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Foreword

This thesis consists of five data chapters that were prepared in the format of manuscripts, with the intention of submission to scientific journals, as encouraged by this University. As such, each chapter is constructed as a unit although there may be some overlap between chapters, especially in the methodology. The chapter-specific abstracts and acknowledgements have been removed and included under the general Summary and Acknowledgements. While the majority of work is based on data collected during the core study periods in 2001-2003, it also incorporates data collected by others during other projects, especially in the case of identification photographs and biopsies; the same applies to historical catch data. These contributors are either co-authors on publications and manuscripts, cited, or acknowledged for their respective contributions. Some of the preliminary results have been included in (unpublished) reports at the Scientific Committee of the International Whaling Commission. Chapter 2 has been published in the *African Journal of Marine Science* (a copy is included in the Addendum), while Chapter 4 has been submitted to the same journal. It is the intention to submit the remaining chapters as papers in due course.

Specific mention should be made of the genetic results reported here, in that they form part of an ongoing regional collaboration examining population structure of Breeding Stock B (and other) humpback whales in the South Atlantic and Indian Oceans. The laboratory work and analyses specific to the processing of the genetic samples was done by two students, Christina Pomilla and Inês Carvalho, for their respective Ph.D. theses under the supervision of Dr Howard Rosenbaum at the Sackler Institute for Comparative Genomics, American Museum of Natural History. Therefore, the involvement of this candidate was limited to the collection of biopsies and the analyses of results after processing of samples, and to information specific to the sub-region, i.e. sex determined and microsatellite matches for the samples collected off west South Africa. All people involved in the genetic analyses are either acknowledged, or are co-authors on the relevant publications.

Acknowledgements

On the cover of one of my favourite Asterix & Obelix books, *Asterix and Cleopatra*, the authors listed all artistic and sundry materials used to create the… "Greatest adventure ever drawn" ….e.g. so many litres of ink, so many paint brushes, etc. I always thought that it would be quite cool to do the same for my thesis, once completed. Listing consumables would have been far too much trouble, but with so many things that can change over a period of nearly 11 years, my list could have looked something like this: used eight different Windows operating system, watched two rugby, three cricket, and three football World Cups, sat on a boat when September 11, 2001 happened, survived a scorpion sting, not to mention the litres of coffee, etc…. I no longer feel any need to compile such a list and it would be something of an understatement to say that I feel very relieved to be able to finally hand in this thesis. Such a piece of work would have been impossible without the contributions of a multitude of people and organisations, and this is something that I will attempt to capture. Some people contributed in more than one way, and so their names may be repeated.

My thanks go to my parents, for their support, thoughts and prayers, for always backing me in whatever I have attempted and for never being prescriptive about following any particular career direction. Thanks also to my two sisters, and the rest of my family (who are too numerous to name) for always showing interest in my (sometimes slow) progress. Special thanks go to the Barendse Family Trust for allowing me to live at our family home for substantial periods of time, although this did sometimes pose unique challenges!

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We are extremely indebted to the South African Navy for granting access to the lookout positions at Baviaansberg and Malgaskop, and allowing us to use a mooring at the Präsident Jetty, and Prof J. Malan and Col N. Slabber of the South African Military Academy for the provision of logistical help, including access to computer facilities and accommodation at Malgaskop. It was a privilege to stay at such a historic site, but also sad to see its dilapidated state in later years. Other members of the SAS Saldanha naval base that deserve special mention are: Capt E. Lochner (for supporting our presence at the base); C.P.O. Tony Cronjé and Sgt Maj Van Eeden (for help with setting up the lookout); Blackie Swart is thanked for tolerating us in ‘his’ Nature Reserve.

At the University of Pretoria, the Department of Zoology and Entomology, and the Mammal Research institute, several members of staff provided excellent support: Babsie Potgieter during the early stages of setting up, Ingrid Vis and Almarie Cronjé (administrative); Human Buirski (software and IT); Marthán Bester, my co-supervisor (special thanks for the loan when I really needed it); staff from the Academic Information Centre (Library) (especially Marié Theron) are thanked for help with obtaining references and providing online access to many journals. At the ‘Whale Unit’ fellow students often provided help and advice (apart from other contributions) which I gratefully acknowledge: Simon Elwen (GIS, mark-recapture); Ingrid Peters (for humpback data collected during her fieldwork, and MARK help); Caryn Berhmann (for help with SOCPROG and how to steer through the administrative challenges of handing-in while pregnant).

Without funding, a project such as this would be impossible. The fieldwork at Saldanha was supported by the National Research Foundation (NRF), South Africa (Grant number 2047517), and in 2002/03 also by the Earthwatch Institute, the Mazda Wildlife Fund (through the provision of a field vehicle), and SASOL (through the donation of two four-stroke engines). PADI Project AWARE (UK) provided funding for refurbishing the lookout, and fuel. I am grateful to the NRF, University of Pretoria, the Society for Marine Mammalogy, and the Wildlife Society of South Africa (Charles Astley Maberley Memorial bursary) for financial support. I received funding from the International Whaling Commission (IWC) to conduct between-region matching, and attend two Scientific Committee meetings.

The following organisations contributed in various ways: IZIKO (office space and computer network), the Naval Hydrographer (tidal data and bathymetry); Institute of Maritime Technology (hydrophone);

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A number of people were co-authors on publications, reports, or manuscripts in progress, or contributed information, comments or data: Cherry Alison (IWC) is thanked for provided catch-related data; members of the Sackler Institute for Comparative Genomics, American Museum of Natural History, Howard Rosenbaum, Christina Pomilla, Inês Carvalho (for responding to my many queries), Dr George Amato, Dr Rob DeSalle, Matt Leslie and Jacqueline Ay-Ling Loo are thanked for their various contributions relating to genetic analyses; permission from Howard Rosenbaum and Nick Gales to cite unpublished documents is much appreciated; Phil Clapham, Simon Elwen, Ken Findlay, Tim Collins, and two anonymous referees are thanked for helpful comments on early drafts or manuscripts; Mike Meÿer is thanked for contributing sighting data from a research cruise. The following photographers (from various affiliations) took pictures that are included in the catalogue: Simon Elwen; Peter Best; Blake Abernethy, Ingrid Peters, Desray Reeb, Shaun Dillon, Lisa Mansfield, Tilen Genov, Stephanie Plön, André du Randt, Darell Anders, Sharon du Plessis, and Rob Tarr. Namibian pictures (used in Chapter 4) were contributed by Simon Elwen, Ruth Leeney, Mike Lloyd, Ute von Ludwiger, Orlanda Sardinha and Francois Visser (Levo Tours).

Last, but not least, I have to thank my promoter Peter Best, for the role that he played. It would be incorrect to say that we got off on the wrong foot – it did however take a while for us to establish an efficient way of communication. It can be likened to a bottle of wine – something of an acquired taste, which mellows with age (I'll leave the metaphor at that…). In the end I came to appreciate his work ethics, his dedication to the field, his incredible knowledge on the subject, and (sometimes) wicked sense of humour. His contribution in finding historical data and sometimes obscure texts and records is especially acknowledged. I also thank him for his careful, thorough reading of draft chapters, a willingness to discuss any issues over the phone or in person, and for always making time to review changes. Finally, I thank him for supporting my involvement and attendance of the IWC Scientific Committee. I still do not share his enthusiasm for strandings though….

All work was carried out under successive annual permits issued to Peter Best by the Minister for Environmental Affairs and Tourism, in terms of Regulation 58 of the Marine Living Resources Act, 1998 (Act no. 18 of 1998).

Jaco-van-die-see (30 August 2011)

Summary

The migration of Southern Hemisphere humpback whales *Megaptera novaeangliae* between their feeding and breeding areas is considered a highly predictable and seasonal event. The west coast of Africa is host to Breeding Stock (BS) B, which has been divided into sub-stocks B1 and B2 based on different catch histories observed between Gabon in the north, and other stations to the south – a notion supported by recent regional genetic analysis, some samples of which were collected during this project. It has thus been assumed that the west coast of South Africa (WSA) functions as a migratory corridor for BS B2 whales. While catch data from Saldanha Bay in 1911-12 supported the existence of two migration peaks, a pilot study in the spring of 1993 (the first dedicated study in over 80 years) suggested a more atypical pattern, with some whales apparently abandoning or suspending their migration, possibly to feed. This has been complicated further by the detection of direct transits of 10 individual humpbacks through microsatellite matches between Gabon and WSA, and has raised questions about the exact function and relationship of WSA to BS B humpback whales.

This thesis presents the results from a study based at Saldanha Bay that included shore-based observations of whale groups during two field seasons (July – December 2001, May 2002 - February 2003), and photographic and genetic data collected during boat intercepts from 1983 to 2008. The observed relative abundance of humpback whales again did not support a classical migration pattern, with the highest sighting rates from mid-spring through summer. Movement patterns of humpback groups tracked by theodolite showed mid-spring to be a turning point in their behaviour, after which they swam significantly slower, showed an increase in ‘non-directional’ movement, and were found farther from shore. Data on group composition and sex showed a significantly female-biased sex ratio during mid-spring, unlike most low-latitude areas where males predominate. The individual identification of humpback whales by means of photographs of ventral tail flukes, left and right dorsal fins, and through microsatellites, yielded numerous resightings at intervals of a year or more, indicating a high level of fidelity to the region and temporary residency by some individuals. Population estimates were calculated using open and closed capture-recapture models and suggest that about 500 animals are present in the area during the spring/summer season.

Direct observation of humpback whales feeding on crustacean prey, short-term association patterns, and the resighting of individuals participating in feeding aggregations in multiple years confirmed this area to be a feeding ground for humpback whales during spring and summer months. Concurrent shore-based observations on southern right whales *Eubalaena australis* showed that this species was present virtually throughout the study period, also utilising feeding opportunities during summer. The potential benefit of this mid-latitude feeding area for humpback females is illustrated by a record of a cow that produced calves in three consecutive years, each of which survived to at least six months of age - the first observation of post-partum ovulation for this species in the Southern Hemisphere. The return of three known calves to the same area is strongly suggestive of maternally derived site fidelity.

General introduction

"Anyone who goes out whaling will make the discovery that whalermen talk most of the time about whales. I do not suggest that these hard-bitten Norwegian seamen ignore entirely such old seafaring topics as wine (or aquavit) and women. Far from it. But in their messrooms I also listen for hours to arguments about whales.

Only in recent years has mankind begun studying whales. The shooting goes on mercilessly, but the scientific investigation of whales and their habits has started. It is not easy to observe the different species of whales, however, and so there are many mysteries to be solved".

Lawrence Green – *Eight Bells at Salamander* (1960)

Migration is one of the life-history events in some animal species or groups that is sometimes highly visible, and can occur at an enormous geographical scale. Though the migration of numerous species have been widely documented and popularised e.g. wildebeest *Connochaetes taurinus mearnsi* in the Serengeti-Mara (Serneels & Lambin 2001) there remain very few places on earth where they still continue unhindered on a scale that resembles their historical extent. This is a result of direct eradication of migratory species, the development and expansion of human habitations and land-use, and importantly, the erection of political and physical barriers. As a result, the range and nature of many migrations have been disrupted, altered irreversibly, or completely obliterated through habitat fragmentation and destruction. Whilst this is especially true for terrestrial animals, some species such as migratory birds are less affected by physical obstruction, though the conditions at either end of their route may influence the migration (Wilcove & Wikelski 2008). In the world's oceans, although not outside the influence of human activities, animals may still continue their migrations in a more or less unhindered way, and some of these count among the longest vertebrate migrations known (Alerstam *et al.* 2003; Rasmussen *et al.* 2007; Stevick *et al.* 2011).

Annual migration is a well known life-history trait of baleen whales (Order Cetacea, Suborder Mysticeti). This is also the case for two species of mysticetes, the humpback whale *Megaptera novaeangliae* (Borowski, 1781) and the southern right whale *Eubalaena australis* (Desmoulins, 1822), their migratory patterns known through direct observation and trends in historical exploitation where the seasonality of catches of certain species at certain localities reflects different stages of the migration (Lockyer & Brown 1981). Individual recognition of whales provided more detailed information about the movement of individual whales; at first it depended on marking experiments (e.g. '*Discovery*' marks), however, the breakthrough in the study of whale movements came through the photography of unique naturally occurring marks (Katona & Whitehead 1981; Hammond *et al.* 1990), and then through advances in genetic methods that allowed individual identification through unique microsatellite DNA 'fingerprints' (Palsbøll *et al.* 1997). Most recently, the use of satellite telemetry has enable 'real-time' monitoring of the movements of individual whales (e.g. Mate *et al.* 1998). All these methods have provided much more detailed information about connectivity between polar feeding grounds and low latitude breeding areas, reinforcing the notion that the migrations of baleen whales are highly predictable events, and that certain species of whales show strong fidelity to the same feeding and breeding areas, and migratory routes (Lockyer & Brown 1981).

Humpback and southern right whales both frequent coastal waters in the Southern Hemisphere during parts of their migrations. The humpback whale has a global distribution and this, coupled with its use of near-shore habitats makes it the best studied of any baleen whale species, with detailed information available on its physiology, biology, reproductive cycle, and feeding and social ecology (Clapham 1996; Clapham & Mead 1999; Clapham 2000). Similarly, the southern right whale has been studied throughout much of its circumpolar range, especially at breeding areas, and its population dynamics well understood as a result of the availability of long-term data series (Payne 1986, Payne *et al.* 1990; Best 1990, 2000). Off the coast of South Africa, the predictability of their migrations and the near-shore distribution of these two species made them relatively accessible to humans from the earliest times: records in the personal journal of the first Governor of the Cape, Jan van Riebeeck, suggest that the indigenous people of the Cape Peninsula (the so-called 'Hottentots', more appropriately referred to as the *Khoi-khoi* or *Khoi-San*) were well acquainted with utilising beached whales. Once, in 1654, they were 'delayed' at a whale stranding and they [the *Khoi-khoi*] ... 'insisted on a feast for two days'. They were also seen burying whale meat in the sand as a method of storage and trying blubber to oil, storing it in the hollow stipes of kelp *Ecklonia maxima* to be used later for oiling their bodies, or to be consumed as food; this is further supported by the discovery of cetacean bones in archaeological excavations on stone-age middens near St Helena Bay (Goodwin 1952; Smith & Kinahan 1984). Later, during colonial times shore-based whaling became an established industry in South Africa (Thompson 1913) with right whales as the main target. These and other catches by American (also French and British) open-boat whalers (Townsend 1935; Best & Ross 1986) and those taken later on by modern whaling operations are relatively well known (Best 1994; Findlay 2000). Following heavy exploitation of both species, southern right whales were afforded full protection in 1935 and humpback whales in the Southern Hemisphere in 1963, although substantial illegal catches were made well after these years (Clapham *et al.* 2009; Tormosov *et al.* 1998). Despite this severe depletion, both these species have shown overall strong signs of recovery (Best 1993; Clapham *et al.* 1999) and are classified under the IUCN category of 'Least Concern' although the status of specific 'sub-stocks' may not be known (Reilly *et al.* 2008a, b).

While the status and recovery of southern right whales that breed in South African waters is well documented (Best *et al.* 2001) this is not entirely the case for humpback whales that use near-shore migratory routes on the west and east coasts. In the Southern Hemisphere the division of different populations of humpback whales and their associated feeding and breeding areas reflect the previously-assigned summer feeding regions or Areas numbered I to VI (Donovan 1991) and the more recently designated 'Breeding Stocks' (BS) A-G (and X) of the International Whaling Commission (IWC) (IWC 1998) (see Figure 1a). The summer feeding areas were by and large based on catch data and information gleaned from '*Discovery* tag' returns (Rayner 1940; Chittleborough 1965). More recently a number of photo identification studies (e.g. Gibbons *et al.* 2003; Garrique *et al.* 2002; Hauser *et al*. 2000; Stevick *et al.* 2004; Rasmussen *et al.* 2007), satellite telemetry (e.g. Zerbini *et al.* 2006) and in particular regional-scale genetic sampling and analysis of mitochondrial and nuclear DNA markers have shed further light on the degree of connectivity between breeding areas and to a lesser extent, the links between breeding and feeding areas (Pomilla & Rosenbaum 2005, 2006; Rosenbaum *et al.* 2009). Though some of these breeding-to-feeding ground links have gained further supporting evidence there are others that remain sketchy due principally to low research effort.

Humpback whales from two breeding stocks migrate through South African waters (Figure 1b): whales that belong to BS C (sub-stock C1) follow the east coast and over-winter off Mozambique, while BS B animals migrate along the west coast and breed somewhere near the equator, presumably off Angola and Gabon (but see later). The former stock was the subject of a shore-based study at Cape Vidal in 1988-1991 (Findlay 1994; Findlay & Best 1996a) and boat-based research in the Mozambique Channel (Findlay *et al.* 1994) and this has allowed the estimation of a population size (Findlay & Best 1996b; Findlay *et al.*, in press). In contrast, BS B is still being assessed as part of the 'Comprehensive Assessment' of the IWC Scientific Committee (IWC 2010) and there remains a number of unresolved issues regarding the possible population sub-structuring, as suggested by genetic analysis (Rosenbaum *et al.* 2009), and the validity of the current division into two breeding sub-stocks, B1 and B2. The humpback whales observed at localities on the west coast of South Africa have been assumed to represent migratory whales that belong to BS B2, although some recent observations of 'out-of-season' presence and non-migratory behaviour, and microsatellite matches between B1 and B2 (Carvalho *et al.* 2009) have brought this into question (Best *et al.* 1995; Findlay & Best 1995). This region is located in what is termed the 'Southern Benguela Ecoregion' based on prevailing oceanographic conditions, geological features, and observed biogeographical patterns (Kerry Sink, pers. comm.) and forms part of one of the world's major eastern boundary upwelling systems, the Benguela (Hutchings *et al.* 2009).

This thesis examines the occurrence of humpback whales off Saldanha Bay (33°02'S, 17°55'E) on the west coast of South Africa, using shore-based observations to elucidate seasonality in relative abundance and movement patterns, and boat-based intercepts to collect photographic and genetic data. By considering these contemporary observations together with historical catch data, it describes aspects of ecology, behaviour, seasonality, and attendance patterns of humpback whales in the region, relates them to information for humpback whales elsewhere on the African west coast, so adding to our current understanding of the structure of Breeding Stock B. Furthermore, concurrent shore based observations on southern right whales provide insight into the seasonality of occurrence and behaviour of this species off the west coast.

FIGURES

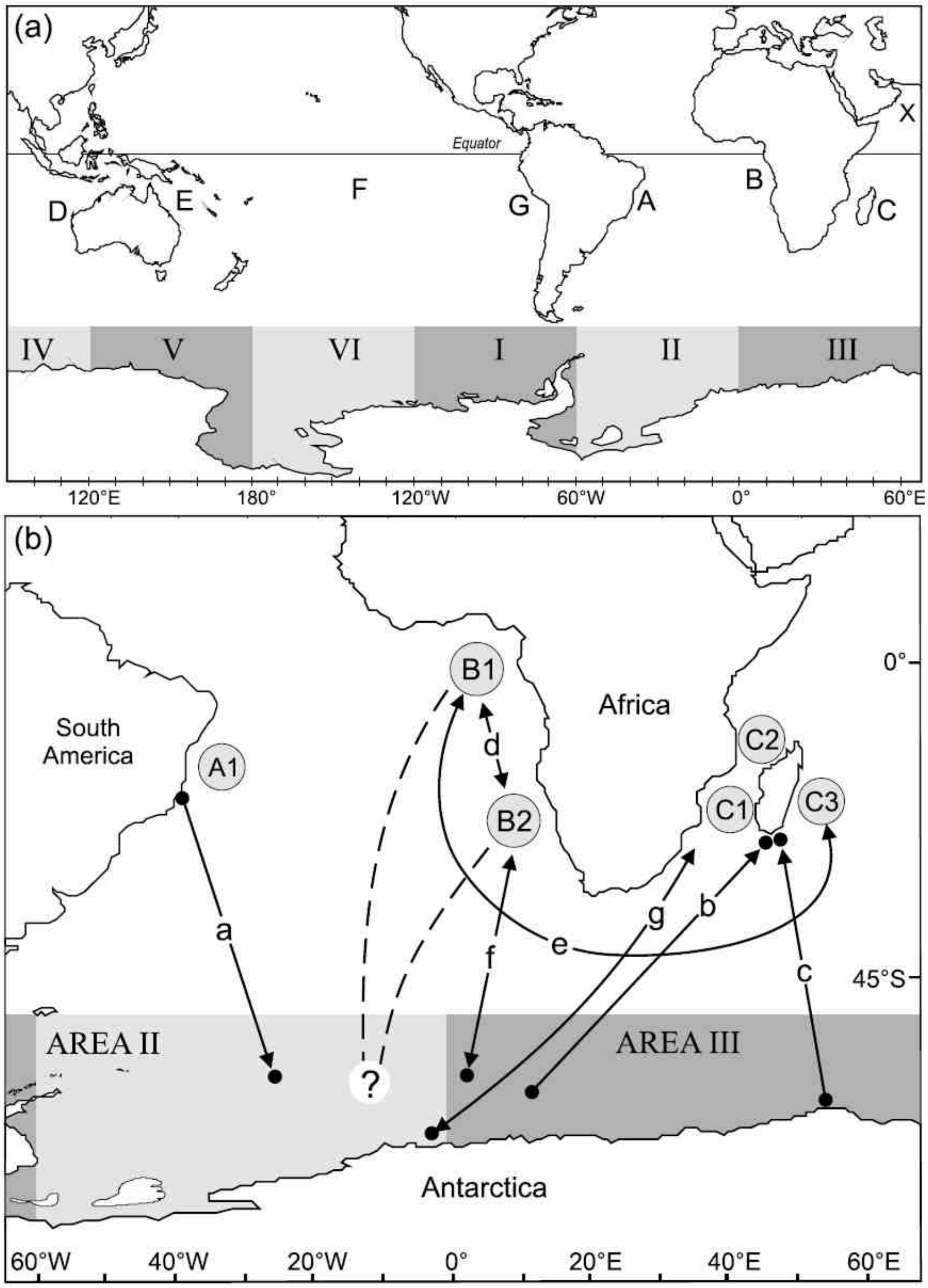

Figure 1. (a) Overview of management areas for humpback whales in the Southern Hemisphere as designated by the International Whaling Commission (IWC) (Donovan 1991; IWC 1998); Breeding stocks indicated by Arabic numerals A – G, and X, and Antarctic Feeding Areas indicated by Roman numerals I – VI; (b) Detail of Breeding Stocks (A1, B1 and 2, C1-C3) and Feeding Areas (II and III) of humpback whales in the south Atlantic and south-west Indian Oceans (IWC 1998). Solid lines indicate actual recorded links (a=satellite tags, Zerbini *et al.* 2006; b and c = *Discovery* tags, Rayner 1940; d, e, f and g = microsatellite matches, Pomilla & Rosenbaum 2005, Carvalho *et al.* 2009). Dashed lines indicate suspected but unconfirmed links.

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Chapter 1 - Patterns of availability and migrations of humpback whales off the west coast of South Africa: evidence from historical catches and observations [1]

“So I said: ‘With Mr Johansen, if it’s not too early for him. Please sir?’

‘Too early, Eyes?’ Thor Larsen was deeply shocked by an idea so unfamiliar. ‘In the hunting of the whale, Eyes, there’s no early or late. There’s the right moment and the wrong moment, not? So you take first watch with Johansen at right moment, not?’

Pleased with a distinction as subtle, almost metaphysical, as I ever heard him make, and still under the influence of his last drink, he laughed before leaving the bridge to smoke his cigarette out on the deck and pace and peer all around his ship, into the sky, and the sea in the dark.

The observation however stayed with me for two reasons. One was the way it had referred to whales in the singular. I had noticed it before. Thor Larsen hardly ever referred to whales in the plural. It was nearly always ‘the whale’, as if every whale we killed were a reincarnation of the ones that had gone before and however cold it lay lashed to the ship‘s side, it would be resurrected for him on our next chase again. The other, of course, was that time, in the normal sense, did not enter into his considerations at all: it was just another dimension wherein one was either right or wrong”.

Laurens van der Post - *The Hunter and the Whale* (1967)

INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) off the African west coast (IWC Breeding Stock B; IWC 2010) were subject to one of the most intensive episodes of commercial whaling ever, with an estimated 17,180 whales being landed in eight seasons from 1909 to 1916. Of these, an estimated 4,488 were taken off the former Congo (now Gabon), 10,109 off Angola, 1,299 off the south-western (Cape) coast of South Africa (WSA), and 1,284 off Namibia (see Best 1994; Best & Allison 2010). In comparison, after 1930 and up to the year of protection (1963) very few humpback whales were caught in the latter three regions: 160 off SW Cape, none off Namibia, and 726 in Angolan waters. Despite (or perhaps as a consequence of) these huge catches in the early years, little scientific information on this stock has ever been published.

Modern whaling on the west coast of South Africa started in 1909, with the operations of two small floating factories (*Vale* and *Svend Foyn*) in the Saldanha Bay region (Best & Ross 1989). From 1910 a land station started whaling at Donkergat in Saldanha Bay, and a second station (Salamander), 1 km to the northwest of Donkergat, in 1911 (Figure 1.1). In 1913 a third land station was opened at Hangklip, about 180 km to the southeast of Saldanha Bay. The only early attempt to investigate the biology of the species in this region was the account of Olsen (1914), who spent almost a year in South Africa in 1912/13, a large part of it at the Donkergat whaling station in Saldanha Bay. Apart from analyses of the whaling statistics themselves (e.g. Budker 1953; Budker & Collignon 1952; Harmer 1931), subsequent biological observations have been confined to the examination of a few humpback whales landed at Donkergat in 1926 (Matthews 1937) and 1962-63 (Best 1967). More recently, evidence of incidental summer sightings off the west coast (Findlay & Best 1995; Best *et al.* 1995) and indications of atypical migratory behaviour in a pilot study (Best *et al.*1995) led to the inception of a

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[1] This chapter contains some data and findings that were previously part of a paper by Barendse *et al.* (SC/54/H21) submitted to the IWC Scientific Committee. The help of Cherry Allison (IWC) with accessing historic catch and positional data is acknowledged.

substantial shore-based study off Saldanha from 2001-2003 (Chapter 2; Barendse *et al.* 2010). Whilst these observations provided unequivocal proof of a non-migratory summer presence of humpbacks in the Saldanha Bay area, it also raised a number of questions; amongst others, on the seasonal variation of the sex ratio (a strong female bias was found in mid-spring), and the possibility of an offshore migrational stream beyond the limit of visibility from land (Barendse *et al.* 2010).

Historical catch, effort, size composition and foetal data from the three whaling stations in the SW Cape, and from Olsen (1914) have been re-examined here as background to contemporary observations, of what are purported to be humpback whales belonging to Breeding Stock B2 (IWC 2010). Furthermore, we look at the offshore distribution of catches made by (mostly) modern whalers off WSA, based on positional data from all known sources.

MATERIAL AND METHODS

Seasonality of catches

The catches made from Saldanha Bay during 1911/1912 (from Olsen 1914) were summed for the two seasons and examined by 10-day period for each month (Figure 1.2). Furthermore, information on seasonality of occurrence, behaviour and/or biology of humpback whales relative to their geographical distribution, as described by Olsen (1914), is summarised in Table 1.1.

Individual catch data were available for the Donkergat, Hangklip and Salamander land stations for each year of operation between 1920 and 1930 (no stations operated in 1921, and only Donkergat and Salamander from 1922 to 1925). This period was chosen because it was one for which a reasonable amount of data was available, and because it pre-dated the introduction of any minimum length or seasonal catch restrictions, and so should be more representative of the population than most of the later catches. The catch data used were those in the records kept by Sir Sidney Harmer at the Natural History, London, except for 1930, for which data in the Cape Archives, the so-called PAN files (‘*Provinsiale Administrasie Natuurbewaring*’ in Afrikaans, translated as ‘Provincial Administration Nature Conservation’) were used.

Sizes of whales caught

Because there was at the time no internationally prescribed method of whale measurement, the lengths of whales given by the companies clearly need some confirmation. We have compared the lengths of four humpback whales (34 ft 6 in to 43 ft 5 in long) as reported by the whaling company at Donkergat in 1926, to the lengths of the same whales as measured by *Discovery* Investigations staff (Matthews 1937). The latter lengths were consistently smaller than those given by the company (0.941, 0.944, 0.96, 0.962, average 0.952). This was presumably because the company was measuring the overall length, whereas the *Discovery* Investigations staff measured from the tip of the snout to the notch in the tail flukes (subsequently adopted as the standard method). To make them more useful for biological analysis, lengths given by all the companies have been adjusted downwards by multiplying by 0.95. (Incidentally, the sexes and dates of capture agreed exactly in the two data sets, with the exception of a disagreement by one day in one of the dates, presumably because the earlier date refers to the capture and the later date to the processing of the whale).

Sex and reproductive biology

Sexually mature males and females were defined as those with adjusted lengths greater than 11.5 m (37 ft 8 in) and 12.0 m (39 ft 4 in) respectively (Lockyer 1984). (As a check on the appropriateness of the length adjustment factor, the two smallest pregnant females had adjusted lengths of 39.9 ft).

Foetal length data were compiled as follows:

Matthews (1937) - six dated foetuses from 1911-1912

Harmer records - 20 dated foetuses from 1920-1929

Best, pers. comm. - 1 dated record from 1962

The lengths of the near-term foetuses from the Harmer database were adjusted to the standard measurement by multiplying by 0.95 (see above).

CPUE

No attempt was made to develop catching effort data for the Hangklip whaling station, as it was considered to be geographically too divorced from the other two whaling stations to reflect relative abundance off Saldanha Bay. As an approximation of catching effort for the two Saldanha Bay whaling stations, the number of days that a catcher was in commission has been used. The dates of commissioning and de-commissioning each catcher were obtained from the Harmer records for the seasons 1922 to 1929. For Salamander in 1920, and for both Donkergat and Salamander in 1930, starting and finishing dates were taken as the days on which the first and last whales were shot, which, together with the numbers of catchers in operation each month, were obtained from the PAN files (see above). For Donkergat in 1920, starting and finishing dates for the fleet were obtained from Harmer's records, but the number of catchers in operation each month were assumed to be the same as in 1919 (obtained from the PAN files), as no direct data could be found.

Distribution and distance from shore of catches

Catch positions of humpback whales from the Saldanha Bay stations, taken anywhere between 28 and 36 degrees south and 20 degrees west and 20 degrees east, were examined to calculate the relative distance of their distribution from the shore. The resolution of positional data collected by whale catchers was generally poor, e.g. captured “within 100 miles radius of Saldanha Bay”, or by one degree grid squares; out of the 41 years of operation, catch positions in degrees and minutes were only available for 14 years. The source was official catch data submitted to the IWC, except for an additional two years (1960/61) that came from copies of Donkergat catch returns held by the Mammal Research Institute (MRI). There were also unreported/illegal Soviet catches in the area during five of the years, made by the *Slava* (1962) and the *Yury Dolgoruky* (1963-64; 1966-67) (Yablokov 1995; Yablokov & Zemsky 2000). The positions of some catches were given as magnetic bearings and distance (in nautical miles) from the station, and latitudes and longitudes calculated (Cherry Allison, IWC, pers. comm.); this was also the case for the 1960/61 data. For the latter the terminal coordinates were calculated using an online calculator[1] with the starting position taken as Donkergat, and the distance converted from nautical miles to km (1 nm = 1.852 km). The azimuth from the bearing was corrected for magnetic declination[2] of the relevant year and rounded to the nearest degree. All positions were plotted in a GIS. An equidistant sinusoidal projection was used, in order to preserve the accuracy of distances along parallels, and the distance to nearest (South African) shore calculated. Distances were rounded to the nearest kilometre, given the low resolution of the original data, the variability of calculations depending on the coordinate system and/or projection used, and the wide range of values.

The only other known sources of catch positions in the specified area were the logbook extracts of 19th century American whaling vessels as compiled by Townsend (1935).

RESULTS

Catch data

CPUE, size and reproductive biology

The raw catch data per 10-day period for 1911 and 1912 combined (Figure 1.2) indicate a very low abundance of humpback whales in March, April and most of May, rising to a peak from late June to early August, and then declining again to a low point in early September. A second peak seems to occur from early October to early December. Without detailed information on catching effort, however, it is difficult to interpret such trends in catches, although this data set is particularly valuable because it more or less represents the peak of the fishery for the species, so that negligible inter-specific effects on the catch are predicted.

The monthly CPUE series for 1920-1930 (Figure 1.3) also indicates that humpback whale abundance was very low in April and May, but rose thereafter to a peak in July, similar to that seen in 1911-12. Abundance then declined again, to a low in early October, before rising to a second peak in November/December, which (although highly variable) seemed to be of the same order as that in July. Whaling clearly stopped before this latter peak had been completed (presumably because the catcher boats had commitments for the Antarctic summer season).

The overall sex ratio in the catch (94 males, 101 females) was not significantly different from parity ($X^2 = 0.25$, $p > 0.5$, df = 1); nor was the sex ratio for sexually immature (48 males, 38 females; $X^2 = 1.16$, $p > 0.25$) or mature animals (46 males, 63 females; $X^2 = 2.65$, $p > 0.10$).

Females carrying near-term foetuses (with adjusted lengths of 12.35 to 16.15 ft, and a mean of 13.62 ft ± 0.21 SE, $n = 19$) were all recorded between 2 July and 25 August, with a mean date of 25 July ± 4 days (Figure 1.4). Females carrying small foetuses (0.19 - 1.17 ft, with a mean length of 0.53 ft ± 0.13 SE, $n = 8$) were all recorded between 10 October and 25 November (mean date 1 November ± 5

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[1] http://www.fcc.gov/mb/audio/bickel/sprong.html
[2] http://www.ngdc.noaa.gov/geomagmodels/struts/calcDeclination

days): due to the timing of the closing of the season, however, it is likely that this mean is under-estimated.

Omitting data from Hangklip, where reporting of foetuses was clearly less efficient than at the other two stations, the pregnancy rate of the mature females from April to August can be calculated as 17/44 or 0.386 ± 0.07 (SE). It is assumed that most near-term foetuses at this time of year would have been discovered, though not necessarily reported. On the other hand, many of the small foetuses from October to December were probably never even discovered, which is why no attempt has been made to include them in the estimation of pregnancy rate.

On 27 June 1923, a 43.7 ft female and a 24.7 ft male (both adjusted lengths) were landed at Donkergat, and in Harmer's records an annotation against the female says "acc[ompanie]d by the preceding, 26'0" ' (7.92 m, uncorrected length). There were no international restrictions on taking lactating females and their calves at that time, and on two other occasions, a mature female and a much smaller animal were taken by the same catcher on the same day. On 30 May 1928 a 42.75 ft female and a 28.5 ft male and on 26 July 1927 a 47.5 ft female and a 28.5 ft female were landed (both at Salamander). These may also represent instances where cows and yearling calves were taken on their way north.

Seasonality

Seasonal changes in availability were accompanied by changes in the proportions of mature animals in the catch (Figure 1.5). Sexually immature animals of both sexes predominated from April to June, forming about 70% of the catch, but in July and August the proportions switched so that mature animals of both sexes formed about 70% of the catch. In September/October the catch was again dominated (65-80%) by immature animals, but by November/December mature animals of both sexes again constituted 70% of the catch. When both mature and immature animals were included, the overall male to female sex ratio did not deviate significantly from parity for any of the season, except November/December when catches showed a female bias (12 males, 24 females, $X^2 = 4$, $p < 0.045501$). This bias was maintained when immature animals were omitted (8 males, 18 females, $X^2 = 3.846$, $p < 0.049861$).

Distribution and distance of catches from shore

A total of 71 catch positions were obtained for humpbacks landed at Donkergat, 14 from Soviet vessels, and two from Townsend's (1935) records (Table 1.2); their localities are shown in Figure 1.6. The Donkergat catches were fairly evenly distributed from 5 km from the shore to about 170 km, with only three taken farther than 200 km (Figures 1.6 and 1.7). This almost certainly represents the effective limit to the range of the shore-based catchers. All Soviet catches were highly pelagic, and with the exception of four, were all located at distances greater than 1,000 km from the coast, and presumably taken during north-south transit to the Southern Ocean at the start of the summer whaling season (Figures 1.6 and 1.7). The single humpback caught by the *Emerald* (Table 1.2) was located in the vicinity of the southernmost Soviet catches, while the one caught by the *Fairy* was located 6 degrees west of this (Figure 1.6).

The majority of catches landed at Donkergat were in winter (Table 1.3), while all Soviet catches were taken in November (13) and December (1). For the Donkergat catches those in June and July (mid-winter) were the farthest from shore (Table 1.3). The two whales caught by the two American vessels were taken in November 1835 and January 1846.

DISCUSSION

Prior to the most recent observations (Chapter 2; Barendse *et al.* 2010), the CPUE data from the commercial whaling out of Saldanha Bay in the 1920s were the best indication we have of seasonal trends in the availability of humpback whales on the west coast of South Africa, although they are naturally limited by (a) the length of the whaling season and (b) the possible confounding effects of effort spent on other species. The data are strongly suggestive of a bimodal peak in abundance, with the two peaks 4-5 months apart (ignoring the possibly incomplete nature of the second peak). Each peak is correlated with an apparent influx of sexually mature animals of both sexes into the population, suggesting that they represent waves of migration.

Such bimodality in occurrence might be expected, given that Harmer (1931) found catches off Angola to be bimodal (July and October) and those off Gabon to be unimodal (July/August). However Harmer claimed that catches off the west coast of South Africa were too small to allow any generalisations to be made, and he inferred that the major migrations of humpback whales in this region touched the coast "at some point N of Cape Town" (see later). Olsen (1914), on the other hand, referred to two clear maxima in the 1911 catch at Donkergat, one at the end of June and the other at the end of October. These he equated with the northern and southern migrations, respectively, and the foetal length data given here would support that assumption (though not necessarily the timing), if birth and conception are assumed to occur north of Saldanha Bay. Despite this, he too stated that although some humpbacks clearly followed the coast during migration, the majority joined the coast north of Saldanha Bay, making use of more offshore routes (Olsen 1914). This would seem especially so for the northward migration, when Donkergat catches were farthest from shore – a pattern also seen for sei whales in the same whaling ground (Best & Lockyer 2002).

Although sample sizes from the commercial catch are small, and the spring migration does not seem to have been fully sampled, there is no sign in the 1920-1930 catch data of the male-biased sex ratio recorded by Brown *et al*. (1995) from biopsy sampling of the migrations off Eastern Australia. It is however, interesting to compare the significant female bias (both when including or excluding immature animals) in November/December with a similar bias found more recently off Saldanha in mid-spring (October), and also mid- to late summer (January/February, calves excluded) from the biopsy samples (also see Chapters 2 and 5; Barendse *et al.* 2010). It should however be noted that these summer catches were virtually all made in the same year, 1920 (Harmer 1931).

