate via the South African coast, the significant differentiation found between Madagascar and East South Africa (Pomilla & Rosenbaum, 2005) and Mozambique (Rosenbaum et al., 2009) would imply these Madagascan individuals only utilise the migration route southwards of north east South Africa. Madagascan individuals would therefore need to depart (northbound) or intercept (southbound) the South African coastline (on route to or from Madagascar), somewhere south of Cape Vidal, South Africa. In turn, this would create variability in relation to the genetic sub-regional composition of the migration route according to latitude. The northern section of the migration route would become less differentiated between South Africa and Mozambique as the proportion of Madagascan individuals reduced. Therefore sample location in South Africa (south coast and east coast) could influence the degree of differentiation found between South Africa vs Mozambique and South Africa vs Madagascar.

However, there is very little evidence to support a distinct east-west migration route between the East Africa and the Madagascar coast, which must exist if some individuals migrating to Madagascar share the southern coast of South Africa as a migration route but do not continue northwards into Mozambique (as shown by highly significant levels of differentiation). It is also inconsistent with the migration route

structures proposed by Best *et. al.* (1998) within the southwest Indian Ocean. Best *et. al.* (1998) speculated that due to differences in catch histories between East Africa and Madagascar during modern whaling, individuals migrating to East Africa must therefore take a separate route to those migrating to Madagascar (Chapter 1, Figure 1.2). Those differences between East African and Madagascan catch histories during modern whaling (Best *et al.*, 1998) do not support Madagascan individuals utilising the south coast of South Africa unless utilisation is at very low levels. Such low level usage would then be inconsistent with the distinct lack of differentiation between South Africa and Madagascar.

On the other hand, during two acoustic transits across the Mozambique Channel in 1994, a small number of singing humpback whales were recorded mid-channel, but otherwise humpback whales were only detected on the continental shelves of East Africa and Madagascar (Best et al., 1998). These isolated singing humpbacks detected mid-channel between East Africa and Madagascar and humpback whale sightings around the Comores and Aldabra (sub region C2) were primarily the basis for the proposed existence of a third mid-channel migratory route (Best et al., 1998). Since then, however, there has been no further evidence to support the existence of this third mid-channel north-south flowing migration route. Pomilla et. al. (2005) hypothesised that, based on their findings of gene flow between sub regions C1 and C3 and a single genotypic recapture between east South Africa and Madagascar, these mid-channel 'singers' could be individuals travelling in either direction between East Africa and Madagascar. On the East African coast, Best et. al. (1998) noted that a smaller secondary stream of animals exists offshore from the main inshore migration route passing Durban. This stream however comprised very few animals sighted by whaling aerial spotters (K. Findlay, pers. comm.) and Findlay (1994) noted that these individuals migrating directly northwards would still strike the coast of Mozambique. Although nothing else is known about its role, it could potentially be linked to the hypothetical passage of individuals between sub regions C1 and C3.

The seven South African genetic samples obtained during this study (the date of the three additional East South African haplotypes are unknown), which showed highly significant differentiation between South Africa and Mozambique were obtained during November during the southbound migration. This is the same capture month

(although different year) and location as one of the individuals recaptured through photo identification off Ponta Mamoli, Mozambique (see Chapter 3). This suggests that for at least the month of November, if multiple sub-regions share this section of the migration route, it does not appear to be temporally differentiated by sub region. In the North Atlantic, temporal differentiation has been found for humpback whales wintering in the West Indies, where the arrival of humpback whales at Silver Bank is temporally segregated by feeding ground origin (Stevick *et al.*, 2003).

Mating behaviour such as singing and surface activity groups has been observed during migration to and from wintering grounds (Best *et al.*, 1998). If individuals from Mozambique share the migration route along the south coast of South Africa with some individuals from Madagascar, successful mating attempts would increase gene flow and thus reduce the level of differentiation between sub regions C1 and C3. The fact that differentiation is considerable may indicate that there is no sharing of the migration route, that successful copulation is not occurring or that individuals are not mixing as a result of some unidentified temporal differentiation.

Sex ratios for South Africa (Plettenberg Bay/Knysna) and Mozambique (Bazaruto and Ponta Mamoli) did not significantly differ from parity. Unfortunately, sample size was too small to investigate the effect that any sex-biased dispersal may have on population structure.

Pairwise comparisons using Φst and Fst indices, have suggested that Antarctic feeding Areas II and III are used by whales from breeding stocks B and C (IWC, 2011a). The longitudinal movements of individuals wintering in C3 and feeding in Area II could potentially be made in low latitude waters by using the migration route along the south coast of South Africa. This would account for the lack of differentiation found between Plettenberg Bay/Knysna and northeast Madagascar. However, as discussed earlier this would require an east-west movement of individuals between South Africa and Madagascar, for which there currently appears to be little evidence.

Such highly significant differentiation found between South Africa and Mozambique, yet a distinct lack of differentiation between South Africa and Madagascar, was unexpected given the current knowledge for these regions. If the migration route

along the south coast of South Africa contains some individuals migrating to or from Madagascar, it provides new insights into southwest Indian Ocean migration routes and more specifically, the role played by the East African migration route. However, for this to be true, an east-west movement of individuals between South Africa and Madagascar must exist. This is currently not supported in the literature. The unexpected levels of differentiation could be a chance result of small sample size, and limited sampling duration, particularly in South Africa. Further genetic sampling of humpback whales over the entire migratory season should be conducted off Plettenberg Bay/Knysna to fully substantiate the results of this study.

5. Chapter 5: The first description of an unidentified skin condition in East African humpback whales

5.1 Introduction

The occurrence of skin disease and lesions in cetaceans has been widely documented (Barr *et al.*, 1989; Geraci *et al.*, 1979; Van Bressem *et al.*, 2008a; Van Bressem *et al.*, 2008b; Van Bressem *et al.*, 1999). The large majority of these reports relate to cases found in odontocetes (Bearzi *et al.*, 2009; Maldini *et al.*, 2010; Wilson *et al.*, 1999; Wilson *et al.*, 1997) but skin disease and lesions have also been reported in mysticetes (Brownell *et al.*, 2007; Castro *et al.*, 2011; Hamilton & Marx, 2005; Henk & Mullan, 1996).

Micro-organisms known or suspected to cause skin disease in cetaceans were reviewed by Van Bressem et al., (2008b) and included viruses (calciviruses, herpesviruses, papillomaviruses, poxviruses), bacteria (Aeromonas spp., dermatophilosis, Erysipelothrix rhusiopathiae, Mycobacterium marinum, Pseudomonas spp., Staphylococcus delphini, Streptococcus iniae, Vibrio spp.), fungi (candidiasis, fusariosis, lobomycosis or lacaziosis, *Trichophyton* spp.) and protozoans. Most of these seemed to be opportunistic pathogens, exploiting some breakdown in the host's defences to initiate an infection. Vitamin deficiencies, diatom growth, anthropogenic pollution, and excessive exposure to ultraviolet radiation are also known to give rise to visible skin changes (Wilson et al., 1997).

Lesions caused by injury, such as from ship strikes (Knowlton & Kraus, 2001b), entanglement in fishing gear (Baird & Gorgone, 2005; Neilson *et al.*, 2009) and interspecific interactions, for example cookie-cutter shark, *Isistius brasilensis*, bites (Brownell *et al.*, 2007), predation by killer whales (Steiger *et al.*, 2008) and predation by gulls (Sironi *et al.*, 2009) have also been documented. In some cases these wounds and specific viral infections (e.g. poxvirus, herpesvirus) may provide routes of entry to opportunistic pathogens (Van Bressem *et al.*, 2008b) resulting in a secondary microbial infection.

A wide range of morphological descriptions for skin lesions of both known and unknown aetiology are found throughout the literature. Wilson *et al.* (1999) categorised types of skin lesions on bottlenose dolphins as black, pale, cloudy, lunar, white fringe spots, dark fringe spots, or orange. Skin lesions on blue whales observed off southern Chile were reported as vesicular lesions and tattoo-like skin disease possibly attributed to the calciviruses and poxvirus respectively (Brownell *et al.*, 2007). Flach *et al.*, (2008) reported on 3 types of skin lesions of unknown aetiology in six species of cetaceans from South America, describing them as whitish velvety lesions, sometimes ulcerated; large, rounded cutaneous lesions and vesicular skin disease. Skin conditions observed on humpback whales from Ecuador included descriptions of velvety white lesions, irregular whitish lesions, "strippled" and rounded lesions, red granulomatous tissue, vesicular lesions, possible lobomycosis-like disease and ulcerated lesions (Castro *et al.*, 2011).

High levels of immunotoxic environmental contaminants such as organochlorine compounds (Jarman *et al.*, 1996; Ross *et al.*, 2000) are known to contribute to the severity of diseases in marine mammals (Aguilar & Borrell, 1994; Ross *et al.*, 1996), whilst chemical contaminants may also affect natural skin barriers (Van Bressem *et al.*, 2008b). Degraded environment, salinity, water temperature, contaminated ship ballast and the heavy use of prophylactic antibiotics in aquaculture are also all thought to be factors influencing the prevalence of skin lesions (Flach *et al.*, 2008; Hamilton & Marx, 2005; Van Bressem *et al.*, 2008b) such as dolphin-pox (Geraci *et al.*, 1979) and lobomycosis (Murdoch *et al.*, 2008). Tattoo-like lesions, characterised by irregular, slightly raised grey, black or yellowish lesions are often associated with the poxvirus and the prevalence of such lesion may be an indicator of poor water quality (Van Bressem *et al.*, 2003).

Assessing the health of free-swimming cetaceans is difficult because most existing knowledge stems from data on captive or stranded individuals. However, photo-identification images are increasingly being analysed to assess and monitor skin condition to provide clues about the health of the cetaceans and the ecosystem in which they live (Hamilton & Marx, 2005).

This study provides the first morphological description for a lesion of unknown aetiology observed on East African humpback whales of the sub-regional breeding stock C1 (IWC, 2011c). Using images taken during a humpback whale photo-identification study, the prevalence and severity of this previously undescribed lesion were assessed among humpback whales photographed along the migration route (off the east coast of South Africa) and the breeding ground off Mozambique in the southwest Indian Ocean.

The study investigates how the prevalence and severity of these lesions vary according to the temporal and geographic distribution of breeding stock C1 humpback whales observed on their breeding grounds and migration route. It examines whether lesion prevalence and severity is linked to differences in age-class and reproductive status and provides a baseline study for future inter-regional comparisons.

5.2 Methods

5.2.1 Data collection

During collection of photo-identification images, the left and right flanks of humpback whales were photographed at field sites along the C1 migration route from May-February (South Africa) and the C1 breeding ground between July-October (Mozambique) (Figure 1.3, Chapter 1). The method for photo-identification and assigning flank images to individuals is described in Chapter 3.

Images of the left and right flank of each photographed humpback whale were assessed, aided by the use of a screen loupe, to determine the presence or absence of lesions among individuals in order to establish the proportion of individuals with lesions (prevalence). Where possible, uncropped images were used, which maximised the area of body visible for assessment. Lesions were then graded according to their severity.

Individuals were classed as mothers, calves or adults of unknown sex:

- Calves were considered to be animals born within the year of the field season, whose body length was less than one third of an adult and observed remaining in close proximity to a particular adult.
- Mothers were considered to be the adult that was consistently closest in proximity to the calf.
- Adults of unknown sex included all other non-calves excluding known mothers.
- All individuals represents the total of the above three categories.

The definitions for the north and southbound migration and wintering ground are taken from those described in Chapter 2. Due to the relatively closer proximity and more similar habitat use of Ponta Mamoli and Bazaruto Archipelago (~650 km) than to Plettenberg Bay/Knysna (~1300 km), data from these two locations were combined for the purpose of this study.

5.2.2 Prevalence

Prevalence was defined simply as the presence or absence of the lesion. Presence included all three categories of severity.

A general visual assessment of the overall health for all individuals with lesions was also made using skin condition (such as scarring, peeling, blistering or other types of lesions), body condition (evidence of emaciation such as protruding vertebral knuckles, concavity behind the blow hole or laterally along the dorsal aspect of the flanks) and infestations of cyamids as indicators of poor individual health (Pettis *et al.*, 2004). This was achieved by viewing uncropped images of individuals, which maximised the area of body visible in each image.

5.2.3 Severity

Severity was categorised as Mild, Moderate or Severe based on tissue colouration and tissue damage (the degree of penetration into the dermal layer) (see Figure 5.1). Mild cases were localised and of a light grey/white colouration; in some cases they also showed a faint yellow colouration. Moderate lesions were those that had an area of

prominent white/yellow colouration located within the surrounding light grey/white area of colouration. In some cases, the skin appeared damaged although penetration into the dermal layer was not clear or appeared superficial. In Severe cases, penetration of the dermal layer was apparent producing a wound-like process, with the appearance of the peripheral tissue being consistent with that described for moderate or mild cases. In some cases classed as severe, red blood vessels were also visible; however it is unclear if these were related to the described lesion.

In using these three categories to describe lesion severity it has been assumed that all these lesions are of a single lesion type of the same aetiology, observed during different stages of development or healing process. This cannot currently be verified because none of the lesion tissue has been examined clinically.

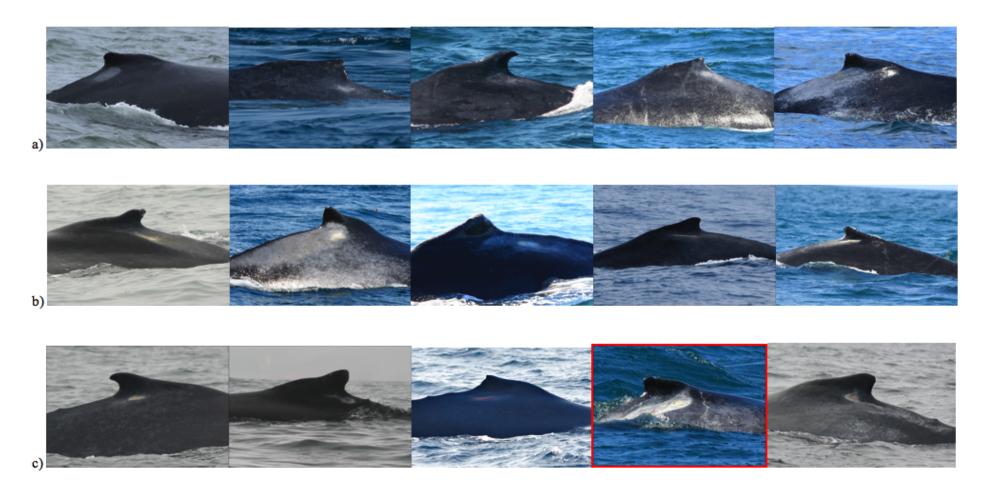


Figure 5.1 (a-c) Lesion severity graded into three categories a) Mild, b) Moderate, c) Severe. Based on tissue colouration and tissue damage (the degree of penetration into the dermal layer). The image outlined in red is of a calf, estimated to be a maximum of approximately four months old.

5.3 Results

The lesions observed and described only occurred in one location on the area of the body photographed (namely on the dorsal flanks latero-ventral to the dorsal fin) and were never observed anywhere else.

A visual assessment of individuals with lesions showed the presence of this lesion type and its severity to be unrelated to the occurrence of other scars, skin deformities, or signs of poor body condition. Lesions were observed on individuals of all skin and body conditions. This ranged from healthy individuals showing no other signs of skin deformities, peeling, scarring and of good body condition to individuals of poor health showing emaciation, blistering and cyamid infestations.

5.3.1 Prevalence

A number of individuals had lesions on both the left and right flank, therefore a total of 175 instances of the lesion was found on 147 individuals (20% of 733 individuals examined), 100 occurrences on 83 adults of unknown sex and 75 (on 36 known mothers and 34 known calves). Of all known mothers (n=71) and calves (n=82), there were 60 mother-calf pairs that had images available for both individuals. There were 41 instances on 36 mothers (60% of mothers) and 31 instances on 26 calves (43.3%) (Table 5.1). Prevalence was almost three times higher for mothers and almost twice as high for calves than for the overall sampled population.

Table 5.1 Skin lesion prevalence in all adults of unknown sex, all known mothers, all known calves and within mother-calf pairs. *Only mother -calf pairs which have images available for both individuals.

	Total	Adults of	All Kr	iown	Mother-calf pairs *	
		Unknown sex	Mothers	Calves	Mothers	Calves
Individuals in catalogue	733	580	71	82	60	60
Individuals with lesions	147	83	36	34	36	26
Percentage of individuals with lesions	20.1	14.3	50.7	35.4	60.0	43.3
Lesion instances	175	100	41	34	41	31

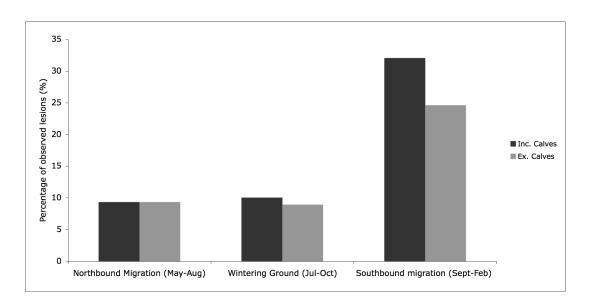


Figure 5.2 The percentage of photographed humpback whales observed with lesions (including calves and excluding calves) during the northbound migration in May-August (n=128) (Plettenberg Bay/Knysna, South Africa), the wintering ground in July-October (n=268) (Bazaruto Archipelago and Ponta Mamoli, Mozambique) and the southbound migration in September-February (n=337) (Plettenberg Bay/Knysna, South Africa).

The earliest observation of a lesion occurred on 7 June during the northbound migration. Prevalence varied markedly according to the temporal and geographic location of individuals (northbound migration, wintering ground and southbound migration, see Figure 5.2), being strongly skewed towards animals in the southbound migration. Lesion instances as a percentage of the number of assessed individuals in each location was low for both the northbound migration (9.4%) and wintering ground (including calves 10.1%, excluding calves 9%) but the observed percentages were markedly higher during the southbound migration (including calves 32%, excluding calves 24.6%) - a threefold increase compared to the northbound migration and wintering grounds. Of the 733 individuals examined, 12 individuals (1.6%) on the northbound migration, 27 individuals (3.6%) on the wintering ground and 108 individuals (14.7%) on the southbound migration were observed with lesions. Skin lesions were present on 68% (n=41) of mother-calf pairs, for which images were available for both individuals (n=60). Lesions were observed on the mother-only in 18 pairs (30%), calf-only in 7 pairs (12%) and on both mother and calf in 16 pairs (27%).

5.3.2 Severity

Mild cases were the most frequent in 'All individuals' and 'Adults of unknown sex' with severe lesions representing less than 10% of those cases (Figure 5.3). The proportion of severe lesions was found to be highest in mothers (22%), whilst lesions of moderate severity were the most common among calves (52.9%). Only 5.9% of lesions on calves were severe - the lowest recorded across all classes of individuals.

In general, the proportion of severe lesions increased over time within a season (Figure 5.4). Severe cases were only observed from Julian-day 247 (4 Sept) and an increase in the proportion of moderate cases and a decline in mild cases occurred after Julian-day 276 (3 Oct).

Sixteen of the 60 mother-calf pairs that had images available for both individuals were found to have lesions on both the mother and the calf. These 16 mother-calf pairs were used to compare the severity of lesions between mother and calf. There were four cases of a higher severity in calves, seven cases of a higher severity in mothers and five cases where lesion severity was equal.

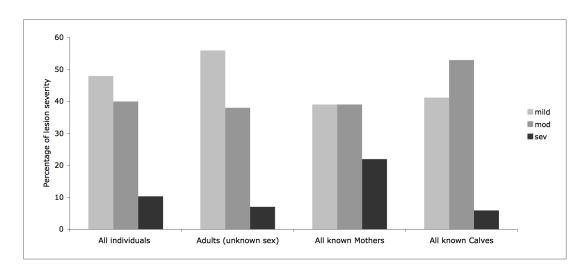


Figure 5.3 The percentage of each class of lesion severity (Mild, Moderate and Severe) for all lesion instances found within four categories of individuals (All individuals with lesions (n=175), All adults of unknown sex (n=100), All known mothers (n=41) and All known calves (n=34) where n=total number of lesion instances.

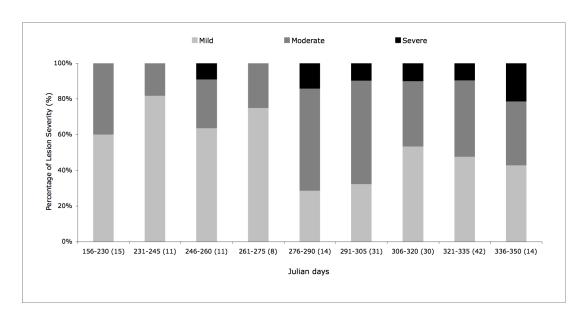


Figure 5.4 The percentage of lesion severities (mild, moderate and severe) for all lesion instances observed on humpback whales in Plettenberg Bay/Knysna (South Africa) and Bazaruto Archipelago and Ponta Mamoli (Mozambique). Data are grouped into 15-Julian day bins with the exception of the first bin which is 75 days (five 15-day bins combined) due to small sample size. Sample sizes in each bin are given in parentheses. Northbound migration = Julian-day 156-244. Wintering grounds = Julian-day 182-304. Southbound migration = Julian-day 245-350

5.4 Discussion

The lesions observed in this study are visually different to the lesions described in other studies (for example - Castro *et al.*, 2011; Knowlton & Kraus, 2001b; Steiger *et al.*, 2008; Wilson *et al.*, 1997). The only similar lesion described elsewhere is of a lesion on the dorsal-lateral surface on a blue whale (*Balaenoptera musculus*), off Isla Grande de Chiloe, Chile (Brownell *et al.*, 2007). However, the lesion is described as a possible open blister or vesicular lesion and appears to be immediately surrounded by tattoo-like lesions. This is therefore slightly different to the lesion described in this study, where the discolouration is less irregular than tattoo-like lesions. Furthermore, there is no evidence to suggest that blistering is the cause of this lesion type. Therefore these observations likely represent the first description for this type of lesion.

It is assumed that the three grades of severity (Mild, Moderate and Severe) represent the same lesion type at different stages of development. No individuals with lesions were seen on more than one occasion; consequently the condition of the lesion could not be tracked over time. Changes in severity throughout the season were therefore based on trends observed within the sampled population rather than on an individual basis.

The specific location of this lesion type appears to be unrelated to other scarring, peeling skin or skin deformities and has not been observed on any other photographed area of the body even though, for many individuals, a large proportion of the area was assessed. This lesion was observed on what appeared to be otherwise healthy individuals as well as some, but not all, individuals showing visual signs of compromised health such as large infestations of lice (Osmond & Kaufman, 1998) and poor body condition. Therefore other visual signs relating to health and skin condition may not be an indicator of susceptibility to this type of lesion.

Without clinical examination of these lesions, determining their cause is problematic. However, a number of potential causes can be ruled out by considering the two main attributes of these lesions:

- 1) The specific location of the lesion was the same on all animals (immediately below the dorsal fin on either or both flanks of the body).
- 2) Lesion severity was apparently progressive and prevalence was strongly skewed towards animals on the southbound migration and mother-calf pairs.

Typical injuries from ship strikes include blunt trauma or laceration type lesions on the body whilst entanglement often results in lacerations or abrasions from body contact with the gear, frequently occurring around the tail stock, mouth, head or body (for example - Knowlton & Kraus, 2001b; Neilson *et al.*, 2009). These types of injuries are inconsistent with the observed localised position of the lesion in this study, found on a recessed area of the body.

Rising levels of ultraviolet radiation (UVR) are thought to cause blistering consistent with acute sun damage in cetaceans (Martinez-Levasseur *et al.*, 2010). However, blisters observed had a regular shape, were not localised to a specific location on the body and were not associated with discoloration of the skin.

Humpback whales have been observed rubbing their bodies on the hulls of boats (pers. obs A. Banks) and on sand (pers. com. V.G. Cockroft). Any lesion caused as a result of this type of behaviour would be expected to appear as an abrasion and could break the skin, potentially encouraging an infection. However the recessed location of the body where the lesion is observed would most likely be protected by the dorsal fin (above) and the wider flank region (below) from abrasion. These regions would also be expected to have more extensive abrasions due to their protruding profile relative to the depression. Apparent bottom feeding by humpback whales on Stellwagen Bank in the North Atlantic resulted in substantial abrasions or "scuffing" along the upper and lower jaw as well as along the dorsal region of the dorsal fin and leading edges and tips of flukes (Hain *et al.*, 1995). However, the type of lesion and its body location described in this study is inconsistent with abrasions caused from bottom feeding – which would be extremely similar to those caused by rubbing or scratching behaviour.

Lesions caused by interspecific and intraspecific interactions such as predation, sexual behaviour, competition, and nursing by mothers would not be expected to be found in one specific location on the body. Lesions caused by predation such as the rake marks of predating killer whales (Steiger *et al.*, 2008) or peck marks on southern right whales caused by kelp gulls (Sironi *et al.*, 2009) are relatively indiscriminate in their body location and are distinct in their appearance. Similarly, sexual, competitive or nursing behaviour would be expected to cause scratches, lacerations or grazes. These would vary according to the degree of body contact between individuals, with lesions being especially present on protruding regions such as the rostral tubercles, caudal peduncles and leading edges of fins and flukes.

All of these causes described above do not provide an adequate explanation and are therefore unlikely causes for this type of lesion. The remaining potential cause is that it is microbial in nature, perhaps as a result of poor water quality (see below) or reduced health condition of the individual. Health condition and the impact of stress-related events may affect the bacterial communities associated with humpback whale skin (Apprill *et al.*, 2011). Therefore, the presence of this skin lesion may suggest that the animal is under stress or of reduced health compared to animals without

lesions. Healthy individual humpback whales in the North Pacific were found to have similar epithelium-associated bacterial communities despite differences between sexes and the immediate geographic sample location, whilst health-compromised whales all showed unique variability in epithelium-associated bacterial communities (Apprill *et al.*, 2011).

It is unknown why the region of body on which this lesion is found is the only area susceptible to its development. One possibility is that this area of the body presents conditions, such as an area of low hydrodynamic pressure, that enable infecting microorganisms to be present. Apprill *et al.*, (2011) found that humpback whales appear to harbour specialized bacterial communities that are both less diverse and phylogenetically distinct compared with seawater and suggested that the skin-associated bacteria are most probably specialised to the substrate on and within the epithelial tissue.

In the mildest of cases, where the lesion is assumed either to be in the very early stage of development or late stage of healing, the visible signs are faint and distinguishing this from natural skin pigmentation or discolouration from other factors was problematic. In these very mild cases and due to the subjectivity of grading severity, it is likely that this led to a small bias in the prevalence of mild cases. The decision to class the lesion as of mild severity or as absent was made after close inspection of the image using a screen loupe. In the most severe cases, penetration of the dermal layer occurs, which may increase the likelihood of a secondary infection whereby wounds may provide entry to other opportunistic pathogens (Van Bressem *et al.*, 2008b). When examining mild cases, there did not appear to be additional signs of skin damage, such as scratches or scars to act as a suitable location for microbial fauna to colonise.