Although not very precise, the apparent pregnancy rate recorded here (0.386 ± 0.07) is similar to pregnancy rates (0.37 - 0.39) reported from other whaling data and values for ‘calves per mature female’ (0.37 - 0.41) from long-term photo-identification studies of humpback whales (Clapham 2000). Nevertheless, given that the data in this paper were collected without any biological supervision, the chances that some foetuses were not reported are high, so that this should be considered as a likely under-estimate of the real pregnancy rate.

The record of at least one cow still accompanied by a large calf in the autumn agrees with Olsen's (1914) observation that some northward-moving humpbacks are accompanied by the calf from last year. Although Baraff and Weinrich (1993) report instances of mother-calf separation on the feeding grounds in the autumn of their birth year, Clapham (2000) records 6 out of 107 calves on the Gulf of Maine feeding grounds that remained with their mothers for two years. Risting (1928) lists seven instances from the 1913 season at the Hangklip whaling station of adult females accompanied by "young ones" between 23 and 29 feet (average 27.1 ft) in length, but these were all were recorded between 21 October and 19 November, and so presumably moving south. One of these females (with a 29 ft calf) was also stated to be pregnant with a 5 in foetus, from which Risting concluded that the female had conceived in successive years. However, even if the lengths were 5% overstated (see above), the calf would have been too big to be a calf-of-the-year, and it is more likely that these were offspring on their second spring migration (i.e. at an age of about 14-15 months, if birth occurred in August). These observations are partially consistent with observations at Saldanha in 2001-2003 when a peak in cow-calf pairs was seen in November, and many of these were large enough to possibly be yearlings or second-year animals (Chapter 2; Barendse *et al.* 2010). An examination of photo identification data from the region provides more insight into calving intervals and accompaniment by calves from previous years (see Chapter 5).

The available positional data, though not representative of the peak of commercial whaling on this species off the west coast, does provide some indication of the offshore distribution of humpbacks in the region. Virtually all the Donkergat catches were located in a fan-shaped area of about 100 km radius and 45^{O} extent, originating from the entrance to Saldanha Bay, presumably representing the extent of the whaling ground for other species. While the extreme inshore (<20 km) zone is probably underrepresented by this pattern of catching, the plot does indicate that humpbacks were available well offshore and out of sight from land. More importantly, it indicates that there were humpbacks present in numbers in June/July at the same latitude (33^{O}S), but at very different longitudes to Saldanha Bay, at a time where sighting rates in the shore-based study were at their lowest (<1 group every 10 hours) (Barendse *et al.* 2010). The low relative abundance and predominantly southward directionality at this time of year did not provide support for the presence of a northward migrational peak near the shore. The catches closer to the coast (both in terms of minima and mean distances) during August, September and October partly correspond to observations described in Chapter 2 in that humpbacks were seen farther away from shore during August/October. The cessation of the whaling season in late spring (presumably for operational reasons as the same catchers had to be deployed in the Antarctic) precludes comparison of the summer seasonality of Donkergat catches with the recent observations, but here the Soviet catches that all (but one) occurred in November, provide evidence for humpbacks occurring about halfway between South Africa and the island of Tristan da Cunha. Also worth mentioning are sightings of humpback whales made by the Ship *Jones* at 36^{O}38’S, 5^{O}00’W and 37^{O}27’S, 8^{O}40’W on 25 and 30 October 1831 respectively (Best 2008), and two recent humpback sightings in November 1985 and January 1990 around the Tristan da Cunha archipelago

(Best *et al.* 2009); all these sightings occurred at times of the year when the whales should have left the coasts of Gabon and Angola, busy with their southern migration. While November sighting rates at Saldanha were lower than those in the preceding and following months, it seems unlikely that whales located between 0^{O} and 10^{O} E would head directly east to reach the coast during December. Townsend's (1935) record of 21 humpbacks taken between 1 October and 30 November 1852 by the bark *F. Bunchinia* in the vicinity of Walvis Bay and Sandwich Harbour, some 400 km north of Lüderitz, compared to the location of the two caught near the Greenwich meridian (one in November 1935) again suggest that humpbacks were present along the coast and on offshore migration routes during the same season.

CONCLUSION

The historical data presented here are too scant to provide a complete picture of seasonal distribution of southern hemisphere humpback whales off the West African coast. However, when considered in conjunction with the evidence from catch histories, such as the low overall catches and no obvious recovery at Saldanha, compared to the breeding ground in Gabon (Best & Allison 2010), a near-shore migration of all whales present in the breeding areas is not supported. Although recent photo-identification and microsatellite matches (Chapter 4; Carvalho *et al.* 2009) confirm that some whales migrate directly from Gabon to an inshore feeding ground on the west coast of South Africa in late spring/summer, simultaneous pelagic catches in the South Atlantic 750–1,400 km offshore at the same latitude indicate that others must take a more direct route to their Southern Ocean feeding grounds (an assumption confirmed by recent satellite-tagging results; Rosenbaum & Mate, submitted manuscript). The latter route would have placed whales well outside the catching range of coastal operations in the SW Cape and Namibia, and in some cases Angola, and if the same whales habitually followed this route in both directions they would have been subjected to much less exploitation pressure than coastal migrators. The observed abundance peaks of humpback inshore at Saldanha Bay therefore do not necessarily indicate migration peaks, and given the female bias in sex ratio detected here (Barendse *et al.* 2010) suggest maternally directed attendance to this region, a hypothesis supported by direct evidence of calves returning to the feeding ground in years subsequent to that of their birth (Chapter 5). Whether the use of migration routes much farther offshore is determined by the same mechanism would be difficult to determine.

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TABLES

Table 1.1. Summarised seasonality, biology and behaviour of humpback whales during their migration along the African west coast, based on observations by Olsen (1914). Refer to Figure 1.1 for localities of whaling stations.

Locality	Biological information	Timing	Behaviour
Saldanha, west South Africa	'Pairs', singles and small groups	End of May	Going north
'Portuguese West Africa' (Angola)	Pregnant cows and others	Appear at beginning of June, most mid-July	Going north
Porto Alexandre (Benguela)	'Pairs', and sometimes cows with newborns	From end of June, beginning July.	Moving north
	Cows with newborns	August, beginning September	Moving north
	Cows with calves	End of September through October. Finished by start of November	1st southward movements
	Cows with no calves	October	Mating
Saldanha	Pregnant cows (small foetus)	November	Going south

Table 1.2. Summary of positional data from various sources, and calculated distances to the South African shore, of all known humpback catch positions in the southeast Atlantic taken between 28 and 36 degrees south and 20 degrees west and 20 degrees east.

Catch information	*n*	Years (and number of catch positions)	Distance range	Mean (median)	Source
Donkergat landings	71	1949 (15), 1950 (7), 1951(9), 1953 (9), 1957 (3), 1958 (2), 1959 (7), 1960 (3), 1961 (4), 1962 (9), 1963 (3)	5 – 236 km	103 (111) km	IWC/MRI
Soviet catches	14	1962 (2), 1963 (1), 1964 (1), 1966 (7), 1967 (3)	756 – 1357 km	1127 (1231) km	IWC
19th century American ships *Emerald* and *Fairy*	2	1835 (1), 1846 (1)	1355 / 1856 km	-	Townsend

Table 1.3. Seasonal variation in distances from shore of humpback catches with known positions off the west coast of South Africa. [* note that all these were pelagic catches taken by Soviet vessels].

Month	Mean distance (km) ± SE	*n*	Minimum distance (km)	Maximum distance (km)
May	79 ±18	5	20	126
Jun.	114 ± 8	16	30	164
Jul.	122 ± 11	30	9	236
Aug.	83 ± 16	10	6	164
Sept.	50 ± 22	5	5	131
Oct.	73 ± 26	5	8	159
Nov./Dec.*	1127 ± 56	14	756	1357

FIGURES

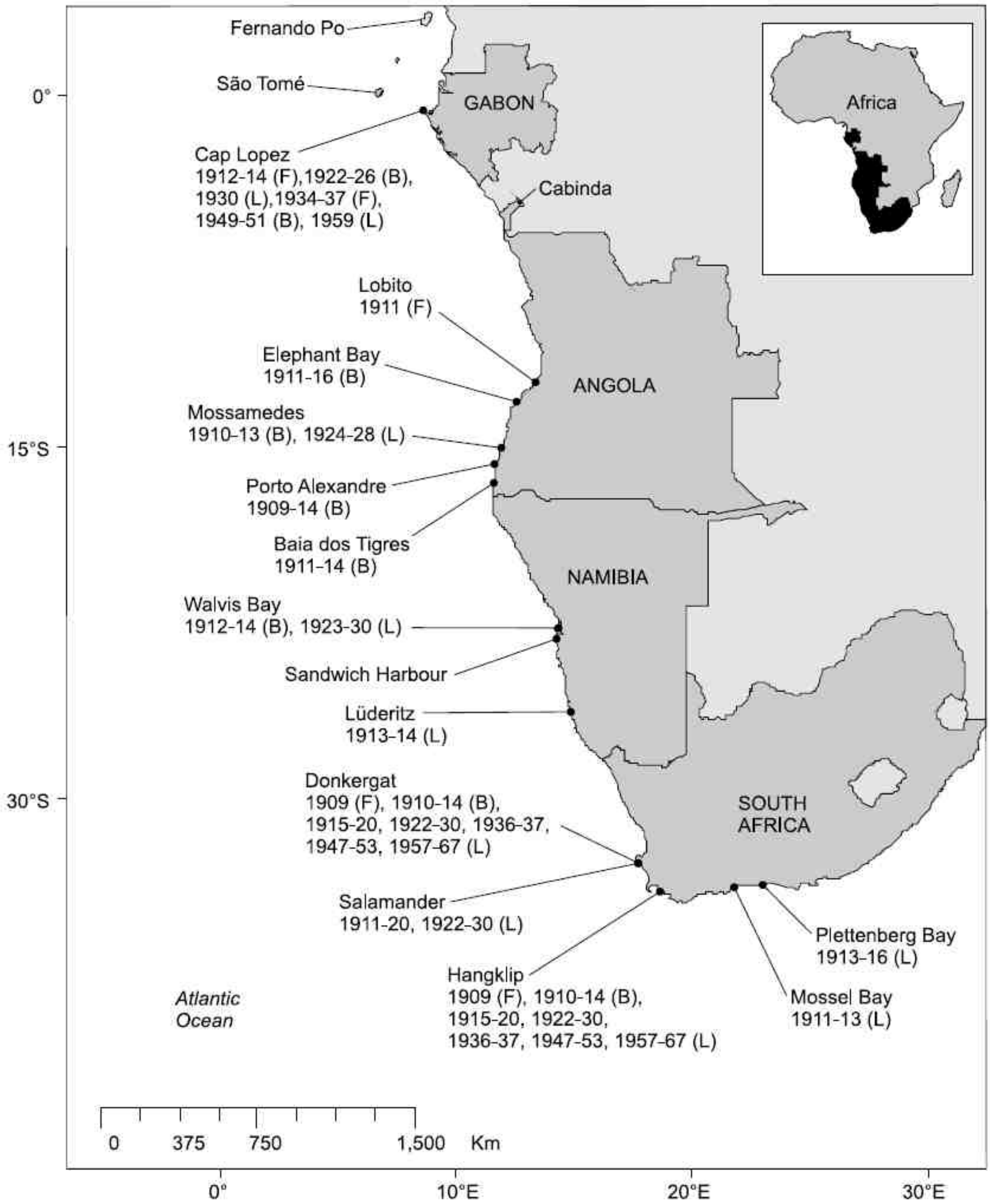

Figure 1.1. Locality of coastal whaling stations and years in operation, along the west coast of Africa (and south coast of South Africa), south of the equator (after Best 1994). (L = land-based, F = floating, B = both).

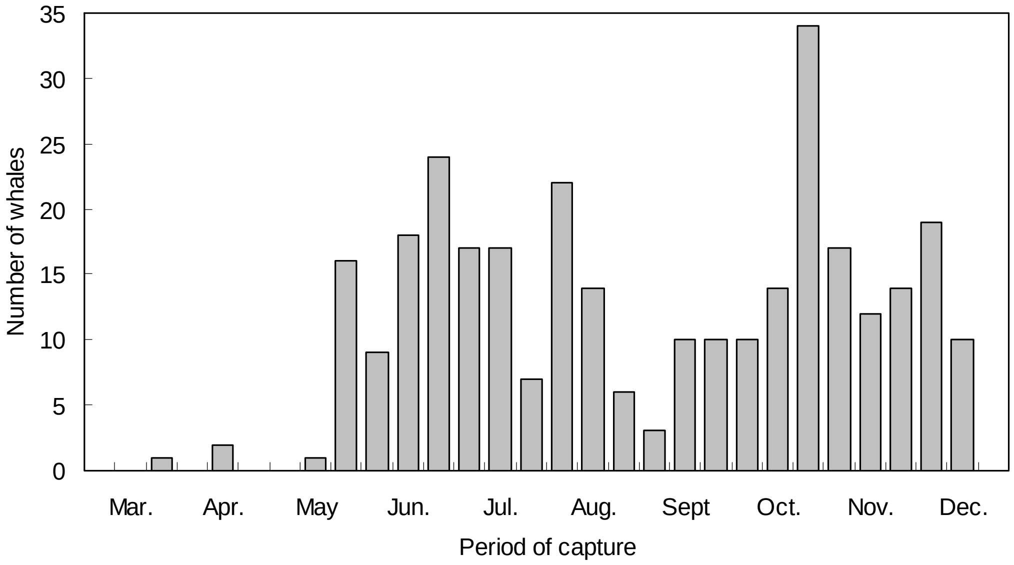

Figure 1.2. Summed catches of humpback whales per 10-day period, Donkergat, 1911-12 (from Olsen, 1914).

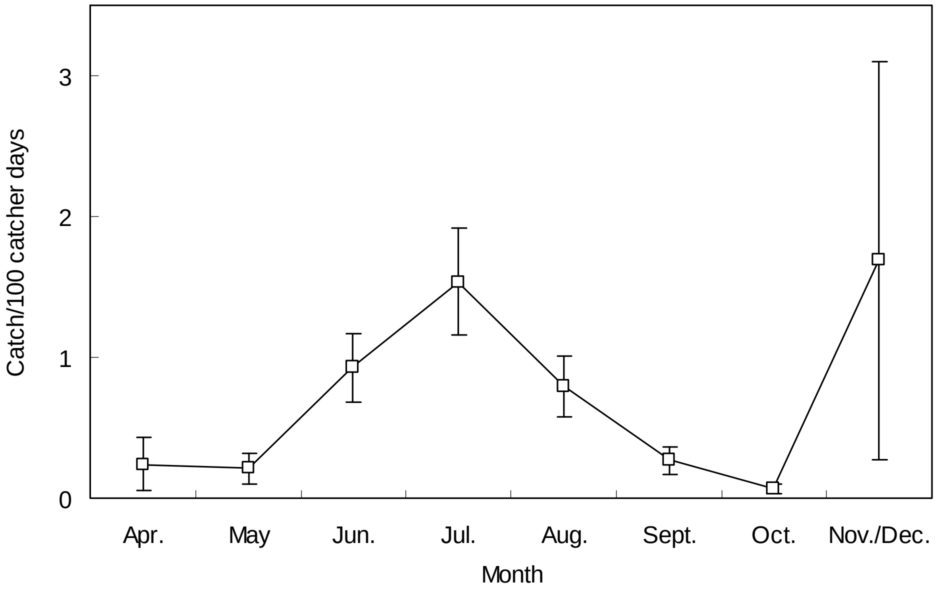

Figure 1.3. Monthly CPUE values (± SE) for humpback whales off Saldanha Bay, 1920-1930.

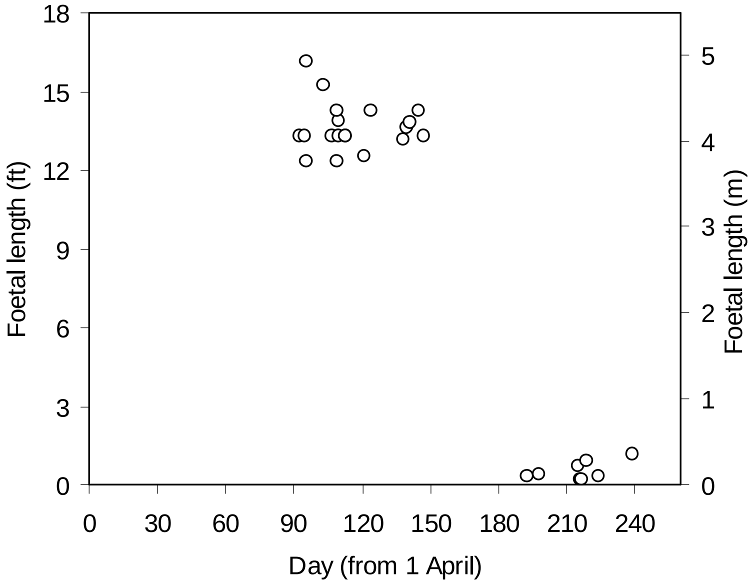

Figure 1.4. Lengths (in m and ft) of humpback whale foetuses, west coast of South Africa, plotted against date of capture of mother.

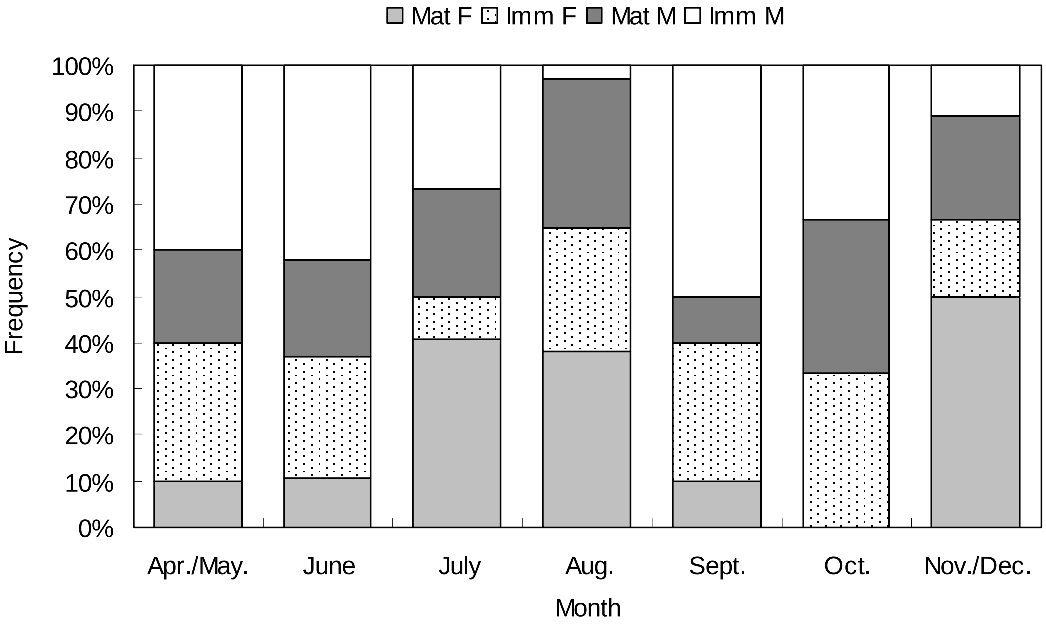

Figure 1.5. Monthly composition of humpback whale catch by sex (M=male, F=female) and maturity status (Imm = immature, Mat = mature), at Donkergat and Salamander, 1920-1930.

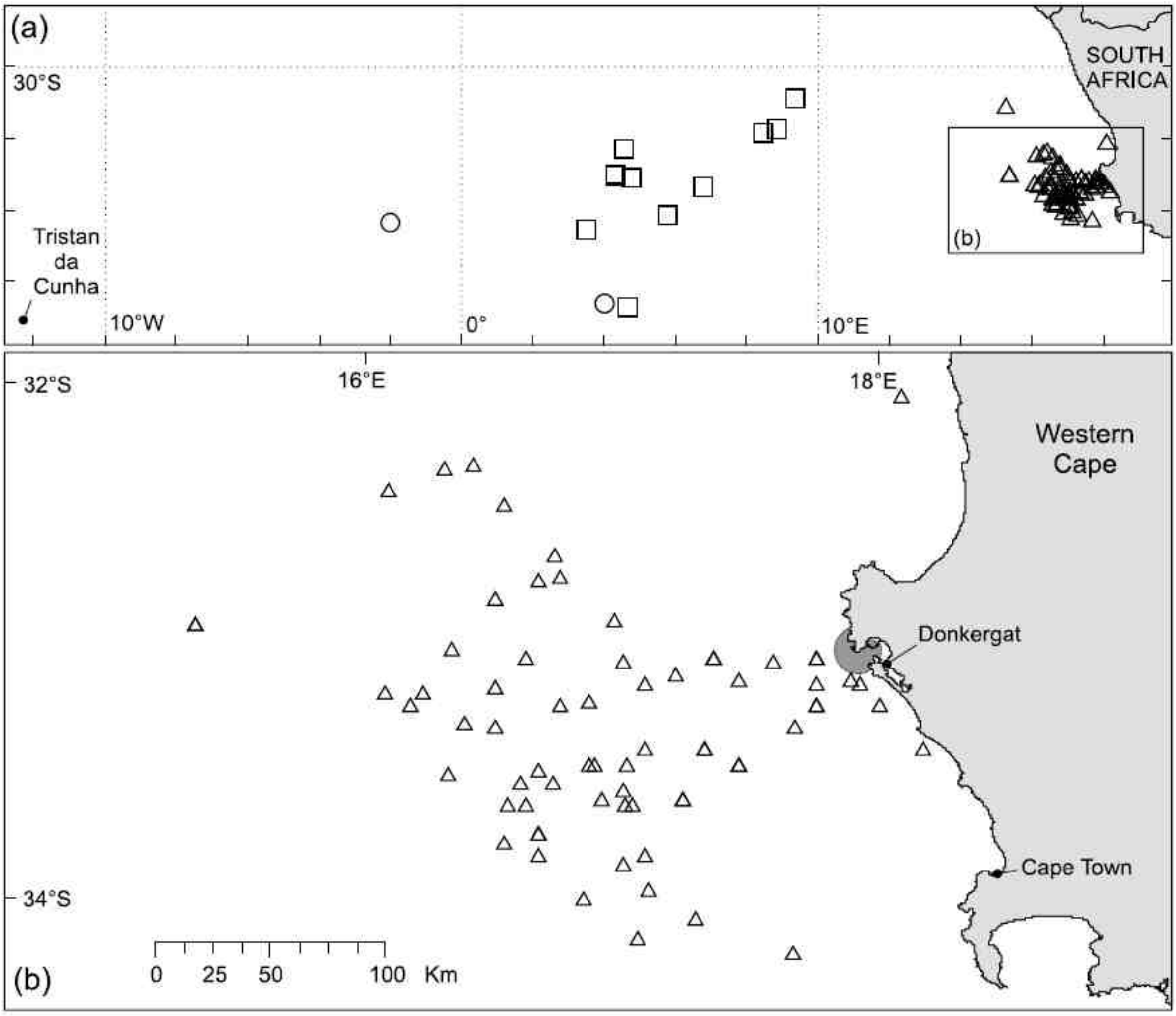

Figure 1.6. (a) Catch positions (*n* = 87) of humpback whales landed at Saldanha Bay (shown by triangles) 1949 - 1967, or taken illegally by Soviet vessels (squares), where accurate positional data were available. Also shown are positions of two whales taken by American whalers (circles) from Townsend (1935). Detail of all legal catches in the vicinity of Saldanha Bay is shown in (b), and darker shaded area shows the extent (±20 km radius) of the visible area for shore-based observations from North Head, Saldanha Bay (reported in Chapter 2; Barendse *et al.* 2010).

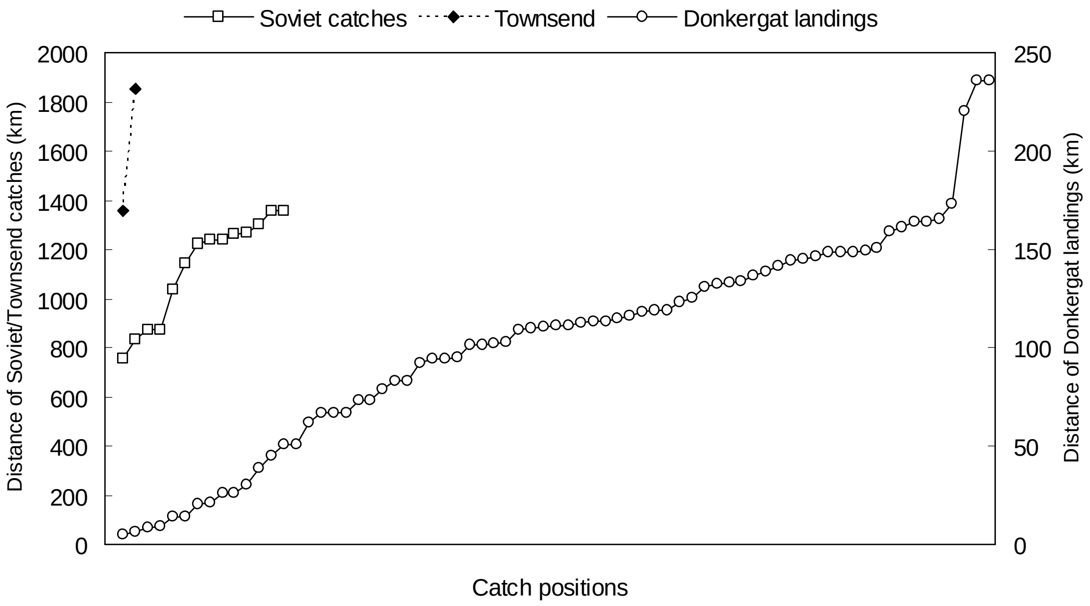

Figure 1.7. Frequency distribution of nearest distance (in km) between 87 catch positions and the South African coastline, of humpback whales taken and landed at Donkergat, or taken illegally by Soviet vessels, between 1949 and 1967 (see Figure 1.6). The two humpbacks taken by American vessels in the 1800's (reported in Townsend 1935) are also included.

Chapter 2 - Migration redefined? Seasonality, movements, and group composition of humpback whales *Megaptera novaeangliae* off the west coast of South Africa[1]

"The colour of the water, as seen at some distance, was like that of a river which has flowed through a red clay district; but under the shade of the vessel's side it was quite as dark as chocolate. The line where the red and blue water joined was distinctly defined. The weather for some days previously had been calm, and the ocean abounded, to an unusual degree with living creatures…"

"…In the sea around Tierra del Fuego, and at no great distance from land, I have seen narrow lines of water of a bright red colour, from the number of crustacean, which somewhat resemble in form large prawns. The sealers call them whale-food. Whether whales feed on them I do not know; but terns, cormorants, and immense herds of great unwieldy seals derive, in some parts of the coast, their chief sustenance from these swimming crabs".

Charles Darwin - *The Voyage of the Beagle*

INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) in general are believed to undertake extensive and predictable migrations from polar feeding grounds in summer, to tropical over-wintering areas, displaying high fidelity to the same breeding and feeding areas (Clapham *et al.* 1993, Clapham 2000, Stevick *et al.* 2003; Rasmussen *et al.* 2007). These migrations frequently follow near-shore migration corridors in the Southern Hemisphere (Dawbin 1966; Bryden 1985). Although behaviour associated with reproduction e.g. male-male competition (Brown & Corkeron 1995) and singing (Clapham & Mattila 1990) is often observed during migration, feeding behaviour during transit is only seen occasionally, and very rarely in the Southern Hemisphere (Best *et al.* 1995; Stockin & Burgess 2005; Stamation *et al.* 2007). The bulk of feeding is thought to occur in the areas of high productivity at high latitudes where the whales spend their summers (Clapham & Mead 1999) with the exception of the unique Arabian Sea population (Breeding Stock X, see Figure 1a in General Introduction) that is apparently resident year-round (Mikhalev 1997; Minton *et al.* in press; Rosenbaum *et al.* 2009).

The division of different populations of humpback whales in the Southern Hemisphere reflects their associated feeding and breeding areas and has been based on their previously-assigned summer feeding regions or Antarctic Areas numbered I to VI (Donovan 1991) and the more recently designated Breeding Stocks labelled A-G (see Figure 1a and IWC, 1998). Whales from Breeding Stock B (BSB) found off western Africa are thought to feed in Areas II (60^{O}W to 0^{O}) and III (0^{O} to 70^{O}E). In some Breeding Stocks there has been some evidence for sub-structuring of stocks based by-and-large on ongoing mitochondrial DNA analyses (e.g. Rosenbaum *et al.* 2009). In the case of BSB the stock has been separated into B1 and B2 (IWC 2001) with the former located in the Gulf of Guinea (north of 18^{O}S) while the humpback whales that migrate past the west coast of South Africa are presumably part of B2, found south of 18^{O}S (see IWC [in press] for details of most recent BS sub-divisions).

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Historical catches from shore-based whaling stations in the Saldanha Bay region have hinted that the whales here conform more or less to a classic migration pattern with two distinct seasonal peaks of abundance thought to correlate with the northward (July/August) and southward (October/November) migrations (see Chapter 1; Harmer 1931; Olsen 1914). On the other hand, Olsen (1914) based on his observations from 1911-1913 did comment that the whaling season at Saldanha was relatively long, lasting till mid-December. More recent and mounting evidence has added further support that this area does not function as a typical migration corridor, and that there may be other contributory factors that influence the timing and duration of visits of humpback whales to this region (Best *et al.* 1995; Findlay & Best 1995).

This study was mounted to examine trends in humpback whale relative abundance, occurrence, and movement across seasons in the Saldanha Bay region, based mainly on shore-based observations. As such it represents the most extensive research effort to date on the species in the region, and, apart from a 6-week long pilot study in 1993 (Best *et al.* 1995), the first since the Discovery Investigations of the 1920s (Matthews 1938). Furthermore, data on group composition were obtained from the most comprehensive genetic collection available for the region, collected during boat intercepts of humpbacks between 1993 and 2008.

MATERIAL AND METHODS

Description of study area and study period

The study was carried out from North Head, Saldanha Bay (33^{O}02'S, 17^{O}55'E) located on the west coast of South Africa, approximately 100 km north of Cape Town (Figure 2.1). This is some 30 km south of Cape Columbine, the western-most headland in the Western Cape Province of South Africa, and the site of an earlier pilot study (Best *et al.* 1995). The region has a Mediterranean-type climate (Kruger 2004) with an average rainfall of 298 mm per annum recorded mostly during winter (Zucchini *et al.* 2003; Zucchini & Nenadić 2006). The wind blows from a predominantly southerly direction in summer and westerly in winter. Saldanha Bay was the site of two modern whaling stations, Donkergat and Salamander, which operated sporadically between 1909 and 1967 (Best 1994; Findlay 2000).

The highly exposed coastline has an approximate north-westerly/south-easterly orientation (330 - 150 degrees true) and is characterised by a rocky shore broken by a number of small bays with sandy or boulder beaches, and a few small near-shore islands and rocks. The tidal cycle is semidiurnal with an average tidal range of about 1.2 m. The bathymetry of the area is shown in Figure 2.1.

In an attempt to gather data across all seasons, a shore-based watch was kept from North Head during two periods of fieldwork: the first for five months from 24 July to 20 December 2001, and the second for nine months from 6 May 2002 to 15 February 2003. See below for seasonal division of sampling effort.

Observations of environmental and sighting conditions

A number of environmental observations were made at the lookout every hour in order to asses the sighting (searching and tracking) conditions, and the following variables recorded:

a) Surface wind speed (in knots) and direction (magnetic bearing): Measured with a handheld anemometer (analogue at first and digital from 25 August 2001 onward) and compass.
b) Cloud cover: Expressed as a fraction of eight (0/8 = no cloud, 8/8 = complete cover) over observation area only (i.e. over the sea).
c) Sea-state: Judged according to the Beaufort scale over the entire observation area.
d) Glare: Magnetic bearing and estimated extent of reflection of sun off the water, expressed as percentage of total search area affected.
e) Swell: Estimated by judging the height of the average swell rising against a rocky islet (Schooner Rock) with a known height of 9 m above sea level (a.s.l.).
f) Visibility at the midline: The midline was set perpendicular to the coastline, at a bearing of 240 degrees True from the lookout. The visibility at this line was the radial distance from the tower to the fix, calculated from the maximum vertical angle at which individual wavelets could clearly be distinguished through the theodolite eyepiece. This distance was assumed to be equivalent to the distance at which a whale could still be accurately tracked. This measurement was not made when the theodolite was being used for tracking whales.
g) Sightability: A subjective index on a scale from 1-5 (1 = very poor, 5 = very good) that summarised how good overall conditions were for spotting whales, and taking into account factors (a) to (f) above.

Search effort was classified into one of three categories, based on prevailing sighting and weather conditions:

a) Optimal watch: Full search effort during suitable conditions over the entire search area, with at least one person searching with binoculars and another with naked eye.
b) Sub-optimal watch: Equivalent to whale vessel surveys where masthead watch discontinued. Conditions were considered sub-optimal at average wind speeds >20 knots for extended periods, Beaufort sea-states of 5 or more, or when more than one half of the search area was obscured by mist or clouds. In practice this was when the sightablity was estimated to be 2 or less (poor to very poor). During sub-optimal watch, searching would be carried out as described above, but sightings would only really be possible within the visible area or within a certain distance from shore. Both optimal and sub-optimal efforts were considered in the calculation of sighting rates.
c) Standby: This mode was entered into under the following conditions - when a sub-optimal watch continued for longer than two hours with no visible signs of improvement; at the sudden onset of extreme weather conditions e.g. continuous rain, thick mist, wind speeds >30 knots, swell height >7 m; or where such extreme conditions already existed at the start of a day. During standby the team would remain at the lookout for some time to assess whether conditions were improving to acceptable levels or not. No searching with binoculars was

attempted and any whales sighted during this time were regarded as incidental sightings and excluded from trackline analysis.

Climatic data

Further environmental measurements (daily minimum and maximum air temperatures in ^{O}C, and air pressure in kPa) were obtained from the South African Weather Services, as recorded at the nearest coastal weather station, Cape Columbine lighthouse (32^{O}49'36"S 17^{O}57'30"E, 68 m a.s.l.). Hourly tidal measurements (in meters) as recorded by a tide meter situated in Saldanha Bay were obtained from the S.A. Naval Hydrographer's office[1]. These were all required for calculating the correction for the effect of refraction during trackline analysis (see below).

Shore-based observations

Data collection

The primary lookout (or tower) was at Baviaansberg, a hill 72.8 m a.s.l. about 700 m (at 240 degrees) from the shoreline on the North Head of Saldanha Bay. The lookout position was located within a military small-arms firing range, and on the rare occasion when the range was active, a secondary observation post at Malgaskop (111.8 m a.s.l.), another hill set 2.65 km farther inland was used (Figure 2.1).

The search area was defined as the area of open ocean to the south, west and north of the lookout, stretching as far as visibility allowed (Figure 2.1). Though Saldanha Bay, Danger Bay, and visible parts of Langebaan Lagoon were also searched from time to time they were not considered as part of the primary search area, although groups of whales that entered these bays were still tracked. Only small sections of the search area were obscured by land, e.g. behind Jutten Island or extremely close inshore.

Teams of 2-4 observers searched for whales for alternating two-hour shifts, starting approximately one hour after sunrise and ending an hour before sunset, weather permitting. Half of the team searched by naked eye and the other half with 7x or 8x wide-angle binoculars, alternating roles every ten minutes. At least one experienced observer (who could also operate the theodolite) was always included with novices. The entire search area was searched by all on watch, regardless of the number of observers.

When a whale or group of whales was spotted, the first cue (i.e. blow, body, splash, breach, slick) was recorded, the species identified if possible and the group size estimated. The most experienced observer would then track the group, using a Wild T1 manual theodolite (equipped with a 22x telescope) that was mounted and levelled on a fixed base. The height of the focal plane at each lookout was calculated through triangulation using a geographically referenced orthophoto (1:10 000) produced by the South African *Chief Directorate: Surveys and Mapping,* and two reference points of known height and position in the field of view: a trigonometric beacon situated at North Head lighthouse, and the highest tip of Schooner Rock. The latter was also used as the fixed reference point

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[1] Visit http://www.sanho.co.za for more information

of known position and bearing on which the horizontal azimuth was calibrated every day. The aim of the tracking was to obtain an accurate 'fix' on the group on at least three different surfacing events, where an event was defined as a number of short-spaced surfacings bracketed by a longer submergence. A fix consisted of the recorded behavioural cue (body, blow, breach, splash or slick), an estimate of group size, the time (to the nearest second) and the vertical and horizontal angles (to the nearest second) as measured by the theodolite. A series of such fixes was termed a 'track'. Searching would resume once a reliable fix was made on the group being tracked. Although groups were tracked for a minimum of three fixes, tracking could continue for several hours if no other groups were seen, or up to an interception by the boat (see below). Revised group size estimates were made as tracking progressed. The group size recorded at the first fix was considered the minimum estimate, whilst the number at the final fix (excluding any feedback from the boat if the group was intercepted) was taken as the best group size estimate available. In the event of a group splitting, the two resultant groups would be treated as new groups. During tracking the search area was still scanned for new sightings by watchers not operating the theodolite, and although the search effort during this time could be considered somewhat reduced, it was assumed during analyses that search effort remained constant during both searching and tracking.

Spatial analyses

Tracks were inspected and for each surfacing event a single fix was selected based on the type of cue recorded at the fix, in the following order of priority: body, splash, and blow. In the few instances where no fixes on such cues were available, a fix on a breach or slick would be used. The horizontal and vertical angles and time recorded at the selected fixes were imported into and analysed using the software program *Pythagoras* (Gailey & Ortega-Ortiz 2000, 2002). The algorithm used is based on the work of Lerczak & Hobbs (1998), and takes into account tidal height (in metres, measured at the nearest hour), and a refraction correction (Glen Gailey pers. comm.; Leaper & Gordon 2001): the latter was based on the air temperature (^{O}C) and pressure (kPA) measured daily at 14:00 at Cape Columbine. The refraction correction was applied to all fixes from both tracks and midline visibility measurements.

The co-ordinates (latitude and longitude) of each fix were calculated by *Pythagoras*, and these positions along with associated sighting data were imported into a Global Information System (GIS) (ESRI ® *ArcMap* ™ 9.2 and ESRI ® *Arcview* ™ 3.3). Accurate digital versions of the coastline, depth soundings and depth contours of the study area were obtained from the S.A. Naval Hydrographer's Office (as used for marine navigational chart SAN 117, scale 1:150 000). Due to its irregular nature, it was necessary to create an "idealised" version of the coastline before calculating the distance of a fix from the shore. This was done by joining the heads of bays within the search area, thus essentially 'removing' these bays in order to provide a more accurate estimate of the distance from this 'smoothed' coastline. In the few cases where whale groups were inside these bays, the distance from the shoreline would be indicated as a negative measurement. At least one reliable fix was taken for 259 groups of humpback whales and the position of this first fix (in some cases the only reliable fix) was used to calculate the distance of the group to the nearest shoreline in a GIS, using the Transverse Mercator Projection with central meridian set at 17.9 degrees east.