A comparison of data from photo-identification studies of ten coastal populations of bottlenose dolphins in Europe, North America and New Zealand found epidermal lesions to be common in all populations (affecting 60% of individuals), but both the prevalence and severity of 15 lesion categories varied among populations (Wilson *et al.*, 1999). No relationship was found between epidermal disease and contaminant levels; however, populations from areas of lower water temperature and salinity

exhibited higher lesion presence and severity. The prevalence of orange films on bottlenose dolphins was found to be lower in the warmer waters off Santa Monica in southern California than in the cooler waters of Monterey Bay in central California (Maldini *et al.*, 2010). In this study, only 9.4% of humpback whales on the northbound migration that were arriving from colder waters were observed with lesions and there were no severe cases. Conversely, 32% of whales observed during the southbound migration coming from the warm waters of the wintering grounds had lesions. This suggests that cooler water is not responsible for the high lesion prevalence for this type of lesion and/or that warmer water may play a part in their formation.

The persistence time of this lesion type is unknown and there were no recaptures of known individuals through photo-identification made during this study (see Chapter 3) of individuals with this lesion. However, if the persistence time for this lesion extends more than a few months, a large number of animals on the northbound migration would be expected to be harboring this lesion from the previous year. The fact that only 1.6% of all individuals with lesions observed during this study were observed during the northbound migration, suggests that the persistence of this lesion is relatively short lived. The increase in prevalence and severity from the northbound migration, to wintering grounds, to southbound migration suggests that these are increasingly severe cases of the same lesion type which persist for at least as long as the whales are present in East African waters. The low incidence rate in the northbound migration suggests that prevalence and severity reduces during the summer feeding period before developing in some animals during the northbound migration. However, it is unknown if this lesion reoccurs on an individual between years, or if the mild cases observed during the northbound migration are partially healed lesions, which have persisted throughout the summer.

Calves observed on the wintering ground are likely to have been born from early July onwards (see Chapter 2). Calves with this lesion were photographed as early as September with moderate severity, which indicates that the development of this lesion is relatively fast. The most severe lesion observed on a calf was photographed in early November off Plettenberg Bay/Knysna, South Africa during the southbound migration (Figure 5.1). The calf had a lesion on its right side only and was

accompanied by its mother with a mild lesion. Both individuals showed no other signs of poor body condition although the calf's skin condition showed additional grey pigmentation extending along its flank and tail stock. This suggests that not only can this lesion develop on animals from a very early age (less than approximately three months old), but that the lesion can become severe within approximately three-four months of the animal's birth.

That lesion prevalence was highly skewed towards mother and calf pairs suggests that this lesion type is related in some way to differences between mother-calf pairs and other animals on the wintering ground and southbound migration. Habitat preference is known to reflect social organization on wintering grounds, where mother-calf pairs are found in shallower waters than competitive groups (Ersts & Rosenbaum, 2003). Line-transect aerial surveys and boat-based surveys conducted in the region of Bazaruto Archipelago and boat-based surveys off Ponta Mamoli, Mozambique conducted during this study (Chapter 2) suggest that mother-calf pairs use the inshore waters of that region. Similarly, a survey of the coastal regions of southern and central Mozambique in 1991 by Findlay et. al., (1994), found more groups with calves over the Sofala Banks than in the rest of the survey area. Although a shipbased survey conducted by Findlay et. al., (2004) over a similar region in 2003 reported a relatively even distribution of such groups across the survey area, lower than expected sighting frequencies in areas of low salinity were found - the lowest being on the Sofala Banks where the Save, Zambezi and Pengue Rivers discharge. These authors suggested the avoidance of turbid waters by humpback whales might have influenced their distribution over the Sofala Banks. Notwithstanding this, mother-calf pairs are generally distributed closer inshore than other animals and are therefore much more likely to be exposed to pathogens and chemical contaminants related to anthropogenic activities. These include agricultural run-off, untreated sewage, and polluted river discharge resulting in an overall degraded water quality. However, Bearzi et. al. (2009) found that skin lesion presence on bottlenose dolphins in Santa Monica were found to be higher in offshore animals compared to those found inshore.

Exposure to chemical contaminants may affect natural skin barriers and suppress the immune system (Van Bressem et al., 2008b). The proportion of individuals with

lesion remained constant for both the northbound migration and wintering ground at around 10% (Figure 5.2). Only after departing from the wintering grounds (the onset of the southbound migration) did the proportion of individuals with lesions and lesion severity substantially increase (32% including calves; 24.6% excluding calves). Mother-calf pairs are likely to be subject to higher levels of pathogens or contaminants due to their inshore habitat preferences and longer residency times whilst over-wintering. The increase in lesion prevalence and severity after over-wintering in the inshore waters off Mozambique is consistent with this increased exposure to poor water quality where sub-lethal effects of pathogens and bio-toxins could possibly weaken a whale's immune system and allow a secondary infection to manifest itself (Hamilton & Marx, 2005).

Lesion prevalence has been shown to differ according to sex and age in other species. The presence of tattoo skin disease (TSD) was examined in 1,392 free-ranging and dead odontocetes comprising 17 species from the Americas, Europe, South Africa, New Zealand and Greenland (Van Bressem *et al.*, 2009). The study found that sex did not significantly influence TSD prevalence except in one species and that, generally, there was a pattern of TSD increase in juveniles compared to calves, attributed to the loss of maternal immunity. There was also a higher probability of juveniles suffering TSD than adults, which was speculated to be a result of adults acquiring active immunity following infection. On the east coast of Scotland, Wilson *et al.*, (1997) found that, in bottlenose dolphins, lesions on adult females and calves covered a significantly greater area of skin than on adult males or sub-adults despite males being unable to off-load bio-accumulated pollutant burdens to their offspring, suggesting that toxin burdens may play only a minor role. Maldini *et al.* (2010) found a high prevalence of pox-like lesions, affecting 80% of the Monterey Bay population of bottlenose dolphins (*Tursiops truncatus*), including mothers and calves.

It has been tentatively suggested that a novel *Tenacibaculum* group of bacteria, apparently prevalent in the North Pacific population of humpback whales, may play a limiting role in the growth of other skin bacteria (Apprill *et al.*, (2011). A prominent association between this lineage of bacteria and a healthy humpback whale calf may indicate that specific humpback skin microbial communities may be established early during either foetal development or post-birth activities such as skin contact during

nursing and close contact swimming. White lesions on North Atlantic right whales (*Eubalaena glacialis*) described by Hamilton and Marx (2005) did not differ according to sex and age class. Out of 15 photo-identified calves nursing from mothers with lesions, only one (6.7%) was found to exhibit lesions. In the same study, blister lesions were also found to be equally present across sex and age classes. Hamilton and Marx (2005) suggested that if the white lesions were spread by contact, then males might be expected to be more susceptible because of the occurrence of large predominantly male-biased surface active groups. Calves that nursed from mothers with lesions were no more likely to have lesions than other calves, which did not support the condition being the result of a contagious disease.

The results from this study suggest that this lesion may be passed from mother to calf during either foetal development or post-birth activities during nursing. However, the lesion was also observed only on the calf in 12% of mother-calf pairs, suggesting that the responsible agent may also be present on or in other individuals that displayed no visible signs of a lesion. Alternatively, individuals that do show signs of this lesion may represent those that have no immunity to the responsible agent or are sufficiently immunosuppressed for the lesion to develop. Mother-calf pairs may be expected to be under increased metabolic stress or experience higher levels of immunosuppression than other animals within the population due to the combined energetic demands of migration, gestation and lactation. For female Balaenopterids, up to 30% of their annual metabolic energy expenditure is estimated to be used during migration (Lockyer, 1981). The metabolic cost of reproduction is substantial, with pregnant females requiring 25% thicker blubber than anoestrus females. This corresponds to an overall body weight increase of at least 60-65% compared with 50% for the resting population during summer feeding (Lockyer, 1981). The initial costs of pregnancy are minimal, only becoming important during the second half of gestation. Most of this extra energy is thought to be used during lactation, which on a daily basis is energetically much more expensive than that of pregnancy (Lockyer, 1981). This high energetic demand could possibly be strong enough to cause variation in reproductive success among individuals (Lockyer, 1981). Levels of immunosuppression among individuals will also vary according to their overall health and fitness.

These lesions are also known to occur on humpback whales wintering off Madagascar (breeding stock C3) and Tanzania (breeding stock C1-N) (Pers. Obs. A.M. Banks) and West Africa (Pers. Comm. Tim Collins) indicating that these lesions are not restricted to whales wintering in breeding stock C1-S. However, an assessment of lesion prevalence and severity in each of these geographic areas has not yet been completed. Recently, an emaciated juvenile humpback whale off the coast of Southern Portugal was also observed to have what appears to be the same type of lesion (Pers. Coms. Ana Marçalo, Portuguese Wildlife Society). Further work is now needed to establish the geographical extent of this type of lesion.

6. Chapter 6: Recent sightings of southern right whales (*Eubalaena australis*) in Mozambique.

6.1 Introduction

Southern right whales (Eubalaena australis) were once widely distributed in the three ocean basins within the Southern Hemisphere (Perry et al., 1999). They were exploited by commercial whaling from about 1770 until receiving protection in 1935 (although some illegal exploitation continued thereafter (Tormosov et al., 1998). During this time, stocks were reduced overall from an estimate of about 60,000 individuals to a critically low estimate of 300 individuals (60 breeding females) in 1920 (IWC, 2001; Jackson et al., 2008b; Tormosov et al., 1998), although these modelled estimates depend heavily on estimates of historical catch levels and population increase rates. The depletion of Southern African right whale stocks has become retracted (southwards) from that of its historical range (Richards, 2009), at least in lower latitudes. Right whales are now primarily occurring along the south and west coast of South Africa. A similar pattern has been observed with North Pacific right whale (Eubalaena japonica) where the size and range of the population is considerably diminished relative to that during the peak period of whaling for this species during the 19th century (Clapham et al., 2004). Using a combination of historical whaling records and contemporary distribution data, the IWC (2001) recognized 11 putative breeding stocks (sub-Antarctic New Zealand, Australia, Central Indian Ocean, Mozambique, South Africa, Namibia, Tristan da Cunha, Brazil, Argentina, Chile/Peru, mainland New Zealand/Kermadec) (IWC, 2001). A number of these stocks (Mozambique; Central Indian Ocean; Namibia; Chile/Peru) are known only from whaling records and have few or no recently documented sightings (IWC, 2001; NMFS, 2007). Southern right whale populations are now apparently limited to four major breeding grounds (Argentina, South Africa, Australia and New Zealand) (NMFS, 2007; Patenaude et al., 2007). Based on historical whaling records and recent sightings from Southern Africa; the stocks of Namibia, South Africa and Mozambique are considered separate management units (IWC, 2001), although their exact inter-relationship is unknown.

Records of right whale catches in Mozambique are poorly documented. Townsend's charts (1935) based on the logbooks and journals of United States whaleships from 1785 to 1913, suggest that right whale catches off Delagoa Bay occurred during the months of May to September. From 1789 to 1804, a minimum of 120 voyages by American, French and British whaleships were made to Delagoa Bay (Figure 6.1) in a fishery directed at both sperm and right whales (Richards & Du Pasquier, 1989), the peak season for both being June and July (Wray & Martin, 1983). Richards & Du Pasquier (1989) noted an average catch of 20 right whales per vessel and Best and Ross (1986) estimated that at least one whale was killed and lost for every five whales landed, thus raising the average whale deaths per vessel to 25 whales. By multiplying the 120 voyages by an average of either 20 catches or 25 whale deaths per vessel, the number of right whales to have caught or killed is estimated to have been 2400 and 3000 respectively, in the Delagoa Bay region from 1789 to 1804. This equates to average of 160 and 200 whales caught or killed respectively, per year over the 15-year period.

Whaling continued sporadically on this ground into the mid-nineteenth century. The ship *Ann Maria* (New London), for instance, visited the bay between 21 June and 1 August 1836 and recorded the presence of another six vessels whaling there: during its stay this fleet accounted for a total of 13 whales (Penobscot Marine Museum, Seasport, Maine). The American whaling vessel *Good Return* in 1842, took a single right whale on 30th June in Sofala Bay (20°24'S; 34°31'E) and a mother-calf pair (23°45'S; 35°24'E) on 21st-22nd July (Wray and Martin, 1983³). However by 1850 whales were apparently scarce (Wray & Martin, 1983). The single right whale taken on 30th June in Sofala Bay (Figure 6.1) is the most northerly right whale capture recorded along the East African mainland, contrary to Richards (2009) who lists the most northern capture to be at Delagoa Bay.

The *Good Return* logbook notes the presence of right whale calves in Sofala Bay during the whaling season (Wray & Martin, 1983), as do the *Alliance* and *Penn* in

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³ Wray and Martin (1983) give this latter position as 25° 45'S but we have cited the position from the original log (Kendall Whaling Museum # 97, microfilm roll 9)

Delagoa Bay in 1793 (Richards & Du Pasquier, 1989). Records of mother-calf pairs provide strong indication that Mozambique was a nursery ground, but the northern extent of this is unknown.

Modern whaling operations occurred in Mozambique waters from 1910 to 1915 and in 1923, during which some 3,524 whales were taken. Although many of these catches were unspecified, there were no recorded right whale catches (Best, 1994), and further south at Durban only 27 right whales were taken in the first 22 years of modern whaling (1908- 1935).

In the absence of any current cow-calf sightings in Mozambique, the IWC (2001) suggested a population size of zero for this sub-stock. But in light of 6 sightings of 10 individuals made in Northern Kwa-Zulu Natal, South Africa (Findlay & Best, 1996) of whales heading towards Mozambique, a nominal population size of <10 mature females was tabled for Mozambique (IWC, 2001).

This chapter documents the first confirmed records of southern right whales (from survey data and incidental sightings) in Mozambique since the cessation of whaling. These provide evidence for the existence of a remnant Mozambique breeding stock or expansion of the South African breeding stock into its historic range. A summary of all surveys which included at least an element of dedicated cetacean observational effort within Mozambique waters (Table 6.1) accompanies the sighting data. We also note a southern right and humpback whale interaction that was observed on at least two days.