Seasonality

Conventional austral seasons, *viz*. autumn (March to May), winter (June to August), spring (September to November) and summer (December to February) were considered. The prefixes 'early'-, 'mid'-, or 'late'- were added to the season name for the first, middle and last month in a season respectively (e.g. mid-spring = October). Where observations were carried out in the same month in different years, these duplicate months were combined into a single seasonal sample, i.e. October 2001 and 2002 formed the mid-spring sample. Sample sizes of tracked whale groups varied considerably between months due to the timing of study periods, variability in sighting rates and associated effort. Some months/seasons with very low sample sizes (<15) were therefore combined in order to increase the available sample size, resulting in seven seasonal groupings: late autumn to mid-winter = May 2002, June 2001/2002, July 2001/2002 (*n* = 23); late winter = August 2001/2002 (*n* = 25); early spring = September 2001/2002 (*n* = 16); mid-spring = October 01/02 (*n* = 55); late spring = November 2001/2002 (*n* = 31); early summer = December 2001/2002 (*n* = 36); mid- to late summer = January 2003, February 2003 (*n* = 26). The term "season" will be used to refer to these seasonal groupings, unless stated otherwise.

Trackline analysis

Three or more reliable fixes at different surfacings could be obtained for 212 groups and these were used in trackline analyses in *Pythagoras* (Gailey & Ortega-Ortiz 2002), and separated according to the seasons described above.

For each trackline the following parameters were calculated:

a) Actual swimming speed (= 'leg' speed): the unweighted mean of the swimming speeds calculated for each 'leg' (the distance travelled between two consecutive fixes in a track) by dividing the distance covered between a pair of fixes, by the time it took to travel between them.
b) Linearity: a form of migration index, calculated by dividing the net distance covered by a track (i.e. the direct measurement between the first and last fix) by its cumulative distance (the sum of all legs). Linearity values range between 0 and 1, with values close to 1 representing a straight track-line, while a value close to 0 represents a track with no constant direction.
c) Net course: the true bearing in degrees of a track, calculated between the first and last fixes.
d) Net speed: calculated by dividing the linear 'distance made good' between the first and last fixes of a track, by the time it took to travel between them (i.e. total duration of track).

Boat-based data collection

Boat intercepts

For the duration of the study, when weather and personnel availability permitted, whale groups were intercepted using a 6 m semi-rigid inflatable boat *Balaena* powered by twin outboard motors. The boat was directed from its mooring inside Saldanha Bay to whale groups by the land-based observers via VHF radio, as soon as they had made an accurate fix on the group. The boat was dispatched to any sighting that appeared to be within reasonable range of a small boat (about 15 km) and that, based on its direction and speed, would not disappear from the search area or field of visibility before the boat could reach it. Groups would generally be intercepted in the order of being spotted; in the case of simultaneous sightings priority would be given to groups that were most likely to be lost (i.e. farther away or faster moving). If other groups were spotted by the boat crew during an intercept, these groups would be visited after data collection was completed.

Intercepts were used to confirm group size, take individual identification photographs and collect skin biopsies using a *Paxarms* biopsy rifle (Krützen *et al.* 2002). Skin samples were placed into individual cryogenic tubes filled with a NaCl-saturated, 20% dimethylsulfoxide (DMSO) solution; the tubes were kept in a cooler box with ice-packs. At the end of each day all skin samples were stored in a domestic freezer (-5 ^{O}C) until they could be transferred to a -15 ^{O}C freezer at the laboratory in Cape Town.

At periodic intervals while the *Balaena* was at sea during or between humpback sightings, a hydrophone would be deployed and an acoustic watch maintained for approximately 10 min at a time.

Group composition and behaviour

A group was considered to be one or more animals that displayed noticeable co-ordinated movement or behaviour and where individuals were no farther than an estimated 100 m from each other (after Whitehead 1983; Corkeron *et al.* 1994). Cow-calf pairs were defined as two whales, one of which about half the length of the other.

All humpback whale groups from which genetic skin and photo-identification samples were collected during other boat-based cetacean studies of the Mammal Research Institute (MRI) in the same region (between 1993 and 2008) were included in the group composition analyses.

Processing of biopsies was carried out by others (See Foreword and Acknowledgements) at the Sackler Institute for Comparative Genomics. Briefly, total genomic DNA was extracted from the epidermal layer of biopsies using proteinase K digestion followed by a standard Phenol/Chloroform extraction method (Sambrook *et al.* 1989) or using DNAeasy tissue kit (Qiagen). Sex determination was carried out by polymerase chain reaction (PCR) amplification followed by *Taq*I digestion of the ZFX/ZFY region of the sex chromosomes (Palsbøll *et al*. 1992), or using multiplex PCR amplification of the ZFX/ZFY sex linked gene (Bérubé & Palsbøll 1996).

Behavioural observations made from the shore were limited to estimating group size and recording overall group behaviour (such as travelling, milling, surface activity, breaching, and possible feeding). Group size, behaviour and composition were also recorded during all boat intercepts. Any incidents of defecation were noted and a faecal sample collected when possible.

RESULTS

Sightings, search effort, and sighting conditions

Shore-based observations were carried out on 102 (or 68 %) of the available days between 24 July and 20 December 2001 and on 177 (or 61.9 %) of the available days between 6 May 2002 and 15 February 2003 for a total of 1,802.18 hours. A total of 1,197 groups of baleen whales was sighted, the majority being southern right whales *Eubalaena australis* (669) followed by humpbacks (289), four mixed species (humpback and right whale) groups, and a single blue whale (*Balaenoptera musculus*). Positive species identification was not possible for 234 other groups of large whales, though 15 of these were recorded as 'like-humpback', 16 as 'like-right whale' and 12 as Bryde's or minke whales (*B. brydei* or *B. bonaerensis*). Only groups that were positively identified as comprising solely humpback whales were considered in the analyses.

Effort during both field seasons was discontinuous, with gaps of up to seven days with no watch, mainly due to poor sighting conditions. In order to create approximately equivalent sub-samples to calculate mean sighting rates and measures of variance during a month or season, daily search effort for days 1-7, 8-14, 15-21, and 22-month end were summed, this resulting in four sub-samples in a full month. Sightings per Unit Effort (SPUE) was calculated by dividing the number of whale groups seen by the total number of hours watched (including both optimal and sub-optimal effort) in a subsample, and transformed to groups per 10 hours of searching (Figure 2.2). This SPUE is not an absolute measure of humpback whale abundance, since *inter alia* it includes all sightings within the search area, not only those that crossed the midline during the watch period, and does not exclude the possibility that a group may have been resighted on more than one occasion on or between days. Furthermore, the number of groups passing through the search area when there was no search effort, or at night, is unknown. A between-season comparison of the mean daily sightability index (calculated by dividing the sum of hourly sightability estimates, by the number made on that day) showed a decrease in mean sightability from autumn/mid-winter (2.95 ± 0.102 SE) through to late summer (2.46 ± 0.14 SE). This difference was significant overall (ANOVA, df = 6, $F = 2.69$, $p = 0.0163$) but post-hoc tests showed no significant difference between specific pairs of seasons. Sightability therefore appeared to be constant enough across seasons to allow the use of SPUE as an index of relative abundance.

In general, effort levels were higher and more consistent during the first part (autumn and winter) of both study periods, but the SPUE was low with only slight peaks in late July/August. During both study periods search effort became more variable from September onwards, mainly due to the frequent occurrence of unfavourable weather conditions that interrupted or prevented searching. Prominent peaks in SPUE were seen at the end of October in both years (peaks A and C in Figure 2.2) and both times these stretched into November. The highest overall SPUE was recorded during the fourth week of October 2002 (peak C) when at least one group was seen per hour. Other above-average peaks in SPUE occurred in December 2002 (peak B) and at the end of January/beginning February 2003 (peak D) despite low and discontinuous search effort (Figure 2.2).

The mean SPUE by season showed an apparent increase in whale availability from mid-spring onwards, despite a strongly decreasing trend in total hours watched from winter to summer (Table 2.1). There were fewer suitable watching days from late-spring onward. All seasons with the exception of mid-spring experienced weeks with no sightings (min SPUE = 0) and despite higher mean sighting rates in mid-spring, and summer (Table 2.1) no significant difference was detected between seasons (Kruskal-Wallis statistic = 10.05229, *n* = 57, *p* = 0.1225). Given the small and variable sample sizes and the big difference in range between minima and maxima of the seasonal groupings (Table 2.1), the median may be a more appropriate measure of central tendency than the mean (Zar 1996), and the multisample median test showed a significant difference between seasons ($X^2 = 12.62920$, df = 6, $p = 0.0493$). When samples were combined into only two seasonal blocks, namely autumn/winter (mean SPUE = 0.96 ± 0.22, *n* = 20) and spring/summer (2.03 ± 0.40, *n* = 37), a t-test showed a significantly higher SPUE for the latter grouping (*t*-value = -2.0252, *p* = 0.0477).

Visibility at midline and spotting distance of whale groups

Overall 1,834 hourly theodolite readings were taken at the midline as indication of the theoretical maximum visibility during periods of optimal and sub-optimal watch. The average visibility from the towers over the entire period was 8.21 ± 0.08 km (SE) ranging from 1.29 to 26.46 km. The average distance from the tower (the ‘sighting distance’) for all 251 humpback groups on which a reliable fix was made (excluding the eight sighted and fixed inside Saldanha Bay) was 7.24 ± 0.26 (SE) and ranged between 1.24 - 25.11 km (Table 2.2). A comparison of the frequency distribution of all midline visibility measurements and radial sighting distances to all humpback groups (placed in 0.5 km bins) showed similarly shaped distributions, with the highest number of visibility observations recorded in the 7.5 - 8.0 km bin, though there was an extended peak from about 5.5 - 8.5 km (Figure 2.3). The distribution of whale sighting distance showed a much flatter peak with a wider range of 2 - 8.5 km, with the 5 - 5.5 km bin containing most groups. Whale groups, in general, appeared to be seen at shorter distances from the tower than the recorded visibilities (Figure 2.3) with a fairly abrupt fall-off of sighting distances beyond 8.5 km, whereas visibility measurements showed a much steadier decrease from 8.5 km and farther. To determine whether the theoretical visibility limited our ability to spot and track whales, we compared the distance at which a group was sighted with the visibility taken at the nearest hour to the time of the fix at which the group distance was calculated (the ‘prevailing visibility’). These measurements were sorted into 1 km bins according to the prevailing visibility, and the mean distance from the tower for whale groups within each bin calculated. A plot of mean sighting distance against prevailing visibility showed that up to about 7 km from the tower, sighting distances were on average higher than the visibility, but after this whale groups were seen at distances well below the prevailing visibility (Figure 2.4). However, the mean distances of whale groups to the nearest shoreline (i.e. perpendicular distance) at prevailing visibility, were considerably less compared to prevailing midline visibility (Figure 2.4).

Seasonal variations of visibility at the midline were tested and showed a highly significant difference (ANOVA, df = 6, $F = 14.4918$, $p < 3.24 \times 10^{-16}$) with significant differences in mean visibility between a number of seasons shown by Tukey’s HSD test for unequal *n* (Table 2.3). The best visibility was measured in late winter with a clear decreasing trend in visibility from late spring to late summer, with the poorest mean visibility recorded in mid-late summer (Table 2.2).

Distance distribution of whales from the shore

Whale groups were seen beyond 15 km from the shore on only six occasions, once in both late winter and early summer, and four times in mid-spring. For all seasons except late winter and mid-spring groups were closer to shore than the overall mean (Table 2.4). Between-season ANOVA showed a highly significant difference of distance of groups from shore (df = 6, $F = 4.41$, $p < 0.0003$) and Tukey's HSD test for unequal samples sizes indicated that this difference was between mid-spring (highest) and early summer (lowest) ($p < 0.004$). A quarter of whales were sighted within 2 km from the shore, including the eight sightings within Saldanha Bay (negative distances). More than half the groups were seen in the range 2 – 6 km and the remaining 25% farther than 6 km and up to a maximum of 20.75 km. There was a rapid fall-off in number of sightings from 10 km onward with only about 6% of groups recorded in this zone (Figure 2.3). When groups were sorted into four distance zones *viz.* inside bays to 5 km, 5-10 km, 10-15 km, and farther than 15 km, a seasonal pattern in distance offshore became evident (Figure 2.5). The majority of groups were seen within 5 km from the shore in all seasons, and the hypothesis that the proportion of groups within and beyond the 5 km mark did not differ significantly (X^2 test) was rejected for all except late winter, mid- and late spring (Figure 2.5).

Group size and composition

The size of 289 groups observed from shore ranged between one and six, with the notable exception of the maximum group size recorded of 15 individuals, and another of 10. These apparent outliers were probably loose association of several smaller groups rather than single groups. The most frequent group size ($n = 122$) was two animals (10 of which were identified as cow-calf pairs by the boat crew) followed by singletons (83). The mean group size based on these best estimates was 2.2 ± 0.08 (SE) ($n = 289$) and excluding the outliers mentioned above, 2.12 ± 0.06 (SE) ($n = 287$). The largest mean group sizes were recorded in mid-spring (2.44 ± 0.12) and early summer (2.5 ± 0.19) and the smallest in late winter (1.69 ± 0.15) and late spring (1.75 ± 0.11) with an overall significant difference between seasons (Kruskal-Wallis $H = 25.5825$, df = 6, $p = 0.0003$). Dunn's multiple comparison *post-hoc* test showed late winter (August) to have a significantly smaller mean group size than both mid-spring ($z = 3.540$, $p < 0.0084$) and early summer ($z = 3.1402$, $p < 0.036$), while the mean of mid-spring was also significantly higher than late spring ($z = 3.1903$, $p < 0.03$) (Figure 2.6).

Group sizes recorded during the 116 boat intercepts ranged from one to seven, except for one grouping recorded as 20, which in reality was a dynamic aggregation of several smaller groups. Excluding this grouping, the mean group size encountered was 1.97 ± 0.084 (SE) (n = 115). Group size was recorded for the same group by both shore observations and boat intercepts 85 times; 61 of these were identical, in six cases boat estimates were higher than the corresponding land ones, and 18 times land estimates were bigger than boat ones. Although the mean size of these groups estimated from land (2.09 ± 0.12) was larger than that made during boat intercepts (1.85 ± 0.086) the difference was not significant (t-test, independent variables, two-sided, df = 168, t-value = -1.7145, p = 0.08843).

Genetic analysis

Sex determination was carried out by others (see Foreword and Acknowledgements) for 216 skin biopsies collected between 1993 and 2006. The majority of samples (104) were taken at Saldanha Bay during the principal study, followed by 92 taken during a St Helena Bay study on southern right whale feeding (2003-2006). The balance was made up of six samples collected at Cape Columbine in 1993, a single sample from Walker Bay (1999) and 13 taken during boat transects for Heaviside's dolphins *Cephalorhynchus heavisidii* along the coast (1999-2000, 2008). Overall 119 females and 91 males were identified while six samples did not yield results. Three duplicate samples of the same individual on the same day and/or from the same sighting were identified from genotyped individuals (using 10 microsatellite loci) (Pomilla 2005; Carvalho *et al.* 2009) and these were removed, leaving a total of 207 sexed samples. The overall female (56.5%) to male (43.5%) ratio, including cow-calf pairs, did not vary significantly from parity (n = 207, X^2 = 3.521739, p > 0.06057, df = 1). A total of 32 groups were identified as cow-calf pairs and from these 20 cows and 12 calves were biopsied: the calves were comprised of nine males and three females. A possible bias may exist towards the sampling of cow-calf pairs due to their generally slower movement (Noad & Cato 2007 and references therein) and more time spent at the surface. Cows and calves that were sampled (32 out of 64 animals) were therefore removed from the overall sample to test this, but the remaining female (53.7%) to male (46.3%) ratio still did not deviate significantly from an 1:1 ratio (n = 175, X^2 = 0.965714, p > 0.32575, df = 1). Following this, the 20 cows were retained in the sample, but the 12 calves excluded. The reasons for this were the presence of calves was presumably dependent on their mothers, and that whaling data on gender included only mature whales. This resulted in a significant female bias in the overall sex-ratio (1.407 females: 1 male, n = 195, X^2 = 5.584615, p < 0.01812).

Other possible biases in selection of intercepted groups

Cows with calves have also been shown to prefer areas closer to shore in a breeding area (Ersts & Rosenbaum 2003), perhaps introducing another source of bias, though this has not been illustrated during migration. To test this, we compared the mean distance from shore of all cow-calf pairs to other groups intercepted by boat between 1999 and 2006 at Saldanha Bay/St Helena Bay, during months when cow-calf pairs were sighted (see Figure 2.7). Distance (calculated using a GIS) was measured between the GPS position of the boat at the time of the intercept, and the nearest coastline. The mean distance to shore of cow-calf pairs (n = 30; 3.49 ± 0.713 km ± SE) did not differ significantly from non cow-calf groups (n = 137; 4.98 ± 0.359 km) (t-test, independent variables, two-sided, df = 165, t-value = -1.77487, p = 0.0778).

To test whether group size affected the likelihood of being intercepted, thus introducing a bias through the selection of larger groups, the mean of the best estimates of group size made from land was compared for whale groups that were intercepted (n = 85; 2.094 ± 0.115) and not intercepted (104;

2.23 ± 0.101). There was no significant difference between the means of these groupings (t-test, independent variables, two-sided, df = 287, t-value = 0.7877, $p = 0.4315$).

In terms of a selection bias of humpback groups intercepts during the other studies, these were all incidental sightings (excepting the six samples from Cape Columbine) during effort directed at other target species, and thus we have to assume that these encounters were random.

A seasonal plot of the numbers of females and males (incl. cows with calves but excluding the calves themselves, Figure 2.7) suggests that during autumn, winter and early spring months, slightly more males than females were sampled, bearing in mind that sample sizes were very small. For the rest of spring and summer more females were available, and for mid-spring and mid- to late summer, this bias was significant (Table 2.5). The number of cow-calf pairs seen during boat intercepts increased from late spring onwards with most seen from December to February (Figure 2.7).

Genetic samples of 76 complete groups of whales (132 individuals) were collected and the overall sex ratio (excl. 8 calves but incl. cows) did not deviate significantly from parity (53 males, 71 females; $X^2 = 2.612903$, $p < 0.106$). Identical numbers (13) of males and females were recorded for lone animals. Most pairs (excluding cows with calves) consisted of a male and female (18) followed by female only pairs (14), and then male only (6). The eight cow-calf pairs included six male and two female calves, while two of the pairs were accompanied by single male escorts. Apart from these cow-calf pairs with escorts, groups of three individuals were completely sampled only another four times; one all-male, two with more males and one with more females. A seasonal breakdown of the gender composition of groups that were completely sampled (Figure 2.8) shows a decrease in the occurrence of single males after early spring, with none recorded in mid-spring. Female-biased groups were found in all seasons except late winter (however, note the low sample size). Male-female pairs and cow-calf pairs (incl. those with escorts) were only seen from mid-spring onwards. No single females were recorded after late spring. Mid-spring was the only season where there was a significant (female) biased sex-ratio of 2.88:1 (Figure 2.8; $X^2 = 7.258$, $p = 0.007059$).

Trackline analysis

Swimming speed

Actual swimming speed (= ‘leg’ speed) ranged from 0.55 to 10.68 km.h^{-1} (Table 2.6), with an overall mean of 4.6 ± 0.15 km.h^{-1} (SE). An examination of leg speed by season reveals a strong decrease in mean swimming speed from autumn through to late summer, and Kruskal-Wallis analysis of variance showed a highly significant difference between seasons (Kruskal-Wallis statistic = 59.21, $p < 0.0001$). Dunn’s multiple comparison between the seasons showed significantly higher swimming speeds in autumn to winter compared with mid-spring to late summer ($p < 0.05$) (Table 2.6). Overall net speed averaged 3.91 km.h^{-1} and ranged from 0.091 to 10.47 km.h^{-1} (Table 2.6). Seasonal mean net speed was always lower than actual swimming speed, with the smallest difference between these parameters observed during autumn to late-winter, while the difference increased from early spring onwards, and was the greatest in mid- to late summer (Table 2.6).

Direction and linearity of movement

Net course and linearity of movement were calculated for all groups with three or more fixes made at different surfacing events (n = 212). A frequency distribution plot of net course (Figure 2.9) reveals a bi-modal distribution, with the larger mode at 100-200 ^{O} and a second smaller peak at 280-360 ^{O}. Taking into account that the orientation of the coastline is at approximately 330 - 150 ^{O} it may be assumed that the first mode (100-200 ^{O}) represents predominantly south-bound, and the second (280-360 ^{O}) north-bound animals. For linearity, the highest number of groups observed (Figure 2.10) had an index in the 0.7 - 1.0 range (where 1 = a straight line) with a definite peak between 0.9 and 1.0. Though there was some variation between 0 and 0.7 levels, the number of observations across this range remained relatively constant and much lower than the peak. It was therefore assumed that a linearity index of 0.9 and greater indicated migration-like movement (swimming in a more-or-less straight line) while indices of < 0.9 represented non-migrating groups.

A plot of cumulative frequency of direction of movement by season, with three directional groupings based on the two modes (north and south), and another containing all groups heading in other directions, shows predominantly southwards movement in autumn to late winter (Figure 2.11). The null hypothesis that mean angles of movement by groups were distributed uniformly each season (i.e. no directionality) was tested using the Rayleigh's test for circular uniformity (Zar 1996). This was rejected (p < 0.05) for autumn/mid-winter (n = 23, avg. degrees = 155.14, Rayleigh's R = 19.78, Rayleigh's z = 17.012) and late winter (n = 25, avg. degrees = 158.52, R = 16.61, z = 11.03) as well as late spring (n = 31, avg. degrees = 148.51, R = 14.77, z = 7.04). Thus, in these seasons, distribution of the mean angle was not distributed uniformly and there was definite directionality in a predominantly southerly direction (Figure 2.11). In the other seasons there were more or less equal numbers of groups moving both north and south while there was an ever-increasing number of groups moving in other directions from early spring onwards.

Non-directionality reached its peak in mid- to late summer when the number of groups moving north, south or in other directions each made up roughly a third of the total groups tracked (Figure 2.11). The incidence of 'migration-like' movement predominated from autumn to early spring after which there were more or less equal numbers of 'migrators' and 'non-migrators' for the remaining spring months (October/November), and a marked decline in groups moving in straight lines (Figure 2.11). Throughout summer 'non-migrating' groups predominated.

Relationships between trackline parameters and other variables

The relationships between the various trackline parameters (linearity, leg speed and direction) and other variables (season, distance from shore and group size) were not always clear. There was no relationship between group size and leg speed (r = -0.0768, p = 0.2655), nor between distance from the shore and linearity (r = 0.078, p = 0.258); but there was a significant and positive correlation between leg speed and distance offshore (Figure 2.12a; r = 0.2081, p = 0.0023) with groups farther offshore travelling at higher speeds. A separation of groups into near-shore (within 5 km from land and inside bays, n = 156) and offshore (beyond 5 km, n = 56) showed the latter to move significantly faster, at a mean leg speed of 4.99 km.h^{-1} compared to the near-shore mean of 4.47 km.h^{-1} (t-test, t-

value = -1.4928, df = 210, p = 0.04775). Leg speed also showed a significant and positive correlation with linearity (Figure 2.12b; r = 0.4586, p < 0.00005) but there was no significant correlation between speed and net course (r = 0.0874, p = 0.2049). A significant and negative correlation between linearity and group size suggests that larger groups tended to display non-migratory movement (Figure 2.12c; r = -0.1511, p = 0.0278).

Seasonal patterns in movement

While the various trackline parameters considered independently showed seasonal differences between winter and summer, a movement pattern was more difficult to define for combined parameters. To test for seasonal patterns in movement, a *post hoc* multivariate approach was attempted using the software PRIMER v6 (Clarke 1993; Clarke & Warwick 2001; Clarke & Gorley 2006). Each whale group was considered a 'sample' with values for the three parameters leg speed, course, and linearity. Parameter values were normalised (the mean subtracted from each value and divided by the standard deviation) and the similarity between every pair of samples calculated based on Euclidian distance. In a non-metric multi-dimensional scaling (MDS) ordination of whale groups (Figure 2.13a; stress-value = 0.1 indicating a good two-dimensional representation), with season selected as the identifying feature (or 'factor', see Clarke & Gorley 2006), the first outstanding feature is two major groupings of samples into the top and bottom halves of the plot. The second major feature is the clustering of most autumn/winter samples into the bottom right of the lower group. Mid-spring samples are the most dispersed, and more or less equally distributed between the top and bottom clusters. While the summer samples are also found in both clusters they are located more to the left of the plot particularly the mid- to late summer samples (Figure 2.13a, all to the left of line A). A one-way Analysis of Similarities (ANOSIM) was applied to samples according to the seven seasonal groupings. This is a non-parametric permutation procedure applied to a resemblance (= similarity) matrix based on the rank similarity of each sample. It calculates a global R-value and overall p-value, as well as a measure of significance of similarity for pair-wise tests between sample groups. The ANOSIM showed an overall significant difference (global R = 0.055, p = 0.005) between seasonal groupings. The pair-wise comparison between seasons (Table 2.7) showed no difference between groups from the two autumn/winter seasons. Late winter and early spring stood out as the least similar to any other seasons, differing significantly from all (including each other) except mid-spring. The latter (October) was the only season that did not differ from any other season. The similarity between late spring and early summer, and the significant difference between both these seasons with mid-to late summer is also noteworthy. To establish which of the three parameters were responsible for the groupings a Principal Component Analysis (PCA) was carried out on the data and the two factors responsible for most of the patterning (in the MDS ordination) shown as an XY scatterplot with the parameters overlaid (Figure 2.13b). From this we can conclude that differences in course were mostly responsible for the separation of the top (northbound) and bottom (southbound) clusters, accounting for 33.1% of the variation, while the strong grouping of winter samples was due to speed and linearity (49% of variation).

Migrators vs. non-migrators

In order to show up possible differences in the movement patterns of 'migrators' and 'non-migrators' according to their linearity of movement, the groups were plotted in an MDS ordination (as described above), this time including the parameters: leg speed, course, and distance from shore, and using linearity as distinguishing factor (migrators ≥0.9 and non-migrators <0.9). The plot (Figure 2.14a; stress value = 0.15 showing a fairly reliable two-dimensional representation, Clarke 1993) shows some degree of separation, firstly between the two groupings (group A = non-migrators, group B = migrators), and secondly within migrators (groups B1 and B2). PCA analysis showed distance from shore and leg speed to be responsible for the separation between migrators and non-migrators, while the two migratory subgroups separated out mainly due to differences in course, B1 containing northbound and B2 southbound groups (Figure 2.14b). Migrators and non-migrators were found to be significantly different when an ANOSIM was applied (global $R = 0.133$, $p = 0.001$).

Feeding behaviour

From land eight groups were observed to display apparent feeding behaviour, which included milling about (slow movement of indeterminate direction) and faster erratic movement with frequent directional changes. Nine groups intercepted by boat also appeared to be engaged in feeding though actual feeding behaviour (lunges at surface) was directly observed during only five of these (Table 2.8). Fourteen groups were observed to engage in surface activity other than feeding, including repeated breaching and competitive behaviour such as flipper slapping. Defecation was observed 37 times for 23 groups intercepted during nine months from 2001-2006. All defecating groups were seen during the months of October 2002/04 (five times), November 2001/04/05/06 (11), December 2001/04 (5) and January 2003 (3). The total number of defecating groups seen from the boat, expressed as a fraction of the total humpback groups intercepted during these nine months (94 groups) results in a defecation incidence of 24.47%. The groups included two of the groups observed to be feeding (Table 2.8). The stools ranged in colour from dark/bright pink to brick red, presumably indicating crustacean prey. Most of the faecal samples collected (preserved in 95% ethanol) were highly diluted and consisted of whitish to pink paste in emulsion or as a particulate suspension. Four samples that contained slightly larger particles were examined through a stereo-microscope and yielded unidentifiable crustacean (possibly euphausiid) exoskeleton remains, with the exception of one collected on 29 November 2006 that contained fairly intact specimens of a Hyperiid amphipod (identified using keys in Dunbar 1963; Gibbons 1999).

The possible relationship between observed/suspected feeding behaviour (including defecation), and whale movement patterns and distribution was explored by labelling all groups tracked on the days where such behaviour was recorded (all groups 30 October 2001 - 26 January 2003 in Table 2.8) as 'feeding' groups, and all groups on other days as 'non-feeding'. Using the same MDS plot (Figure 2.14, based on the parameters leg speed, course and distance from shore) this time with feeding/non-feeding as distinguishing factor, we see a strong similarity between the grouping based on linearity (Figure 2.14a) and feeding behaviour (Figure 2.14c).

Acoustic stations

In all, 33 acoustic stations were surveyed, for a minimum of 10 minutes each, from 2001 – 2003 during August, September, October, November, December and January. During a total time of 141 minutes monitored, no humpback vocalisations were detected.

DISCUSSION

Despite variable and, at times, discontinuous search effort, the summer seasonal coverage of this study meant across-year effort was more extensive than during any previous attempt at shore-based monitoring of Southern Hemisphere humpback whales. All seasons, with the exception of autumn, were well surveyed. This allowed us to compare whether the observation of a 'suspended migration' made by Best *et al.* (1995) during spring was indeed unusual, or whether the observed whale availability and behavioural patterns were applicable to other seasons and years.

Sighting conditions, visibility and distance of whales from shore

On days where searching occurred the mean sightability, based on the various environmental observations, appeared to have been constant enough to allow comparison of sighting rates across seasons. The significant seasonal variation of mean visibility at the midline between some seasons may raise concerns about whether whale groups were missed in the search area due to limited visibility. Such conditions were most prevalent during summer months when not only the lowest visibility was recorded, but also the maximum distances at which whales were tracked exceeded visibility maxima estimates. It suggests that visibility was difficult to judge during these months, in all likelihood as a result of the frequent occurrence of coastal fog, persistent south-easterly winds, or strong refraction due to the strong gradient between high air and low sea temperatures. Despite this some of the highest sighting rates were still recorded during summer.

Compared to the radial sighting distances to whales, the overall mean visibility was always greater, excepting mid-spring and mid-to late summer. However when the mean sighting distance was compared to the mean visibility measurement prevailing at the time of sighting, it was greater than the visibility up to about 7 km. This apparent contradiction might be the consequence of the visibility measurements being taken on the midline, while most sightings were made well away from the midline. If alongshore visibility should be greater than offshore visibility in times of moderate-poor visibility (for instance, owing to the majority of haze being over the sea rather than the land) this could account for the apparent discrepancy. When visibility was good, i.e. 7 km and farther, this effect seems to disappear. Considering that the seasonal mean distance from shore of whale groups never exceeded 6 km, and was less than 4 km in all but two seasons (see below), and assuming that north- or southbound whales would remain at a more or less constant distance from the shore as they travel through the search area, it seems likely that the majority of whale would have passed within the visibility range at some stage. This is apparent when comparing the mean radial distance, at which whales were sighted, to the calculated distance to the nearest shoreline. Groups were evidently sighted well before they passed the nearest point to the tower. Visibility as measured through the theodolite is probably a conservative estimate of the distance at which whales may be sighted (but not necessarily tracked), given that cues such as blows are visible with the naked eye, and not only at the 22x magnification.

The mean distance of whales from the shore was fairly similar for most seasons at around 3.5 km with the notable exceptions of late winter and mid-spring when it was about 5.5 km. Not surprisingly these two seasons saw a greater proportion of groups in the 5 – 10 km range. On the whole though, the majority of whales were still seen in the 'inshore' zone (<5 km) with very few beyond 10 km, and this was unlikely to be as a result of restricted visibility offshore. This is compatible with observations at Cape Columbine during mid- to late spring (Best *et al.* 1995) though the mean offshore distance of 3.1 km ± 0.2 (SE) recorded in that study was lower than both our overall mean (4.41 km ± 0.21, SE) and that of the same season (5.78 km ± 0.48, SE). This may be because Cape Columbine is situated slightly more to the west than Saldanha Bay and so possibly acts as a headland that coastally migrating whales have to navigate around.

Seasonality of occurrence and movement patterns

Mid-spring (=October) stands out in more than one respect as a seasonal 'turning point'. First, the highest sighting rate was recorded at this time of year and it remained relatively high from then onwards, this despite the decreased search effort and reduced visibility. Second, there were also noticeable changes in the whale movement parameters from autumn to early spring, and the remaining seasons. Mean actual swimming speed started decreasing significantly from mid-spring onwards, from >6 km.h^{-1} in winter, to <3 km.h^{-1} in late summer. The corresponding mean net swimming speeds are well within the range of recorded 'migration' speeds of humpback whales recorded off the east coast of South Africa (Findlay 1994), and elsewhere (Noad & Cato 2007; Lagerquist *et al.* 2008). However, the low actual and net speeds recorded in mid- to late summer certainly fall in the lower end of the range and are very similar to the low speeds recorded at Cape Columbine (Best *et al*. 1995).

Sightings in mid-spring were distributed almost evenly between the near and offshore zones, recording the overall highest mean distance from shore. It was also the month where non-directionality in movement became a prominent feature and where almost equal numbers of groups either milled around or moved in near-straight lines, in all major directions. Multivariate representation of the movement variables in combination confirms mid-spring as a period where whale movement was less distinctive than in any other seasons, sharing similarities with both the preceding and following seasons. This is in strong contrast with groups from the winter months that all displayed movement patterns that were, with few exceptions, very alike in terms of speed, course and linearity. From this one could speculate that mid-spring represents a period where we observed an overlap of two behaviourally distinctive 'sub-groups' of humpbacks; one component migratory, although judging by the observed direction both north - and southbound, and the other distinctly non-migratory, and each perhaps occurring at different distances from the shore. Olsen (1914) reported similar 'anomalous' behaviour off Saldanha during 1912/13, and speculated that there may be two components to humpbacks moving past during the northern migration. One consisted of animals that moved straight to the north and had empty stomachs when caught, while the other was seen to move 'wildly back and forth' along the coast apparently in search of food (see later discussion on feeding).

Olsen (1914) also reported on whales frequently seen by vessels farther offshore that presumably met the coastline north of South Africa on their northward migration. Reeves *et al.* 2004 made similar inferences during an estimate of historical seasonal distributions of humpbacks and blue whales from 18th and 19th century logbooks of catches in the North Atlantic. They concluded that the humpbacks migrated over an extended period making use of both near-shore and offshore routes, and that sporadic feeding took place well south of 'traditional' feeding grounds, a behaviour that may persist to the present. Our finding that groups farther offshore moved slightly faster may support this, though the distance that Olsen (1914) refers to was presumably well beyond the visibility range of our station. It therefore remains difficult to distinguish different 'components' of the population based on movement patterns alone.

Defining migrators/non-migrators

High availability or relative abundance of whales in an area, whether based on direct observations or historical catches, is not necessarily conclusive evidence of a migration peak, but could represent a local feeding aggregation (see later discussion on feeding). The multivariate comparison of migrators versus non-migrators did show a difference between these groupings on the basis of actual swimming speed and distance from shore. Furthermore, within the 'migratory' group two sub-groups separated out on the basis of their course; this suggests the existence of two migrational streams heading in opposite directions. Although we saw a definite increase in the proportion of groups showing non-migratory (non-linear) movement from autumn through to late-summer, linearity alone can thus not be considered a reliable indicator of migrational behaviour without taking into account direction of movement, and speed. For example, in early spring more groups showed linearity ≥ 0.9 but the number of groups heading south and in other directions were about equal.

Our observations in October/November (mid- to early spring) are consistent with those made earlier at Cape Columbine (Best *et al.* 1995) during the same months, in that the groups showed both southerly and northerly directionality. Perhaps more difficult to explain is the dominance of south-bound groups, moving at higher speed during the winter months, at a time when we would still expect to observe at least the tail-end of a northern migration (Olsen 1914). It would appear that although groups that displayed both strong directionality and linearity were present during almost all the seasons, there was a shift in movement pattern from October/November onwards when we saw both strong directed movement (both north and south), as at Cape Columbine, but also an increase in the 'non-migrating' and slow swimming components. Whether the 'fast-and-straight' swimmers were actually migrating or simply moving up or down the coast, perhaps between Cape Columbine and Saldanha, in a determined manner (as suggested by Olsen 1914) remains uncertain. What is clear is that the dominant movement pattern changed between winter and summer: fast movers became fewer towards summer, especially ones heading south, and by mid- to late summer almost all groups moved slowly. This is supported by the significantly low average speed of 2.9 $km.h^{-1}$ and the virtual disappearance of the fast-moving and straight-swimming component that characterised groups sighted during winter months.

Other behaviours observed elsewhere during migration have included singing (Clapham & Mattila 1990) and non-acoustic means of communication such as breaching, tail slapping and other surface behaviour (Dunlop *et al.* 2007, 2008). Although surface active behaviour was observed, we did not detect any vocalisations, though we have received a reliable report of singing on 29 December 2003 from an observer in a steel-hulled yacht near Dassen Island, approx. 50 km south of Saldanha (P. Evans, pers. comm.).

Group size, sex-ratio, and composition

The changes observed in mid-spring were not limited to movement patterns alone. Group sizes recorded were larger than average, and it was the only season where the overall sex-ratio varied significantly from parity with a strong female bias of about 2:1 even when cow-calf pairs were excluded. This is in marked contrast to the findings of Brown *et al.* 1995 who described a migration (both north- and southward) off the Eastern Australian coast from May-October that was overall highly skewed towards males. Similar apparent male-dominated sex ratios have been seen on breeding grounds (Craig & Herman 1997; Palsbøll *et al.* 1997). With no evidence for any stock-level deviations from an approximate 1:1 sex ratio (see discussion in Clapham & Mead 1999) it has been speculated that male bias during migration may be a result of some females possibly remaining in 'feeding' areas (presumably high latitude) throughout winter. On the breeding grounds such a bias might be explained by a longer residence time of males (Craig & Herman 1997). Our discovery of a region with a significant female bias may offer a plausible explanation as to where the 'missing' females go while males complete the full migration, with mid-spring falling roughly between the northward and southward migrations. Compared to ours, the study site of Brown *et al.* 1995 was situated much closer to the Feeding Group V northern destination (breeding area), but unfortunately they did not provide a seasonal (monthly) breakdown of recorded sex-ratios which prevents more detailed comparisons. A number of questions thus still remain: (1) Where were these females during winter? Did they spend time in an unknown area or merely travel at a more leisurely pace from the feeding grounds, compared to males, to reach the coast of Saldanha during mid-spring? (2) Do male-biased sex ratios occur at localities farther up the west coast of Africa? Whaling data from 'Congo' (now Gabon) at about 1^{O} S indicated that in 1949 males made up nearly 65% of all catches, 47.55% in 1950 and about 50% in 1951 (Budker & Collignon 1952), implying that the situation is not markedly different than in the breeding grounds for humpbacks. Pomilla and Rosenbaum (2006) however, more recently reported a male-biased sex-ratio at breeding grounds off Gabon, as well as Madagascar.

Apart from the sex ratio at any given site, a number of authors have commented on differential timing of migrating humpbacks based on sex, age and reproductive state (see summaries in Clapham 1996, 2000), as well as group composition (Brown & Corkeron 1995). Typically, for Southern Hemisphere humpbacks, lactating females with 'yearling' calves are believed to head north from the feeding grounds first. They are followed by immature whales of both sexes; then mature males and resting females, and finally pregnant females (Dawbin 1997). Resting and recently impregnated females are the first to leave on the southward migration, followed by immature whales and mature males. The last to leave breeding areas are cows with new-born calves (Chittleborough 1965; Dawbin 1966). Bearing in mind that we could not assess the reproductive condition of female whales except when they were accompanied by small calves, we did observe seasonal changes in composition of completely sampled groups, suggesting some staggering in migrational timing. The proportion of singletons (both males and females) decreased from winter to summer, with single females disappearing altogether after late spring. Again, mid-spring stands out with the first appearance of male/female pairs; this was also the most commonly recorded grouping off East Australia (Brown & Corkeron 1995), especially during the northward migration. The decrease in singletons of both sexes and increase in mixed gender pairs from mid-spring may be evidence of increased breeding interactions. This may be due to ‘mate guarding’, as suggested by Brown and Corkeron (1995), a notion supported by Clapham’s (1993) finding of male-female dyads on feeding grounds (also see discussion in Valsecchi *et al.* 2002). We did not test for the relatedness of pairs (but see Chapter 5), so males accompanying females could conceivably include some large male yearlings not identified as calves.

From late spring onwards the number of cows accompanied by calves was highest, although some cow-calf pairs were sighted in most months. The peak birth month for southern hemisphere humpbacks is early August (Matthews 1938, Chittleborough 1958, 1965). Though not explicitly measured, the size of calves observed off Saldanha (estimated relative to the size of the accompanying female) ranged from about new-born size in a few instances (3.96 - 4.57 m) to the suggested size at independence (between 8 and 10 m; Clapham *et al.* 1999) with the majority falling in roughly ‘half the mother’s length’ or between 5 and 6 m. This suggests considerable variation in the departure time from breeding areas, and arrival at, or transit through the study area, or may reflect some yearlings or second-year animals still accompanied by their mothers. There is some support for the latter possibility from the records of adult female humpback whales accompanied by calves/juveniles, as described in a Norwegian Whaling Statistics form (obtained from Sue Burkett, IWC), annotated by the manager of the Hangklip whaling station (K. Bernsten) in 1913 (Table 2.9). Between 21 October and 19 November, eight small whales were landed that were described as being accompanied by their mothers (or whales assumed to be their mothers) at the time they were taken, seven of which were also killed and proved to be females of adult size (12.8-15.24 m). Six of the small whales were 8.53–8.84 m long, or about the size humpback whales at 10 -11 months of age (8–10 m, Clapham *et al.* 1999). These were presumable calves from the previous year. The other two were considerably smaller (7–7.3 m), and may represent calves-of-the-year, about three months old, a finding not inconsistent with some estimates of early growth in humpback whales (Stevick 1999).

Feeding behaviour

Humpback whales have been observed to shift their feeding areas as a response to changes in prey availability in the Gulf of Maine, North Atlantic over a period of <10 years (Weinrich *et al.* 1997). At traditional feeding grounds in the Southern Ocean, Murase *et al.* (2002) showed that humpback whales associate strongly with high concentrations of euphausids and that their distribution was determined by the availability and location of prey species. They suggested that humpbacks should be able to feed equally efficiently during migration in high-density krill swarms. Such swarms of the krill belonging to the dominant species in the Southern Benguela, *Euphausia lucens*, do occur periodically off Saldanha (Stuart 1986; Pillar *et al.* 1989, 1992), though numerous other meso- and macro zooplanktonic crustaceans (other euphausids, amphipods, mysids) and small pelagic fish are found in the area that could be potential candidates for humpback prey (Hutchings *et al.* 1991; Gibbons *et al.* 1995; Gibbons & Hutchings 1996). Historical records of humpback stomach contents from the region (Olsen 1914) include copepods (‘rodaate’ in Norwegian) and fish: a stomach full of ‘herrings’ from a humpback whale taken at Donkergat in 1912 or 1913 was illustrated by Olsen (1914), while the stomach contents of four humpbacks examined there in 1926 were empty (2) or contained fish (2). One of the latter, taken on 25 June was crammed with fish noted as "?clupeoids", while the other (taken on 20 September) was filled with a pasty mass of fish scales and bones (Matthews 1938). However, four stomachs examined at Donkergat in 1962 and 1963 in the months of June (1), July (2) and August (1) were all empty (Best 1967).

Feeding by humpbacks during migration has thus far been considered opportunistic, such as the surface feeding on small ‘baitfish’ by a single humpback associated with bottlenose dolphins (*Tursiops aduncus*) observed off Queensland, Australia (Stockin & Burgess 2005) and the more recent description of a ‘supplemental’ feeding ground by Stamation *et al.* (2007), also for the Area V stock. However, Dawbin (1956) suggested that feeding opportunities could cause deviations or interruptions in the southward migration of humpback whales past New Zealand, recently confirmed by satellite telemetry (Gales *et al.* 2009), and a similar situation seems to occur off the west coast of South Africa. Although we observed actual feeding only five times, defecations were observed in almost a quarter of all groups, during months when defecation was recorded. In many cases we saw movements and concentrations of whales that suggested feeding, similar to observations at Cape Columbine in 1993 (Best *et al.* 1995). These groups almost always consisted of two or more animals, and on several occasions these smaller ‘sub’-groups formed loose aggregations of up to 20 animals that moved around in a fairly large general area. Such aggregations were first seen in December 2001, and again in the months of October 2002 and November 2007. The strong correspondence of groups seen or suspected to be feeding (based on behavioural observations) and ‘non-migratory’ groups (based on movement parameters) as shown by multivariate analysis, suggests that most groups in the general area were probably engaged in feeding.

The regular incidence of defecations seems to support the fact that feeding occurred over a number of days in the vicinity (following the reasoning of Danilewicz *et al.* 2008). We observed swarms of zooplankton containing euphausids, mysids and gelatinous organisms at the surface on at least one occasion next to feeding humpback whales (17 October 2002). Massive swarms of the krill species *Euphausia lucens* were also observed to wash up on the beach of North Bay inside Saldanha Bay during October 2002 and 2006. A plankton haul carried out near a feeding group on 26 January 2003 contained specimens of *E. lucens* and the amphipod *Themisto gaudichaudi* (identified from keys in Gibbons 1999). These findings, along with the amphipod remains found in one faecal sample, and an earlier record by Findlay and Best (1995) of an entangled juvenile humpback that had fed on stomatopods before its death, suggests that crustacean prey is not confined to euphausids.

As in October/November 1993 (Best *et al.* 1995), an examination of humpback movement patterns off the South African west coast failed to provide strong supporting evidence for a conventional bi-directional humpback migration, this despite longer seasonal coverage and clear seasonal peaks in relative abundance during early-spring and summer. These peaks, when considered in combination with the observed movement pattern pointed to activities other than migration, in particular localised feeding. In the light of this, it seems that Olsen's (1914) observations nearly a century ago, as well as those of Best *et al.* (1995) were not anomalous for the region, and that a significant component of humpback whales may make use of the area as a feeding ground. This occurs at least from October to February/March, well beyond the expected peak of the southern migration. The prevalence of this behaviour during the time when the southward migration should take place may relate to the nutritional condition of the animals, as suggested by the much lower oil yields of southward migrating humpbacks compared to north-bound ones off West Australia (Chittleborough 1965). Specifically, females that are either pregnant or nursing are likely to have a greater urgency to feed at the first available opportunity. Males humpbacks would presumably also have expended considerable energy in the breeding areas, as demonstrated for sei whales *Balaenoptera borealis* heading south that had significantly reduced testis-mass compared to during the northern migration (Best & Lockyer 2002).

The spatial extent of this feeding/non-migratory behaviour remains unclear. If we assume it to be associated with upwelling cells of high productivity in the southern Benguela system (Weeks *et al.* 2006), the range could span for about 1,000 km from Lüderitz in the north, to Cape Point in the south. Some historical observations in summer of humpback whales off the Namibian coast at Hollam's Bird Island (see John Keeler's 1830 account mentioned in Best & Shaugnessy 1979), and catches in the 19th century off Walvis Bay up to January (Townsend 1935) may support this. There are notable differences in the nature of these upwelling cells: Cape Columbine and the Cape Peninsula cells are synchronous but seasonally variable, with highest upwelling in spring and summer while the Namaqua cell (Lüderitz) is more perennial and extends farther offshore (Weeks *et al.* 2006). Movement between different cells could explain the determined northerly and southerly directionality seen from mid-spring through summer.

CONCLUSION

The movement patterns and behaviour observed in this study do not exclude the presence of a strictly migratory population component, but make it virtually impossible to identify it from these data. Grey whales (*Eschrichtius robustus*) that feed opportunistically in 'pockets' along their migration route in the eastern Pacific (Moore *et al.* 2007) are now considered to be flexible foragers. The putative migration of humpbacks appears to represent not only a continuum in terms of breeding behaviour as suggested by Brown and Corkeron (1995), but also includes a component of foraging. Based on our findings, as well as an ever-growing number of records of feeding during migration (such as Stamation *et al.* 2007), in traditional 'wintering' areas (Danilewicz *et al.* 2008; de Sá Alves *et al.* 2009) and 'rediscoveries' of previously unknown feeding grounds (Gibbons *et al.* 2003), 'flexible forager' is a label which seems equally appropriate for humpback whales.

The possibility exists that such feeding behaviour may occur at other mid-latitude locations with similar oceanographic conditions to the southern Benguela, provided that suitable prey organisms are present at sufficiently high densities. The resident population of humpback whales in the Arabian Gulf certainly proves that they are able to subsist off the monsoon and upwelling driven productivity found off Oman (Mikhalev 1997). A better understanding of the scale of this behaviour off the west coast of South Africa may only be achievable through satellite telemetry or a sub-region wide survey (ship or aerial) during the spring to summer peak, similar to the study by Moore *et al.* (2007) on grey whales.

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TABLES

Table 2.1. Summary of mean sightings per unit effort (SPUE, whale groups per 10 h of search effort), range and search effort by seasonal grouping based on monthly sub-samples (four per month).

Season	*n*	Mean SPUE (groups.10h^{-1}) ± SE	Range SPUE (min-max)	Total hours on watch	Days on watch	Daily hours on watch
Late autumn to mid-winter	12	0.69 ± 0.28	0 - 3.06	459.08	69	6.65
Late winter	8	1.19 ± 0.32	0 - 2.46	293.3	46	6.38
Early spring	8	0.71 ± 0.18	0 - 1.45	260.8	38	6.86
Mid-spring	8	3.07 ± 1.25	0.43 - 10.46	242.23	42	5.77
Late spring	8	1.51 ± 0.40	0 - 2.99	238.63	35	6.81
Early summer	7	2.46 ± 1.16	0 - 8.73	180.95	32	5.65
Mid to late summer	6	2.59 ± 0.92	0 - 6.48	127.18	20	6.36
All seasons	57	1.63 ± 0.28	0 - 10.46	1802.18	282	6.39

Table 2.2. Seasonal mean radial sighting distance from the tower to humpback groups on which a reliable theodolite fix was made (*n* = 251, shaded columns), and mean hourly visibility measured at the midline. Eight whale groups sighed within bays were excluded from this analysis. [* Seasons between which sighting-distances from tower to whales were significantly different, $p < 0.05$, Tukey's HSD test for unequal samples sizes].

Season	Means ± SE (km)		*n*		Minimum (km)		Maximum (km)	
	Whales	Visibility	Whales	Visibility	Whales	Visibility	Whales	Visibility
Late autumn to mid-winter	7.46 ± 0.74	8.20 ± 0.16	27	496	2.68	1.28	18.98	23.46
Late winter	8.61 ± 0.74	9.22 ± 0.21	25	293	2.16	2.02	16.62	26.46
Early spring	5.29 ± 0.82	8.94 ± 0.26	16	256	1.77	2.98	11.46	25.00
*Mid-spring	8.67 ± 0.55	8.18 ± 0.22	71	237	1.24	2.14	23.28	21.51
Late spring	6.40 ± 0.60	8.18 ± 0.22	32	233	1.34	2.50	13.89	23.80
*Early summer	6.18 ± 0.56	7.20 ± 0.27	49	185	2.21	1.50	25.11	19.63
Mid- to late summer	6.22 ± 0.59	6.20 ± 0.23	31	134	2.25	2.18	17.47	14.68
All seasons	7.24 ± 0.26	8.21 ± 0.08	251	1834	1.24	1.29	25.11	26.46

Table 2.3. Between-season comparison of visibility measurements at midline using Tukey's HSD test for unequal sample sizes. [* indicates significant difference between seasons, $p < 0.05$].

Season	Late winter	Early spring	Mid-spring	Late spring	Early summer	Mid- to late summer
Autumn to mid-winter	*0.010203	0.592470	0.999879	1.000000	0.091302	*0.000111
Late winter		0.752770	*0.010471	*0.025587	*0.000026	*0.000026
Early spring			0.409064	0.581084	0.000538	*0.000026
Mid-spring				0.999984	0.186617	*0.000309
Late spring					0.113501	*0.000147
Early summer						0.259254
Mid- to late summer						

Table 2.4. Seasonal mean distance from position of first reliable theodolite fix on whale groups to nearest coastline (km) and minimum and maximum distances of whales from shore.

Season	Mean ± SE (km)	*n*	Minimum	Maximum
Autumn to mid-winter	3.69 ± 0.35	27	0.48	9.34
Late winter	5.58 ± 0.75	25	1.34	15.65
Early spring	3.35 ± 0.58	16	0.58	9.93
*Mid-spring	5.81 ± 0.48	71	0.37	19.01
Late spring	3.74 ± 0.43	32	0.37	7.73
*Early summer	3.36 ± 0.45	49	0.038	20.75
Mid- to late summer	3.86 ± 0.56	31	0.58	14.55
All seasons	4.42 ± 0.21	251	0.37	20.75

Table 2.5. Seasonal sex-ratios in humpback whales biopsied in the region of Saldanha Bay, South Africa 1993-2008. [* indicates sex ratio differs significantly from parity, *p* <0.05].

Season (month/s)*	Female (%)	Male (%)	*n*	X^2	*p*
Including cows and calves (*n* = 207)					
All seasons combined	56.52	43.48	207	3.5220	0.06057
*Autumn to mid-winter (Mar.-Jul.)	21.43	78.57	14	4.5700	0.03251
Late winter (Aug.)	40.00	60.00	5	0.2000	0.65472
Early spring (Sept.)	45.45	54.55	11	0.0910	0.76303
*Mid-spring (Oct.)	66.00	34.00	50	5.1200	0.02365
Late spring (Nov.)	57.69	42.31	52	1.2310	0.26726
Early summer (Dec.)	51.43	48.57	35	0.0286	0.86577
Mid- to late summer (Jan./Feb.)	65.00	35.00	40	3.6000	0.05778
Excluding calves (*n* = 195)					
All seasons combined	58.46	41.54	195	5.5850	0.01812
Autumn to mid-winter (Mar.-Jul.)	23.08	76.92	13	3.7690	0.05221
Late winter (Aug.)	40.00	60.00	5	0.2000	0.65472
Early spring (Sept.)	45.45	54.55	11	0.0910	0.76303
*Mid-spring (Oct.)	67.35	32.65	49	5.8980	0.01516
Late spring (Nov.)	57.14	42.86	49	1.0000	0.31731
Early summer (Dec.)	51.52	48.48	33	0.0303	0.8618
*Mid- to late summer (Jan./Feb.)	74.29	25.71	35	8.2570	0.00406

Table 2.6. Mean actual swimming speed (or ‘leg’ speed) and net speed by season, with significant results from Dunn’s multiple comparison post-test on actual swimming speeds (ns = not significant).

Season	Actual swimming speed and net speed (in brackets) (km.h^{-1})				Dunn’s multiple comparison of actual swimming speeds between seasons: *z*-value (*p* value)		
	n	Mean ± SE	Min.	Max.	Autumn to mid-winter	Late winter	Early spring
Autumn to mid-winter	23	6.07 ± 0.35 (5.80 ± 0.42)	1.68 (0.94)	8.47 (8.55)	-	ns	ns
Late winter	25	6.53 ± 0.29 (6.04 ± 0.36)	3.46 (2.09)	9.32 (9.29)	ns	-	ns
Early spring	16	5.77 ± 0.61 (5.18 ± 0.71)	1.89 (0.64)	9.62 (10.47)	ns	ns	-
Mid-spring	55	4.14 ± 0.33 (3.30 ± 0.34)	0.55 (0.16)	10.68 (9.18)	3.19 (0.00313)	4.71 (0.53x10^{-4})	ns
Late spring	31	4.23 ± 0.37 (3.60 ± 0.40)	0.91 (0.091)	8.62 (8.77)	3.13 (0.0367)	3.92 (0.00183)	ns
Early summer	36	4.28 ± 0.31 (3.31 ± 0.33)	1.04 (0.41)	8.37 (7.85)	3.09 (0.0417)	3.91 (0.00191)	ns
Mid-to late summer	26	2.67 ± 0.20 (1.90 ± 0.21)	1.01 (0.13)	5.28 (4.10)	5.5 (0.1x10^{-5})	6.31 (0.6x10^{-6})	4.24 (4.78x10^{-4})
All seasons	212	4.61 ± 0.15 (3.91 ± 0.17)	0.55 (0.091)	10.68 (10.47)			

Table 2.7. Summary results from ANOSIM of pair-wise, between-season comparisons based on the trackline parameters speed, course and linearity. [* indicates significant differences between pairs of seasons, $p < 0.05$].

Season	Autumn to mid-winter	Late winter	Early spring	Mid-spring	Late spring	Early summer
	R (*p*)	*R* (*p*)	*R* (*p*)	*R* (*p*)	*R* (*p*)	*R* (*p*)
Late winter	-0.023 (0.937)					
Early spring	0.189 *(0.003)	0.174 *(0.007)				
Mid-spring	0.014 (0.352)	0.059 (0.106)	0.017 (0.371)			
Late spring	0.061 (0.054)	0.115 *(0.003)	0.188 *(0.038)	-0.038 (0.878)		
Early summer	0.061 (0.075)	0.114 *(0.009)	0.118 *(0.031)	-0.014 (0.681)	-0.018 (0.814)	
Mid- to late summer	0.014 (0.352)	0.478 *(0.0001)	0.256 *(0.005)	-0.009 (0.545)	0.101 *(0.005)	0.065 *(0.033)

Table 2.8. Description of groups showing feeding or feeding-like behaviour seen from land and/or boat. [Asterisk indicates direct observation of feeding; Def. = defecation seen, yes (y) or no (n)].

Date*	Seen from	Group size	Def.	Description of behaviour
30 Oct 01	Land	2	n	Milling about, apparently feeding
03 Nov 01	Boat	3	y	Dark pink defecation
10 Nov 01	Boat	2	y	Bright pink defecation
06 Dec 01	Land	3	n	Slowly moving south, apparently feeding. Associated with seven dusky dolphins (*Lagenorhynhcus obscurus*)
16 Dec 01	Boat	2 and 2	y	Two groups seen defecating
17 Dec 01	Land/boat	±20 and 3	y	Large, loosely associated group identified as 11 smaller groups from land. Milling and suspected feeding behaviour. Defecation seen in this group and during a later sighting of three animals
19 Dec 01	Land	15-20	n	At least two sub-groups of animals scattered over large area, milling about
11 Sept 02	Land/boat	1	n	Small animal with erratic movements, long dives, spending brief time at surface, Cape fur seals (*Arctocephalus pusillus*), seabirds and unidentified dolphins displaying feeding behaviour nearby
*17 Oct 02	Boat	8	y	Combination of seven earlier sightings. Pairs of animals doing sideways co-ordinated surface lunges, mouths open and ventral grooves distended. Jellies, euphausids and mysids seen in water. Defecation seen
29 Oct 02	Land	2 and 3	y	Two separate groups, one milling and possibly feeding. Second group surface active, defecation seen
30 Oct 02	Boat	6 and 2	y	Defecation seen in first group that was made up of a cow-calf pair and escort, later joined by another pair and singleton. Later sighting of two also defecated
*13 Dec 02	Land/boat	2	n	Milling and feeding lunges, erratic movement in circles, apparently along thermal divide (16^{O}C on one side and 17^{O}C on other)
10 Jan 03	Boat	2 and 1	y	Cow-calf pair and later single animal. Bright, brick red defecation by both groups
*26 Jan 03	Land/boat	3 and 2	y	One group seen from land to be lunging, also surface active and milling about. A different group seen from boat also lunged. Bright pink defecation seen during intercept. Blue whale *Balaenoptera musculus* sighted displaying suspected feeding behaviour, swimming along a foam line parallel to shore
12 Oct 04	Boat	5	y	Two humpbacks and three southern right whales. Defecation seen
08 Nov 04	Boat	2 and 2	y	Defecation seen in two groups
29 Nov 04	Boat	1	y	Individual travelling slowly while defecating. Later resighted and defecated whilst lobtailing (five stools produced in five minutes)
02 Dec 04	Boat	9	y	Single humpback with eight southern right whales, defecation by both species
*23 Mar 05	Boat	2	n	Lunge feeding
24 Nov 05	Boat	3	y	One animal slightly separate from others and evasive. Defecation seen
*12 Oct 06	Boat	3	n	Two humpbacks and one southern right both apparently feeding. Humpbacks made sideways lunges through “mysid” patch. Plankton sample collected
19 Nov 06	Boat	1 and 5	y	Single animal, later resighted as part of larger group, defecation seen both times
22 Nov 06	Boat	2	y	Defecation seen
26 Nov 06	Boat	2	y	Evasive group, defecation seen
29 Nov 06	Boat	1	y	Evasive pair, apparently feeding. Defecation seen
14 Nov 07	Boat	14-20	n	Large association of several sub-groups, apparently feeding, associated with feeding seabirds

Table 2.9. Details of humpback whales accompanied by 'calves' taken at Hangklip whaling station, South Africa, in 1913 (length data converted from whole feet or inches) from notes by the manager of the station, K. Bernsten.

Date	Length of adult female (m)	Accompanying 'calf'		Notes on records (translated from Norwegian)
		Length (m)	Sex	
21 October		8.53	F	In company of mother that escaped
31 October	14.33	8.53	M	These two animals together so assumed to be mother and calf
01 November	14.63	7.32	M	ditto
	12.80	7.01	F	ditto
10 November	15.24	8.84	M	Young one shot 1st then the mother. Adult pregnant with 12.7 cm foetus
15 November	14.02	8.53	F	These two animals together so assumed to be mother and calf
18 November	14.02	8.84	M	ditto
19 November	14.63	8.84	M	ditto

FIGURES

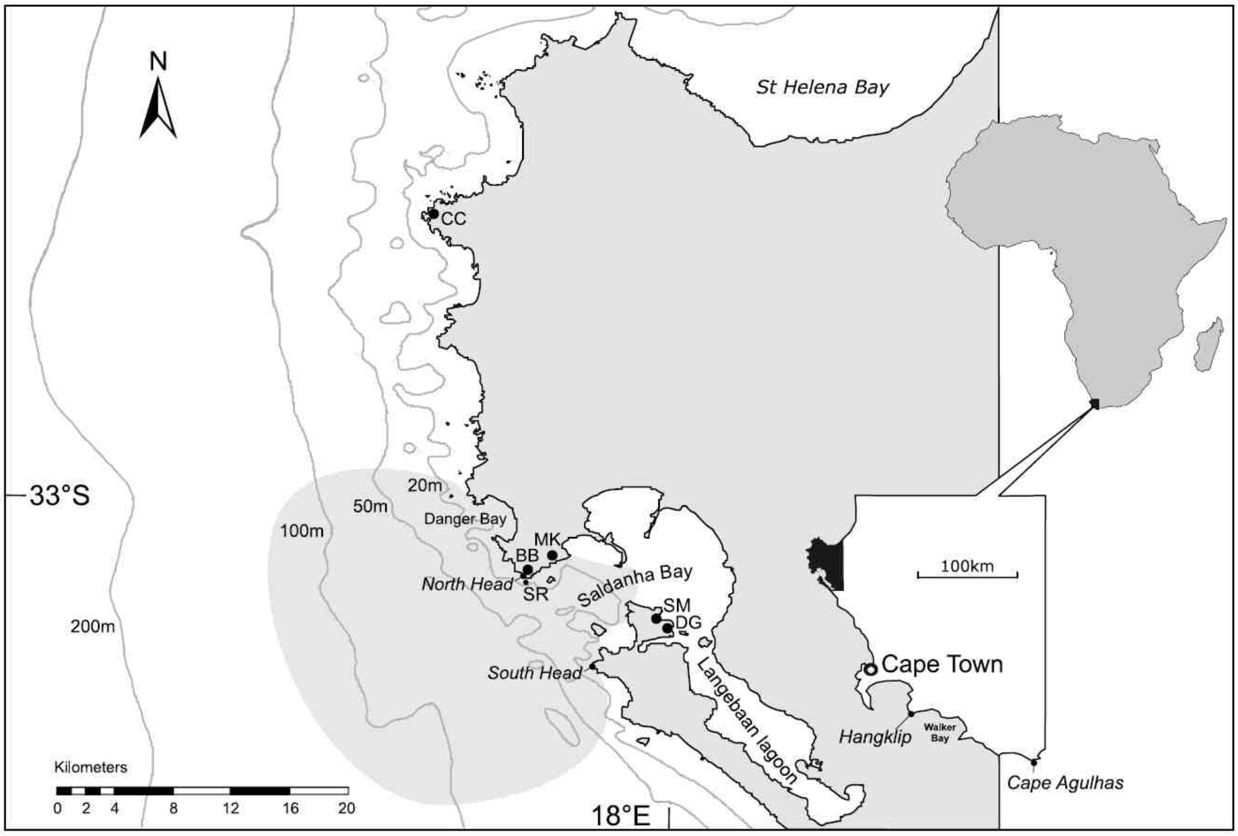

Figure 2.1. The location of the study area on the west coast of South Africa and detailed localities mentioned in the text (BB = Baviaansberg, MK = Malgaskop, CC = Cape Columbine, DG = Donkergat, SM = Salamander, SR = Schooner Rock). The approximate extent of the search area is indicated by lightly shaded area.

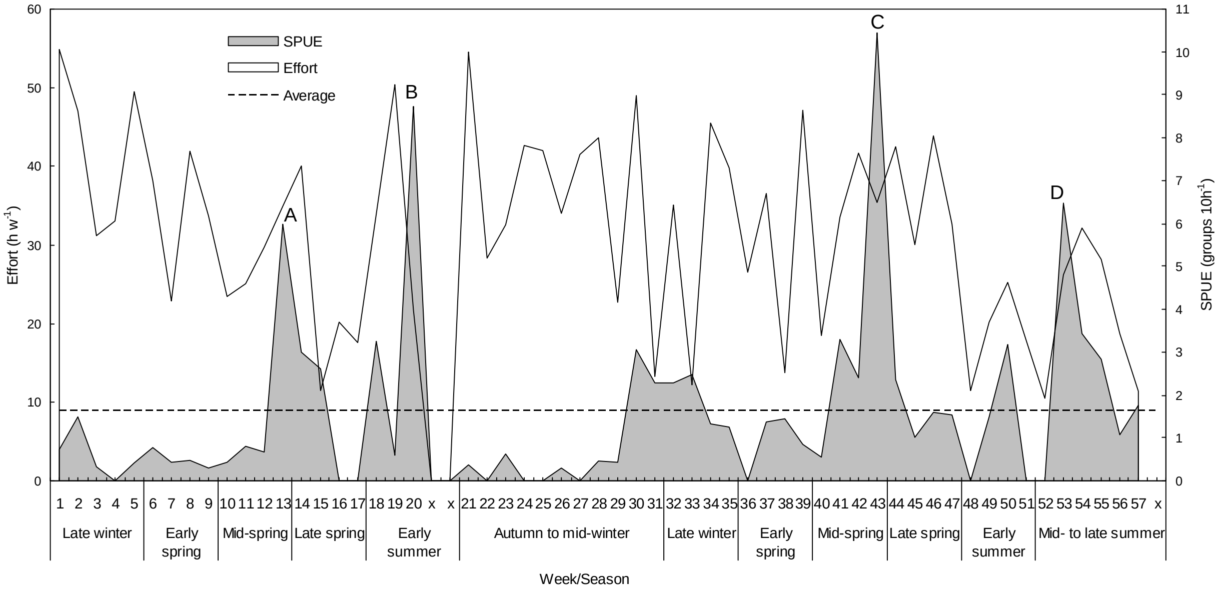

Figure 2.2. Sightings per unit effort (SPUE) of humpback whale groups and search effort per week for two field seasons 24 July – 20 December 2001 (wks 1-21) and 6 May 2002 to 15 February 2003 (wks 22-58). Solid line is average SPUE (1.63) over entire study period. Peaks marked A - D are referred to in the text.

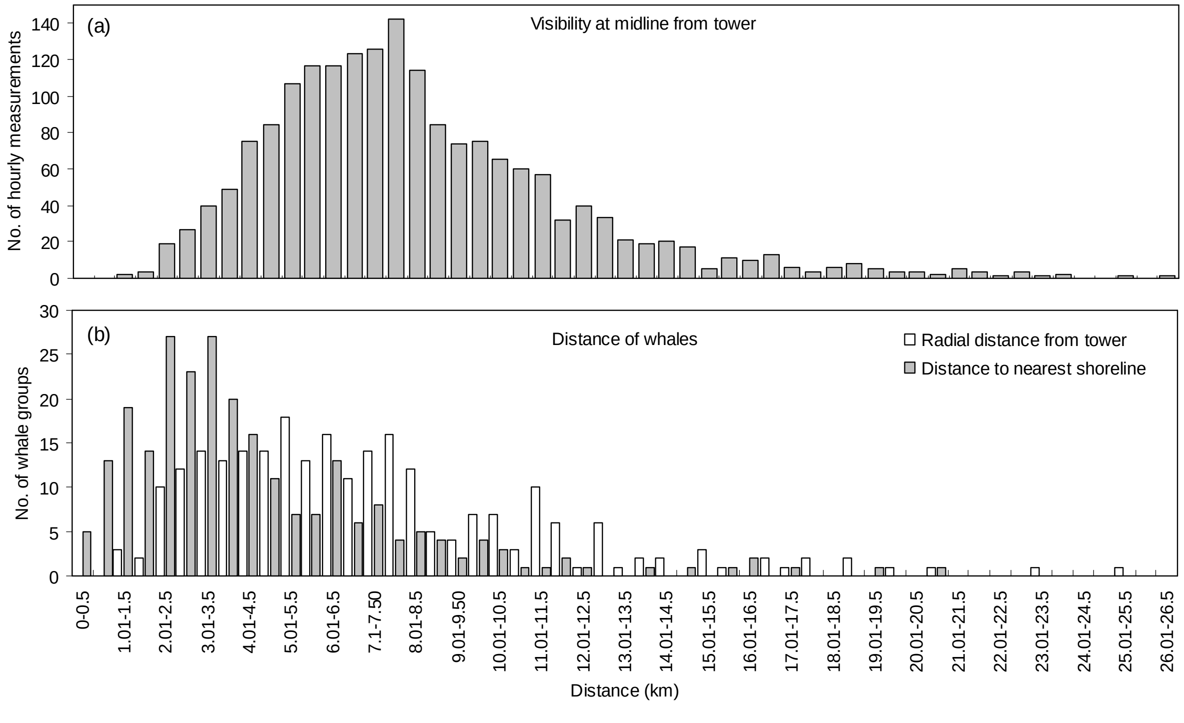

Figure 2.3. Frequency distribution of radial sighting distances measured to all humpback groups fixed by theodolite (*n* = 251, excluding eight groups sighted within bays) and hourly midline visibility measurements taken (*n* = 1834) per 0.5 km bin.

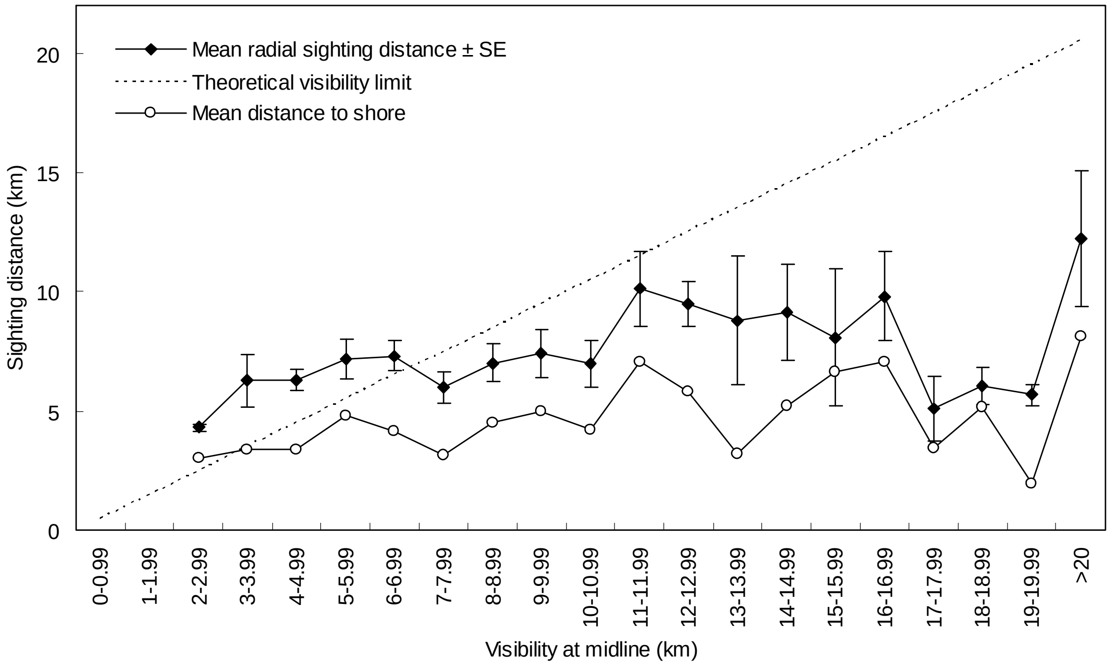

Figure 2.4. Mean radial sighting distances (km ± SE) from tower, and calculated distances to nearest shoreline, of whale groups at prevailing visibility at the midline (per 1 km bin) as measured by theodolite. Dotted line indicates theoretical visibility limit.

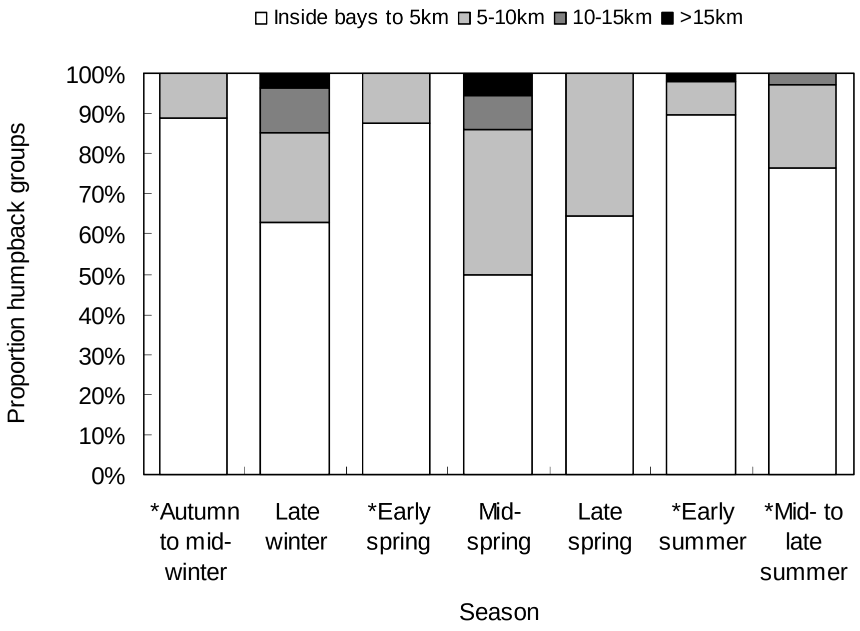

Figure 2.5. Seasonal breakdown of distance from shore (km) of humpback groups (*n* = 259). Seasons where numbers of groups within and beyond 5 km zones differ significantly (X^2, $p < 0.05$) are indicated by asterisk.

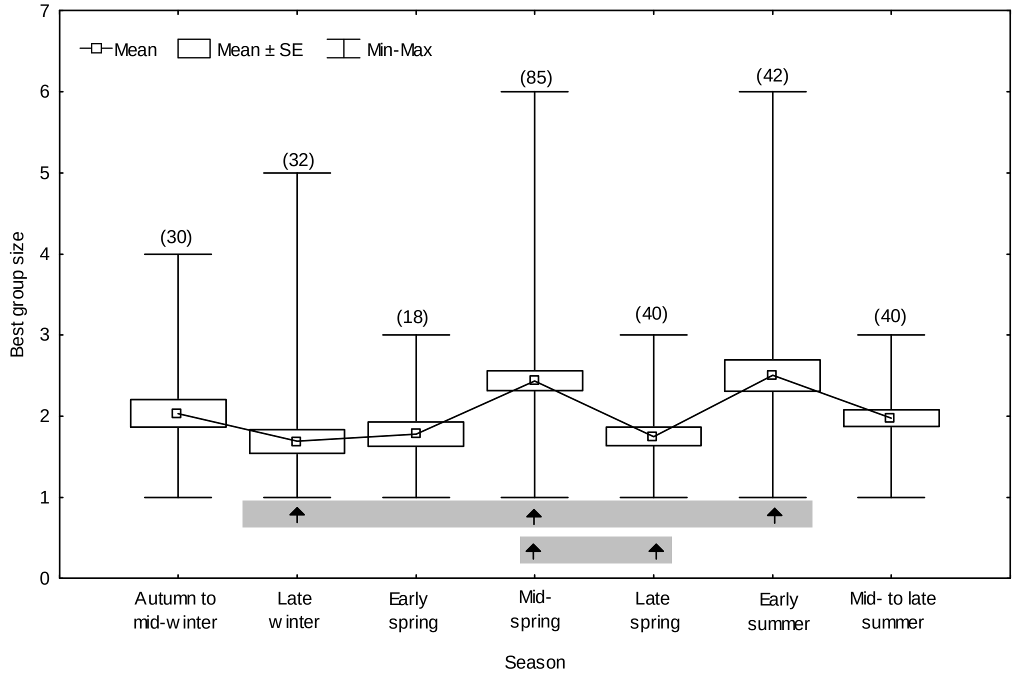

Figure 2.6. Seasonal mean (range = whiskers and SE = boxes) of best estimates for group size (sample sizes in parentheses) as observed from land, excluding two outlier groups (*n* = 287). Shaded rectangles below plot summarise significant results from multiple comparison *post-hoc* test with arrows indicating significantly different seasons.