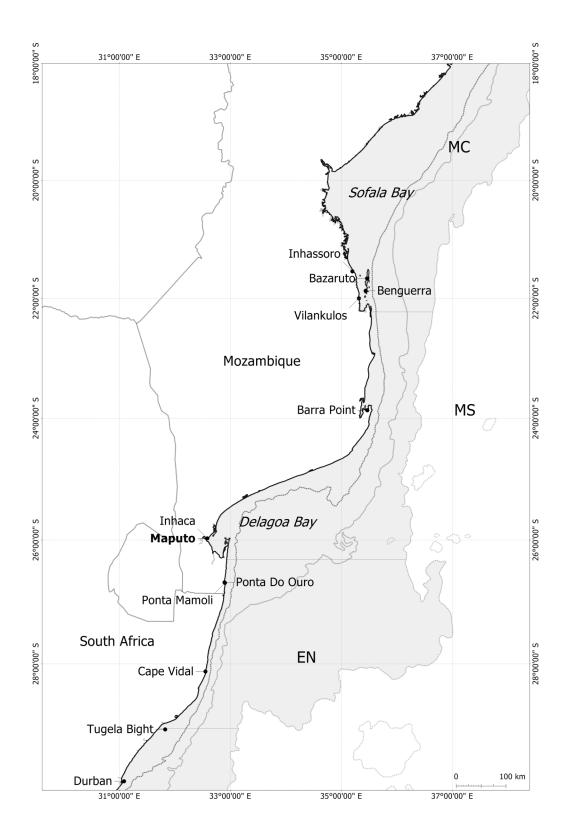


Figure 6.1 Survey area in Southern Mozambique and northern KwaZulu-Natal, South Africa. Historical right whale catches occurred at Durban, Delagoa Bay, and Sofala Bay, whilst recent sightings have been made at Barra Point, Ponta Mamoli, Ponta Do Ouro and Cape Vidal. MS=Central Mozambique, MS=Southern Mozambique, EN=North-eastern South Africa.

Table 6.1 Summary of surveys and associated effort where cetacean observations have taken place in Mozambique between 1977-2009.

Year	Survey Type	Description	Effort/Coverage	Southern right whale sighting
1977- 1978	Boat-based (Multi-day)	Fisheries survey, Mozambique. ¹ Vessel: 46m combined stern trawler/ purse seinern R/V "Dr.Fridtjof Nansen". Date: 24 Aug 1977-20 Jun 1978. Limited cetacean survey conducted.	Four complete coverage's of the whole Mozambique coast (10° 30'S to 26° 50'S).	None
1991	Boat-based (Multi-day)	Humpback whale line transect survey, Southern Mozambique. ² Vessel: 20m ketch yacht " <i>Zanj</i> ". Date: 15 Aug-15 Sept 1991	630 nautical miles steamed on effort in coastal waters of Mozambique between Maputo (25° 58'S) and 18° 00'S. Three leg return trip.	None
1995- 1997	Boat-based (Single-day)	Bottlenose and humpback dolphin survey, Maputo (Delagoa) Bay, Mozambique. Vessels: 4.5m R.I.B. and 9m fibreglass boat. Throughout 1995-1997.	146 trips totalling 302 hours of sea time. Survey area within Maputo (Delagoa) Bay (26°S; 32°E)	None
1997	Aerial	Southern Mozambique whale shark surveys. ⁴ Aircraft: Cessna 182. Date: Jun, Aug, Oct, Nov 1997	Flight speed and altitude: 70-80knts and 500-1000 ft. 9 coastal flights between Maputo (25°58'S; 32° 34'E) and Ponto do Ouro (26° 50'S; 32° 50'E), 1 flight within Maputo (Delagoa) Bay only. Approx 70 Nm/flight.	None
2003	Boat-based (Multi-day)	Cetacean line-transect survey, Mozambique. Vessel: FRS Algoa. Date: 26 Aug-27 Sept 2003.	952 nautical miles of search effort between Cabo Inhaca (26° 00' S; 33° 05' E) and the north of Mozambique Island (14° 26' S; 40° 53' E) between the 20 and 200 m isobaths.	None
1997- 2009	Boat-based (Single-day)	Inshore dolphin encounter surveys as part of "DolphinCare-Africa / EnCOuntours" ecotourism operation, Ponto do Ouro, Mozambique. ⁶	2669 trips totalling 4004 hours (1.5hr/trip). Inshore waters of Ponta do Ouro. (26° 50'S; 32° 50'E)	Six sightings Six individuals
2007	Boat-based (Single-day)	Dugong and humpback whale surveys, Bazaruto Archipelago, Mozambique. Vessel: 6m R.I.B. Date: Jun-Nov 2007.	85 trips totalling 469 hours of sea time. Survey Area extended 16 nautical miles north and 10 nautical miles east of Bazaruto Island (21° 30'S; 35° 28'E).	None

2007	Aerial	Dugong distribution and abundance surveys, Bazaruto Archipelago, Mozambique. ⁸ Aircraft: Cessna 210, Cessna 182 and Cessna185. Date: Apr 2006-Nov 2007.	Flight speed and altitude: 80knts and 150m. 27 Line transect Flights between Save River and Sao Sebastiao, Bazaruto Archipelago between 0 and 20m isobaths. 135 Hours, covering 9052 miles, mean 5.0 hour/flight	None
2008	Aerial	WWF Dugong distribution and abundance surveys, Bazaruto Archipelago, Mozambique. Aircraft: Cessna 206. Date: 25-29 May 2008.	3 surveys totalling 10.57 hours between Bartolomeu Dias and Sao Sebastiao Peninsula, Bazaruto Area.	None
2009	Land-based	Humpback whale survey, Ponta Mamoli, Mozambique. 10 Date: Aug-Sept 2009.	17 surveys totalling 26.5 hours of observation time. Ponta mamoli, Mozambique (26° 42'S; 32° 54'E)	One sighting One individual
2009	Boat-based (Single-day)	Humpback whale survey, Ponta Mamoli, Mozambique. 11 Vessel: 6m R.I.B. Date: Aug-Oct 2009.	13 trips totalling 34 hours of sea time. Survey area extended approximately 10 nautical miles north and offshore of Ponta Mamoli (26° 42'S; 32° 54'E).	None
2009	Aerial	Marine mammal survey, northern Mozambique. 12 Aircraft: Cessna 206. Date: 24-25 Nov 2009.	Flight speed and altitude: 80knts and 150m. 2 surveys consisting of 8 eastwest transects between the coast and 1500m isobath, totalling 6.48 hours of flight time between Pemba and Memba plus a north-south coastal flight.	None

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⁹ WWF (2008) Dugong Aerial Survey Report. May 25-29, 2008. Bazaruto Archipelago National Park Inhambane Province, Mozambique. 29p.

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Table 6.2 Sightings of southern right whales in Mozambique 1977-2009. Key: Juv.=Juvenille; Ad.=Adult; M-C=Mother Calf Pair; P=Probable; C=Confirmed. SRW=southern right whale, HBW=humpback whale, BND=bottlenose dolphin. * Exact date uncertain. ** Possible re-sighting. ^Multiple sightings on at least two days.

Date	Location	Lat (S)	Long (E)	Platform	Group Size	Group Composition	Mixed Species Group	Behaviour	Direction of Travel	Depth (m)	Substrate	Class
20 Sept, 1997	Ponta Do Ouro	26° 49' 00" (Approx location)	32° 53' 00" (Approx location)	Boat (Incidental)	1	Juv. ♂ (Brindle)	n/a	Milling	n/a	6m	Sand & Reef	С
2-12 Sept, 2003*^	Ponta Do Ouro/Ponta Malongane	26° 48' – 26° 50'	32° 53' – 32° 54'	Boat (Single-day)	1	Ad.♀	SRW - (prolapsed uterus) HBW BND	Milling	n/a	7-10m	Sand & Reef	С
30 Aug, 2008	Barra Point, Inhambane	23° 47' 00'' (Approx. location)	35° 32' 00'' (Approx. location)	Boat Incidental	1		n/a			<20m	Sand & Reef	P
18 Sept, 2008	Ponta Do Ouro	26° 49' 6.7''	32° 53' 40.4''	Boat (Single-day)	2	AdAd.	n/a	Travel	South	>10m	Sand	C
13 Aug, 2009	Ponta Do Ouro	26° 50′ 8.3′′	32° 53' 31.8''	Land based Incidental	2	М♀-С	n/a	Travel	South	5-10m	Sand	P
16 Aug, 2009	Ponta Madajanine	26° 44′ 6.6′′	32° 54' 16.9''	Boat (Single-day)	1		n/a	Travel	South	5-10m	Sand	P
14-21 Aug, 2009*	Barra Point, Inhambane	23° 47' 00'' (Approx. location)	35° 32' 00'' (Approx. location)	Boat Incidental	2		n/a	Resting	n/a	<20	Sand & Reef	P
26 Aug-10 Sept, 2009**	Barra Point, Inhambane	23° 47' 00'' (Approx. location)	35° 32' 00'' (Approx. location)	Boat Incidental	2		n/a			>20	Sand & Reef	P
4 Sept, 2009	Ponta Mamoli	26° 35' 8.1''	32° 54' 49.4''	Boat Incidental	1	Juv.	n/a	Travel	South	>10m	Sand	С
16 Sept, 2009	Ponta Mamoli	26° 42' 5.2''	32° 54' 23.4''	Land based	1	Juv.	SRW BND	Travel	South	5-10m	Sand & Reef	C

6.2 Methods

Surveys for which a measure of effort was available are included in the survey and effort summary (Table 6.1). Boat-based surveys were considered to be 'multi-day' if the vessel was not required to return to shore at the end of each day (large survey or sailing vessels). 'Single-day' surveys were completed by vessels required to return to shore each day (boats <7 meters in length and range-limited). An attempt has been made to provide a measure of effort; for 'multi-day' boat-based surveys (Table 6.1), where available, this includes the total number of hours on survey effort and where known, the distance surveyed. For 'single-day' boat-based surveys, effort is described by trip duration and trip frequency (Table 6.1) and stratified by area (Figure 6.4 and Figure 6.5). Aerial surveys are described by area covered, flight speed, altitude and/or flight time/distance flown. Aerial surveys were conducted using a Cessna 182, 206 and 210 flying at an altitude between 500-100ft over inshore waters. All recent sightings of southern right whales in Mozambique (n = 10) were classified following the protocol used by Roux et al. (2001) whereby sightings are rated as doubtful, possible, probable or confirmed (Table 6.2). Allocation of each category was based on the experience of the observers, conditions of the sighting (distance and visibility) and the supporting evidence provided (notes, sketches, photographs and video footage).

6.3 Results

Effort for 'single-day' boat-based cetacean surveys increased overall from 1995 to 2009 with a peak in 2007 of just over 700 hours (Figure 6.4). Intra-annual 'single-day' boat-based effort was lowest in February and highest in December, of which a large proportion took place at Ponta Do Oura and Ponta Mamoli (Figure 6.5). Multi-day surveys (Table 6.1) occurred at a greater distance from shore than 'single-day' surveys and consisted of two humpback whale line transect surveys (1991 - 25° 58'S; to 18° 00'S and 2003 - 26° 00' S to 14° 26' S) and a fisheries survey that had limited cetacean survey effort but completed four complete coverages of the Mozambique coast (10° 30' S to 26° 50' S) between 1977-1978. Sightings of right whales during

these 'multi-day' surveys may have been less likely due to the distance at which they were conducted from shore and so comparing sightings with 'multi-day' survey effort should be regarded with caution.

No sightings of right whales were made during 'multi-day' or aerial surveys. Of the 10 sightings (Table 6.2), five sightings were considered to be "confirmed" and five were considered to be "probable". Seven sightings were made inshore or from land between Ponta Do Ouro and just north of Ponta Mamoli (26°50'S to 26°35'S) (Figure 6.1 and Table 6.2). Three incidental inshore sightings were made off Barra Point, Inhambane (23°47'S - 35°32'E) (Figure 6.1 and Table 6.2). The maximum distance from the coast of any sighting was 900 meters. Although the highest frequency of sightings occurred in 2009 (Figure 6.2), this increase is most likely attributed to increasing search effort through dedicated surveys or increased tourism activities such as scuba diving, whale and dolphin watching and 'swim-with' operators within inshore waters at Ponta Do Ouro, Ponta Mamoli and Inhambane. Six sightings were incidental and four sightings were made during dedicated cetacean survey effort. Sightings only occurred during August and September (Figure 6.3) even though survey effort extended outside of these two months (Figure 6.5 and Table 6.1). This differs from the historical right whale records from Sofala Bay, which occurred during June and July (Wray & Martin, 1983) and the extensive catches illustrated by Townsend (1935) between May and September. The mean date was calculated for all sightings (n=10) using the exact date (n=8) or where this was unknown, the mean date within the approximate date range was used (n=2). The inclusion of one possible resighting at Barra Point, Inhambane (Table 6.2) gave a mean sighting date of 2 September (SD=14 days, n=10) whilst its exclusion produced a mean sighting date of 1 September (SD=15 days, n=9). Where data on age class (adult/juveniles/calves) and group size were recorded for sightings and excluding the possible re-sighting, adults (n=4) were sighted most frequently, followed by juveniles (n=3). Only one calf was seen.

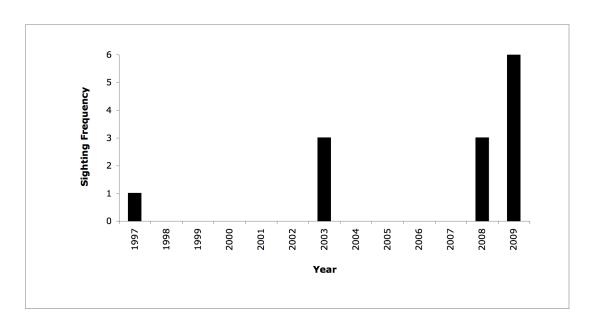


Figure 6.2 Frequency of southern right whale sightings in Mozambique between 1997 and 2009 without adjustment for effort.