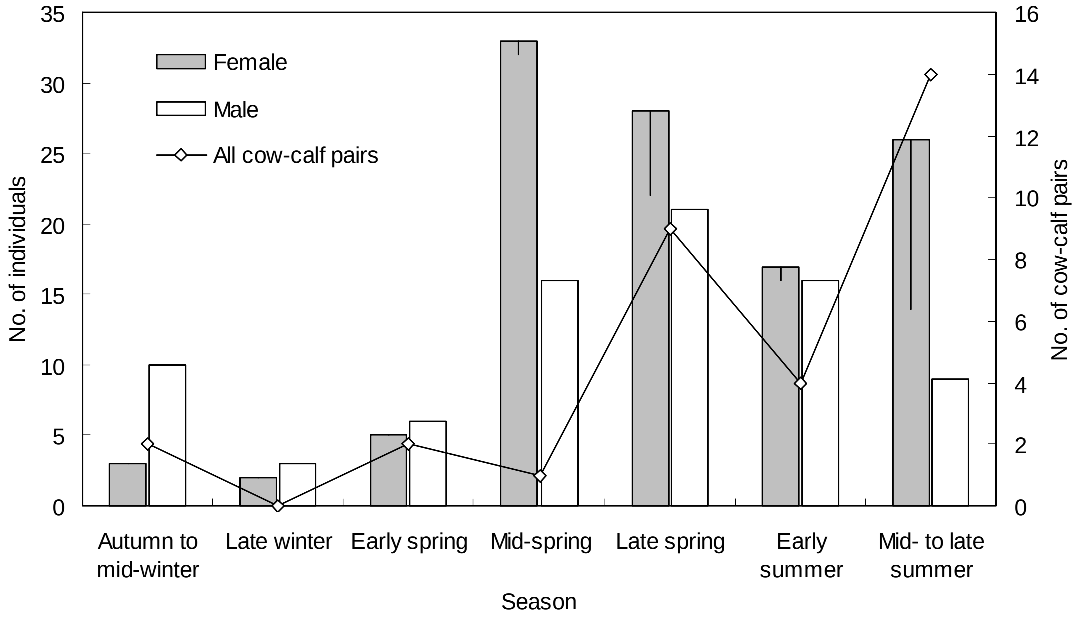

Figure 2.7. Numbers of male and female whales (including 20 cows, as indicated by the solid lines within the bars) per season as determined genetically (*n* = 195). Calves (12) were excluded, but total number of cow-calf pairs seen per season is indicated by line plot.

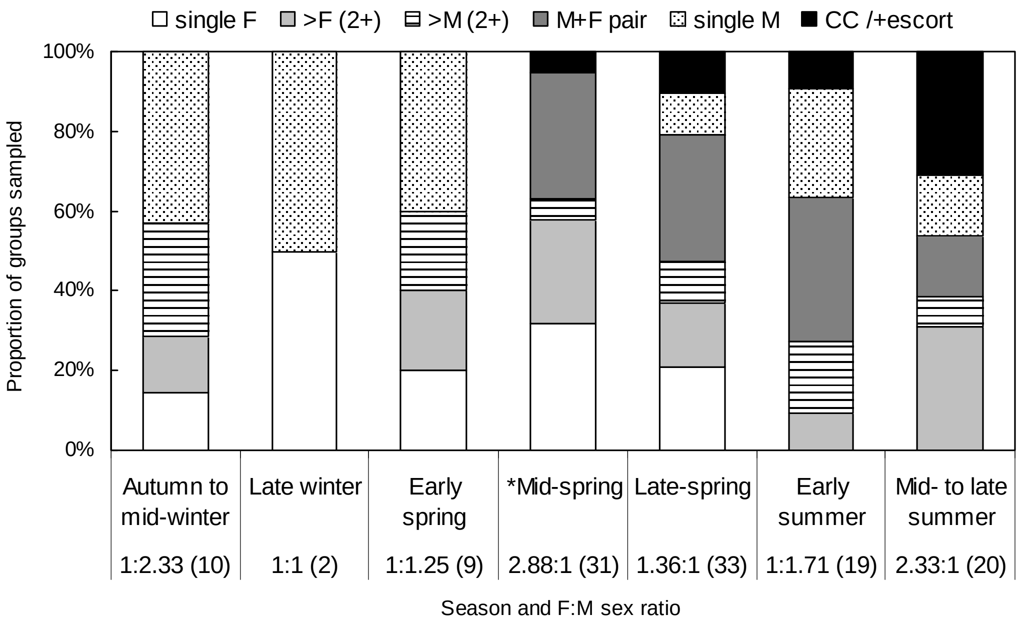

Figure 2.8. Seasonal composition of humpback whale groups that were completely sampled genetically, 2000 - 2006. Female to male sex ratio and total number of individuals (in parentheses) indicated below each season. Asterisk = significant female bias ($X^2 = 7.258$, $p < 0.05$). Key to legend: CC = cow calf pairs, including two with (male) escorts; M + F pair = male and female; >F = all-female duos and groups of three or more with female bias, >M = all-male duos and groups of three or more with male bias; single male (M) and single female (F).

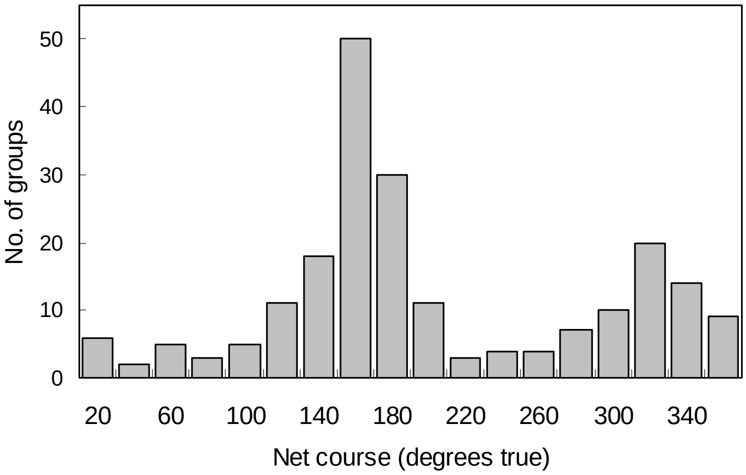

Figure 2.9. Frequency distribution of net course in degrees true of 212 humpback whale groups tracked from North Head, Saldanha Bay.

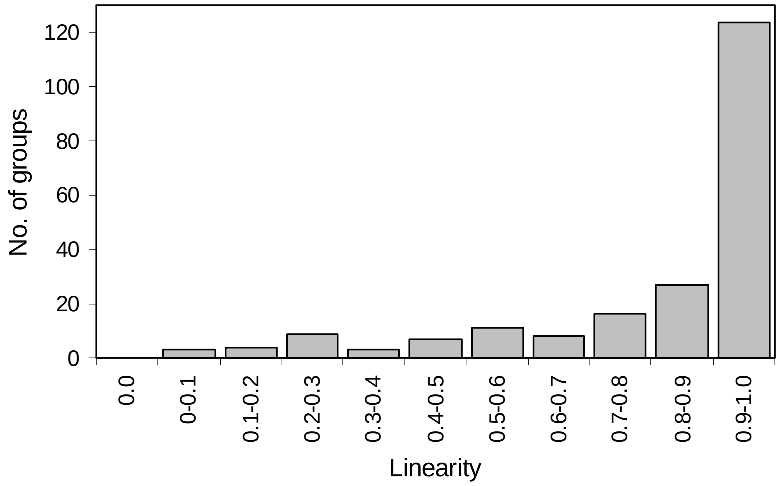

Figure 2.10. Frequency distribution of linearity of movement of 212 humpback whale groups tracked from North Head, Saldanha Bay.

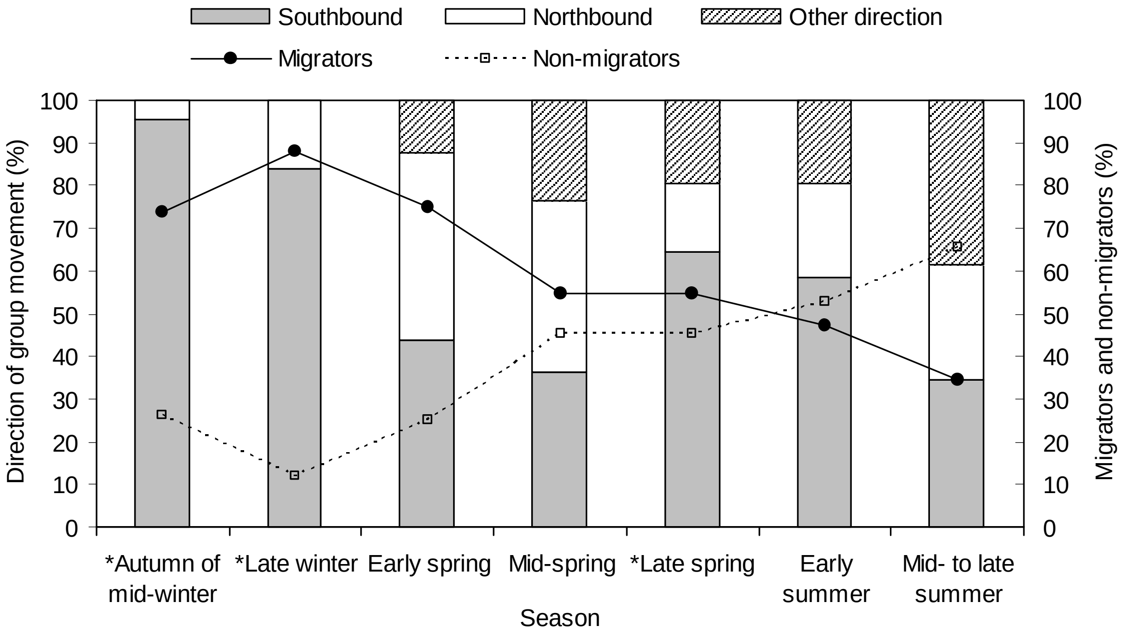

Figure 2.11. Directionality (net course) and linearity of movement of humpback whales groups (*n* = 212) by season. Bars show cumulative frequency of occurrence of groups that were southbound (100-200^{O}), northbound (280-360^{O}) or heading in other directions, based on net course (degrees true). Asterisk indicates seasons with significant ($p < 0.05$) directionality as determined by Rayleigh's test. Line plots show percentage of "migrating" (linearity ≥0.9) or "non-migrating" (<0.9) groups seen.

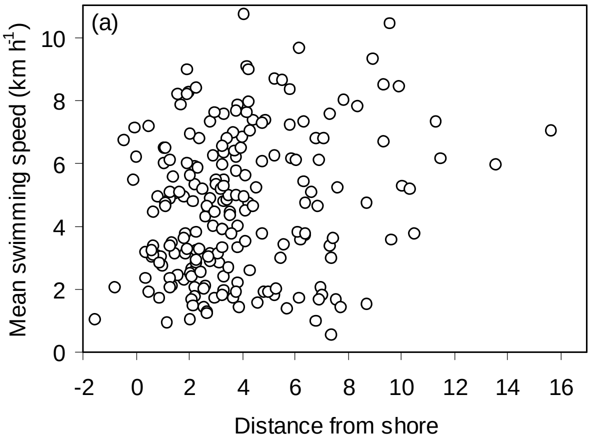

Figure 2.12(a). Relationship between mean swimming speed (km.h^{-1}) and distance of whale groups from the shoreline (km).

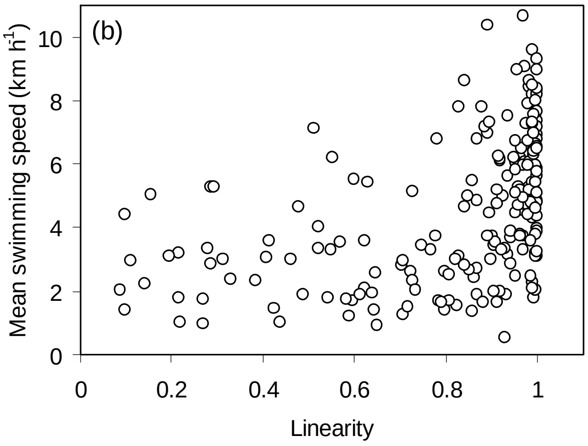

Figure 2.12(b). Relationship between mean swimming speed (km.h^{-1}) and linearity of movement of humpback groups.

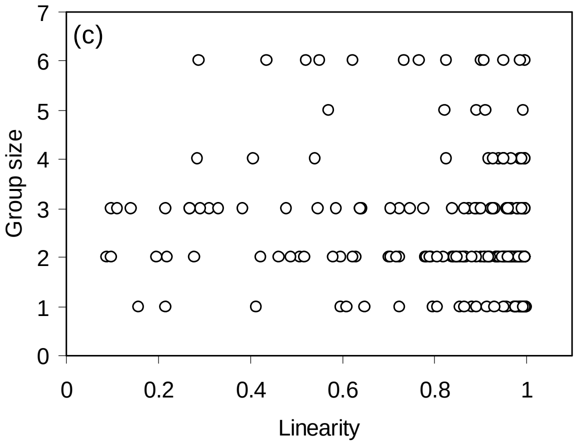

Figure 2.12(c). Relationship between size of humpback groups and linearity of movement.

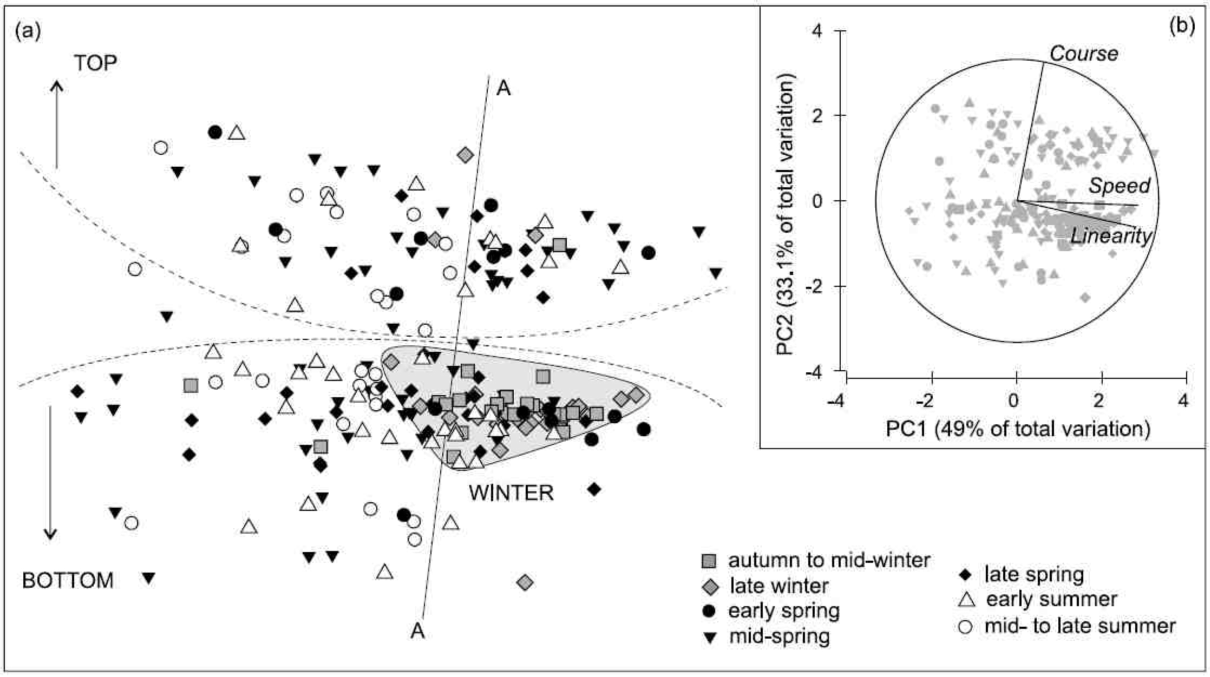

Figure 2.13: (a) Non-metric multi-dimensional scaling (MDS) ordination plot of seasonal samples based on the combination of movement parameters (normalised, Euclidian distance, stress-value = 0.1). Dashed lines indicate the top and bottom groupings and shaded shape encloses the majority of autumn/winter samples. Line A represents the right-hand limit of all mid- to late summer samples. Shape B1 includes the northbound (280-360 ^{O}) groups and B2 the southbound (100-200 ^{O}) groups; and (b) Principal Component Analyses (PCA) of seasonal samples of whale movement parameters with those responsible for most variation (speed and linearity horizontally and course vertically) overlaid onto the scatter plot.

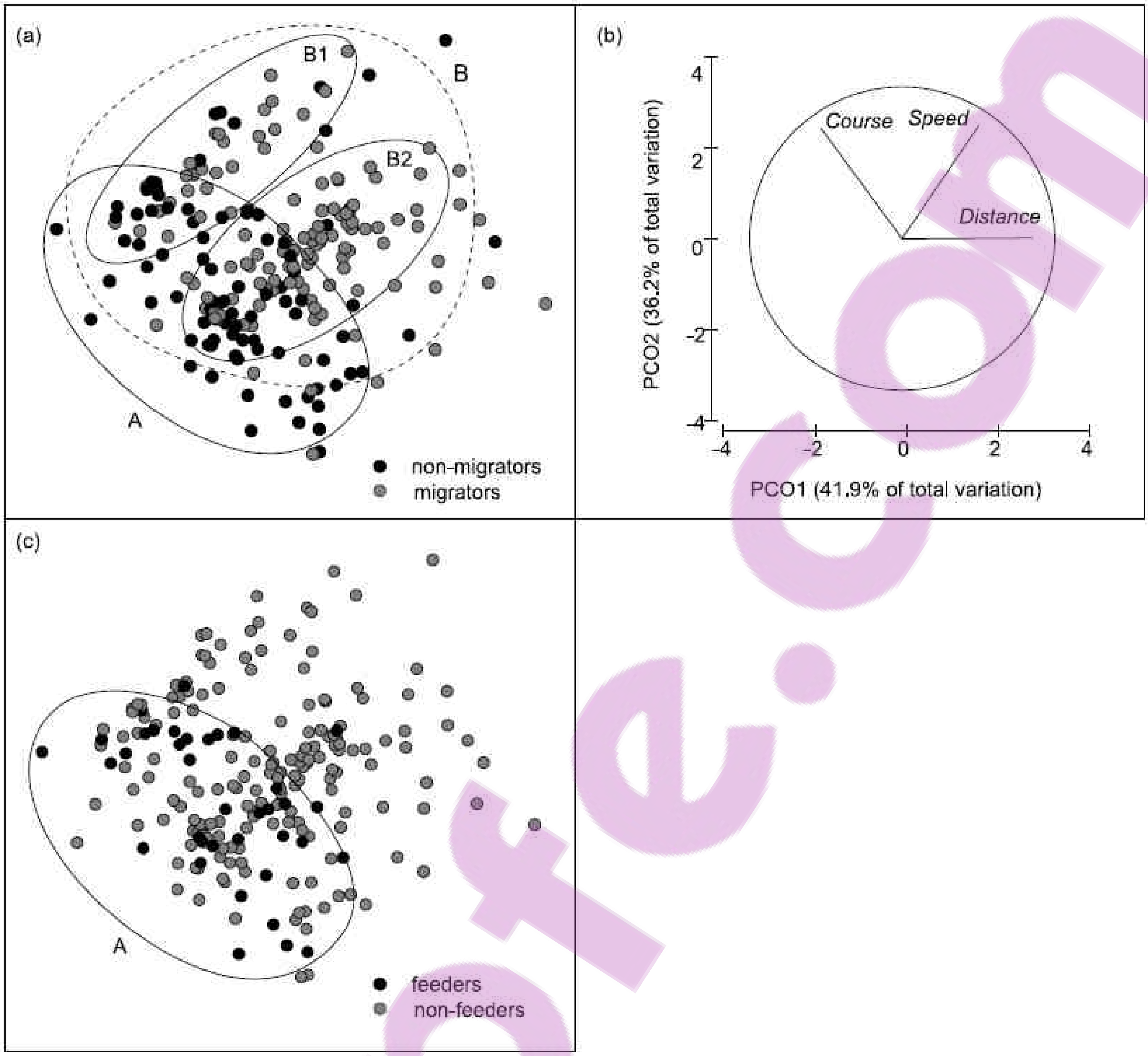

Figure 2.14: (a) Non-metric MDS ordination of migrators (linearity ≥0.9) and non-migrators (<0.9) based on the parameters speed, course and distance from shore (normalised, Euclidian distance, stress-value = 0.15). Group A (enclosed by the solid line) indicates non-migratory grouping, and group B (dashed line) migrators; (b) shows the PCA axis and parameters that best explain the clustering seen in 2.14(a); and (c) shows the same MDS plot with feeding and non-feeding as the distinguishing factor.

Chapter 3 - Shore-based observations of seasonality and movements of southern right whales *Eubalaena australis* off Saldanha Bay, South Africa

"The Council of Seventeen brought up the question [of whaling] again in 1723, suggesting Saldanha Bay as a good locality, but the project was not viewed with any favour by the officials at the Cape. It was pointed out that the whales were not 'walvischen' (Greenland whale) but 'noord-kapers' (small South Sea black or 'right' whale), and that they were not met with permanently either in Table or Saldanha Bays, but came in mostly during the rainy season when the sea was rough and whaling proportionately more difficult; further, that the water being comparatively shallow the harpooned fish rose more frequently and thus retained its strength longer, carrying boats far out to sea and causing loss of gear, etc. when cut loose."

"…According to that document [a 'Memorandum regarding the whale fishery at the Cape' by Governor the Earl of Caledon, 1807], Hendrik Bundle, in the employ of Mr. van Hall, deposed 'that in the year 1790 in St. Helena Bay there were so many whales that the Americans cut merely their heads off for the whalebone and let their carcases with the blubber float away; that there were about 20 ships which procured together about 400 whales in the course of three months'. Another employé, James Castles, affirmed 'that in the year 1791, he lay with 32 sail of whalers in St Helena Bay; that his ship procured in nine weeks 1500 barrels of oil, and that all the other ships completed their cargoes'… ".

"…It may be well to sound a warning note here. Since this chapter was written there has been immensely increased activity in the [whale product] trade; attracted by dazzling dividends of from 30 per cent. to 100 per cent. earned by pioneer companies at the Cape and Natal, many new establishments are being started on the coast……… Looking to the enormous slaughter of whales that must inevitably occur if all these ventures are to succeed, it becomes a serious question whether legislative action should not at once be taken to enforce a Close Season or other protective measures, before whales are utterly exterminated in our seas".

W.W. Thompson – *The Sea Fisheries of the Cape Colony* (1913)

INTRODUCTION

The first whales to be encountered by early European explorers near the coast and in the bays of the south-western Cape of South Africa were most probably southern right whales *Eubalaena australis* - then referred to as the 'small South Sea black, or right whale'. Accounts by Dutch colonists in the 1600s make mention of the presence of whales in Table Bay, and describe some of the (often unsuccessful) early attempts at harpooning them (Thompson 1913). They further mentioned a number of other localities including Saldanha and St Helena Bays, that, together with Table Bay were known as the 'Cape of Good Hope' grounds (see Figure 3.1a), where whales were apparently abundant, thus showing good potential for shore-based whaling. However, it only became an established industry shortly before British occupation in 1795 (Thompson 1913; Best 1970). At St Helena Bay, French, British and American whaling vessels (Richards & Du Pasquier 1989) had by this time (between the years 1785-1792) already taken a minimum estimated total of 1,484 right whales (Best 2006). By the 1830s the 'local populations' of right whales in these bays had essentially been depleted, a situation that persisted until comparatively recently, despite full protection of the species since 1935 (Best 1970; Best & Ross 1986). Right whales in St Helena Bay were not only abundant during those early years, but they also appeared to occur outside of the expected seasons, including during the summer months (Richards & Du Pasquier 1989; Best 2006).

Arguably the best studied of any large whale species in South African waters the southern right whale's recovery from whaling has been monitored since 1969 by means of aerial surveys (Best 1990, 2000). Apart from elucidation of the population's demography (e.g. Best *et al.* 2001), data from these surveys have been used to describe their coastal distribution (Best 2000), group composition (Best *et al.* 2003), and environmental factors that may affect these (Elwen & Best 2004a, b). It is now well understood that sheltered bays on the south coast (particularly those at St Sebastian Bay, de Hoop, and Walker Bay; Figure 3.1a) are favoured by (principally) right whale females for calving and nursing of new-born calves during winter (Elwen & Best 2004c), with the peak calving season being in August (Best 1994). Nevertheless, aerial surveys routinely covered only the south coast between Muizenberg (34^{O}07'S, 18^{O}28'E) and Nature's Valley (33^{O}58.8'S, 23^{O}33.6'E) and on the few occasions on which the survey had been extended up the west coast, coverage was limited to September or early October (Best 2000). Similarly, shore-based observations in this area have been confined to a single month's duration (October/November) as part of a pilot study directed at humpback whales at Cape Columbine (Best *et al.* 1995). Consequently, the distribution and seasonal occurrence of right whales off the west coast of South Africa have until recently, gone largely undescribed.

Here we present observations on the seasonality, movements and behaviour of right whales made during a shore-based project on humpback whales *Megaptera novaeangliae* off Saldanha Bay (Barendse *et al.* 2010), the duration and seasonal coverage (14 months over two years) of which greatly exceeded those of any previous studies in the region.

MATERIAL AND METHODS

Study area and data collection

The study area, period and data collection were identical to those described fully in Chapter 2 (Barendse *et al.* 2010) for humpback whales. In brief: a watch was kept on days with suitable sighting conditions from a shore-based lookout situated on the North Head of Saldanha Bay (Figure 3.1b), during two periods of fieldwork: 24 July to 20 December 2001, and 6 May 2002 to 15 February 2003. The area was searched both by naked eye and binoculars by teams of 2 - 4 observers. Attempts were made to track all groups of whales sighted, using a Wild T1 manual theodolite (equipped with a 22x telescope), where a group was defined as one or more individuals that were no further than about 100 m from each other, and showing similar movement patterns and/or behaviour. The minimum data collected for each whale group at each surfacing event (from hereon referred to as a theodolite 'fix') included a time (to the nearest second), simultaneous vertical and horizontal angles (to the nearest second) of the sighting as measured by the theodolite, the behavioural cue (body, blow, breach, splash or slick) that was fixed upon, and the best estimate of group size. Because the primary study animal of this project was the humpback whale, the theodolite tracker would prioritise obtaining fixes on this species first, in the few situations where more than one species of whale were sighted simultaneously. However, the aim throughout was to track all whale groups sighted and as a minimum, to obtain a fix on at least three separate surfacings, regardless of the species. Observers would still continue to monitor the movements of a group after successfully tracking it, and record another fix from time to time.

Weather permitting, a 6 m semi-rigid inflatable boat was directed by the shore-based personnel to all sightings within a reasonable distance (<20 km) from the mouth of Saldanha Bay for a small vessel to intercept. Furthermore, the boat would also intercept groups spotted by its crew, without assistance from land. Although priority was given to intercepting humpback whales, attempts were made to intercept all available whales. Data collected by the crew and reported here for right whales are limited to GPS position, group size, composition, and selected behaviours (see below).

Seasonality

Seasonal groupings of data identical to those described in Chapter 2 (Barendse *et al.* 2010) were used; *viz.* data collected in the same month in different years were combined into a single seasonal sample, and are referred to by the season's name, unless stated otherwise. This resulted in a total of seven 'seasons': autumn to mid-winter (May and June 2002, July 2001/2002), late winter (August 2001/2002), early spring (September 2001/2002), mid-spring (October 2001/2002), late spring (November 2001/2002), early summer (December 2001/2002), and mid- to late summer (January and February 2003).

Trackline and spatial analysis

The methodology followed here to construct a trackline from theodolite fixes is identical to that described in detail in Chapter 2. In the event of more than one fix taken per surfacing, a single one was selected giving priority to cues in the following order: body, splash, blow, slick and breach. Three or more fixes taken during sequential surfacings made up a trackline (or 'track'). The software program *Pythagoras* (Gailey & Ortega-Ortiz 2000, 2002) was used to calculate the longitude and latitude from theodolite readings at each fix, with corrections for tidal fluctuations and refraction included. These co-ordinates (in decimal degrees) were imported into a Global Information System (GIS) (*ArcMap* ™ 9.2 and *Arcview* ™ 3.3 from ESRI ®, Redlands, CA) for further spatial analysis and mapping, and the distances of whale groups (from the first fix of a track) to the nearest 'smoothed' coastline (i.e. excluding major bays) were calculated for all groups with at least one reliable fix (n = 450).

Trackline analysis was conducted in *Pythagoras* (see Chapter 2 for detailed account) for all tracks with three or more reliable fixes at different surfacings (n = 362), and the following parameters calculated: (1) mean actual swimming speed or 'leg' speed in $km.h^{-1}$ (the unweighted mean of swimming speeds calculated for each leg); (2) net speed ($km.h^{-1}$), the linear distance travelled between the first and last fixes of a track divided by the duration of the track; (3) linearity, a migration index, expressed as a decimal fraction between 0 and 1, where near-straight lines have values closer to 1; and (4) net course, the bearing calculated between the first and last fixes of a track, in degrees true.

Behavioural observations

No focal animal behavioural observations were made during sighting and tracking, but the general behaviour attributed to the entire group was noted. Behaviour was classified as one of seven broad types: (1) 'Milling', or slow, non-directional movement; (2) 'Passive', or non-energetic behaviour other than milling, such as logging and sailing; (3) 'Aerial active', or high energy behaviour such as breaching, tail or flipper slapping, or combinations of these; (4) 'Possible feeding', or movements that suggested feeding such as frequent short dives, open mouth, etc.; (5) 'Individual surface active', or individual whales displaying surface activity other than described under (3); (6) ‘SAGs’, or surface activity in groups of two or more (excluding aerial displays), presumably associated with courting or mating (see Best *et al.* 2003); and (7) ‘Travelling’, or noticeably directional movement, sometimes associated with other active and passive behaviours. In cases where both passive (including milling) and active behaviours were seen in the same group, the most active behaviour was selected. Behavioural data collected during boat intercepts were limited to noting encounters with cow-calf pairs and surface active groups (SAGs), and observations of possible feeding and actual defecations.

RESULTS

Search effort and sightings

Search effort took place on 282 days for a total of 1,802.18 hours, during which 669 groups of southern right whales, and four groups containing both southern right and humpback whales, were sighted on 188 separate days. The relative sighting rate was calculated as Sightings per Unit Effort (SPUE), and expressed as number of whale groups seen per 10 hours of searching (Figure 3.2). Although attempts were made to avoid duplicate recording of the same sighting on any one day, it is possible that the same individuals or groups were recorded more than once on the same day, either after being ‘lost’ by observers and re-sighted, or by groups splitting or combining with others, so these numbers should be considered indicative of relative rather than absolute abundance. The search effort was highly variable, sometimes being absent for up to a week (Figure 3.2) as a result of unfavourable sighting conditions (see Chapter 2 for a full discussion). A notable feature of SPUE distribution (Figure 3.2) is that right whales were present in all but four weeks of the study period, the exceptions being weeks 21 and 22 (from 7 - 20 May 2002), week 31 (22 - 31 July 2002), and week 57 (8 - 15 February 2003). There was an overall significant difference between monthly SPUE values based on the weekly (pooled) seasonal samples (Table 3.1; $n = 57$, Kruskal Wallis ANOVA, $H = 25.83$, df = 6, $p = 0.001$). The sighting rates in all winter months were generally lower than the overall average rate of 4.14 groups per 10 hours (Figure 3.2), this despite high and relatively consistent search effort. During autumn to mid-winter the SPUE was the lowest recorded and differed significantly from early spring ($z = 3.45$, $p < 0.012$), mid-spring ($z = 3.60$, $p < 0.007$), and early summer ($z = 4.26$, $p < 0.004$), as determined by a Dunn’s multiple comparison post-test. In both field seasons from about the last week of late winter (indicated by ‘A’ in Figure 3.2), there was a sharp increase in SPUE up to a peak in mid-spring (‘B’, Figure 3.2). The sighting rates then dropped, to rise again in late spring, although this was more the case during the first field season (indicated by ‘C’). The highest overall SPUE was recorded during an extended period of two months with generally high sighting rates, starting on 1 December 2002, the first week of summer (week 48) and lasting until the end of January 2003 (week 55), with the highest peak recorded in the first week of that month (‘D’ in Figure 3.2). Early summer was also the season with highest mean SPUE, at almost one group seen every hour (Table 3.1).

Distance from shore

A frequency distribution of distance of sightings from shore (Figure 3.3) shows southern right whales to have an extreme near-shore distribution. The groups sighted within 1 km from the coastline abutting the open ocean, between the heads of bays, or in the visible areas inside bays (80 in Saldanha Bay/Langebaan Lagoon, four in Danger Bay, and one in Plankiesbaai - see Figure 3.1b for localities) made up nearly half (48.7%) of the total of the 450 groups seen from the shore. The majority of the remaining groups (45.8%) were located in the 1 – 5 km zone, while only 25 groups (5.6%) were spotted beyond 5 km. However, the share of groups between the inshore (bays and <1 km, n = 219) and offshore zones (≥1 km, n = 231) did not vary significantly from an expected 1:1 ratio (Table 3.3). The distribution of boat intercepts from the shore (Figure 3.3) shows an even stronger near-shore distribution than shore sightings, with 49.6% (118 groups) of intercepts occurring inside bays (compared to 18.9% of shore sightings). Moreover, unlike groups tracked from land, the overall proportional distribution of the intercepts between inshore (bays and <1 km) and offshore (> 1 km) zones varied significantly from an expected even distribution, with the majority (n = 159) occurring in the inshore zone (X^2 = 26.89, df = 1, p < 0.001). This is strongly suggestive that the boat favoured intercepting right whale groups located inside bays or close to the shore, although the two distributions are not entirely independent, since the boat was informed about some sightings by the land-based observers.

The overall mean distance from the shore, excluding those seen in the bays, was 2.14 km ± 0.09 (SE) (Table 3.2, n = 365) and the maximum distance recorded from the shore was 9.16 km. A Kruskal-Wallis ANOVA by ranks showed a highly significant difference of distance from the shore between seasons (H = 46.564, p < 0.0001, df = 6, n = 365) and a Dunn’s multiple comparison post-test showed that early summer differed significantly from late winter and all three spring seasons (September, October, November) respectively, while mid-to late summer differed significantly from late winter (Table 3.2). These two summer seasons had mean distances farther than the overall average; 2.94 km ± 0.18 (SE) for early summer and 2.60 km ± 0.25 (SE) for mid-to late summer; this despite the maxima recorded during these seasons not being the highest. A seasonal breakdown of distance of tracked whale groups by distance zone, *viz.* inside bays, 0 – 1 km, 1 - 2 km, 2 - 4 km and >4 km (Figure 3.4) reveals that from mid-winter to early spring, the majority (>60%) of groups were sighted either inside bays, or within the 1 km range from the shore. Conversely, in summer months groups beyond 2 km made up about 60% of sightings while the bay-dwelling and near-shore (<1 km) components dwindled. Whale groups in the 1 - 2 km range remained relatively constant across seasons with the exception of autumn to mid-winter, when a sizable proportion of groups was located in this zone, and the ‘inside bays to 1 km’, and >2 km components were more or less equal (Figure 3.4). Given that overall, the shore sightings were distributed evenly between the inshore and offshore zones (see above) the hypothesis that this distribution was maintained during all seasons was tested. This was rejected for five of the seasons, with more groups being seen inshore in late winter, mid- and late spring, and more groups offshore in all summer seasons (X^2, Table 3.3).

Trackline analysis

The four mixed-species groups mentioned above were excluded from trackline analysis. For 450 right whale groups at least one reliable fix was obtained, and the distance to the nearest shore calculated, while trackline analysis could be carried out for 362 groups. These groups were tracked on average for 1.018 h ± 0.043 (SE) with the shortest track lasting only 4 min and the longest 5.64 h. With southern right whales known to show preference for sheltered bays on the south coast (Elwen & Best 2004a), and given the prominence of the bay-dwelling component as shown above (Figures 3.3 and 3.4), the movement parameters for groups tracked inside and outside the major bays were compared, where possible.

Direction and linearity of movement

Since movement for whale groups located inside the bays would be constrained by topography, the calculated net courses were plotted separately for groups inside (n = 70) and outside bays (n = 292). This showed that while there was strong bimodality for the open ocean whales, there was no clearly discernible pattern for those in bays (Figure 3.5). The axis between the two directional peaks (about 330 – 150^{O}) for offshore whales corresponds closely with the orientation of the coastline at Saldanha Bay. The mean angle of direction (based on net course) for all whale groups in bays was 33.32^{O} and Rayleigh's test for circular uniformity (Zar 1996) showed that their directionality did not differ significantly from a random distribution (Rayleigh's R = 11.798, z = 1.988, p > 0.05), while whales tracked outside of the bays showed significant directionality in a south-easterly direction (127.98^{O}, Rayleigh's R = 48.261, z = 7.976, p < 0.05). The groups inside bays were therefore excluded for the examination of seasonality of direction of movement. The remaining groups were binned into four 90^{O}-quadrants with a 30^{O} offset to the west from true north, to compensate for the direction of the coast (Figure 3.6). The resultant quadrants were therefore: (1) alongshore north-bound (286 – 15 ^{O}); (2) alongshore south-bound (106 – 195 ^{O}); (3) offshore (westward, 196 – 285 ^{O}); and (4) onshore (eastward, 16 – 105 ^{O}). The seasonal breakdown (Figure 3.6) shows no offshore movement during autumn to mid-winter, a season dominated by southward moving groups. The latter was also the predominant component in late winter, early spring and late spring, while north- and southbound groups were more or less equal in the remaining seasons except for mid-spring, where northbound groups were in the majority. Groups displaying offshore movement made up less than 10% of all groups during any season, although there appeared to be a slight increase in this component from late winter through to summer. The onshore component was very small during both autumn to mid-winter, and mid- to late summer (<5%), while it was more or less constant at about 18% of groups for the remainder of seasons except late spring (7.7%). The mean courses (Table 3.4) further confirm changes in direction between seasons. Starting in early spring, the mean course changed by over 90^{O} on four occasions between successive seasons, alternating between an alongshore to slightly onshore southerly, and a northerly or north-easterly (onshore) direction (Table 3.4). In three of the four seasons with a mean net course in a southerly alongshore direction (*viz.* autumn to mid-winter, early and late spring - Table 3.4), the directionality was found to be significantly non-randomly distributed (p < 0.05) as determined by Rayleigh's test for circular uniformity (Zar 1996).

Nearly half (47%) of all the whale groups (n = 362, including those in bays) had linearity of movement values between 0.95 and 1.0, forming the only prominent peak in the frequency distribution of linearity (Figure 3.7). Groups with linearity of movement from 0.95 - 1.0 (i.e. moving in an almost straight line) were classified as showing 'strong' and those with less than 0.95, 'weak' linearity. When examined by season (Figure 3.8) there was an overall decline in the proportion of groups exhibiting strong linearity with advancing season. Thus, from autumn to mid-winter the proportion of groups with strong linearity was significantly greater than parity (X^2 = 8.33, df = 1, p < 0.004) while in the summer seasons the groups with weak linearity predominated (early summer: X^2 = 15.21, df = 1, p < 0.0001; mid- to late summer: X^2 = 3.90, df = 1, p < 0.048). There was no significant difference (t-test, t = -0.438, df = 360, p > 0.662) between mean linearity of groups inside (0.82 ± 0.24 SE, n = 70) and outside (0.83 ± 0.013 SE, n = 262) bays.

Swimming speed

Actual swimming speed for all groups ranged from 0.2 to a maximum of 7.6 km.h^{-1} with a mean of 2.71 km.h^{-1} ± 0.08 (SE), while net speed ranged from almost stationary (0.03 km.h^{-1}) to 7.7 km.h^{-1} with a mean of 2.32 km.h^{-1} ± 0.09 (SE) (Table 3.5). The net speed of the majority of groups fell in the 0.5 – 3.5 km.h^{-1} range (Figure 3.9). Kruskal-Wallis ANOVA showed actual swimming speeds across seasons to differ significantly (H = 35.872, n = 362, p < 0.0001). The highest mean leg speed was recorded in autumn- to mid-winter at 4.11 km.h^{-1} ± 0.37 (SE), and a Dunn's multiple comparison post-test showed this season to differ significantly from early spring (z-value = 4.222, p < 0.001), mid-spring (z = 3.830, p < 0.003), and early summer (z = 4.813, p < 0.0001). Furthermore, early summer differed significantly from mid- to late summer (z = 3.528, p < 0.009); the latter season had the second highest recorded mean swimming speed. The lowest means for both actual and net speeds (2.2 km.h^{-1} and 1.68 km.h^{-1} respectively) were measured in early summer, the season when the lowest minimum net speed was recorded (Table 3.5). Both actual and net swimming speed showed a significant and negative relationship with the duration of the track (leg speed: r = -0.203, p < 0.0001; net speed: r = -0.278, p < 0.0001). Actual swimming speed for groups tracked inside bays (2.01 km.h^{-1} ± 0.14 SE, n = 70) was significantly lower than those in open water (2.88 km.h^{-1} ± 0.094 SE, n = 292) (t-test, t = 4.258, df = 360, p < 0.0001). This was also the case for net speed within (1.65 km.h^{-1} ± 0.133 SE) and outside bays (2.48 km.h^{-1} ± 0.103 SE) (t-test, t = 3.764, df = 360, p < 0.0002).

Group characteristics and behaviour

Group size

Although 669 southern right whale groups were seen from land, group size estimates and behavioural observations were only considered for those on which at least one reliable theodolite fix was made (n = 450). A total of 241 groups were intercepted by boat (on 97 different days) and 91 of these could be confidently linked to groups that were also fixed by theodolite, and so are known duplicates of some of the groups mentioned above, although there may be others. Comparative results from both these datasets, when presented, are therefore not purported to be independent but may help to assess whether comparable observations were made from the two different observation platforms.

The mean group size estimated from land was 1.82 ± 0.042 (SE) (Table 3.6), with a maximum of six, and singletons were the most frequently encountered, followed by groups of two (Figure 3.10). The mean group size for all boat intercepts was 2.17 ± 0.11 (SE) (Table 3.6), with the maximum estimated at 12 and groups of one also the most common, followed by dyads (Figure 3.10). For whales tracked from the shore and located inside bays, mean group size (1.90 ± 0.096 SE, n = 85) did not differ significantly from that for groups tracked in the open ocean (1.80 ± 0.0.047 SE, n = 365) (t-test, t = -0.893, df = 448, p > 0.372), assuming that there was no bias in sighting groups of different sizes at different distances from the shore. However, for boat intercepts, the mean group size inside bays (2.48 ± 0.182 SE, n = 118) was significantly bigger than those outside (1.88 ± 0.109 SE, n = 120) (t-test, t = -2.84, df = 236, p < 0.005). Furthermore, the mean group size for bay dwellers intercepted by boat was significantly larger than for those tracked from shore (t-test, t = 2.56, df = 201, p < 0.011), but not for whales outside bays, again assuming that there was equal chance to spot whales at any distance.

A breakdown of group size by season estimated from both land (Figure 3.11a) and boat (Figure 3.11b) showed a more or less similar proportion of singletons for both, with most seen in autumn to mid-winter and a decreasing trend though to early spring. Groups of three or more only became a feature from early spring onwards; however, it is evident that group sizes larger than four were rarely recorded from land during most of the seasons, giving the impression that there was either some underestimation made from land, or a selection of larger groups by the boat (Figures 3.11a, b).

For groups tracked from land, actual swimming speed showed a significant (negative) correlation with group size (r = -0.132, p < 0.011) (Figure 3.12), but this was not the case for linearity (r = 0.020, p > 0.703).

Possible biases influencing size estimates made from land and boat

The different mean group sizes obtained from land and boat estimates (especially for whales inside bays), and the seasonal differences in group size composition (see above and Figures 3.11a, b) are also reflected by the seasonal mean group sizes (Table 3.6). These show that boat-based estimates, especially during the early seasons (autumn through to mid-spring) were larger than those made from land, whereas they more or less concurred from late spring onward. Assuming that size estimates for the same group assessed from the boat would be more accurate than those made from land, the observed differences in estimates from the two platforms suggests that was a (possibly seasonal) source of bias leading to an underestimation of land group sizes, or some bias in selecting larger groups for interception by the boat. To further examine this, group sizes estimated for the same 91 groups from both boat and land were compared. Although the overall means (1.97 ± 0.12, SE for boat, 1.84 ± 0.097, SE for land) were found not to differ significantly (t-test for dependent samples, t = 1.5613, df = 90, p > 0.122), this masked a definite trend with group size (Figure 3.13). Assuming the boat-based estimates are ‘true’, it appears the land-based observers tended to underestimate group sizes of three or more (in agreement with the seasonal distribution, see above and Figures 3.11a, b).

The two most plausible sources of the above bias are (a) that (radial) spotting distance affected the ability for shore-based observers to accurately estimate group sizes, or (b) that larger group sizes were more easily seen at greater distances, or a combination of both. Group sizes estimated from the shore when plotted against the radial spotting distance, showed a significant and positive correlation (Figure 3.14; $r = 0.146$, $p < 0.002$). This relationship remained true when the spotting distances to the 91 groups that were seen by both land and boat, were compared to the respective group size estimates (land: $r = 0.239$, $p < 0.022$; and boat: ($r = 0.327$, $p < 0.002$). This implies that the significant positive correlation (Figure 3.15; $r = 0.207$, $p < 0.0001$) between distance to (the nearest) shore and group size (excluding those groups in bays) may indicate that larger groups were found farther from shore, or alternatively, it may reflect enhanced detection of bigger groups at greater distances. The latter explanation is supported by boat group size estimates (excluding groups in bays) that showed no significant relationship with distance to nearest shoreline ($r = 0.018$, $p > 0.847$) (bearing in mind the possible near-shore bias of intercepts and non-independence of data). This suggests that the most reliable estimates of group size made by land-based observers would be the ones for groups seen closest to shore, say within 3 km.

Behaviour and group composition

Out of the 450 right whale groups, the behaviour of 19 groups (4.2 %) was not specifically recorded, possibly because of the short duration of sightings, nondescript behaviour, or exceptionally high sighting rates that restricted detailed observations on multiple groups at the same time.

Groups specifically recorded as ‘surface active groups’ (SAGs) were intercepted on 21 occasions by the boat, and identified from the shore 76 times. Looking at both land and boat sightings, most SAGs contained three animals ($n = 42$) followed by groups of two ($n = 34$) (Figure 3.10), and eight groups of four, with only 13 SAGs containing more than four individuals (but see results above describing potential biases in group size estimation). SAGs started to appear from late winter (Figures 3.11a, b and 3.16) and their numbers were consistently high from early spring through to early summer, with some variation between the numbers observed from land and boat. In both instances there was a virtual disappearance of SAGs in mid- to late summer (Figures 3.11a, b); these seem to be replaced by milling groups and individual surface activity during this season (Figure 3.16). SAGs intercepted by boat were located predominantly inside the greater Saldanha Bay (14 out of 21 groups, Figure 3.17).

Cow-calf (c-c) pairs were intercepted by the boat 18 times during the study period, of which two were resighted on different occasions. One of the resighted c-c pairs was first seen unaccompanied, and again later on the same day as part of a group of seven individuals, with defecations observed. This was one of the four instances where c-c pairs were associated with other whales in larger groups. One of these larger groups showed a high degree of surface activity, with other individuals apparently harassing the c-c pair. The size of calves seen ranged from an estimated length of 4 m to about 9 m. Three of the c-c pairs were located inside Saldanha Bay (Figure 3.17) while the others were seen in shallow water (<80 m depth), mostly less than 3 km from the shore. All cow-calf pairs were seen in spring or summer (Figure 3.16) with the exception of one pair in May, where the calf was large, presumably from the previous year, and the cow appeared to be in poor physical condition.

Defecations were observed from the boat on 16 occasions (Table 3.7), including once by a cow accompanied by a calf (18 December 2002, No. 9) and thrice associated with apparent feeding behaviour (Table 3.7, No’s. 18, 19, 20). All defecations were seen in November/December 2002, and

January 2003. Behaviour that was interpreted as relating to feeding included the flushing of baleen and swimming with the mouth open, often in conjunction with the observation of zooplankton in the water at the sighting, or frequent and short fluke-up dives. Feeding behaviour was sometimes associated with surface activity, reminiscent of sexual activity related to typical SAGs, although this was more likely to be individual surface activity by members of the larger feeding groups (see below). The first two of the nine intercepts where suspected feeding was observed occurred in spring (in September 2002 by a small animal, and in October 2002 in association with humpback whales), while the majority of observations were in December (four times) and January (three) (Table 3.7). Possible feeding groups ranged in size from singletons up to five individuals, with only two groups larger than three, and dyads the most commonly seen (four times). Feeding groups were seen in water depths ranging from 8.3 – 100 m and were all located outside Saldanha Bay, with the exception of the one seen on 13 September 2002 (Figure 3.17, No. 1), near the entrance of Langebaan Lagoon. Twice, at shallower depths (21.8 and 43.1 m; Figure 3.17, No's. 4 and 20 respectively) patches of what appeared to be sediment particles rose to the surface during bouts of repetitive short dives, suggesting feeding close to the bottom.

DISCUSSION

The presence of southern right whales at the study site virtually throughout the study period was unexpected. Sightings on the west coast south of 32^{O}S during the eight extended aerial surveys between 1970 and 1986 were made in the months of September/October but these accounted for only 10% of the total recorded per survey (Best 1990). In the wider context however, it is difficult to interpret the observed relative abundances on the west coast in relation to the numbers seen on the south coast, due to the restricted seasonal coverage of the aerial surveys. The observed SPUE at Saldanha in October/November was about three times higher than that recorded at Cape Columbine for right whales in 1993 (68 groups seen in 424 hours of watching = 1.6 groups.$10h^{-1}$) reported in Best *et al.* (1995), an increase greater than can be accounted for by the overall population increase, but its significance is difficult to establish because of the slightly different locales.

The seasonal availability of right whales off Saldanha had much in common with that observed previously at De Hoop on the south coast (Best & Scott 1993) where they first were seen in April, and numbers rose to a peak in mid-spring (October) before starting to decline again. A similar pattern was observed almost 20 years earlier (1967 and 1968) in Walker Bay by two shore-based volunteers (Best 1970), when right whales started to arrive in May, reached a peak of abundance during September/October, and left the bay by the end of November. The timing of this decline in abundance in both localities agrees with the period that has been described by others as the onset of the migration away from the coast (Burnell & Bryden 1997), or at least the beginning of an alongshore dispersal prior to the main migration, especially by unaccompanied whales (i.e. those without calves, see Best 2000). However, in contrast to the south coast, this decline in late spring/early summer was short lived off Saldanha, and the mean SPUE rose again sharply in December to an overall high of nearly a group every hour. At a mean group size of two (estimated from both land and boat) this translates to about 20 whales available on a daily basis in the immediate area; still well below maximum counts reported for De Hoop in Best & Scott (1993). Whether this relatively high sighting rate represented an influx of whales into the area, or merely resightings of the same groups that were moving around, is uncertain, and may only be revealed by individual identification; however, it is consistent with the historical summer presence of right whales on the west coast (Best 2006), and also with results from a satellite telemetry study where at least one tagged right whale remained in St Helena Bay till early January (Mate *et al.* 2011). Sighting rates dropped back down closer to pre-spring levels during the last two weeks of January and first two of February, when observations were terminated. There was no coverage during March and April, and for only one week in May.

Distance from shore and occurrence in bays

There was a clear tendency for the boat to intercept whales closer to the shore. This was probably as a direct result of the greater availability of whales in the bay, and a heightened likelihood of their being encountered as the boat left its mooring and moved out of the bay. The bigger group sizes and greater numbers of SAGs seen and intercepted from late winter onward, and their location inside Saldanha Bay, were presumably due to preferential selection of these groups by the boat over groups that were further away. Because of the reduction in the numbers of whales inside the bay during the summer seasons, the offshore distribution of boat intercepts at that time may have more closely reflected the availability of groups with distance from the shore. In contrast to the boat intercepts, the distribution of sightings seen from the shore did not appear to be subject to the same near-shore bias, although it is possible that smaller groups were missed at greater distances. However, the groups seen from land probably reflect actual distance distribution more accurately than boat intercepts.

Overall, the distances to the shore for right whales were congruent with aerial survey results in emphasising the strongly inshore distribution of the species (Best 1990; Elwen & Best 2004a), with two thirds of all groups found inside bays or within 2 km from shore. While this proportion is less than the 90% of whales seen within 1.85 km during a special fixed-wing aircraft survey off the south coast in September 1987 (Best 1990), this single survey did not address seasonal variation in the distance distribution from the shore. At Saldanha, the months that were equivalent to the timing of the standard aerial survey did contain a higher proportion of whales within 2 km (about 80%) than the other months. There was a seasonal change in the offshore distribution of right whales from a more or less even distribution between bays, 0-1 km, and >2 km offshore in autumn to mid-winter, to a significantly near-shore one during late winter and mid– to late spring. These seasons saw up to a quarter of all groups inside major bays, mostly the greater Saldanha Bay. This distribution again changed markedly in the summer months when fewer groups were seen inside bays or near the shore, and a significant majority were located beyond 1 km from the shore. The maximum distances of 9.16 km recorded from land (in October) and 9.12 km by boat (in January) were similar in range to the 9.63 km recorded during the 1987 survey mentioned above, and reported in Best (1990). The component of groups seen beyond 4 km was greatest during the summer months.

Alongshore movement patterns and directionality

Southern right whales are known to be highly mobile, and long-range movements between coastlines of different continents (or islands) are not altogether unusual (Best *et al.* 1993; Pirzl *et al.* 2009; Rowntree *et al.* 2001). Movements at a smaller scale (along the same coastline) have been described from shore-based observations or aerial surveys (Burnell & Bryden 1997; Best 2000). On the South African south coast during October (the time of the annual survey), dispersal of cow-calf pairs tended to be of short distance (about 30-40 km) apparently in a westerly direction, and mainly completed within a day, although the restricted seasonal coverage, short duration and nature of the survey (e.g. flights in a westerly direction) severely limited the inferences that could be made (Best 2000).

More recently, results from a satellite telemetry study of right whales with tags deployed at two localities on the South African coast, one off the west coast and another off the south coast, have shown local movement patterns to be somewhat more complex than a simple westward movement in the latter part of the season (Mate *et al.* 2011). Satellite tagged individuals were seen twice during the present study, one of which was a cow (No. 847 in Best & Mate 2007) that was tagged on 12 September 2001 in St Sebastian Bay. This whale was re-photographed in the same bay during the aerial survey on 11 October 2001, still accompanied by a calf. The tag transmitted for 57 days and during this time the whale moved westward to Walker Bay, where the signal was lost on 8 November (Mate *et al.* 2011). The individual (bearing a satellite tag scar, see Best & Mate 2007) was resighted off Saldanha Bay again on 5 December 2002 as part of a feeding group, offering a suggestion of its possible destination after the tag stopped transmitting in the previous year. Such a movement pattern in the same season was confirmed by two other satellite tagged individuals (a male and unaccompanied female) that were tracked from St Sebastian Bay to the west coast (Mate *et al.* 2011). Satellite tracking also revealed movement in the opposite direction: two whales, a male and a female, tagged off Saldanha in late September travelled south and then east to False Bay and St Sebastian Bay respectively. Another three male whales tagged off Saldanha in late September moved northwards into St Helena Bay where they remained in the vicinity for up to 107 days before leaving the coast.

Other incidental evidence of transit from the south to the west coast was given firstly by an entangled whale that was seen and photographed twice during summer (16 and 23 December 2001). The whale had green nylon line and torn black netting wrapped around its tail stock and through the notch of its flukes, with a number of coloured floats trailing on about 15 m of rope. The entangled whale had been photographed on 9 October 2001 off Mossel Bay (34^{O}04.19’S, 22^{O}12.9’E) during the annual aerial survey. Another instance of movement from the south to west coast was provided by an albinistic juvenile seen as a calf when its mother was satellite-tagged on 13 September 2001 in St Sebastian Bay (34^{O}22.85’S, 20^{O}53.74’E), and re-photographed there with its mother during the aerial survey on 10 October. This whale was intercepted off Saldanha Bay on 30 September 2002, and again in 13 January 2003, when about 13-17 months old, both occasions on its own.

Movement of right whales past North Head, Saldanha (based on mean angle) was initially in a southerly direction in winter through to early spring, before changing to a northerly one in mid-spring.

From then on it switched each season by over 100 degrees between a northerly and southerly direction, ending with predominantly southward bound groups in mid-to late summer. Apart from autumn/mid-winter, early and late spring, when this trend was backed up by significantly greater proportions of southbound groups, other seasons had more or less equal shares of south- and north-bound groups. The groups moving onshore increased from late winter to early summer, in agreement with the greater proportion of bay dwellers, although it remained a minor component, as did offshore moving groups. The dominance of southbound groups early in the season is more difficult to explain, as it suggests that right whales were entering the area from somewhere to the north, rather than lower latitude feeding grounds to the south. The numbers seen during this season were however very low. The balance between north and south bound groups in most of the other seasons appears consistent with the somewhat variable directionality of whales, satellite tagged in September off the west coast (see above, and Mate *et al.* 2011). It therefore appears that right whales move up and down the coast, hugging the shoreline closely with no evidence of whales arriving from directly offshore, nor leaving in that direction in noticeable numbers. This agrees with the considerable variation in the coastal residence times, timing, and location of departure from the coast on the southern migration, for satellite tracked right whales (Mate *et al.* 2011).

Speed and linearity of movement

The distribution of net speeds resembled that reported by Mate *et al.* (2011) for satellite tagged right whales, with a peak at 1 km.h^{-1}, while the mean net speed from this study falls somewhere between that recorded for the tagged whales close to shore (1.6 km.h^{-1}) and those offshore (3.3 km.h^{-1}). The mean actual and net swimming speeds for mid-spring (=October) were however more than double those calculated for 34 ‘undisturbed’ (by boat) southern right whales tracked by theodolite at Cape Columbine in October/November 1993 (Best 2000). Only groups that were tracked for longer than an hour were used in the latter analysis, whereas in the present study all tracks with three or more reliable fixes were used, irrespective of the duration of the track (131 tracks were longer than 1 h). Off Saldanha, mean swimming speeds were found to decline significantly, the longer the duration of the track. When only tracks of longer than 60 min were used, the mean actual swimming speed was 2.51 km.h^{-1} ± 0.13 (SE) and net speed 1.91 km.h^{-1} ± 0.13 (SE), still substantially faster than the equivalent speeds recorded at Cape Columbine (1.67 km.h^{-1} ± 0.85, SE and 1.01 km.h^{-1} ± 0.91, SE respectively). Although any tracking data collected after the boat had closed with whales were not used for trackline analysis, the approaching boat may have affected swimming speed in some cases. Furthermore, unlike Cape Columbine, the area between and outside the heads of Saldanha Bay is a busy shipping lane with an active fishing fleet, and bulk carriers frequently moving through the bay to and from the iron ore jetty (see below). There are also differences in the physical characteristics of the two locations (e.g. bathymetry, degree of exposure, and availability of sheltered bays) that may influence movement patterns (Elwen & Best 2004a, b). These factors may all have contributed to the higher swimming speeds compared to those recorded at Cape Columbine, although northern right whales (*Eubalaena glacialis*) have been shown not to respond greatly to approaching vessels (Nowacek *et al.* 2004).

Groups showing strong linearity of movement made up more than three quarters of those tracked in autumn to mid-winter, a period that coincided with the highest swimming speeds recorded in a season. The inverse was partly true for summer months when weak linearity dominated, and swimming speed during early summer was at the lowest recorded level, although groups moved significantly faster again in mid-to late summer. Late winter and all spring months had about equal numbers of groups showing strong and weak linearity, and swimming speeds were closer to the average of 2.21 km.h^{-1}.

Group composition and behaviour

When considered in combination with behavioural observations, southern right whale movement patterns and distribution from shore at Saldanha Bay suggested three distinct episodes:

(1) Autumn and winter seasons were characterised by a low abundance, small groups (1 – 3 individuals) travelling fast in a predominantly southerly direction, with strong linearity (decreasing between early and late winter), and an even distribution between distance zones from the shore;

(2) Spring months had in common higher abundances, larger group sizes, a strongly inshore distribution (<1 km and inside bays), with somewhat lower swimming speeds. This episode signalled the start of directionality alternating between a mean southerly to a northerly bearing, significantly south-bound in early and late spring. Furthermore, neither strong nor weak linearity dominated at any time. Groups of more than three individuals became more common and from early spring, SAGs became a regular feature, especially in bays.

(3) Early summer saw the highest relative abundance recorded, a retention of large groups, that occurred farther from shore and moving at significantly lower speeds. While the north-to-south alternations continued, the onset of the summer feeding season was signalled by random directionality, very low linearity of movement coupled with an increase in milling behaviour, and observations of actual feeding and defecations. Groups with individual aerial activity increased, and although low numbers of groups displaying surface activity were still seen, we believe these were cases of larger groups with individual surface activity, rather than true SAGs as would be expected in the core nursery areas (as described by Best *et al.* 2003).

Saldanha Bay and its environs as a habitat for right whales

Apart from the evidence for the historic importance of the St Helena Bay area as a summer feeding ground (Best 2006), there is no *a priori* reason to expect that the habitat use by southern right whales along the west coast should be very different from that observed off the south coast. The west coast north of Table Bay is certainly more exposed to the prevailing westerly swells and winds (in winter) and the shelf edge is much closer to the shore compared to the south coast, with a lower water temperature (Shannon 1989). Locations on the south coast are known areas of concentration for cow-calf pairs presumably due to the favourable conditions, such as shelter from prevailing open ocean swells and winds, and sandy floors with gentle slopes that they offer (Elwen & Best 2004a, b, c). Maternal philopatry has also been implicated with the preference shown for certain areas (Best 2000). There are, however, very few large or sheltered bays available on the west coast, apart from the coastline between St Helena and Saldanha Bays. There were discernable differences in the movement parameters of whales outside and inside major bays (slower swimming speeds and random directionality). In spring and early summer SAGs appeared to favour the inside of the bay, especially North Bay. Saldanha Bay is effectively a large bay containing a number of smaller ones, offering variation in physical characteristics such as shore type (rocky vs. sandy), slope, orientation, and depth.

Groups seen off the west coast during aerial surveys mostly consisted of unaccompanied whales, in contrast to those off in the south coast standard survey area, where cows and their calves made up more than 50% of all counted (Best 1990). This is consistent with the low numbers of cow-calf pairs seen during the present study, and suggests that the west coast and the Saldanha Bay area in particular is not an important nursery ground for right whales, but for most of the year is utilised mainly by unaccompanied whales transiting the coast or interacting socially until summer, when the area functions as a feeding ground. The historical range of right whales in coastal waters is known to have extended to at least 17^{O}S off the west coast, and 27^{O}S on the east coast (Richards 2009). Seasonal trends in 19th century southern right whale catches between 30^{O}W and 80^{O}E south of the equator (based on Townsend’s 1935 chart, and presented by Best 1970), did show most catches during June and July to have occurred between 20 – 30^{O}S; that is north of the latitude of Saldanha Bay. This is of particular interest, given the observed southerly directionality at Saldanha Bay during these months, although the current distribution of right whales during winter on the south coast of South Africa is in strong contrast to impressions created by the historical catch data, and the relationship between right whales off South Africa and those further north, such as off Namibia and Mozambique, has not been clearly illustrated (Best 2006). Possibly with the gradual shift (from east to west) in right whale distribution along the south coast over the last 40 years, and a population growth in the region of 7% per annum (Best 1990, 2000; Best & Scott 1993), right whales (including cow-calf pairs) may ultimately begin to re-occupy some of their former range on the west coast. At Peninsula Valdéz, Argentina, it has been observed that the patterns of habitat use by southern right whales has changed over a period of decades (Rowntree *et al.* 2001), including shifts in the location of areas of peak density (i.e. nursery grounds). These changes are in some ways comparable to those observed along the south coast of South Africa, although an additional factor exists in Argentina, namely, kelp gull *Larus dominicanus* attacks on whales, which causes disturbance of especially mother-calf pairs (Rowntree *et al.*1998). Furthermore, a relationship has been demonstrated between right whale population dynamics (such as breeding success) and global climate signals, which could relate to fluctuations in food availability as a result of changes in climate (Leaper *et al.* 2006). Environmental and biological regime shifts (due to climatic factors) have been observed in the Benguela upwelling system (Cury & Shannon 2004), although it is not clear how this might impact on right whale habitat use.

CONCLUSION

Our results show that right whales are present virtually throughout the year at Saldanha Bay, and generally very close to the shore. The increased incidence of right whales off the west coast, whether due to changes in habitat use, saturation of breeding habitats, disturbance, or even climatic shifts, could increase potential interactions with human activities, given that this area is the hub for several important commercial fisheries, such as the trap fishery for west coast rock lobster *Jasus lalandii* (Johnston & Butterworth 2005) and purse-seining for small pelagic fish (Coetzee *et al.* 2008). It is also at the centre of a growing oil and gas industry, and there is pressure to expand such activities even to the core right whale nursery areas on the south coast (Best & Findlay 2010). As the locality of South Africa's largest natural port, Saldanha Bay already experiences considerable volumes of ship traffic; in the 2008/2009 financial year it handled 452 ships and total cargo of more than 50 million tonnes, of which two thirds was exports[1]. This implies on average about three transits of the mouth of the bay every 24 hours by cargo vessels, with an additional unknown number of transits by fishing vessels and other smaller craft. Right whales, including SAGs and cow-calf pairs, showed no sign of avoiding the mouth of the bay (Figure 3.17). With work now completed on an upgrade that increased the capacity of the iron ore railway line and jetty to handle 93 million tonnes per annum (Anon. 2006), it is important to continue the monitoring of southern right whale numbers in the area, especially given the species' potential vulnerability to ship-strikes, as described for its North Atlantic counterpart (Nowacek *et al.* 2004).

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TABLES

Table 3.1. Mean and range of sightings of southern right whales per unit effort (SPUE) and search effort by seasonal grouping, Saldanha Bay, South Africa (where *n* = number of monthly quartile subsamples).

Season	*n*	Mean SPUE (groups.10h^{-1}) ± SE	Min-max (SPUE)	Total h on watch	Days on watch	Hours day^{-1} on watch
Autumn to mid-winter	12	0.84 ± 0.21	0 - 2.52	459.09	69	6.65
Late winter	8	2.23 ± 0.61	0.61 - 5.42	293.30	46	6.38
Early spring	8	4.85 ± 0.95	1.83 - 10.6	260.80	38	6.86
Mid-spring	8	5.94 ± 1.39	1.62 - 10.81	242.23	42	5.77
Late spring	8	3.63 ± 1.05	0.57 - 9.87	238.63	35	6.82
Early summer	7	9.40 ± 2.09	0.92 - 15.64	180.95	32	5.65
Mid to late summer	6	4.50 ± 1.81	0 - 12.34	127.18	20	6.36
All seasons	57	4.14 ± 0.54	0 - 15.64	1802.18	282	6.39

Table 3.2. Mean, minimum and maximum distance from position of first reliable theodolite fix on southern right whale groups to the nearest shoreline, and significant results of Dunn's multiple comparison post-test between pairs of seasons, Saldanha Bay, South Africa.

Season	Mean distance in km of whale groups from shore, excluding those in bays (number shown in parentheses))				Dunn's multiple comparison of distance to shore between seasons: *z*-value (*p*-value), ns = not significant	
	n	Mean ± SE	Min.	Max.	Early summer	Mid-to late summer
Autumn to mid-winter	30	1.87 ± 0.24	0.22 (3)	4.97	ns	ns
Late winter	25	1.08 ± 0.18	0.11 (9)	3.11	4.99 (0.000012)	3.80 (0.003027)
Early spring	64	1.84 ± 0.22	0.09 (26)	6.80	4.34 (0.000300)	ns
Mid-spring	71	1.76 ± 0.21	0.18 (22)	9.16	4.61 (0.000084)	ns
Late spring	41	1.86 ± 0.29	0.14 (14)	8.36	3.97 (0.00154)	-
Early summer	94	2.94 ± 0.18	0.03 (7)	8.81	-	ns
Mid- to late summer	40	2.60 ± 0.25	0.10 (4)	6.63	ns	-
All seasons	365	2.14 ± 0.09	0.03 (85)	9.16	-	-

Table 3.3. Seasonal comparison of the distribution of southern right whale groups from the shore, showing the numbers located inshore (within bays and 1 km from shore) and offshore (beyond 1 km), and results of Chi-square test on whether this distribution deviates significantly from parity; Saldanha Bay, South Africa.

	Season							
	All seasons	Autumn to mid-winter	Late winter*	Early spring	Mid-spring*	Late spring*	Early summer*	Mid- to late summer*
Inshore	219	11	26	57	56	35	22	12
Offshore	231	22	8	33	37	20	79	32
Chi-square (df = 1)	0.32	3.67	9.53	6.4	3.88	4.09	32.17	9.09
p	0.572	0.555	0.002	0.114	0.049	0.043	0.0001	0.0026

Table 3.4. Mean net direction of swimming (in degrees true) by season for southern right whale groups in the open ocean tracked by theodolite from North Head, Saldanha Bay, South Africa (n = 292) [* indicates seasons where directionality as calculated by Rayleigh's test for circular uniformity is significantly non-random ($p < 0.05$)].

Season	*n*	Mean net course (^{O})	Rayleigh's *R*	Rayleigh's *z*	*p*-value
*Autumn to mid-winter	25	137.96	19.9974	15.9959	<0.000001
Late winter	23	118.78	6.1255	1.6314	0.196957
*Early spring	52	126.13	19.6931	7.4580	0.000468
Mid-spring	55	25.92	7.9303	1.1434	0.320145
*Late spring	39	151.77	15.8047	6.4048	0.001361
Early summer	71	45.85	4.4952	0.2846	0.753603
Mid to late summer	27	161.51	4.1082	0.6251	0.539466

Table 3.5. Mean actual swimming speed and net speed by season for all southern right whale groups tracked from North Head, Saldanha Bay, South Africa (*n* = 362).

Season	Actual (and net) swimming speed (km.h^{-1})			
	n	Mean ± SE	Min.	Max.
Autumn to mid-winter	27	4.11 ± 0.37 (3.99 ± 0.38)	0.58 (0.42)	7.60 (7.62)
Late winter	29	3.06 ± 0.35 (2.80 ± 0.38)	0.30 (0.13)	7.28 (7.22)
Early spring	71	2.34 ± 0.15 (1.93 ± 0.16)	0.33 (0.15)	7.64 (7.67)
Mid-spring	76	2.52 ± 0.17 (2.17 ± 0.18)	0.29 (0.06)	7.23 (7.43)
Late spring	52	2.93 ± 0.19 (2.63 ± 0.21)	0.30 (0.28)	5.60 (5.53)
Early summer	76	2.20 ± 0.16 (1.68 ± 0.16)	0.19 (0.03)	6.53 (5.76)
Mid- to late summer	31	3.35 ± 0.28 (2.71 ± 0.32)	0.89 (0.19)	6.14 (6.06)
All seasons	362	2.71 ± 0.08 (2.32 ± 0.09)	0.19 (0.03)	7.64 (7.67)

Table 3.6. Mean group sizes for southern right whales by season off Saldanha Bay, South Africa, based on best estimates made from land (*n* = 450) and during boat intercepts (*n* = 241). Note that these are not independent datasets, i.e. there is some overlap of groups tracked and intercepted.

	Land			Boat		
Season	*n*	Mean ± SE	Maximum	*n*	Mean ± SE	Maximum
Autumn to mid-winter	33	1.36 ± 0.09	2	17	1.65 ± 0.24	5
Late winter	34	1.65 ± 0.11	3	26	2.19 ± 0.32	6
Early spring	90	1.86 ± 0.09	5	62	2.69 ± 0.27	12
Mid-spring	93	1.74 ± 0.10	6	31	2.42 ± 0.30	8
Late spring	55	1.84 ± 0.13	5	33	1.88 ± 0.22	7
Early summer	101	2.08 ± 0.10	6	38	2.03 ± 0.24	9
Mid- to late summer	44	1.73 ± 0.11	4	34	1.71 ± 0.20	7
All seasons	450	1.82 ± 0.04	6	241	2.17 ± 0.11	12

Table 3.7. Timing and description of apparent feeding behaviour and defecations by southern right whales observed during boat intercepts around Saldanha Bay, South Africa during research in 2001-2003. Numbers in first column corresponds to those in Figure 3.17.

No.	Date	Time	Group size	Description and behaviour	Depth (m)	SST (^{O}C)
1	13-Sep-02	08:39	1	Possible feeding. Smallish (8 m) animal; mouth open, swimming up and down and arching back	8.3	16
2	17-Oct-02	16.24	2	Possible feeding. Associated with humpback whales, breaching at same time as humpback; one animal seemed to lunge with open mouth, zooplankton visible in water	85.5	17.5
3	11-Nov-02	15:09	1	Defecation	70.1	14.1
4	05-Dec-02	11:54	2	Possible feeding. Repeated short dives (ca. 5 min) at mouth of Danger Bay. Sediment particles came to surface; one animal carried satellite tag	21.8	12.2
5	06-Dec-02	07:56	5	Possible feeding. Frequent vertical dives after 1-3 blows on surface, some baleen shown with surfacing, dives lasting less than 3 min; one individual with satellite tag scar	63	12.5
6	06-Dec-02	11:24	2	Defecation	85	13.7
7	06-Dec-02	12:50	1	Possible feeding, vertical dives	92.8	15.5
8	16-Dec-02	12:13	3	Defecation; one individual entangled, net caught around peduncle and through fluke notch, yellow floats and black netting. Animal sighted earlier on aerial survey and resighted later in season	34.5	16.8
9	18-Dec-02	11:00	2	Defecation. Cow of mother-calf pair	56.8	17.2
10	18-Dec-02	11:36	1	Defecation	47.2	18.5
11	18-Dec-02	12:23	1	Possible feeding. Flushed baleen	49.8	18.7
12	20-Dec-02	11:25	2	Defecation	45.1	19.6
13	20-Dec-02	13:20	2	Defecation. SAG	57.6	18.4
14	23-Dec-02	13:01	3	Defecation	65.3	20.8
15	23-Dec-02	16:36	1	Defecation	67.5	20.6
16	23-Dec-02	16:54	2	Defecation. SAG. Same entangled animal as above	67.6	20
17	10-Jan-03	15:43	2	Possible feeding	57.6	18.1
18	13-Jan-03	16:10	1	Defecation during spy-hop: groaned and then defecated. Also opened mouth, apparently skimming and flushing baleen	77.7	14.6
19	14-Jan-03	15:10	2	Defecation. SAG	100	16.7
20	24-Jan-03	14:07	3	Defecation/Possible feeding. All animals doing dives of ca. 3 min, erratic surfacing, could see brown patches coming to surface after dives - possible feeding near bottom. Baleen flushing also seen	43.1	18.5
21	31-Jan-03	14:21	1	Defecation	57	14.8
22	31-Jan-03	15:45	4	Defecation	48.7	14.8
23	31-Jan-03	16:14	7	Multiple defecations; includes cow-calf pair	50	14.3

FIGURES

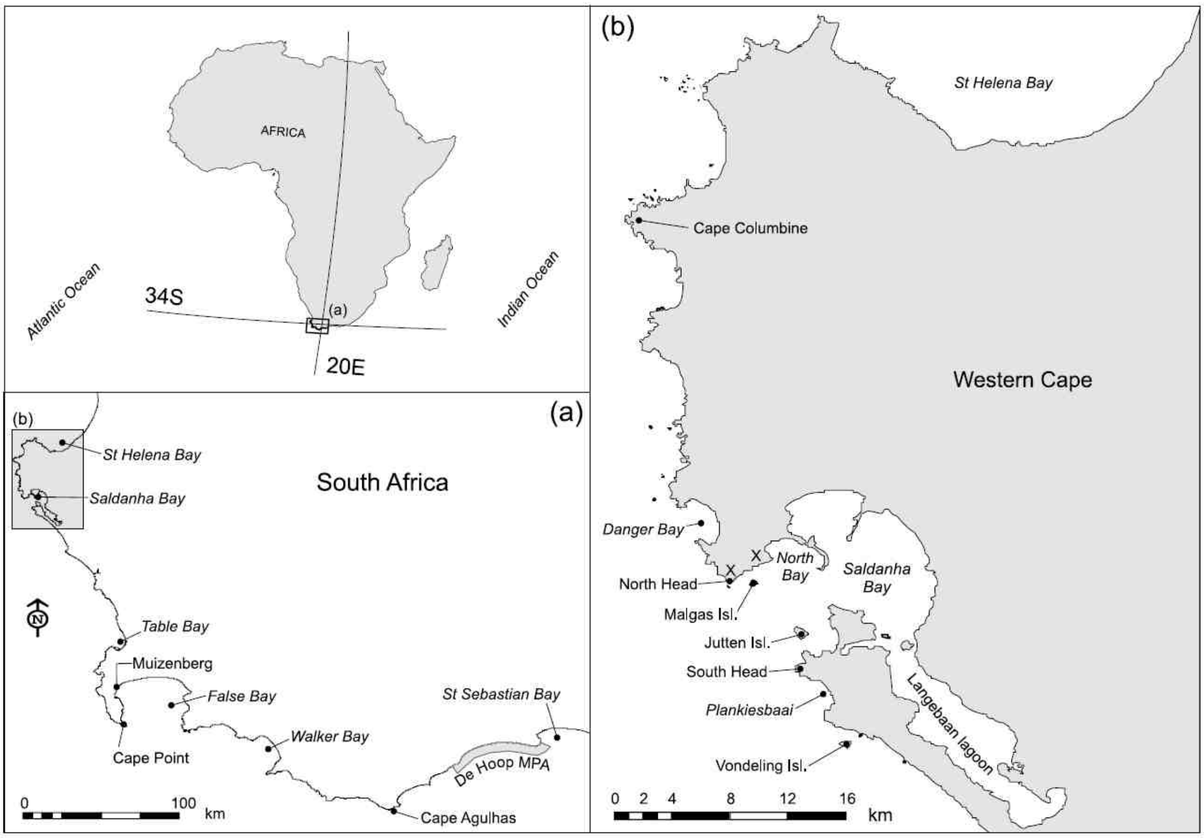


Figure 3.1. (a) The south-western Cape coastline of South Africa, with major features and areas of importance for southern right whales, such as major bays and the De Hoop Marine Protected Area (MPA); and (b) showing detail of the Saldanha Bay study area and nearby localities referred to in text. Positions of the two shore-based lookouts used during the study are indicated by ‘X’.