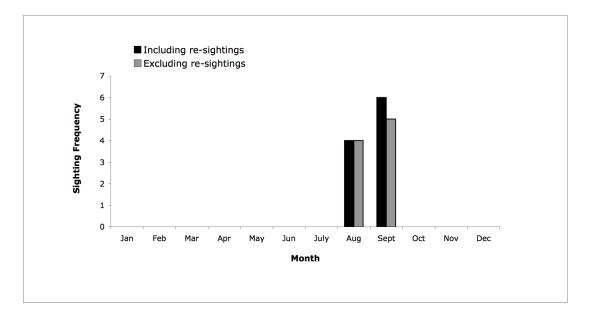


Figure 6.3 Seasonality of all southern right whale sightings, including and excluding confirmed re-sightings, in Mozambique (1997-2009) without adjustment for effort.

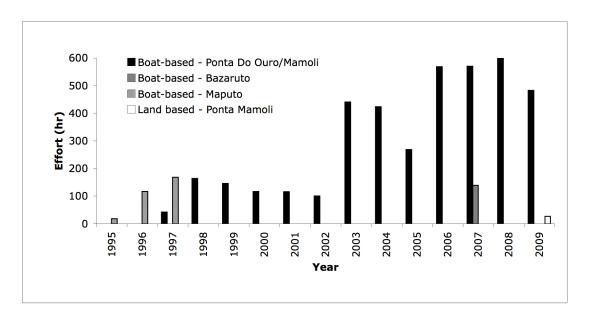


Figure 6.4 'Single-day' boat-based and land-based effort per year stratified by area for Ponta Do Ouro/Ponta Mamoli (combined due to there immediate proximity), Maputo and Bazaruto Archipelago, Mozambique, 1995-2009. Effort = hours of sea time or land-based observations.

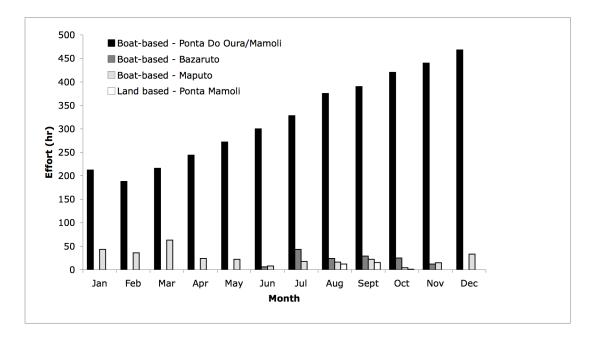


Figure 6.5 'Single-day' boat-based and land-based effort stratified by area per month for Ponta Do Ouro/Ponta Mamoli (combined due to their immediate proximity) Maputo and Bazaruto Archipelago, Mozambique, 1995-2009. Effort = hours of sea time or land-based observations.

Excluding one possible re-sighting (n=1), groups were of either one individual (n = 6) or pairs (n = 3). The first sighted pair consisted of two adults whilst the second was of a mother-calf pair. A mixed species group consisting of a southern right whale and

a humpback whale were sighted on a number of occasions on at least two days (see below). One of the single juveniles was a brindle southern right whale (= grey morph, Schaeff *et al.*, 1999). Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) were also observed on two occasions swimming with southern right whales. The behaviour and predominant direction of travel was available in the majority of cases (n=8); one sighting was described as 'resting', two sightings were described as 'milling' and five sightings were described as travelling. All travelling groups were travelling in a southbound direction.

6.3.1 Re-sightings and humpback whale interaction

It is possible that a sighting of two southern right whales on 26 August 2009 at Barra Point, Inhambane, was a re-sighting of a previous sighting of two southern right whales made in the same area between 14-21 August 2009 (exact date unknown) (Table 6.2). However, this cannot be confirmed either way as no photographs were taken of either sighting. On at least two days in early September 2003, a number of sightings were made of a mixed species group consisting of one adult southern right and one adult humpback whale observed in shallow water (<10m) at Ponta Do Ouro. During the sightings, the two animals were observed slowly milling around in the area together, or indulging in increased social interaction with rolling, waving of pectoral fins, fluking and breaching. Underwater photographs of the interaction taken by A. Gullan also revealed a protrusion of what was taken at the time to be the right whale's penis: subsequent inspection of photographs however revealed that this was more likely to be a prolapsed uterus (Figure 6.6). The humpback whale was not observed from underwater and no determination of its sex was made. Indo-Pacific bottlenose dolphins were also observed on at least one occasion with the mixed species group. After the examination of photographs the humpback whale appeared to be the same individual observed on different days whilst for the right whale, this remains unconfirmed. It should be noted that Table 6.2 records this mixed species group, which occurred on at least two days, as a single entry due to uncertainty regarding the exact dates and number of sightings.

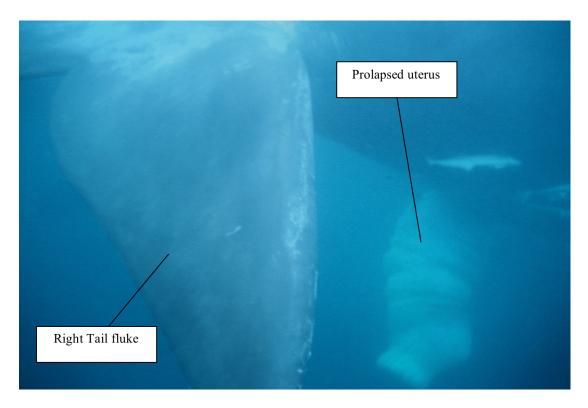


Figure 6.6 Underwater view of the southern right whale with possible prolapsed uterus (right) and tail fluke (left) during its interaction with a humpback whale. Photograph: Angie Gullan.

6.4 Discussion

The existence of a Mozambican right whale sub-stock is recognised by the IWC (IWC, 2001), although this recognition stems from historical catch data alone. The five confirmed and five probable sightings reported in this chapter provide the first clear evidence for the existence of southern right whales utilizing the coastal waters of Mozambique since the cessation of whaling. Moreover the majority of recent sightings have occurred in the last 10 years, of which half occurred during 2009. However, survey effort has increased considerably during the last ten years (Figure 6.4) and the increase in sightings is likely to be due to this. Naive observers or those not expecting to sight southern right whales in Mozambique waters could fail to detect or recognize southern right whales, particularly when humpback whales are also very abundant. Although this could account for low numbers of incidental sightings from non-cetacean specialists, it would not account for low sightings during extensive cetacean survey effort (boat based, land based and aerial) using experienced observers. All of the current right whale sightings in Mozambique were made within

900 meters from the coast. This is consistent with the reported nearshore distribution of southern right whales in South Africa (Best, 1990), where 90% of sightings occurred within 1.85 km from the coast. Best (1990) also noted that some right whales were seen up to 9.63 km from the coast. The lack of right whale sightings during the 'multi-day' surveys could well be due to disparity between offshore effort coverage and right whale distribution where the offshore effort primarily occurred beyond the nearshore range of right whales.

It is difficult to establish if these animals are a remnant population or represent a range expansion of the South African sub-stock. The complete lack of records from Mozambique until the late 1990s could well be due in part to limited survey effort confined to Maputo Bay or areas further offshore (Table 6.1). During a land-based survey of humpback whale migration at Cape Vidal between 1988-1991 (Figure 6.1), Findlay and Best (1996) recorded six southern right sightings totalling ten individuals. These animals were recorded traveling both northbound and southbound and sighting dates are consistent with those recently recorded in Mozambique. It is not unreasonable to consider that those observed by Findlay and Best (1996) may have been migrating to and from Mozambique from the South African sub-stock. Best and Ross (1986) note the possibility of a range retraction as a result of extensive whaling. It would follow that a recovering population might expand back into its historical range and that the sightings at Cape Vidal between 1988-1991 (Findlay & Best, 1996) were the first evidence of this repopulating expansion. No genetic information is available from any of these sightings and no photo-identification matches have yet been attempted with other catalogues. However, Rosenbaum et al. (2001), found that the maternal lineage haplotype from one individual sampled in Madagascar matched one of the two most common haplotypes found only in the South Atlantic Ocean, providing some evidence of common ancestry. The greater proximity of Mozambique would suggest even readier 'overflow' for southern rights from the growing South African population. Alternatively, these recent sightings could be of a remnant population, which due to their extremely low numbers have remained largely undetected until the recent increase in survey effort in the near-shore regions of the Mozambique coast.

Roux *et al.* (2001) reviewed sightings of southern rights along the coast of Namibia between 1971 and 1999. The seasonal distribution of sightings (June to December) was wider than those reported here for Mozambique. Interestingly though, the mean sighting date of the Namibian population was 4 September (SD=45 days, n=36). This peak compares very closely with the recent Mozambique sightings reported here, and is similar to the south coast of South Africa, where whales reach a peak in September (Best & Scott, 1993) or September/October (Best, 1981).

Individual movements can differ radically from the generalized distributions of their origin stock (Best et al., 1993; Mate et al., 1997; Rowntree et al., 2001). Male southern right whales have been found to display significantly less site fidelity than females (Burnell, 2001). Within-year movements of southern right whales during their breeding season have also shown that movements over large distances are not uncommon (Burnell, 2001). Burnell (2001) documented 18 within-year movements ranging from 211-1,490km, made over periods of 3-59 days. The longest within-year distance of 1,490km was in fact made by a female in less than 41 days and in a Southern African context, Southern Mozambique would be within range for such a within-year movement by a South African southern right whale. It is also possible that southern right whale(s) join (or follow) humpback whales to and from their Mozambique breeding grounds as the migration of East African humpback whales coincides with the occurrence of southern right whales on their South African breeding grounds. The presence of coronuline barnacles on a right whale have also been taken as possible evidence of visitation by an adult female right whale to a humpback breeding ground (Best, 1991).

Interspecies associations have been documented for a variety of cetacean species (Baird, 2002; Herzing *et al.*, 2003; Rossi-Santos *et al.*, 2009; Willis *et al.*, 2004). However, these interactions typically involve odontocetes and are often associated with foraging, cooperation or aggression (Rossi-Santos *et al.*, 2009). Whilst hybrids of mysticetes are known to have been taken through commercial whaling operations (Arnason *et al.*, 1991; Berubé & Aguilar, 1998), observations of interactions between mysticetes are less frequently documented. However, interactions between southern right whales and humpback whales are known to occur. In Hawaii, Salden and Mickelsen (1999) describe how a North Pacific right whale appeared to initiate a

social interaction with a group of humpback whales. Sekiguchi *et al.* (2010) describe an interaction between a southern right and humpback whale in Antarctica (64°31'S - 107°58'E) and on several occasions southern right and humpback whales have been seen travelling together in South African waters (including one of the sightings from Cape Vidal). The nature of the interactions in the present instance is unknown, but is unlikely to be sexual given the patently non-functional condition of the female right whale.

Whaling records show that Sofala Bay and Delagoa Bay were known areas of southern right whale concentrations in winter, and these locations are consistent with the direction of travel observed in this study. Sighting data from Ponta Do Ouro (26°53'S) and Ponta Mamoli (26°42'S) show a southerly direction for all groups recorded travelling. This suggests that those whales were ranging further north from where they were sighted which is also consistent with the three "probable" sightings from Barra Point, Inhambane (23°47' S), approximately half way between Ponto Do Ouro and Sofala Bay. Although no recent sightings have been made north of Barra Point, Inhambane, it is reasonable to suggest that in light of historic whaling at Sofala Bay, right whales might be found at least 225 nautical miles further north of Barra Point, Inhambane.

6.4.1 Threats

Although current estimates of population size are lacking, exceptionally low sighting rates despite increased effort using a variety of survey platforms, suggest that the abundance of southern rights in Mozambique is very low. This suggestion of low abundance in turn raises concern about the effects of possible anthropogenic threats. Right whale injury and mortality due to ship strike and entanglement in fishing gear can be serious problems when populations are small (IWC, 2001; Johnson *et al.*, 2005; Knowlton & Kraus, 2001a; Moore, 2009; Nowacek *et al.*, 2004). The use of coastal gill nets and long lines along the Mozambique coast also poses a potential entanglement threat for southern right whales utilizing inshore waters. There are no specific management plans in Mozambique, which deal solely with whales. However, the Coastal Zone Management Strategy, Fisheries Law and Regulations and the Forest and Wildlife Law offer generic protection, which list whales and dolphins

as species that cannot be exploited or killed. In light of this new information regarding the presence of southern right whales off the coast of Mozambique, we recommend that management plans be revised and updated to include and consider the seasonal occurrence of southern right whales within the inshore waters of southern Mozambique. Recommendations should include measures to control disturbance from boat traffic and fishing and to prevent critical habitat degradation. Further surveys are now required to determine the overall distribution and numbers of right whales frequenting the coast of Mozambique. Genetic and photo-identification information should also be acquired to determine the identity of the right whales off Mozambique and their inter-relationship with other southern right whale populations.

7. General Discussion

7.1 General overview – background and aims and findings of this study

7.1.1 Background

Southwest Indian Ocean humpback whales have been fairly extensively studied but information from Breeding Sub-stock C1-S is sparse. Prior to this study, this breeding sub-stock was known only from whaling catch data during the years of exploitation (reviewed by Findlay, 2001) and through a small number of more recent scientific studies. Contemporary information on the wintering ground off Mozambique was limited to two ship-based surveys designed to investigate humpback whale distribution and population size (Findlay et al., 2011; Findlay et al., 1994). The northern section of its proposed migration route had been documented from shore-based visual surveys undertaken each winter at Cape Vidal, from 1988-1991 (Findlay & Best, 1996). The only information relating to the western section of the migration route came from records of humpback whales passing the Knysna Heads on the south coast of South Africa between 1903-1906 (Best & Ross, 1996). Molecular studies investigating population structure within Breeding Stock C have included Breeding Sub-stock C1-S, but genetic samples were only collected in the region northwards of northeast South Africa (the northern section of the migration route and Southern Mozambique) (Pomilla et al., 2005; Pomilla & Rosenbaum, 2006; Rosenbaum et al., 2009). Similarly, the tail fluke images collected from the same region have been used to assess the degree of interchange between the wintering grounds of Mozambique and Madagascar (Cerchio et al., 2008b).