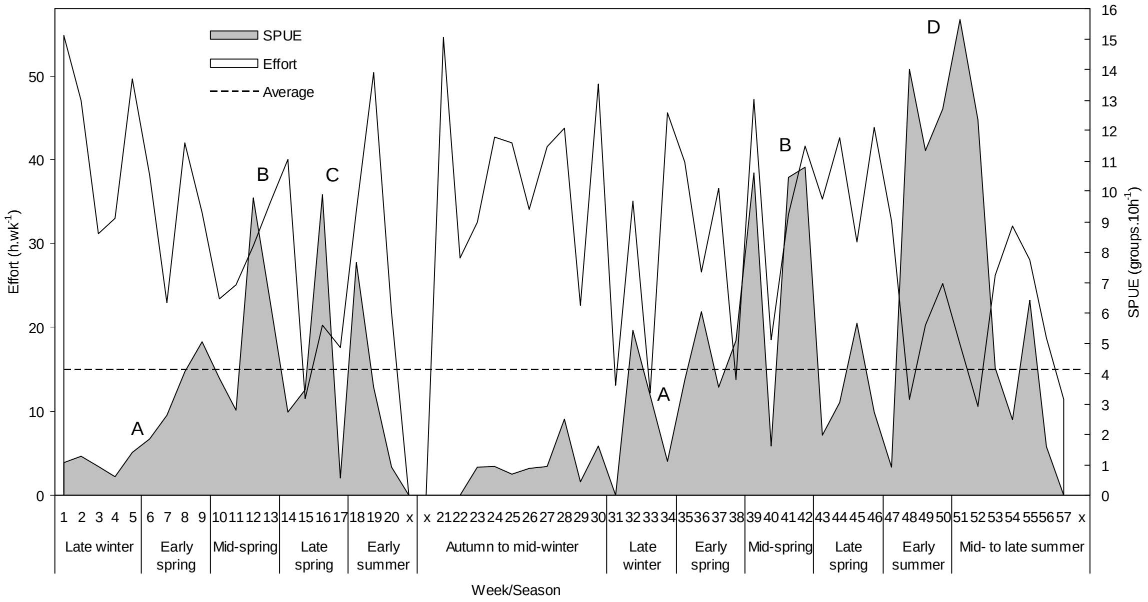


Figure 3.2. Sightings per unit effort (SPUE) of southern right whale groups off North Head, Saldanha Bay, and weekly search effort between 24 July – 20 December 2001 (weeks 1-21) and 6 May 2002 – 15 February 2003 (weeks 22 – 58). Dashed line is the average SPUE over the entire study period. ‘x’ indicates gaps in the fieldwork.

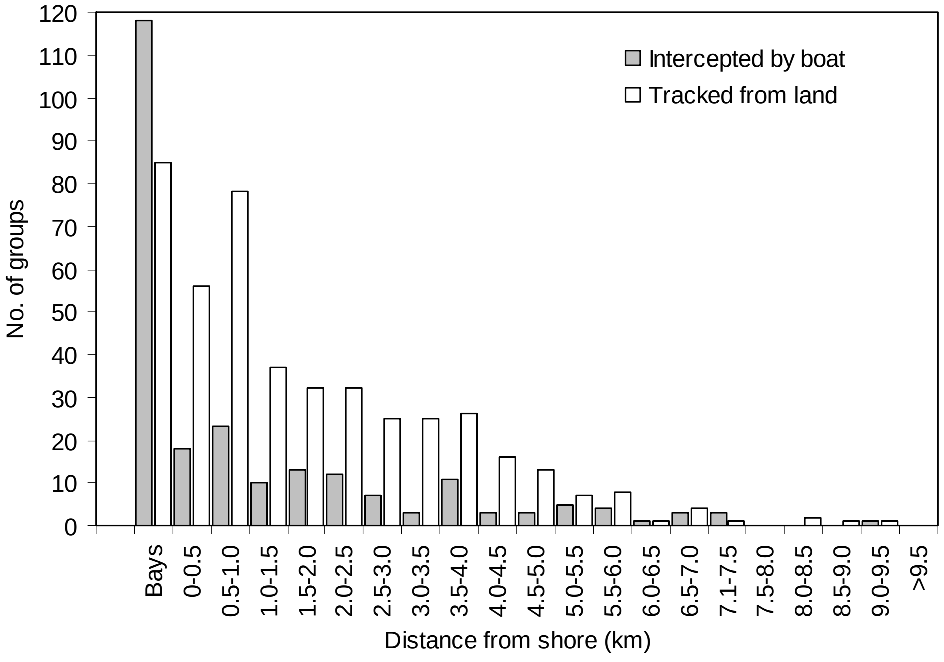


Figure 3.3. Distance distribution of southern right whale groups from the coast when tracked from the shore (calculated from first reliable theodolite fix), or intercepted by boat (GPS position) to the nearest ‘smoothed’ shoreline (km), or located inside major bays.

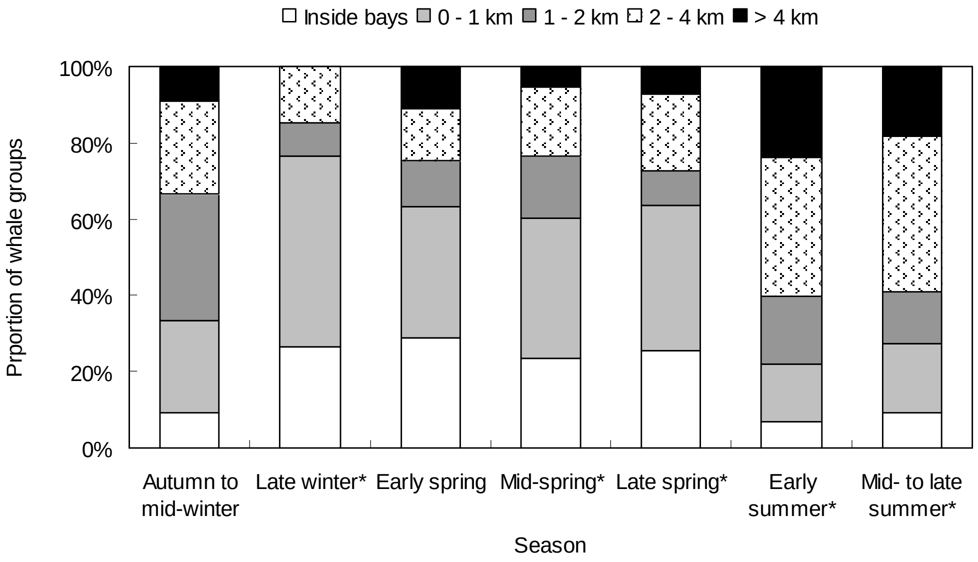


Figure 3.4. Binned distances of 450 southern right whale groups from shore each season, calculated from the first reliable theodolite fix to the nearest shoreline. Asterisk indicates where numbers of groups found in the inshore (bays and <1 km) and offshore (≥1 km) zones differ significantly (*p*<0.05) from parity (Chi-square, see Table 3.3).

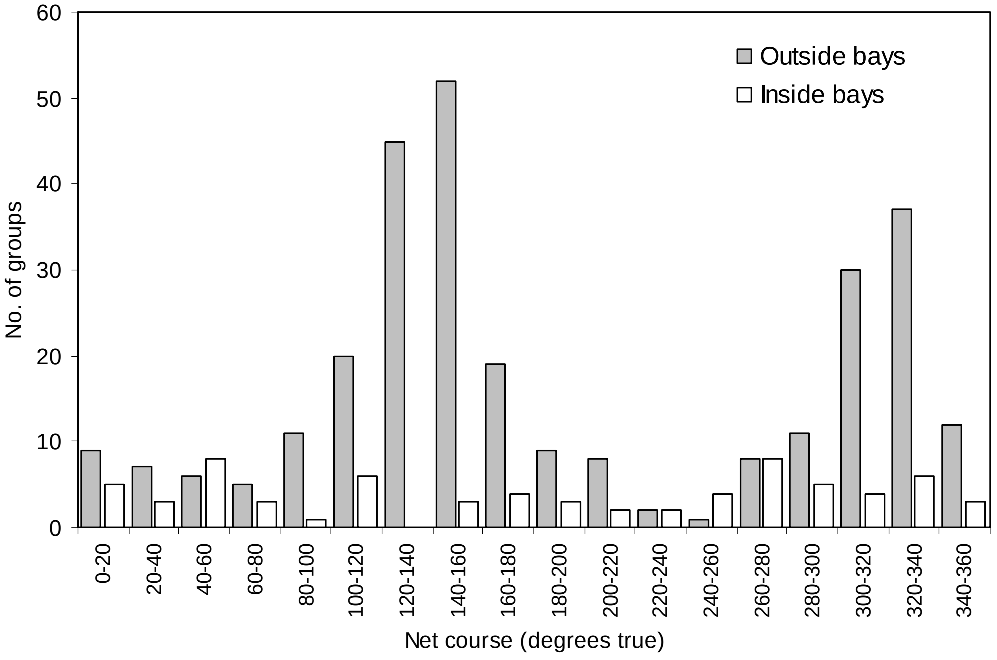


Figure 3.5. Frequency distribution of net course of 362 southern right whale groups tracked from North Head, Saldanha Bay, 292 in the open ocean and 70 inside bays.

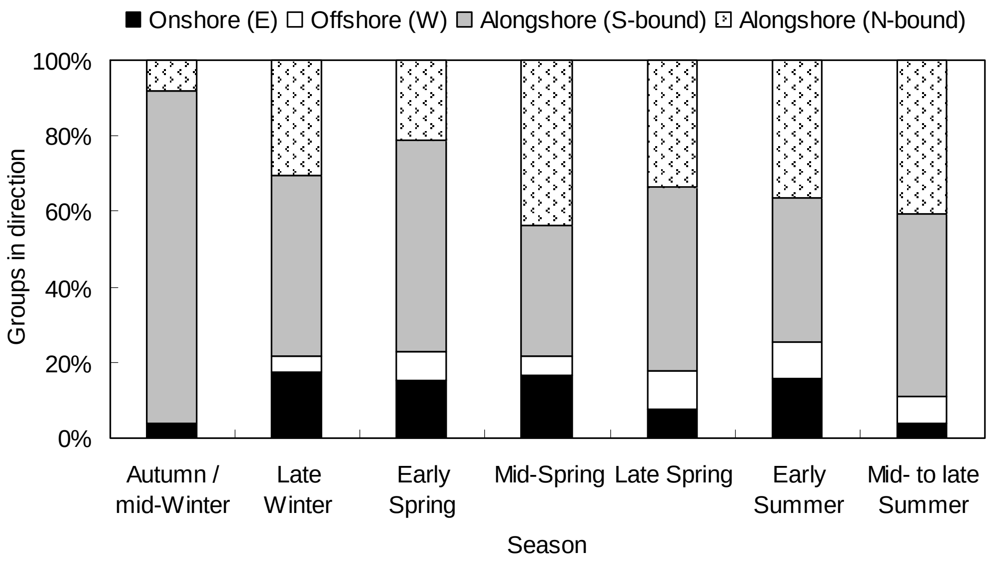


Figure 3.6. Seasonal breakdown of directionality of movement (net course in ^{O} true) of 292 southern right whale groups (excluding those inside bays) tracked from North Head, Saldanha Bay. Key to legend: South-bound = 106-195^{O}; north-bound = 286-15^{O}; offshore (westward) = 196-285^{O}; and onshore (eastward) = 16-105^{O}.

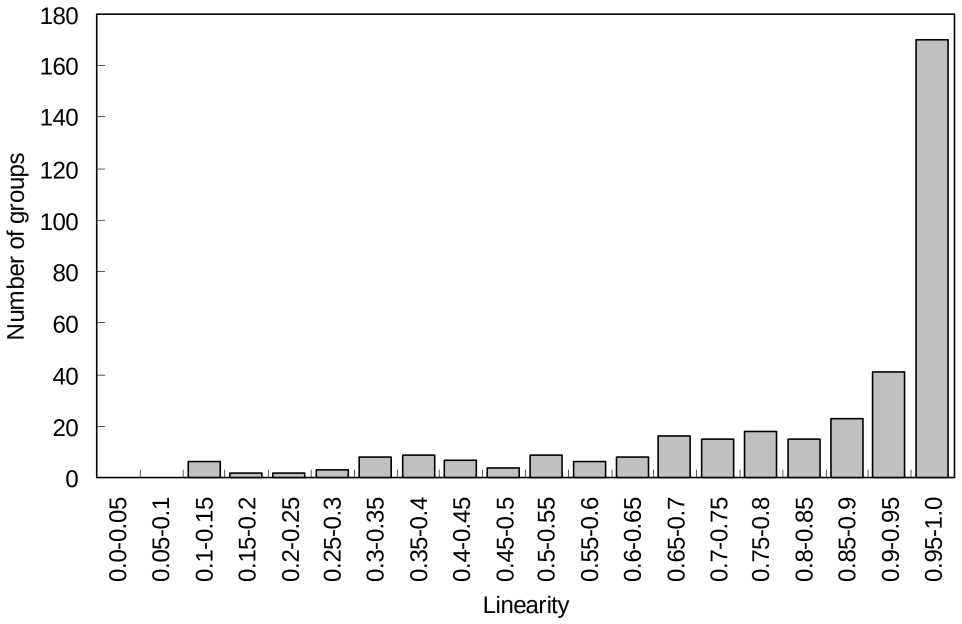


Figure 3.7. Frequency distribution of linearity of movement of 362 groups (292 in the open ocean and 70 inside bays) of southern right whales tracked from North Head, Saldanha Bay.

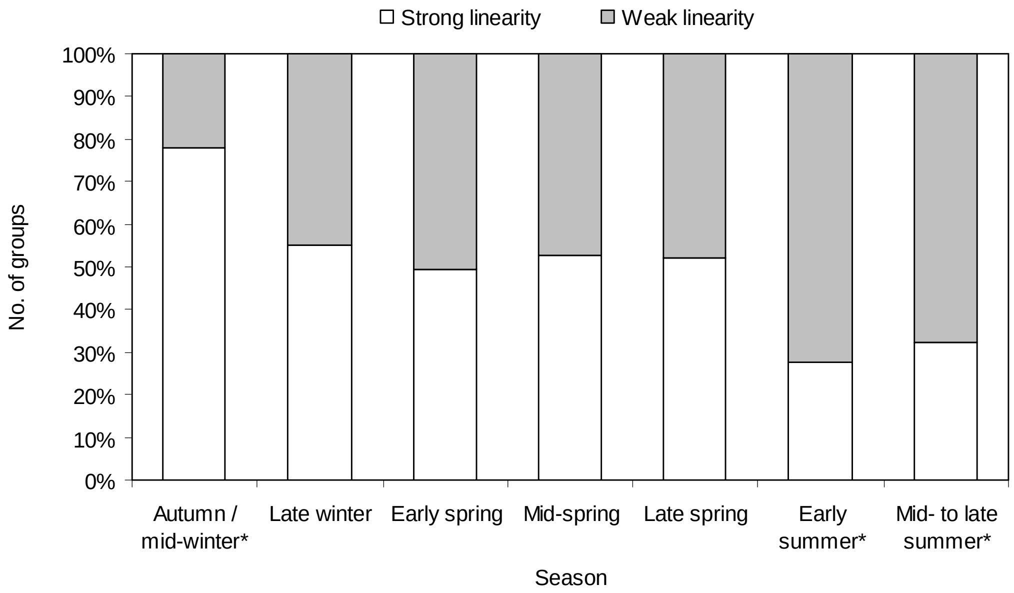


Figure 3.8. Seasonal breakdown of strength of linearity of movement (strong ≥ 0.95, weak < 0.95) of 362 southern right whale groups tracked from North Head, Saldanha Bay. Seasons where the proportions deviate significantly from parity (χ^2, $p > 0.05$) are indicated by an asterisk.

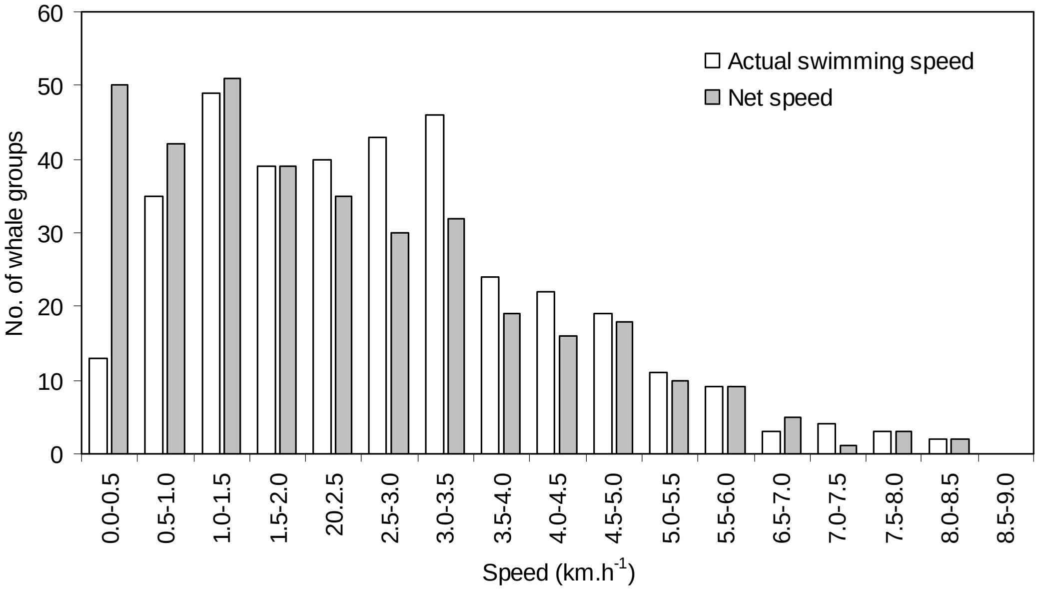


Figure 3.9. Frequency distribution of actual ('leg') and net swimming speeds (km.h^{-1}) of 362 southern right whale groups tracked by theodolite from North Head, Saldanha Bay.

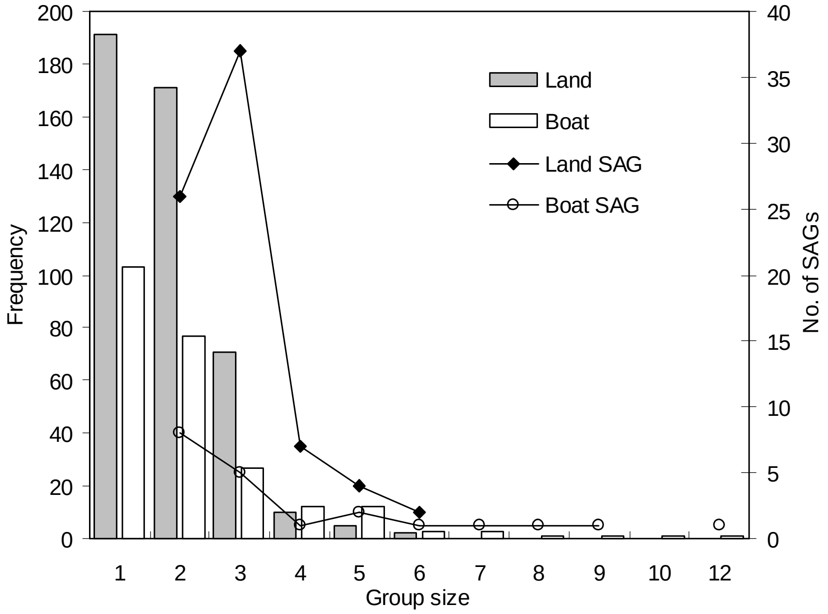
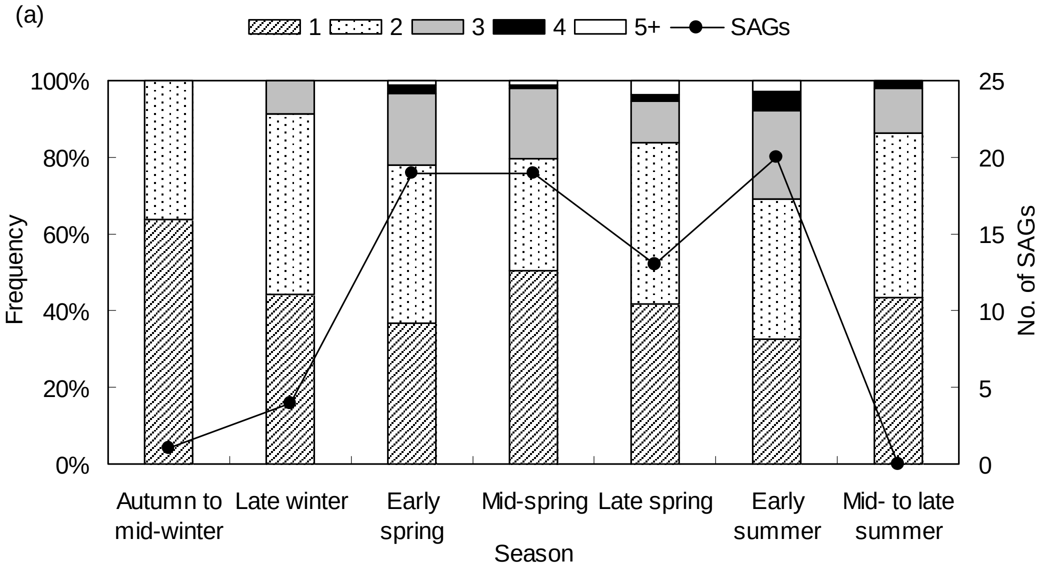


Figure 3.10. Frequency distribution of all group sizes of southern right whales, and of surface active groups (SAGs), estimated from land and during boat intercepts at Saldanha Bay.



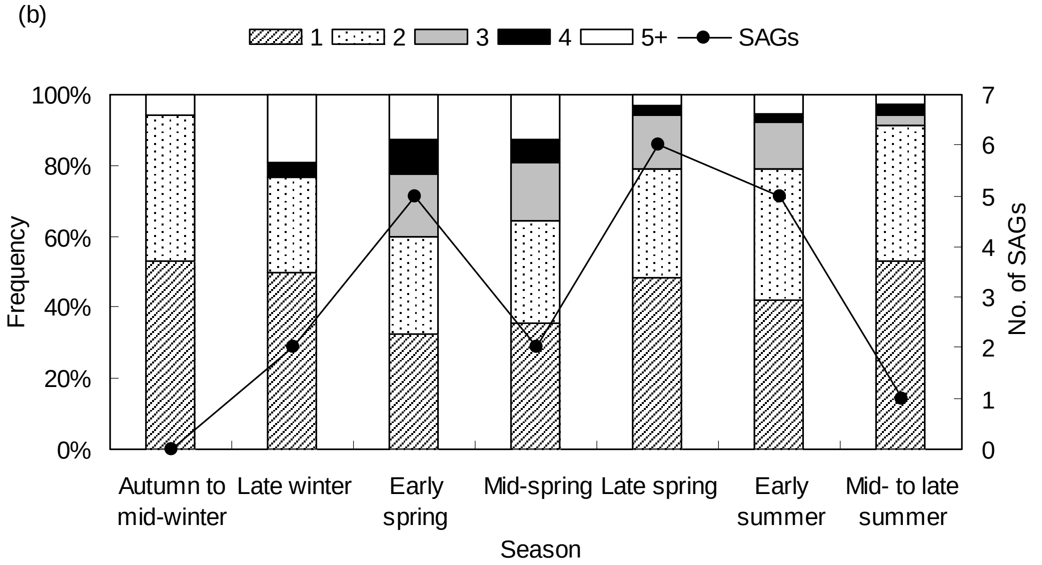


Figure 3.11. (a) Seasonal distribution of different group sizes of southern right whales estimated from land and; (b) during boat intercepts, and number of Surface Active Groups (SAGs) recorded during different seasons from each observation platform, North Head, Saldanha Bay.

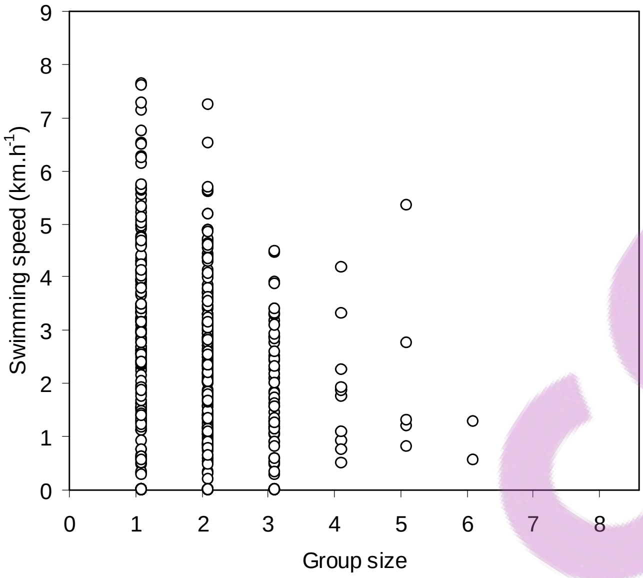


Figure 3.12. Relationship between group size estimates of southern right whales made from land at North Head, Saldanha Bay, and actual swimming speed in km.h^{-1} (whales in bays included).

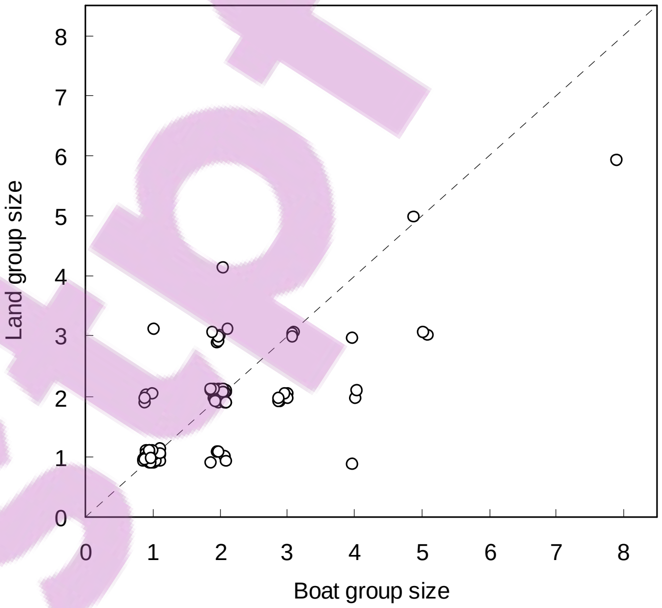


Figure 3.13. Relationship between group sizes estimated from boat and land for the same 91 groups of southern right whales, North Head, Saldanha Bay. A random offset factor of 0.25 has been introduced to group sizes to make overlapping points more visible. Dashed line indicates perfect fit.

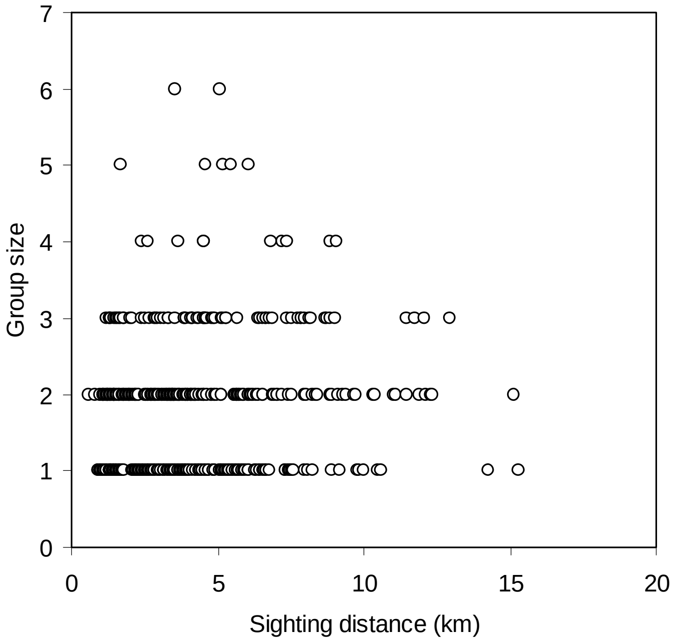


Figure 3.14. Relationship between group size estimates of southern right whales made from shore and radial sighting distance (km) from the lookout to the calculated position of the first theodolite fix, North Head, Saldanha Bay.

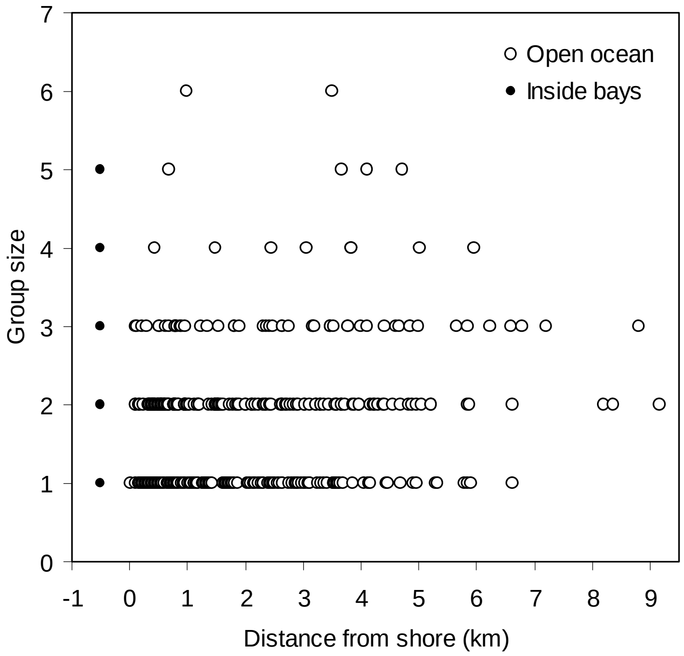


Figure 3.15. Relationship between group size estimates of southern right whales made from land at North Head, Saldanha Bay, and distance to nearest shoreline from the position of the first theodolite fix on a group (whales inside bays have been included for illustrative purposes and assigned an arbitrary distance of -0.5, but were excluded from the analysis).

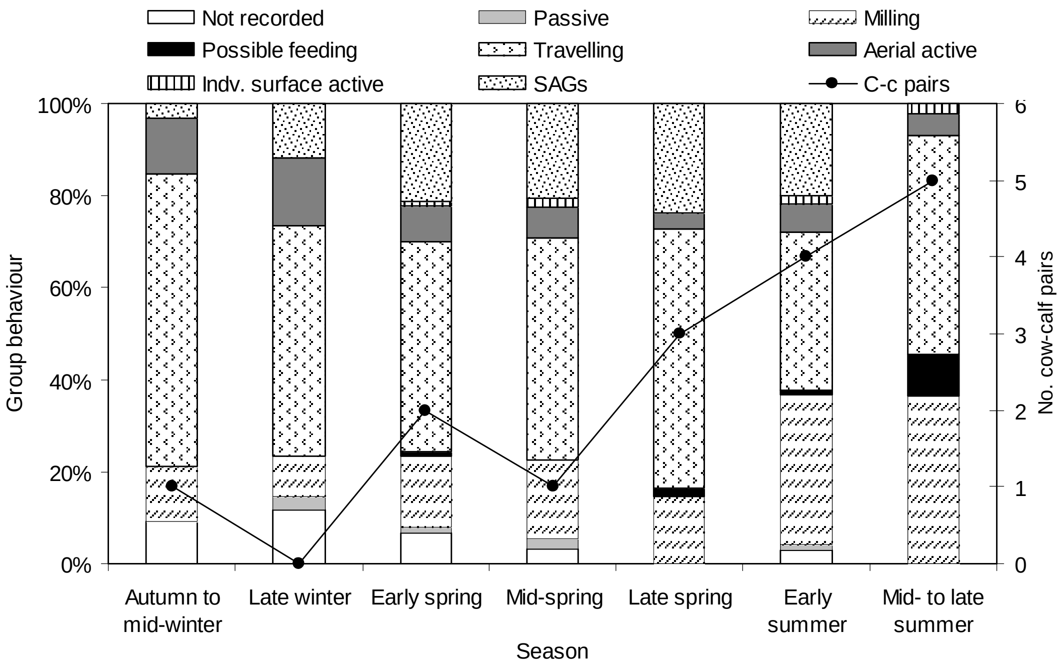


Figure 3.16. Seasonal breakdown of predominant behaviour attributed to 450 southern right whales groups seen from North Head, Saldanha Bay, and number of cow-calf pairs intercepted by boat during each season (*n* = 16, known resightings excluded).

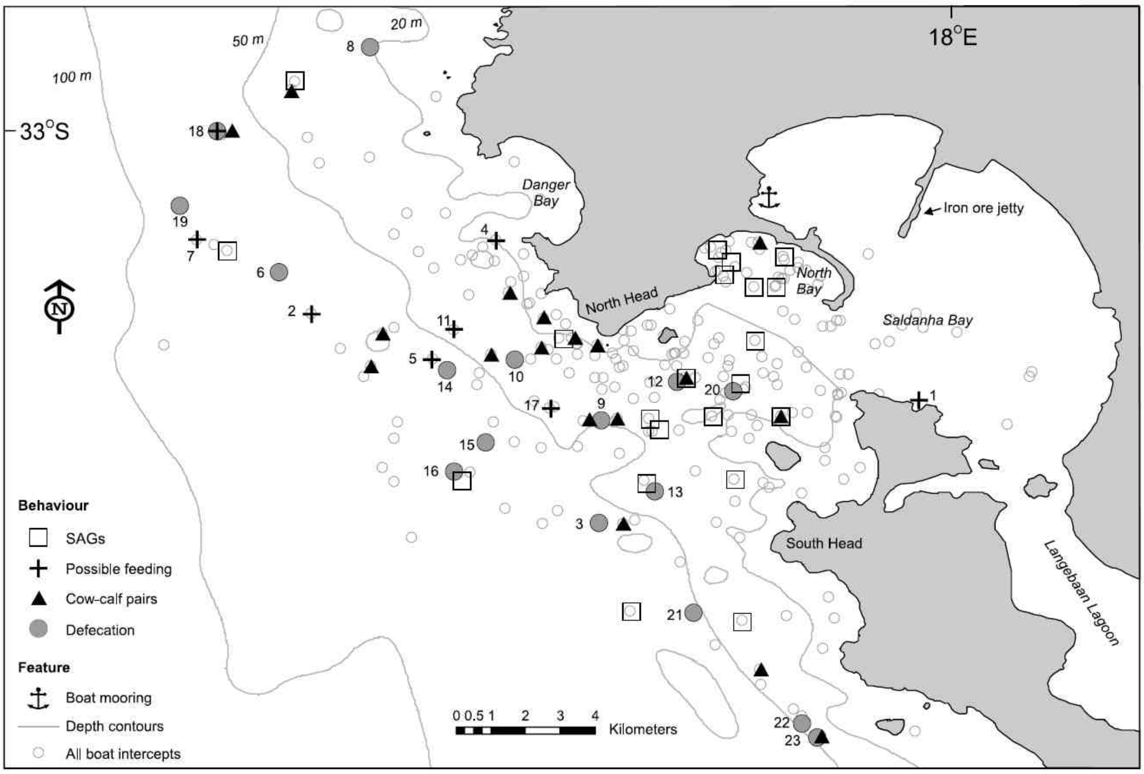


Figure 3.17. Saldanha Bay study area showing localities of all right whale intercepts by boat and those associated with specific group and behavioural observations. Numbers correspond to those in Table 3.7 or mentioned in the text. Note that during some sightings more than one feature may have been recorded, and positions of markers have been adjusted to improve their visibility.

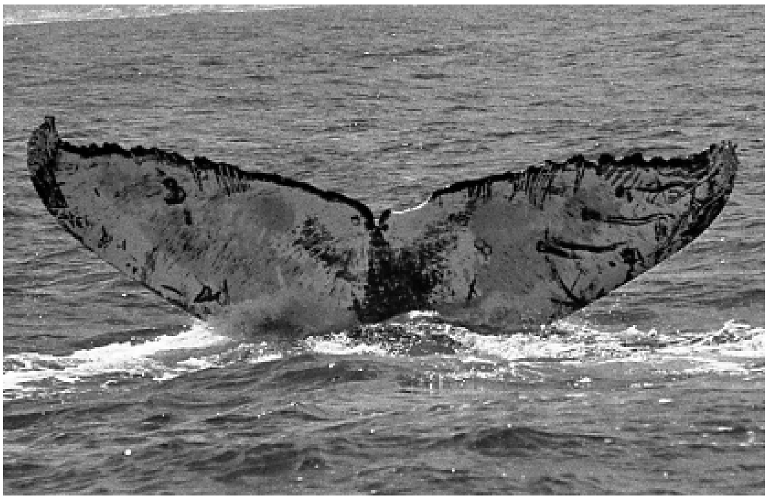
Chapter 4 - Transit station or destination? Attendance patterns, regional movement, and population estimate of humpback whales *Megaptera novaeangliae* off west South Africa based on photographic and genotypic matching[1]

“There is one great difficulty with a good hypothesis. When it is completed and rounded, the corners smooth, and the content cohesive and coherent, it is likely to become a thing in itself, a work of art. It is then like a finished sonnet or a painting completed. One hates to disturb it. Even if subsequent information should shoot a hole in it, one hates to tear it down because it once was beautiful and whole…”

“…A learned institution sent an expedition southward, one of whose many projects was to establish whether or not the sea-otter was extinct. In due time it returned with the information that the sea-otter was indeed extinct. One of us, some time later, talking with a woman on the coast below Monterey, was astonished to hear her describe animals living in the surf which could only be sea-otters, since she described accurately animals she couldn’t have known except by observation. A report of this to the institution in question elicited no response. It had extincted sea-otters and that was that. It was only when a reporter on one of our more disreputable newspapers photographed the animals that the public was informed. It is not known whether the institution of learning has been won over.