The limited number of scientific studies in Breeding Sub-stock C1-S and the fact that data did not extend southwards of northeast South Africa meant that a substantial proportion of the migration route remained unstudied. In addition, the two surveys to investigate distribution in the coastal waters of Mozambique were of relatively short duration.

After the completion of the comprehensive assessment of Breeding Stock C humpback whales in 2009, the IWC made a number of recommendations based on the limitations of the current data for this stock. These included increasing the number of boat based surveys to gain information on estimates of abundance, as well as other life history information, and the increased collection of genetic samples to help resolve population structure (Annex H - IWC, 2011).

7.1.2 Aims and general findings

This study aimed to improve overall understanding of humpback whales in Breeding Sub-stock C1-S and southern right whales in Southern Africa, with the intention that new information will help to inform and improve the accuracy of future assessments of their status in the southwest Indian Ocean. The work undertaken thus aimed to provide a comprehensive description of how humpback whales utilize the east African coastline from the western section of the migration route along the south coast of South Africa to the winter grounds off Bazaruto Archipelago on the coast of Mozambique. In addition it aimed to evaluate the presence of southern right whales off the coast of Mozambique.

Data collected during boat-based and aerial surveys were used to describe population structure, movements, temporal patterns of migration and skin condition of humpback whales in breeding sub-stock C1-S off southern Africa. Results confirmed that the migration route along the south coast of South Africa is linked to the winter ground off Mozambique. A lack of exchange between breeding sub-stocks C1-N and C1-S was found. This may suggesting that these breeding sub-stocks are independent of each other. Molecular analysis revealed unexpected levels of population structure between the migration route and the winter ground of C1-S, as well as the possibility that this migration route is also utilised by some individuals from breeding sub-stock C3. A skin condition of unknown aetiology that primarily affects humpback whale mother-calf pairs was identified. The first assessment of its prevalence and severity was made, providing a baseline for future monitoring. Humpback whale abundance in an inshore region of Bazaruto Archipelago, Mozambique was estimated and attempts were also made to use the limited information off Plettenberg Bay/Knysna, South Africa. In addition to improving our understanding of humpback whales from

Breeding Stock C, knowledge about another baleen whale species utilising the southwest Indian Ocean was extended. The first evidence of southern right whale presence off the coast of Mozambique since the cessation of whaling was documented. It remains unknown whether this is a remnant sub-stock or the recovering South African sub-stock reoccupying its historical range.

This chapter considers the results of this study in the context of informing comprehensive assessments to evaluate the status of a species. It also discusses these findings in relation to factors that affect population recovery.

7.2 Informing comprehensive assessments

The status of marine mammals has often been characterized using two principal measures: (1) abundance and (2) mortality from various causes (Reynolds et al., 2009). Marine mammal scientists are gradually expanding this limited construct to include the factors that influence or determine abundance and trends such as animal health, population demography, and current and future threats to the population. Classifying the extent to which species or sub-populations are at risk of extinction using criteria developed by the IUCN requires knowledge of geographic range, population size and trends, habitat and ecology and past, recent and ongoing threats (IUCN, 2012). The IUCN Red List classification of extinction risk for mammals has been used in numerous studies, including the identification of traits associated with high extinction risk, prioritization of species for conservation action and recommending global conservation priorities (Schipper et al., 2008). Evaluating the population status of whale stocks requires examination of current stock size, recent population trends, carrying capacity and productivity, all of which requires knowledge of population structure and population dynamics (IUCN, 2012) (IWC, 2011c). Estimating the former abundance of whale populations or 'stocks', and reconstructing the historical trajectory of decline and recovery (if any), are essential to an assessment of the true impact of whaling on the marine ecosystem, and to provide a baseline for judging current and future recovery of whale stocks (Jackson et al., 2008b). This baseline has important implications for the management of any future whaling and for understanding the ecological role of whales.

The complex stock structure of Breeding Stock C has meant that more information is required on movements and population structure of humpback whales within the South West Indian Ocean to evaluate their status appropriately. In this study, three field sites, separated by up to 2000 km enabled both the migration route and winter ground of breeding sub-stock C1-S to be described. The migration route along the south coast of South Africa clearly serves as a route to winter grounds of Southern Mozambique. This finding was expected given what was already known for this region. The temporal distribution of humpback whales off Plettenberg Bay/Knysna was found to be bimodal, a pattern typical of migration routes in a wide range of taxa including birds (Stotz & Goodrich, 1989), fish (Welton et al., 1999) and marine mammals (Brown & Corkeron, 1995). The northbound migration was found to occur between May and August and the southbound migration between September and mid-February. These timings are consistent with humpbacks migrating to and from the winter grounds off Mozambique where their temporal distribution off Bazaruto Archipelago, was found to be between the end of June and the end of October, with a unimodal peak in August/September. The temporal patterns found in this study were generally consistent with those found during shore-based surveys off Cape Vidal, northeast South Africa (Findlay & Best, 2006) which had also suggested that that humpback whales were migrating to and from winter grounds in Mozambique. However, the southbound migration off Plettenberg Bay continued into the middle of February, several weeks longer than was expected given that whales were not observed after the end of October off Bazaruto Archipelago or December off Cape Vidal. The breeding and feeding ground location of these "late" whales remains unknown but the implications of the timing of these sightings is discussed below and in section 7.3 & 7.4.

Some individuals showed remarkable timing synchrony with a mean 10 day difference between years. This has also been found elsewhere (Burns *et al.*, 2012; Cerchio *et al.*, 2008a; Felix & Haase, 2001) and has been noted as a source of bias in mark-recapture studies when sampling is temporally unequal (Cerchio *et al.*, 2008a).

Connectivity between the south coast of South Africa and the winter grounds of Mozambique was identified through the recapture of two individuals between Plettenberg Bay/Knysna, South Africa and Ponta Mamoli, Mozambique. This

provides the first direct evidence that the migration route along the south coast of South Africa, which extends at least as far west as Plettenberg Bay/Knysna, conveys whales to and from the Mozambique winter grounds (Sub-region C1-S). This is consistent with the timings described above and the proposed South African coastal migration route for sub-region C1 (Best *et al.*, 1998).

On the other hand, analysis of the mtDNA control region found a highly significant level of population structure both at the haplotype and nucleotide level between the migration route along the south coast of South Africa and the Mozambique winter grounds. This was unexpected given the temporal distributions and photographic recaptures found between these locations in this study and the lack of population structure found between northeast South Africa and Mozambique (Pomilla *et al.*, 2005). In addition and equally unexpected was the complete lack of differentiation found between Plettenberg Bay/Knysna and the north east coast of Madagascar. This is inconsistent with the current understanding of population structure for breeding Stock C, where significant differentiation has been found between sub-regions C1-S and C3, where levels of exchange between these regions have been estimated to be low (Rosenbaum *et al.*, 2009).

Previously, in the context of sub-region C1-S, population structure has been investigated only using samples collected northwards of Cape Vidal, South Africa. This suggests that although significant population structure exists between the winter grounds of breeding stock C1-S and C3, the migration route along the south coast of South Africa may contain individuals from both sub-regions. However, currently, there is little evidence to suggest a migration stream flowing east-west between the coasts of South Africa and Madagascar. The sample size for molecular analysis for Plettenberg Bay/Knysna was too small (n=10) to determine whether the level of population structure found in this study is representative. Nonetheless, this raises important questions regarding whether or not the south coast of South Africa migration route supports more than one sub-region, which until now had only been assumed to link with the coast of Mozambique (Best *et al.*, 1998; IWC, 2011c). This can only be fully answered by increasing the number of samples for molecular analysis from Plettenberg Bay/Knysna and by making further comparisons of tail fluke images between the migration route of C1-S and sub-region C3.

Although Breeding Stock C1 has been divided into two sub-regions, C1-N and C1-S, for management purposes the IWC has suggested that C1 should be treated as one sub-stock (IWC, 2011c). However, if humpback whales observed off the coast of east Africa represent a single sub-stock, then complete mixing should occur throughout the winter ground and between the winter ground and its migration route. The lack of recaptures between C1-N and C1-S (including the C1-S migration route along the south coast of South Africa) provides some evidence to suggest that mixing does not occur between these two sub-regions, which may represent two independent sub-stocks utilising the east coast of Africa. The incorporation of these two regions into a single stock (IWC, 2011c) may therefore need to be reconsidered if additional photographic comparisons continue to reveal a lack of connectivity between these two sub-stocks. If individuals from sub-region C1-N were not migrating along the south coast of South Africa, then the most obvious alternative route would be one which passes through sub-region C2 and C3.

This study revealed that the southbound migration off Plettenberg Bay/Knysna continued into mid-February and consisted mainly of mother-calf pairs and associated escorts. Mother-calf pairs are on average the last cohort to depart from winter grounds (Dawbin, 1997). This study has shown that although the departure of mother-calf pairs is skewed towards the end of the breeding season, individual departures range from the first to the last individuals to leave the winter grounds. For mothers accompanying their recently born calves, a late departure from the winter ground could increase the calf's chances of survival by providing and extending the period of time to grow and develop before enduring the southbound migration. On the other hand, an earlier departure would maximize foraging time at the feeding grounds.

Humpback whales have been observed feeding in the productive Benguela upwelling region off the west coast of South Africa during spring and summer (Barendse *et al.*, 2011a; Barendse *et al.*, 2010b; Findlay & Best, 1995). As well as the possibility of inter-regional exchange during winter, the relatively close proximity of sub-region B2 to Plettenberg Bay/Knysna compared to the Antarctic feeding grounds would make sub-region B2 a viable feeding ground location for some C1-S humpback whales.

However, comparisons of tail fluke images from sub-regions C1-S and B2 revealed no recaptures. The high rate of site fidelity found in B2 (Barendse *et al.*, 2011a) combined with the lack of recaptures between C1-S and B2 suggests no exchange between these two sub-regions during summer or winter. The late departure from winter grounds is likely to result in a reduction in foraging time at the feeding grounds unless travel time or distance is reduced. Reducing travel time by increasing swimming speed seems an unlikely option for mothers accompanying their recently born calves.

7.3 Recovering populations

The "state of a marine mammal population" covers a number of concepts including demographic status and health status (ASCOBANS, 2009). Changes in vital rates, *i.e.* fecundity and mortality, which may lead to future changes in abundance and distribution, describe the demographic status of a population whilst the nutritional state, main pathologies and causes of death, and contamination by pollutants are often used to describe its health status. Their proper understanding helps in identifying relevant mitigation or management actions. Assessing the health of free-ranging marine mammals is difficult and this is particularly so for cetaceans (Wilson *et al.*, 1999). Visual assessments are increasingly being used to identify and monitor the skin conditions of marine mammals (for example- Brownell *et al.*, 2007; Hamilton & Marx, 2005; Van Bressem *et al.*, 2009; Wilson *et al.*, 1997); however, identifying their cause is much more problematic.

Cetacean populations, along with populations of other large mammals (and animals in general) are regulated through density dependent changes in reproduction and survival (Fowler, 1984). A decline in birth rate and neonate survival is commonly associated with a decrease in per-capita prey availability. In large mammal populations, non-linearity in density dependence leads to the most important changes in population parameters likely occurring at population levels close to carrying capacity (Fowler, 1984).

Density dependence has been suggested as the cause of changes in migration timing in baleen whales. Lockyer (1981) suggested that in the 1930s-1950s, the rapid

decrease in blue, fin and humpback whale abundance in the Southern Ocean led to an increase in prey for sei whales, which altered their migration timing causing their peak abundance to occur in January rather than March in the Southern Ocean. However, on the whole, interspecific competition between baleen whale species is thought to be limited, due in part to resource partitioning mediated by food preferences and the biomechanics of body size (Clapham & Brownell, 1996).

Population dynamics modeling has suggested that the humpback whale sub-stocks of C1 and C3 had recovered to nearly 65-98% and 76-83%, respectively, of their pre-exploitation abundances (IWC, 2010). As these recovering stocks approach carrying capacity, density dependent factors will begin to limit population growth rates. Humpback whales show maternally driven site fidelity to feeding locations (Stevick *et al.*, 2006) and increased competition for food resources will likely have a negative impact on an individual's ability to maintain its annual energy requirements. If a reduction in foraging time is large enough, the energy requirements of female Balaenopterids, which when pregnant require a 25% increase in blubber thickness more than anoestrus females (Lockyer, 1981), may not be met. Most of this extra energy is believed to be used during lactation, which on a daily basis is energetically much more expensive than that of pregnancy (Lockyer, 1981). If the metabolic requirements of pregnancy and lactation are not met, this could cause variation in reproductive success among individuals.

The skin lesions described in this study were much more prevalent among mother-calf pairs and lesion severity was lowest during the northbound migration and highest during the southbound migration. It seems likely that the lesion is microbial in nature, but this cannot be confirmed until samples of tissue can be acquired and analysed. A higher prevalence and severity found in mother-calf pairs than the overall sampled population could indicate that its occurrence is related to the inherent biological stresses associated with pregnancy and lactation. Alternatively, these lesions may indicate poor water quality along the coastal regions of East Africa (see section 7.4). An increase in the prevalence of skin conditions may be one indication of metabolically stressed individuals caused by density dependent factors (or density independent factors discussed in section 7.4) on feeding grounds, resulting in immuno-suppression or metabolic fatigue due to energetic demands not being met by

a reduction in foraging efficiency. Observations of a pair of adult humpback whales off Plettenberg Bay/Knysna provided the first evidence of Breeding Stock C animals feeding on shoaling fish during migration, indicating that prey availability along the migration route may be utilised during migration. However, the very low incidence of feeding humpbacks along this migration route suggests that feeding is limited to occasional bouts. This is consistent with an increasing number of reports where humpbacks have been observed feeding opportunistically during migration (Danilewicz *et al.*, 2008; de Sá Alves *et al.*, 2009; Stamation *et al.*, 2007; Stockin & Burgess, 2005; Swingle *et al.*, 1993).

Populations at high risk of extinction are considered to be those for which abundance is known or thought to be very low (considerably fewer than a thousand individuals) (Clapham *et al.*, 1999). For populations or sub-populations of marine mammals that have limited or no information to enable their status to be evaluated, understanding their distribution is a critical starting point in this process. Until an assessment can be made, a precautionary conservation approach should be taken, whereby potential threats that could increase its risk of extinction are identified and mitigated against.

After the near extirpation of southern right whales from intense open-boat and pelagic whaling during the eighteenth and nineteenth centuries and modern whaling during the twentieth century (Best & Ross, 1986; Richards & Du Pasquier, 1989; Wray & Martin, 1983), their populations appear to be recovering (IWC, 2001). Following a range retraction during the years of exploitation, recovering populations appear to be undergoing a steady northward expansion in their distribution (Richards, 2009). However, although these populations appear to be reoccupying their historical range, their present distribution is still far short of that recorded over a century ago (Richards, 2009). The only sub-stock of southern right whales in Southern Africa, which shows strong signs of recovery, is off the south coast of South Africa and is arguably the largest breeding stock in the Southern Hemisphere (IWC, 2001). In contrast, the southern right whale sub-stock off the coast of Mozambique was considered to have a population size of less than ten individuals (IWC, 2001) after six sightings of ten individuals were made off Cape Vidal, South Africa (Findlay & Best, 1996).

Whether these recent right whale sightings are of an existing remnant population or the result of range expansion by a recovering South African population (IWC, 2001) is unknown. Either way, these findings represent a valuable addition to our understanding of current right whale distribution. The temporal distribution of southern right whales off the coast of Mozambique falls within that found for humpback whales wintering off the coast of South Africa. Southern right whale sightings all occurred within 900 meters of the coast, which is consistent with the nearshore distribution of southern right whales in South Africa (Best, 1990). This preference for very inshore regions is in contrast to humpback whales observed off Bazaruto Archipelago, where they were encountered up to 43 km from the coast, with blows being seen much further out to sea. Although their temporal distributions overlap, the utilisation of only the most inshore regions by southern right whales means that the risk posed by near-shore anthropogenic activities may be considerably higher for southern right whales than for humpbacks.

Ship-strikes and fishing gear entanglement are two of the biggest threats to right whales globally (Caswell et al., 1999; IWC, 2010; Johnson et al., 2005; Knowlton & Kraus, 2001a; Lodi & Rodrigues, 2007). Artisanal fishing is widespread along the Mozambique coastline, often operating from open beaches or using boats less than 10 m long and is the predominant fishery in Mozambique (Hara et al., 2001). In the greater Bazaruto Archipelago region alone, 79 fishing centers and 1,425 informal fishing camps exist (Everett et al., 2008), demonstrating the intensity of this widespread fishery. The most common method is beach seining where a 150-meter wide net is pulled either to shore or to an anchored vessel (Everett et al., 2008). The use of monofilament line, gill nets and stake nets are also common in the artisanal fishery. These types of fishing gear and methods are likely to present a significant risk to southern right whales (Meyer et al, 2011) and should be considered a critical concern given the lack of information about this small population. In addition to the artisanal fishery, semi-industrial and industrial fishing also operate along the coastal region of Mozambique. This involves lager vessels, which are mostly involved in line fishing, trawling and trap fishing (Everett et al., 2008). Due to the overlap in the temporal distributions of southern right and humpback whales, any effort to reduce disturbance to humpback whales caused by anthropogenic activities off the coast of Mozambique will also likely aid southern right whales.

The proposal for a deep-water port development on the border of South Africa and Mozambique is another potential threat to this population of southern right whales. Increased shipping traffic through its migration route or winter ground will increase vulnerability of individuals to ship strike as well as increasing levels of acoustic disturbance and pollution. Regardless of the origin of these right whales, their abundance off the coast of Mozambique is very low and every effort should be made to protect and conserve them while the identity, abundance and distribution of the population are studied further.

7.4 Small and large-scale environmental impacts

Extrinsic (density independent) factors can affect populations irrespective of population size (Wolff, 1997). These can be medium-to-long term changes in the environment such as climate change (Learmonth *et al.*, 2006; Tynan & DeMaster, 1997) and water contaminant levels (Wilson *et al.*, 1999) caused by human activity or short term, small scale changes such as local perturbations in the environment (Chambert *et al.*; Urbán *et al.*, 2003).

Degraded water quality is well known to have potentially negative impacts on marine mammal populations (Van Bressem *et al.*, 2008a; Van Bressem *et al.*, 2008b; Wilson *et al.*, 1999). However, the impact of water contamination is difficult to quantify because its effect is indirect. High contaminant levels in tissue are known to cause immuno-supression in individuals that can lead to increased susceptibility to disease, which may reduce the reproductive output of individuals and ultimately populations (Van Bressem *et al.*, 2008a).

Understanding the effects of climate change on marine mammals and their ecosystems has become a priority in recent years (IWC, 2010; Learmonth *et al.*, 2006; Tynan & DeMaster, 1997). The potential impacts of climate change on marine mammals can be direct, such as reduced sea ice and rising sea levels reducing the number of seal haul-out sites, or the need for some species to track a specific range of water temperatures in which they can physically survive (Learmonth *et al.*, 2006). Indirect effects of climate change include temporal or spatial changes in the

distribution of prey, abundance and migration patterns, community structure, susceptibility to disease and contaminants (Learmonth *et al.*, 2006; Nicol *et al.*, 2008).

Changes in the temporal and spatial distributions of baleen whales on feeding grounds are thought to reflect similar changes in the temporal and spatial distributions of their prey (Friedlaender *et al.*, 2008; Friedlaender *et al.*, 2006; Weinrich *et al.*, 1997). In turn, this may affect their migration timings (Visser *et al.*, 2011). A change in temporal distribution of whales could indicate a wide-scale ecosystem change that is causing changes to the spatial or temporal distribution of their prey. The Scientific Committee of the IWC recently made recommendations to examine existing long term data sets of humpback and southern right whales populations to investigate changes to the arrival and departure times on the breeding grounds as a result of climate change (IWC, 2010).

Observations made in this study of humpback whales being present off the coast of east Africa between late-May and mid-February are inconsistent with records of humpback whales being present between April and December during the early part of the Century. This may indicate that the timing of migration has shifted, becoming one or two months later during the last 100 years. A shift of this nature is not unexpected given the similar patterns observed in other population of baleen whales, such as grey whales in the North Pacific (Rugh *et al.*, 2001; Shelden *et al.*, 2004; Swartz *et al.*, 2006) and humpback whales in the North Atlantic (C. Ramp pers. comm.). This may be the first evidence for a change of this kind to be observed in a Southern Hemisphere humpback whale population. However, given that the robustness of the historical data cannot be confirmed, interpreting these results must be treated with caution.

A change in prey distribution could cause a reduction in foraging efficiency unless the prey shift is successfully tracked either spatially or temporally. As described in section 7.3, if a reduction in foraging time or efficiency at feeding grounds is large enough, an individual's energetic demand (which for pregnant females is substantially higher than for anoestrus females) may not be met. The evidence of a shift in the migration timing of humpback whales during the last 100 years (Chapter 2) may be

indicative of humpback whales tracking temporal changes in prey distribution and abundance on their feeding grounds. Alternatively, a reduction in foraging efficiency could be overcome by increasing the time spent at feeding grounds, which in turn would cause a delay in migration.

The temporal and spatial distribution of humpback whales during migration is considered to be predictable and cyclical (Prideaux, 2003) and wide-scale migration patterns are thought to be largely unaffected by current regimes (Dawbin, 1966; Rosenbaum et al., 2009). However, results from this study suggest that the temporal and spatial structure of the Agulhas Current may have influenced humpback whale migration. During August 2008, a Natal Pulse measuring 150 km in diameter was recorded offshore of Port Elizabeth for approximately one month (Rouault et al., 2010). The location, timing and effects of such a large Natal Pulse, combined with its close proximity to Plettenberg Bay/Knysna appeared to correlate closely with differences in encounter rates observed off Plettenberg Bay/Knysna between 2006 and 2008. This substantial disruption to the flow and structure of the Agulhas Current, which has flow rates of up to 2 m s⁻¹ (7.2km/h) (Lutjeharms, 2007) appears to have caused northbound migrating humpback whales to deviate away from this southward flowing high velocity water mass by moving closer inshore. This suggests that the temporal and spatial structure of the Agulhas Current can influence humpback This could positively or negatively affect their energetic whale migration. expenditure, depending on whether the influence was to their advantage or disadvantage.

Humpback whales, like most other baleen whales, acquire all or the majority of their annual energy budget during the summer feeding period (Lockyer, 1981). Once away from the feeding grounds, they remain largely dependent upon their lipid reserves, which were stored as blubber in the previous feeding season. During this fasting period away from the feeding grounds, any increase in energy expenditure caused by having to make unexpected migratory deviations to avoid short-term changes in a current's structure or flow, could ultimately affect reproductive output. Spatial or temporal changes caused by changes in current regimes could also cause whales to be present at an unexpected time or place. If this is not taken into account in

conservation assessments, an increased risk of disturbance from anthropogenic activities, such as fishing, oil and gas operations or shipping could be overlooked.

The movement of individuals inshore may have introduced heterogeneity of capture probabilities of individuals in this study. Where data can be used to estimate abundance, heterogeneity introduced through the effects of currents might be important to consider.

7.5 Future work

As information continues to be acquired for baleen whales in the South West Indian Ocean, our understanding for this region continues to develop. This study has added to this information and to our understanding of how humpback and southern right whales utilize the coastline of East Africa in the region.

Nevertheless, many questions remain unanswered or warrant further investigation. More information is needed before conclusions can be drawn regarding the levels of exchange and population structure of humpback and southern right whales off the east coast of Africa.

7.5.1 Humpback whales

Although this study has increased our knowledge of humpback whales in Breeding Stock C, a number of issues need to be addressed or further investigated. Identifying the width of the migration steam off Plettenberg Bay/Knysna will allow the number of individuals that passed by undetected to be estimated, which will increase the accuracy of future abundance estimates for this region. Although the Agulhas Current regime appears to affect the migration timing and distribution of humpback whales, its impact remains un-quantified. Its quantification is important in terms of understanding the energetic expenditure of migrating humpback whales and may be important when estimating abundance as well as assessing the levels of conservation and management needed outside of their "normal" distribution.

A reconciliation of the photographic catalogue held by Oceans and Coasts with the catalogue created in this study will allow a greater sample size for photo identification comparisons. A comparison between this region (C1-S) and C3, C2 and B1 should be conducted to further investigate levels of exchange between sub-regions. Similarly, the C1-S and C1-N comparison should be repeated in the future to include new, unmatched tail fluke images collected in Northern Mozambique, Tanzania and Kenya. Information on the migration route westward of Knysna remains limited and the point at which the migration route departs the coast is unknown. Identifying the point at which the migration route departs from the coast could provide information towards identifying the location of the offshore component of this route. Further genetic sampling is required off Plettenberg Bay/Knysna to substantiate the levels of genetic differentiation found in this study. Similarly, extending sampling effort (photo identification and genetic) beyond December will allow the sub-stock identity of the "later" whales observed off Plettenberg Bay/Knysna between Dec and mid-February to be determined. Before the cause of the skin lesions found on East African humpback whales can be confirmed, samples must to be obtained and analysed to determine their aetiology.

7.5.2 Southern right whales

Identifying southern right whale presence in Mozambique is the first step towards increasing our knowledge for this sub-stock. In order to evaluate the status of this sub-stock, its distribution and abundance must be determined. In addition, skin samples must be acquired for genetic analysis to investigate population structure, which will help answer the question of stock identity. Photo identification studies and satellite tagging of these individuals will allow for levels of exchange between Mozambique and South Africa to be estimated as well as revealing the extent of their migration route and breeding ground habitat. The small population size of this substock heightens its high risk from threats caused by anthropogenic activities. Therefore, it is recommended that every effort be made to enhance conservation strategies and reduce the impact of anthropogenic activities until such time that their status is adequately evaluated and the stock identity is understood.

8. Appendices

8.1 Appendix 1a: Example of the research permit issued to the Centre for Dolphin Studies each year for the collection of data in South Africa which used in this study



Private Bag X2, ROGGEBAAI, 8012. Foretrust Building, Martin Hammerschlag Way, Foreshore, CAPE TOWN, 8001 Tel: (+ 27 21) 402 3911 Fax: (+ 27 21) 402 3964

Enquiries: Dr C.J. Augustyn Tel: 021-4023102

Fax: 021-4023639 E-mail: augustyn@deat.gov.za

24 March 2009

Dr V G Cockcroft Centre for Dolphin Studies PO Box 1856 Plettenberg Bay

Attention: Dr V G Cockcroft

PERMIT FOR THE PURPOSES OF A SCIENTIFIC INVESTIGATION OR PRACTICAL EXPERIMENT IN TERMS OF SECTION 83 OF THE MARINE LIVING RESOURCES ACT, 1998 (ACT NO. 18 OF 1998).

I, the undersigned, Chief Director: Research, Antarctica & Islands, Branch Marine and Coastal Management, Department of Environmental Affairs and Tourism (the Chief Director) acting in pursuance of the delegated authority conferred upon me by the Honourable Minister of Environmental Affairs and Tourism as contemplated in terms of Section 79 of the Marine Living Resources Act of 1998 (Act No. 18 of 1998) ("the Act") hereby permit, in terms of Section 83 of the Act, the following person(s)/institution to engage in the scientific investigation or practical experiment referred to below:

PERMIT REFERENCE NUMBER: RES2009/29

PERSON(S)/ INSTITUTION: Bayworld Centre for Research and Education, Port Elizabeth Museum, SCIENTIFIC INVESTIGATION OR PRACTICAL EXPERIMENT: Collection, transportation and possession of dead stranded whales, dolphins and seals or any parts thereof,

subject to the following conditions:

GENERAL CONDITIONS

- This permit is issued subject to the provisions and regulations of the following laws:
 - (a) The Marine Living Resources Act, 1998 (Act No. 18 of 1998) ("the Act"), and all regulations published in terms
 - (b) The National Environmental Management Act, 1998 (Act No. 107 of 1998) ("NEMA"), and in particular, the regulations that control vehicle use in the coastal zone (as amended);

 - (c) The National Environmental Management Blodiversity Act, 2004 (Act No. 10 of 2004); (d) The National Environmental Management Protected Areas Act, 2003 (Act No. 57 of 2003);
 - (e) The Sea Birds and Seals Protection Act, 1973 (Act No. 46 of 1973); and
 - (f) Prevention of Pollution from Ships Act (Act No. 2 of 1986).

- 1.2. If, in the opinion of the Chief Director there are sound reasons for doing so, the Chief Director may amend the conditions of the permit.
- 1.3. Any reference to the Permit Holder in these permit conditions includes the entity or person, his/her or its employees (whether permanent, full-time or part-time), his/her or its contractors, agents or advisers, being cognisant of the course and scope of their contractual relationship.
- 1.4. A breach of the provisions of the Act, regulations or these permit conditions by the Permit Holder may result in the initiation of legal proceedings (civil or criminal). A breach includes:
 - (a) furnishing information to which the Department of Environmental Affairs and Tourism (the Department) is entitled, which is not true or complete;
 - (b) contravening or failing to comply with a permit condition or with the provisions of the Act;
 - (c) being convicted of an offence in terms of the Act; or
 - (d) failing to effectively utilise the permit.
- 1.5. The Permit Holder shall store at their registered place of business/residence the original permit issued. The Permit Holder shall at all times, have available a <u>true certified copy</u> of this permit which should be produced on demand by any Fishery Control Officer or any other law enforcement official.
- 1.6. This permit shall only be utilized by the individual whose name appears on the permit.
- 1.7. If the permit is in the name of an institution/company/close corporation the individual utilizing the permit shall in addition to a certified copy of this permit, be in possession of identification and/or a letter which identifies the individual as an authorized person or employee of the permit holder.
- 1.8. Any individual utilizing this permit shall in addition to the above conditions have a certified copy of any other permit/exemption required in terms of other legislation including any permit or exemption in terms of the Marine Living Resources Act, 1998 (Act No. 18 of 1998).
- 1.9. An application for a permit may be refused if the conditions of a previously issued permit had not been adhered to.
- 1.10. In terms of the Act, the permit holder is obliged to report to the Minister any contravention of the provisions of the Act by any other person.
- 1.11. The Permit Holder must safely store all inorganic waste material, garbage and pollutants on board the vessel or at the site of research activities. Should the Permit Holder discard any inorganic waste material, garbage or pollutants into the sea or coastal environment, this permit will be suspended for a period determined by the Department and the Permit Holder shall take those steps considered necessary in terms of NEMA to remed y any pollution caused.
- 1.12. Report(s) that include descriptions of all collections that took place under this permit must be submitted to the Chief Director: Research, Antarctica and Islands, Department of Environmental Affairs and Tourism, Bıranch Marine and Coastal Management (Attention: Dr Kim Prochazka), Private Bag X2, Roggebaai, 8012. This should be submitted within one month of the expiry date of this permit, or with the application for renewal of the permit.

- 1.13. Specimens collected in terms of this permit shall not be sold or offered for sale.
- 1.14. This permit does not in any way absolve the holder from the obligations of and adhering to the remainder of the provisions and conditions of the Act.

2. SPECIFIC CONDITIONS

- 2.1. This permit allows for the collection, transportation and possession of dead stranded whales, dolphins and seals or any parts thereof, for the bona fide research projects of Dr Vic Cockcroft and the Centre for Dolphin Studies, as authorized by the Director of Bayworld, Port Elizabeth Museum.
- 2.2. All skeletal material and soft parts collected from stranded animals in the possession of the Centre for Dolphin Studies must be transported to Bayworld, Port Elizabeth, for permanent curation as per Bayworld protocols (Attention: Dr M Smale) within the following timeframes:
 - Collections made during 2009 should be transferred within one month of the expiry date of this permit.
 - Collections made before 2009 should be transferred by 31 December 2009.

All copies of cetacean and pinniped data forms must be included in the collection.

- 2.3. A Memorandum of agreement must be signed by both parties with respect to intellectual property of the collection. A copy of this agreement must be forwarded to the Chief Directorate: Research, Antarctic and Islands (Attention: Dr Kim Prochazka).
- 3. PERMIT VALIDITY PERIOD

This permit is valid from date of issue until 31 December 2009.

A.S. JOHNSON

DR C.J. AUGUSTYN
CHIEF DIRECTOR: RESEARCH, ANTARCTICA AND ISLANDS

8.2 Appendix 1b: CITES Export permits

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PERMIT/CERTIFICATE No. 0138888

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PERMIT/CERTIFICATE No. 0138888

8.3 Appendix 1c: CITES Import permits

European Community Exporter/Re-exporter	Permit/Certificate 404236/02				
PORT ELIZABETH MUSEUM	No. 494226/02				
AT BAYWORLD BEACH ROAD	☐ EXPORT 2. Last day of validity (See Condition ☐ RE-EXPORT 08/11/12				
HUMEWOOD	OTHER 08/11/12				
PORT ELIZABETH					
SOUTH AFRICA	Convention on International				
Importer	Trade in Endangered Species				
SEA MAMMAL RESEARCH UNIT	of Wild Fauna and Flora				
SCOTTISH OCEANS INSTITUTE UNIVERSITY OF ST ANDREWS	4. Country of (re) export SOUTH AFRICA				
ST ANDREWS	the Mark on Solyon reproducts				
FIFE	5. Country of Import UNITED KINGDOM				
KY16 8LB Authorised location for live wild-taken specimens of Annex A species	7 Landan Management Authority				
	Department for the Environment, Food and Rural Affairs				
The state of the same of the same	Floor 1, Zone 17, Temple Quay House 2 The Square, Temple Quay				
The second secon	2 The Square, Temple Quay				
The state of the s	Bristol, BS16EB Tel 0044 (0)117 372 8749 Website www.ukcites.gov.uk				
Description of specimen(s) (incl. marks, sex/date of birth for live animals	s) 8. Net Mass (kg) 10. Quantity				
Twenty seven skin biopsy samples.					
Total no more than 81g.	11. CITES Appendix 12. EC Annex 13. Source 14. Purpose S				
Safar take trainings are to the control of the cont	15. Country of Origin Mozambique				
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and the state of t	18. Country of lest ré-export: South Africa				
the south ago at dolds for the same with the	19. Certificate No 0131201 20, Deta 11/06/12				
1. Scientific name of species Megaptera novaeangliae					
A STATE OF THE STA	The second second real the second submitted a second secon				
2. Common name of species Humphacked Whale					
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European Community Exporter/Re-exporter	Permit/Certifica	te	40	20	15987	
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AT BAYWORLD	RE-EXPORT		2. Last day of validity (See Condition 4			
BEACH ROAD				08/11/12		
HUMEWOOD	OTHER					
PORT ELIZABETH						
SOUTH AFRICA	C AR	Co	nvention	on Int	ernational	
Importer		Tra	ade in End	ange	red Species	
SEA MAMMAL RESEARCH UNIT	, 11	of	Wild Faun	a and	Flora	
SCOTTISH OCEANS INSTITUTE	4. Country of (re)-expe					
UNIVERSITY OF ST ANDREWS	SOUTH AFR	ICA				
ST ANDREWS FIFE	5. Country of Import				CARLES IN	
KY16 8LB	UNITED KIN	GDOM			TOTAL BEAUTY	
Authorised location for live wild-taken specimens of Annex A species	7. Issuing Managemen	nt Authority				
	Department for the Wildlife Licensing	Environment,	Food and I	tural A	Allairs	
	Floor 1, Zone 17, 7	emple Onav	House			
	2 The Square, Tem					
	Bristol, BS1 6EB Tel 0044 (0)117 372 8749 Website www.ukcite				tac gove uk	
	9. Net Mass (kg)	8/49 Websi	THE RESERVE AND PERSONS NAMED IN	uantity	,cuc.	
Description of specimen(s) (incl. marks, sex/date of birth for live animals)	5. 1461 Wass (NG)		10.0		7	
Seven skin biopsy samples. Total no more than 21g.	11. CITES Appendix	12. EC Anner	13. Sc	urce	14. Purpnea	
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	15. Country of Origin South Africa					
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Scientific name of species Megaptera novaeangliae	F - 1 - 1 - 1 - 1 - 1 - 1 - 1 - 1 - 1 -					
				3		
Common name of species Thumbhacked Whale						
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8.4 Appendix 1d: DEFFRA Animal Heath Import License

Authorisation No: TARP/2012/82(a)

DEPARTMENT FOR ENVIRONMENT, FOOD AND RURAL AFFAIRS

AUHORISATION FOR THE IMPORTATION FROM THIRD COUNTRIES OF RESEARCH SAMPLES

European Communities Act 1972

TRADE IN ANIMALS AND RELATED PRODUCTS REGULATIONS 2011 ANIMAL BY-PRODUCTS (ENFORCEMENT) (ENGLAND) REGULATIONS 2011

The Secretary of State for Environment, Food and Rural Affairs, by this authorisation issued under the terms of Paragraph 4 of Schedule 3 of the Trade in Animal and Related Products Regulations 2011 authorises:

Sea Mammal Research Unit Scottish Oceans Institute St Andrews Fife KY16 8LB	Name and full postal address
Subject to and in accordance with the conditions set out below, the landing in Engls	and of:
Humphack Whale Skin Biopsies, intended for particular studies or analyses	Product
From	
Mozambique & South Africa	Countries of origin
At	
All London Airports	Ports of entry
Until	
02 September 2012	Expiry Date
The same of the sa	Talthough Na
Dated: 13 June 2012 Officer of the Department Environment, Food and	nt for Safe

8.5 Appendix 2: Abundance estimation for humpback whales migrating past Plettenberg Bay/Knysna, South Africa

The very low recapture rate found in this study (Table 3.2, Table 3.3) prevented the calculation of a robust abundance estimate for humpback whales off Plettenberg Bay/Knysna. Nonetheless, in an attempt to obtain as much information as possible from the data, a method developed to estimate the maximum population size for studies in which no recaptures were made was utilised (Bell, 1974; Edwards, 1974) for the years 2006-2008. Assuming that all the usual conditions for mark-recapture analysis are met, the method uses the following equation to describe the probability, p, that none of n recaptures is marked:

$$p = \frac{(N-a)!(N-n)!}{N!(N-a-n)!}$$

where a = number of marked individuals and N = population size. For given values of a and n, the value of N at which p = 0.5 can be found. There is then a 50% chance that the true population size is no greater than N.

95% confidence limits around this value can be found by finding the value of N where p = 0.025 and 0.975 This method was implemented in software R (R Development Core Team, 2010).

The Chapman estimator was used to estimate abundance for 2006-2007 and 2007-2008 in which both pairwise estimates were each based on one recapture, where n_1 = number of individuals captured on first occasion (year), n_2 = number of individuals captured on second occasion (year), m_2 = number of recaptures, \hat{N} =estimated abundance:

$$\hat{N} = \frac{(n_1 + 1)(n_2 + 1)}{(m_2 + 1)} - 1$$

with estimated variance:

$$V\hat{a}r_N = \frac{(n_1+1)(n_2+1)(n_1-m_2)(n_2-m_2)}{(m_2+1)^2(m_2+2)}$$

The lower and upper confidence intervals were calculated as $\frac{N}{C}$ to $N \cdot C$, where:

$$C = e^{1.96\sqrt{ln(1+CV^2)}}$$

Table 8.1 Abundance estimate for humpback whales migrating past Plettenberg Bay/Knysna, South Africa. n = number of individuals captured on first occasion (year), a = number of individuals captured on the second occasion (year), m_2 = number of recaptures, \hat{N} =estimated abundance. P-values in parentheses.

Pairwise years	n	а	m_2	Ñ	Lower 95% confidence interval	Upper 95% confidence interval
2006-2008	54	75	0	5,907 (0.500)	1,163 (0.0250)	160,031 (0.975)

Table 8.2 Abundance estimates for humpback whales migrating past Plettenberg Bay/Knysna, South Africa using Chapman's estimator. n_1 = number of individuals captured on first occasion (year), n_2 = number of individuals captured on second occasion (year), m_2 = number of recaptures, \hat{N} =estimated abundance.

Pairwise years	n_I	n_2	m_2	Ñ (CV)	Lower 95% confidence interval	Upper 95% confidence interval
2006 -2007	54	24	1	687 (0.544)	433	1863
2007-2008	24	75	1	949 (0.547)	348	2590

Due to limited mark-recapture data for Plettenberg Bay/Knysna prior to 2006 (Table 3.1), only data between the years 2006 and 2008 were used to estimate the abundance of humpback whales migrating past this region (Table 8.1 & Table 8.2). Of the three pairwise abundance estimates, 2006-2008 contained the largest sample sizes but was the only pair of years to contain no recaptures. The resulting abundance estimate of

5907 individuals (95% CI 1,163; 160,031) was both the highest and least precise estimate. A p-value of 0.5 means that the expected population size has a 50% chance of being higher than the estimated population size \hat{N} . For the two pairwise estimates derived from the Chapman's estimator, which contained one recapture, their estimates were both considerably lower. Unfortunately, the extremely low precision in all of these estimates makes them uninformative but they are presented in the spirit of providing some new information for this region.

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