This is not to set down criticism; it is no light matter to make up one’s mind about anything, even about sea-otters, and once made up, it is even harder to abandon the position. When a hypothesis is deeply accepted it becomes a growth which only a kind of surgery can amputate. Thus, beliefs persist long after their factual bases have been removed, and practices based on beliefs are often carried on even when the beliefs which stimulated them have been forgotten”.

John Steinbeck - *The log from the Sea of Cortez*



Tail flukes of “Ampersand” (ZAW-006), a female humpback whale seen on 11 occasions over 15 years - the most for any individual.

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[1] Content from this chapter was presented at the first African Marine Mammal Colloquium (AMMC) held in Kleinbaai (18-21 May 2010), and in a paper (SC/62/SH2) to the IWC Scientific Committee in Agadir, Morocco, June 2010. It has subsequently been prepared as a similarly titled manuscript and submitted to the *African Journal of Marine Science* by authors: J. Barendse, P.B. Best, M. Thornton, S, H. Elwen, H.C. Rosenbaum, I. Carvalho, C. Pomilla, T.J.Q. Collins, M. Meÿer & R.H. Leeney.

INTRODUCTION

The west coast of South Africa should function as a near-shore migration corridor for humpback whales *Megaptera novaeangliae* based on its mid-latitude geographical position and occurrence of such behaviour along the east coast of South Africa (Findlay & Best 1996) and at similar locations elsewhere in the Southern Hemisphere (Bryden 1985; Dawbin 1966). However, in the vicinity of Saldanha Bay (at about 33^{O}S) historic and more contemporary observations have shown humpback whales to display seasonal residency from October to February (Best *et al.*1995; Findlay & Best 1995; Olsen 1914). Most recently, a shore-based survey there with near-complete seasonal coverage (Chapter 2, Barendse *et al.* 2010) has shown that the high relative abundances recorded during these spring and summer months did not correspond to the timing of expected migration peaks, but rather to aggregations of whales feeding on krill *Euphausia lucens* and other crustacean prey.

Humpback whales found in the south-eastern Atlantic are designated to the International Whaling Commission's (IWC) Breeding Stock (BS) B (IWC 1998) as included in the 'Comprehensive Assessment' of the IWC Scientific Committee (IWC 2010) for Southern Hemisphere populations. This region, particularly the west coast of Africa south of the equator, was characterised by extremely high catches from 1908 to 1914 and episodic catches thereafter (Best 1994). The whales from BS B are thought to migrate primarily to Antarctic Areas II (60^{O} W to 0^{O}) and III (0^{O} to 70^{O} E) for the austral summer, especially to the so-called 'nucleus feeding area' located between 10^{O} W and 10^{O} E (Figure 4.1a; IWC 2010). Based on mitochondrial and more recently, nuclear genetic evidence of population sub-structuring (Carvalho *et al.* 2010; Pomilla 2005; Pomilla & Rosenbaum 2006; Rosenbaum *et al.* 2009) BS B has been divided into two breeding sub-stocks, B1 and B2, with the Walvis Ridge or Angola/Benguela Front at about 18^{O} S proposed as a possible boundary (IWC 2010). However, the majority of sampling to date has been limited to only two widely separated localities: on the breeding ground off Gabon (Collins *et al.* 2008) which is thought to represent BS B1, and off the west South Africa (WSA) that presumably belongs to BS B2. Since no breeding behaviour has been observed (or is expected to take place) in WSA, the actual geographical location of the breeding ground for BS B2 remains unknown, and the proposed northern boundary at 18^{O}S would be inconsistent with the sea surface temperature regimes found for other humpback whale breeding grounds (Rasmussen *et al.* 2007). The detection of 10 whales biopsied off both Gabon and WSA (Carvalho *et al.* 2010) using microsatellite genotyping (Palsbøll *et al.* 1997) has raised questions about the BSB sub-division. Given that the whole coastal region between about 7 – 30 ^{O}S, comprising the territorial waters of Angola and Namibia (Figure 4.1a) is more or less unsampled it remains difficult to construct a more conclusive population structure model for the region.

The shore-based observations presented in Chapter 2 do not add to the current understanding of how these humpback whales relate to others in the region as derived from the genetic structure and microsatellite matches between Gabon and WSA (see above), nor provide information on whether the same individuals appear off Saldanha Bay during any of the same seasons in different years, or an accurate measure of how many whales utilise the area as a feeding ground. Individual photo identification (Katona & Whitehead 1981) may help to address these questions. Humpback whales are individually recognisable from two physical features that may be readily photographed: (1) their tail flukes, which includes the trailing edge, and the occurrence of natural marks, scarring, and pigmentation of their ventral surfaces (Katona & Whitehead 1981; Mizroch *et al.* 1990); and (2), the lateral view of their dorsal fins, that takes into account the shape of the fin, the prominence and distribution of knuckles on the caudal peduncle, and any scarring or pigmentation on the fin and/or flank (Kaufman *et al.* 1987). Although the use of dorsal fins and lateral body markings has yielded successful matches (Gill *et al.* 1995), the more distinctive flukes are favoured for use in regional photo identification catalogues. Such catalogues have been employed widely to identify migratory links (e.g. Stevick *et al.* 2004), examine regional movement patterns and population structure (e.g. Calambokidis *et al.* 2001), and calculate population sizes (e.g. Straley *et al.* 2009).

We present here results from the most comprehensive photo identification and genetic collection to date from the west South Africa region in order to examine within- and between-year attendance patterns, and investigate inter-regional movements between WSA, Namibia, Gabon, and Antarctic Areas II and III by comparing all available tail fluke collections from these areas. Furthermore, although not specifically collected for this purpose, the type of capture-recapture data obtained from the within-region photographic and genotypic matching may be suitable for the calculation of abundance estimates (Hammond 1986; Hammond *et al.* 1990). We try to estimate the number of humpback whales that may feed in the area during spring and summer using different approaches, including capture-recapture methods on selected sub-sets of data using different identification features (tail flukes, right and left dorsal fins, and microsatellites). Both closed and open population models are used, as is the norm in many published abundance estimates for large whales, including humpbacks (e.g. Calambokidis & Barlow 2004; Larsen & Hammond 2004; Straley *et al.* 2009). To our knowledge, this is the first time dorsal fins have been used to calculate abundance for this species, in addition to the more favoured flukes. The exposure of the latter is known to vary for individual whales which may affect individual capture probability (Perkins *et al.* 1984, 1985), while dorsal fins are always exposed and more easily photographed (Gill *et al.* 1995). Therefore, we examine potential sources of capture heterogeneity, sampling bias, and error that may result from the use of dorsal fins vs. tail flukes as photographic identification features, using double-marked animals (i.e. identified by more than one feature). The results are compared and discussed in terms of the estimation method or model applied, and identification feature used.

MATERIAL AND METHODS

Data collection and sighting database

The sighting database and photographic catalogue were compiled from a number of data sources (Table 4.1), but as a minimum requirement for inclusion had to be collected from within the Exclusive Economic Zone (EEZ) of South Africa, west of Cape Agulhas (20^{O} E). These included data from humpback whales encountered incidentally during research work directed at other cetacean species, or during routine multi-disciplinary scientific cruises in the region, in the years 1983 - 2008 (Figure 4.1b). It further included all boat intercepts made during the work reported in Chapter 2 in the years 2001-2003, and those from another study dedicated to humpback whales at Cape Columbine in 1993, described by Best *et al.* (1995) (Figure 4.1c). Although it was attempted throughout to photograph the ventral side of the tail flukes and both left and right sides of the dorsal fin, and from 1993, to collect a biopsy from every whale encountered, any whale was included for which at least one of these were taken/collected and the date (day, month and year) and locality (latitude and longitude) of the sighting known. In most cases additional data (including group size, composition and behaviour, SST, depth, and duration of encounter) were also collected. Discrimination between individuals in the field (and association of specific images/biopsy attempts with individuals) was aided by onboard notes and sketches of body features, and by recording all photographic (film roll/data card numbers and frames) and biopsy sampling effort for each individual. This information was later used in the database to associate identification features with specific individuals seen during a sighting.

Prior to 2004 most images were recorded on high speed (ISO 400 and higher) black-and-white or colour negative, and colour positive film using motor-driven 35 mm single lens reflex (SLR) cameras with 100-300 mm manual focus zoom lenses; from January 2005 onwards these were replaced by digital autofocus SLR cameras. Once processed (film) or downloaded (digital), photo frames or images were associated with specific individuals within specific groups on each day, using the field notes mentioned above. Film was scanned using either a dedicated film scanner (Canocraft FS2) or flatbed scanner with filmstrip adapter (EPSON SmartPanel or Canoscan FS8400). The scanning protocol and structure of the photographic database were based on those developed by P.J. Ersts (later modified by S. Cerchio and T. Collins, Wildlife Conservation Society) as part of an ongoing regional Atlantic/Indian Ocean humpback whale research collaboration. Film frames were scanned at 600 dots per inch (dpi) and cropped to maximise the coverage of the area of interest (i.e. tail fluke or dorsal fin plus caudal peduncle). Black and white negatives were scanned as colour film and later converted to 8-bit greyscale images (following the protocol developed by Santos-Tieder *et al.* 2003) and saved in the TIF format. Scanned images and digital photos were imported into the Microsoft© Access database in JPG format. Each image was individually assessed for photographic quality and orientation of the subject and a score based on a 5-point scale assigned to each of these categories (1 = not useable, 2 = poor, 3 = fair, 4 = good, and 5 = excellent). Every tail fluke (TF) image was further classified according to its ventral pigmentation pattern (or ‘type’) on a scale from 1 - 5, where 1 is all white (no central black bar between the left and right flukes) and 5 all black (see Rosenbaum *et al.* 1995). Flukes were rated for the part visible above water, i.e. whole, left fluke only, right fluke only, and trailing/leading edge. An additional classification type ‘0’ was introduced for TF where it was impossible to assign types 1 - 5, either due to the unfavourable orientation or partial obscuring of the subject, or where the tail flukes were severely scarred or mutilated due to injury, such as killer whale (*Orcinus orca*) bites. Images were also assigned a score from 1 – 5 for individual distinctiveness of the subject although this rating was not used in any of the present analyses.

Skin biopsies were collected using the *Paxarms* rifle system (Krützen *et al.* 2002). Some samples were lost during early sampling attempts as plastic darts cracked on impact at the thread holding the brass heads. This loss was eliminated by attaching a nylon monofilament tether between the main body of the dart and the head (from 4 October 2001 onwards) to prevent it from falling off and sinking. All biopsy heads were sterilised by flaming after use. Samples were placed into individually labelled cryogenic tubes filled with a NaCl-saturated, 20% dimethylsulfoxide (DMSO) solution and placed on ice bricks in a cooler box. At the end of each day all skin samples were stored in a domestic freezer (-5 ^{O}C) until they could be transferred to a -15 ^{O}C freezer at the laboratory in Cape Town. Processing of samples was carried out by others (see Foreword and Acknowledgements) at the Sackler Institute for Comparative Genomics (American Museum of Natural History).

Within-region matching

The matching described below was done separately for each identification feature. Thumbnail (100 dpi) or medium resolution (200/250 dpi) copies of the original pictures for all useable images (i.e. with photo and orientation quality ratings of poor and better) were viewed on 38 – 48 cm (15 -19 in) thin film transistor (TFT) computer screens. Original (large format) images were viewed for final decision making. Tail flukes were compared by pigmentation type to reduce the number of possible comparisons, first to all images of the same type, and then to all images from the preceding and following types (e.g. type 2 was compared to types 1, 2, and 3). Type 0 flukes were compared to all available images from all other types. In the case of dorsal fins, each image was compared with every other image. Within-year matching was carried out first, i.e. checking for matches of the same individuals on different days in the same year. Once completed, representative images of individual whales from each year were compared in chronological order to those of the subsequent year in the database and matches identified. The processes of within- and between-year matching were repeated by a second person. Where a match disagreed, it was reviewed and a consensus decision made to accept or reject it. Once all matching was completed, the best image(s) available per individual and identification feature were selected for representation in the overall catalogue, and a unique identification number assigned per identification feature.

Genotyping was carried out by others (see Foreword and Acknowledgements) and the methodology of using 10 microsatellite loci is detailed in Carvalho *et al.* (2010). Each biopsy was associated to an individual sighting incident by its original biopsy number. In the case of a positive match between two skin biopsies, the laboratory code assigned to the earliest collected sample was retained as the identification number for that individual.

Periodicity and seasonality of resightings

Although matching was carried out for each feature independently a maximum of four identification features, *viz.* tail flukes (TF), right dorsal fins (RDF), left dorsal fins (LDF) and microsatellite (MS) could be collected for an individual whale at any given encounter. Wherever a common identification feature was identified between two or more different sightings, these could be linked. Thus, a full sighting history could be built based on all matches made through all available identification features between different encounters, even though these were not all collected at every sighting. It is important to note that failure to positively link one feature to another for the same individual could result in missed matches between different sightings. The problems of having multiple separate records for the same animal in a combined feature catalogue were highlighted by Gill *et al.* (1995), especially when dealing with large numbers of individuals. However, given the small total number of humpback whales identified, we believe the use of combined identification features was warranted in order to optimize the sample size for the purposes of examining trends in the growth of the catalogue and attendance patterns.

Within- and between (calendar) year occurrences of resighted individual whales were examined using combined identification features (genotype and photos of usable quality) for the entire database. The time interval between the dates of first and last sightings (excluding the first day) was calculated for all individual whales that were resighted on different days, both within and between years. For whales sighted on successive days, the time between sightings was assumed to be one day, i.e. rounded up to 24 h. Between-year time calculations took leap years into account. The number of days between sequential sighting events was also calculated for each individual whale. The seasonality of resightings for the entire sighting database was examined by sorting them by month, and separated on the basis of their overall resighting histories, i.e. seen only once, resighted within years only, and resighted between different calendar years. Note that the latter may have included some within-year sightings, but were not included in the ‘within-year only’ category.

Between-region photographic matching

The representative images of 154 individual humpback whales identified by TF that resulted from the WSA within-region matching (see above) were compared to TF collections from four other regions (see Figure 4.1a for localities):

Cabinda – Twenty-five individual whales of which identification pictures of TF (45 images in total) were taken during September 1998 off Cabinda, Angola, around oil production platforms some 50 nautical miles south of Congo River mouth (Best *et al.* 1999) were compared to the WSA, Namibia and Gabon catalogues.

Gabon – A total of 1,297 individuals represented by 9,776 images collected from 2001-2006 was compared to the WSA and Cabinda images. The database, area of collection, and matching procedures are fully described by Collins *et al.* (2008).

AHWC (feeding Areas II/III) - The Antarctic Humpback Whale Catalogue (AHWC) is a compilation of almost 5,000 photographs (TF, LDF and RDF) taken by miscellaneous contributors, both by scientists and non-scientists since 1987. The images originate from regions throughout the southern hemisphere, and the overall aim of the AHWC is to investigate movements of humpback whales between the Southern Ocean and lower latitude waters through an internationally collaborative project (Allen *et al.* 2008). It is currently maintained by the College of the Atlantic (Maine, USA) and is publicly available on the web-based photo-sharing platform *Flickr*® (http://www.flickr.com/ahwc). The photostream can be viewed as a whole, or by sets, using the search tool to select any combination of tags or text, such as TF pigment type or locality of picture (for example, the tag ‘T1 areaIII’ would display all images of type 1 from Area III) (Judy Allen pers. comm.). The type 0 is not used in the AHWC. A total of 186 images representing 130 individuals, tagged as being from Areas II and III, were compared to the WSA images.

Namibia – There is presently no formal humpback whale catalogue for Namibia, but images have been collected at Walvis Bay, (23^{O}00'S, 14^{O}30'E) during research cruises directed at Heaviside's (*Cephalorhynchus heavisidii*) and bottlenose (*Tursiops truncatus*) dolphins, or by dolphin- and whale-watching operators in winter (June – August) and summer (January – March) of the years 2008, 2009 and 2010. Preliminary sorting and matching of these yielded 35 individuals (61 images).

Images of both whole and partial TF of all quality ratings except 'not useable' were considered. The AHWC does not catalogue non-useable images as individuals (Judy Allen pers. comm.). No matching was conducted between the Gabon catalogue and the images from AHWC and Namibia. Representative images of each individual in one database were systematically compared to those of the other, bracketed by fluke type (as described above for within-region matching) to avoid mismatches due to the variable assignment of TF types. All matches were checked and confirmed by a second person.

Abundance estimates

Catalogue size adjusted for annual survival

For each of the four identification features, a measure of the absolute minimum abundance was derived from the number of individual whales contained in the respective databases. This was done similarly to the method used by Straley *et al.* (2009) where the number of whales ($\tilde{N}_x$) alive in any given year (x) is calculated by adding the number of unknown (or 'new') individuals identified in that year ($\tilde{n}_x$), to the number estimated to have survived from the preceding year ($\tilde{N}_{x-1}$), the latter adjusted by an annual survival rate (ϕ) (Equation 4.1). The term $\tilde{N}_{x-1}$ is the sum of $\tilde{n}_{x-1}$ and $\tilde{N}_{x-2}$ (again adjusted with ϕ) and so forth. No variance can be calculated.

$$\tilde{N}_x = \tilde{n}_x + \phi(\tilde{N}_{x-1}) \tag{4.1}$$

The value for ϕ was set at 0.96 as calculated for humpback whales in the North Pacific (Mizroch *et al.* 2004). Although this value is probably lower for non-adults (see Zerbini *et al.* 2010 for discussion), it is considered a reasonable estimate for annual adult survival, given that the area is not a breeding ground and very few calves were seen (Chapter 2; Barendse *et al.* 2010).

Data selection for capture-recapture estimates

The only time period for which sufficient data were available for several years in sequence, and offered adequate seasonal coverage to permit estimation of abundance for whales that engage in spring/summer feeding, occurred during 2001 – 2007 (Table 4.2). This included the sighting data from the boat-based component of the work described in Chapter 2 (see above) and the remainder, of humpback whales encountered during work on feeding southern right whales (2003 – 2007) at Saldanha Bay (in September), and St Helena Bay (in October - December, rarely January) – note that this study had no shore-based watch (see Table 4.1). By restricting the data sub-sets to only certain seasons, the possible heterogeneity in capture probability introduced by different seasonal attendance patterns of individuals should be reduced. Six successive capture occasions (j) of six months each were identified, starting in September of one year and ending in February the following year (e.g. j_1 = 01 September 2001 to 28 February 2002, both dates inclusive) (see Appendix 4.1).

Variation in photographic quality and the distinctiveness of natural marks can affect the ability to correctly match different photographs of the same individual, and hence the likelihood of a successful resighting (Friday *et al.* 2000; Gunnlaughsson & Sigurjónsson 1988; Hammond 1986; Stevick *et al.* 2001). For example, on images of poor quality, highly distinctive individuals may still be identified while matches of less distinctive animals are more likely to be missed (i.e. an increased probability of false negatives). To reduce such errors we applied the commonly used approach (e.g. Cerchio 1998; Straley *et al.* 2009; Friday *et al.* 2008) of excluding images below a certain quality; in this case those of quality and/or orientation rating of ‘poor’ and ‘not useable’ were not used for capture-recapture calculations and no partial TF pictures (halves or trailing edges) were included.

Closed population model

The two-sample Chapman’s modified Petersen (CMP) estimator (Seber 1982) has been used elsewhere to calculate the size of feeding aggregations of humpback whales (e.g. Larsen & Hammond 2004; Straley *et al*. 2009). When applied over relatively short time periods (e.g. one-year intervals), it is considered an acceptable approach for a long-lived mammal with relatively low rates of natural mortality and recruitment, despite such populations generally not meeting the assumptions of closed population models. These assumptions (adapted from Seber 1982), applicable when using natural marks, are: (1) a constant population during the sampling period (no immigration/emigration, or births/deaths); (2) no loss of marks between sampling periods; (3) all marks are correctly recorded; (4) all whales have an equal chance of being recorded in the first sample; (5) both previously identified and newly sighted whales have equal probability of recapture in subsequent samples.

We employed the CMP estimator here due to its relative simplicity, and to illustrate issues that relate to different identification features used (see later), with the formula (Seber 1982):

$$N^* = \frac{(n_1+1)(n_2+1)}{(m_2+1)} - 1 \qquad (4.2)$$

where N^* = estimated population size, n_1 = the number of whales identified during j_1, n_2 the number of whales identified during j_2, and m_2 the number of whales identified (i.e. matched) in both periods. The estimated variance (*v or* vâr) of N^* and the estimated coefficient of variation (CV*) of N^* were calculated according to formulas in Seber (1982):

$$\hat{\text{var}}(N^*) = v = \frac{(n_1+1)(n_2+1)(n_1-m_2)(n_2-m_2)}{(m_2+1)^2(m_2+2)} \qquad (4.3)$$

and

$$\text{CV}^* = \sqrt{\hat{\text{var}}(N^*)} \Big/ N^* \qquad (4.4)$$

Confidence intervals (95%) for the CMP estimator were calculated with the log-normal transformed method as proposed by Burnham *et al.* (1987).

$$r = \exp\left(1.96\sqrt{\ln(1+(\mathrm{CV}(N^*))^2)}\right) \tag{4.5}$$

The lower confidence interval (CI) was calculated by dividing N^* by r, and the upper by the product of N^* and r.

The CMP calculation was restricted to the first pair of capture periods ($j_1 – j_2$) as these were the only ones with the primary effort directed at humpback whales, had the largest sample sizes, and where recaptures were detected for all identification features. Furthermore, sampling during j_1 - j_2 occurred at the same site of limited extent (i.e. within ±25 km radius from North Head, Saldanha Bay); this should reduce capture heterogeneity, a factor not accounted for by the CMP estimator between individuals, or over time (Hammond 1986). Such heterogeneity is regarded as highly likely to be a factor for all natural populations, resulting in underestimation of the true size of the population, sometimes considerably (Carothers 1973).

Open population models

Maximum-likelihood models of the Jolly-Seber (JS) type (Jolly 1965; Seber 1965; Schwarz & Seber 1999) are frequently used when the assumption of population closure is unlikely to be met, and when data from multiple capture periods are available. The POPAN option, included in the software Program MARK 5.1 (White & Burnham 1999; Schwarz & Arnason 2006) is one of the JS model formulations most readily available to biologists (Arnason and Schwartz 1999). It has therefore enjoyed wide application for generating population estimates from photographic and genotypic capture-recapture data for several cetacean species (e.g. North Pacific right whales *Eubalaena japonicus* - Wade *et al.* 2011; Indo-Pacific bottlenose dolphins *Tursiops aduncus* - Reisinger & Karczmarski 2010; killer whales - Reisinger *et al.* 2011), including humpback whales (Larsen & Hammond 2004), and other large marine fauna such as whale sharks *Rhincodon typus* (Meekan *et al.* 2006); in some cases for very small populations for which limited data are available.

The POPAN model estimates the following parameters: the super-population size *N*; the apparent survival rate ϕ; the probability of entry into the population, or '*Pent*' with the alternative notations of *b* or β (the latter used here); and capture probability (*p*) at capture occasion *j* (Schwarz & Arnason 2006). The prescribed link functions (GC White, Program MARK Help files) namely, the Logit link for ϕ and *p*, and multinomial Logit (MLogit) link for β were used. Different variations of the model were applied to datasets for six successive capture occasions (j_1 - j_6) for all four identification features (TF, LDF, RDF, and MS) including all parameters fixed (.), full time-dependence (t) for ϕ, β and *p*, and with ϕ fixed at the biologically realistic value of 0.96 (see above). While the β parameter accounts for the contribution of births to the overall entry rate (Arnason & Schwarz 1999), and though there are published annual rates of increase (ROI) available for humpback whales (see Zerbini *et al.* 2010) it was not attempted to fix this at a specific value, given that our data are not likely to be (fully) representative of a discrete breeding population. Selection of the best models was done using Quasi-

Akaike's Information Criterion (QAICc), adjusted for small sample sizes as implemented in MARK (Cooch & White 2006).

Biases in abundance estimates derived from different photographic identification features

Given that dorsal fins have never been used to calculate abundances for humpback whales, their reliability as a naturally marked feature for this purpose is untested. It is expected that the use of identification features with less information or that are less distinctive would be more difficult to match, which can result in misidentification (Hammond 1986), as is the case for other species where dorsal fins are used (Gowans & Whitehead 2001). Therefore, we examine the incidence and effect of missed matches, when using dorsal fins. Furthermore, we assess the possible impact of variation in individual fluking behaviour (on estimates) as it is a known idiosyncratic behavioural feature (see Perkins *et al.* 1984, 1985) and there was a sense during the data collection that it was more difficult to photograph the flukes of some individuals, a notion reinforced by fewer individuals identified by this feature compared to dorsal fins (see later). While we acknowledge that the use of genotypes is not completely free from error and may cause an upward bias in abundance estimates due to misidentification of microsatellites (see Lukacs & Burnham 2005; Wright *et al.* 2009), detailed consideration of this issue is beyond the scope of this paper, although we did compensate for it where applicable or possible in the analyses below.

Tests for false negative rates

Microsatellites were used as an independent (non-photographic) identification feature and all individuals (n = 32) that were identified by this feature and resighted on different days, were used as the sample. For each capture occasion (day) it was assessed whether a specific photographic feature of useable quality (>poor) was recorded; then, whether or not a specific feature confirmed the matches made by microsatellite. The sample size per identification feature was the number of times both a MS match and a photograph of the feature in question were available ('matching opportunities'). Failure to detect a photographic match constituted a false negative. As a simple test to quantify the positive bias caused by the detected false negative error rate (e), the pair-wise CMP estimator (see above, Equation 4.2) was calculated for the applicable dataset, using the false-negative correction developed by Stevick *et al.* (2001). The identification events (s) per sampling period (j) were taken as the sum of every time a whale was identified as an individual, excluding same-day resightings, therefore assuming that the boat crew recognised such individuals in different groups on the same day. Thus, to correct for the higher-than-actual total number of whales 'identified' due to missed matches within each sampling period, the numbers of individuals identified during j_1 and j_2 (n_1 and n_2) are calculated as

$$n'_j = \frac{n_j - e.s_j}{1-e} \tag{4.6}$$

The number of individuals matched between these samples (m_2) was increased by the error factors to correct for missed matches between j_1 and j_2 in the following manner

$$m'_2 = \frac{m_2}{(1-e)} \tag{4.7}$$

A comparison of the resultant population estimates with the uncorrected ones provided an indication of the magnitude (%) of the overestimation.

Variation in recording of tail flukes for resighted whales relative to other features

All whales resighted on different days (n = 60) were used as the sample, and the identification features collected during intercepts on these different days were compared. First, the number of times TF were recorded (of any photographic quality) during all intercepts of resighted whales was compared to that of other features. Second, the frequency with which TF were recorded in the case of multiple resightings was examined. Third, the duration of intercepts where TF were recorded was compared to those where no TF were recorded. Finally, the probability of recording TF or dorsal fins (left or right) for an individual whale was calculated by counting the number of intercepts during which the feature was recorded and expressing it as a fraction of the total number of times that the resighted whale was intercepted.

Use of double marks

Here we used TF as one type of mark, and LDF, RDF and MS respectively as alternative marks. For the two adjacent sampling periods (j_1 and j_2), the n_1 consisted of animals that were identified by both TF and the other mark in question, i.e. double-marked animals. The n_2 consisted of the total number of whales identified by either TF, or the alternative mark in the following sampling period; with recaptures (m_2) being those double-marked animals that were identified by whatever feature was used for n_2. This approach is intended to compare the relative capture probabilities of the two marks used: if they are equal, then recapture rates (and by inference, abundance estimates) should be similar whichever feature is used for the second sample. During the calculation using the CMP estimator (Equation 4.2), an error correction factor (e) was applied to dorsal fins and MS similar to that described above (i.e. n_2 was adjusted downward and m_2 adjusted upward, after Stevick *et al.* 2001), but n_1 was left unadjusted because the animals were already identified without error from their TF. The correction factors used for dorsal fins were those calculated from LDF and RDF false negative tests (see below). When MS was used as alternative identification feature it was adjusted by the mean allelic error rate of 0.065 calculated for the samples collected off WSA (Inês Carvalho, unpublished data).

RESULTS

Range and seasonality of collection effort

Due to the *ad hoc* and variable manner in which much of the photographic and genetic data were obtained, effort is loosely defined here as ‘collection days’, i.e. any day on which such data were collected. There were only 28 such days from 1983 to 2000, compared to 108 over the next eight years (Table 4.2). The greatest number (and days with boat availability) of collection days occurred between 2001 and 2006 during the two studies highlighted earlier (at Saldanha Bay and St Helena

Bay) and made the greatest overall contribution in terms of number of images and individuals identified after matching was completed (Table 4.1). Other notable periods of data collection were during the earlier study at Cape Columbine (Best *et al.* 1995) and incidental humpback sightings made during a project on Heaviside's dolphins *Cephalorhynchus heavisidii* (described in Elwen *et al.* 2009). Collection days, as a proportion of days where a boat was deployed, ranged from 12.8% (in 2000), to a high of 38.8% in 1993, and most years were at around 20 – 30 % (Table 4.2). Overall, at least one collection day was recorded during any given month, but effort was not evenly distributed across seasons. The autumn and winter months (March – August) had the poorest overall coverage with 10 or less collection days per month, while spring and summer months (September – February) were better sampled. Most collection days occurred in November (*n* = 30), and fewest in June (*n* = 1) (Table 4.2). The spatial extent of miscellaneous data collection along the west coast was fairly extensive (approx. 700 km between the northern- and southernmost sites; Figure 4.1b); however, the majority of data were collected within a fairly limited area of about 1 x 1 degree latitude/longitude grid square, no further than 25 km from the shore (Figure 4.1c), and included the major study sites mentioned above.

Within-region matching

Sighting database/catalogue

The WSA catalogue up to February 2008 included a total of 1,820 images, made up of 510 TF, 694 RDF, and 616 LDF (Table 4.1), representing 446 individual sighting histories collected during 225 boat intercepts/encounters. Excluding images that were deemed 'not useable', 154 individuals were identified using only TF, 237 by RDF, and 230 by LDF (see Table 4.5). Microsatellite genotyping of 216 skin biopsies yielded 56 samples matched to one or more other samples, representing 156 individuals, three of which were identified by microsatellite only (i.e. were not photographed). By linking different individual identification features to common sightings, a total of 289 individual whales were identified with 'combined features', although eight only had 'not useable' images and were thus excluded (*n* = 281). Few animals (<10 per annum) were identified before the advent of dedicated field work in 2001 (Figure 4.2), when most individuals were identified in a single year (80). New additions remained at fairly high levels for the following five years (> 25 individuals per annum) although there was a steady decrease in the growth rate of the database (Figure 4.2).

Resighting rates, intervals and seasonality

Using combined identification features (*n* = 281), 214 individual whales were seen once only, seven were resighted on the same day (i.e. in more than one group), and 60 (21.35%) on different days. Forty-four whales were resighted between calendar years, the majority once only (30), followed by twice (7) to a maximum of five resightings (i.e. in six different years) (see Table 4.3). Only 12 of these between-year sightings were not seen on multiple occasions in the same year, with one individual recorded a total of 11 times (the same whale that was seen in six different years).

The shortest interval between first and last sighting events was one day and the longest 18 years, with the mean interval being 3.4 yr and the median 1.5 yr. Most whales were resighted within one year

(23), followed by a 1 - 2 yr interval (17). For 14 whales, the interval was longer than four years, and for six of these, longer than 12 years (Figure 4.3). A breakdown of time intervals between sequential sightings (Figure 4.4) of all resighted whales showed that most individuals were resighted on the same day (35 times), or within a week of the previous sighting. Resightings at intervals of more than a week, but less than six months, were relatively few (<10). The next most commonly observed resighting intervals were at 6 – 12 mo and 1 – 2 yr (Figure 4.4). Intervals of between 2 and 3 yr and longer than 5 yr were recorded less than 10 times each, while between 3 and 5 yr was not very common.

None of the 32 individual whales seen during winter months (June to August) were resighted (Figure 4.5). During all other months some of the whales seen were resighted on other occasions, the majority between calendar years. Between October and January, a small proportion of resighted individuals were same-year resightings only; however, from February to May all resighted individuals were between years and 50% or more of whales seen during these three months had been seen previously (Figure 4.5).

Between-region matching

None of the images from Cabinda or Namibia matched a whale in any of the catalogues they were compared with. Three matches were made between the WSA and Gabon catalogues, and two between WSA catalogue and the Area II/III images contained in the AHWC (Table 4.4; also see Figure 4.1b). Three of these whales (ZAW-096, ZAW-213 and ZAW-292) were also resighted in different years off WSA (Tables 4.3 and 4.4). The matches with the AHWC were found to be with two humpbacks sighted together on the first day of the IWC-SOWER (Southern Ocean Whale and Ecosystem Research) cruise that departed on 22 December 2005 from Cape Town for the Antarctic; the images were inaccurately tagged in the database as being from Area III. Both were males (determined from biopsies collected off WSA) and the one animal (ZAW-290) was seen less than a month before in St Helena Bay, some 150 km to the north (Table 4.4). The second animal had been seen previously in St Helena Bay in December 2004 when it was accompanying a cow-calf pair, and was identified as a possible yearling calf. It was also seen subsequently, on 22 November 2006 (also in St Helena Bay) with a different female, when several defecations were observed, presumably an indication of recent feeding.

A northward transit with duration of about 230 d between sequential sightings was recorded for two of the WSA-Gabon matches (Table 4.4). Shorter southward transit periods (40 - 80 d) between Gabon and WSA for sightings in the same calendar years were recorded. The one male (ZAW-096) provides an interesting perspective in that it was sighted off WSA during the years before and after being photographed in Gabonese waters. It was first seen off Saldanha on 16 December 2001 as part of a group that defecated. On 6 August 2002 (233 d later) it was identified off Gabon, before appearing off Saldanha Bay 88 d later, where it apparently remained in the vicinity for a period of over two months, to be resighted on 14 January 2003. It was again resighted on 7 November 2006 when it approached the research boat during a plankton haul in St Helena Bay (Table 4.4).

Abundance estimates

Quality control criteria excluded 122 out of 1,409 images (all photographic features) from the datasets used for abundance estimates. The summary capture-recapture tables of data used in the models (given in Appendix 4.1) show the overall small sample sizes and few recaptures, especially for TF. During the first two sampling periods more individuals were identified by dorsal fins than other methods, and more matches were made, although for the remaining four periods most whales were identified by MS. The latter feature generally had the highest recapture rate relative to total number of whales identified, and between all pairs of recapture periods. Fewer resightings were recorded for LDF than RDF.

Adjusted catalogue size

The total number of individual humpback whales in the database (after correction for annual survival) represented by TF was over 30% lower than for LDF or RDF, while almost the same as MS, bearing in mind that biopsy sampling only started in 1993 (Table 4.5). Given that failure to match dorsal fins (or genotypes) that belong to the same individual contained in the database would inflate the catalogue size for the relevant feature, the total catalogue size was reduced (after correction of survival) by the calculated false negative rate for the respective feature (see Table 4.8). The numbers of whales identified by LDF and RDF were still greater than for TF (by 22.4% and 29.7% respectively).

Closed population models

The CMP estimates from TF data were the lowest overall, even less than the lower 95% confidence intervals of the estimates for all other identification features (Table 4.6) and less than the adjusted TF catalogue size. Tail fluke estimates were between 70 and 80% lower than uncorrected dorsal fin estimates, and about half the uncorrected MS estimates. Even when these features were corrected for false negative errors (see later) the TF estimates were still 45 - 75 % smaller. The highest overall estimate was from RDF, then LDF and MS, although all estimates had fairly wide 95% CI's. The estimates from the genotypic recaptures had the lowest CVs.

Open population models

Model configurations with all or most parameters constant or fixed $\{\phi_{.}\ \beta_{.}\ p_{.}\}$ and $\{\phi_{0.96}\ \beta_{.}\ p_{.}\}$, or with capture probability set to vary between capture periods, and other parameters constant or fixed $\{\phi_{0.96}\ \beta_{.}\ p_{t}\}$ showed very poor fit, or failed to converge, and were not considered. The remaining model variants applied were:

(1) full time-variance for all parameters $\{\phi_{t}\ \beta_{t}\ p_{t}\}$;

(2) full time-variance for two parameters with ϕ fixed at 0.96 $\{\phi_{0.96}\ \beta_{t}\ p_{t}\}$;

(3) ϕ fixed at 0.96, β set to vary fully over time, and p constant $\{\phi_{0.96}\ \beta_{t}\ p_{.}\}$.

Using the $\Delta QAIC_c$ as indication, model 2 showed the best fit for all identification features except for the LDF data for which the full time-variant (model 1) fitted best (Table 4.7). For TF, model 3 with p fixed had almost equal support to model 2 ($\Delta QAIC_c < 2$) although yielding a considerably lower estimate for *N*. Model 3 was also fairly well supported for MS data although model 2 performed better (Table 4.7); estimates based on this feature showed the least variation between model variants, and the tightest confidence intervals. All other identification features showed considerable variation and very wide CI's, especially those derived from dorsal fins. For all identification features model 3, the variant with fewest parameters, yielded the lowest CVs, although it was not well supported (zero likelihood) for the dorsal fin data (Table 4.7). The estimates for TF (with the exception of model 2) were lower than for other features. The estimates derived from dorsal fins were about double the highest TF or MS estimates, but with high variance and CI's (Table 4.7). Goodness-of-fit tests available in MARK did not yield results due to inadequate data availability. Given the sparse data and low number of recaptures, no attempt was made to model more complex configurations.

Potential biases in abundance estimates for different photographic identification features

False negatives

Assuming that the microsatellite identifications were correct, photographs of LDF and RDF when used alone as an identification feature resulted in 13.8% and 9.1% missed matches respectively, whereas no missed matches were detected for tail flukes (Table 4.8). No false positives were detected for dorsal fins. To test for misidentifications using microsatellites, individuals resighted by tail flukes on different days using pictures of quality and/or orientation > 'poor' were used as a control (11 individuals, intercepted 24 times), and were compared to matches obtained by microsatellite (where biopsies were taken). No false negatives were detected in seven matching opportunities. The values for N^* for the LDF and RDF recapture data and corrected for by the respective error rates (0.14 and 0.09) were 18% and 10% lower than the respective uncorrected values (Table 4.6). Although no microsatellite mismatches were detected, an abundance estimate corrected for the mean allelic error rate (0.065) is included for comparison: it was 17% lower than the uncorrected estimate (Table 4.6).

Individual variation in fluke exposure relative to other features

For 21.67% of the whales resighted on different days (n = 60), no pictures of TF were collected, for 20% no biopsies, 3.33% no RDF, and 1.67% no LDF photographs. In the majority of cases, TF photographs (for the 47 whales) were obtained during the first intercept/encounter (65.96%), 27.66% during the second, and 6.38% during the third and fourth. Furthermore, during all intercepts involving these resighted whales (n = 183 - some whales were in the same groups), TF pictures were collected during only 57.4% of intercepts, compared to 92.9% for dorsal fins. There was no significant difference between the mean duration of intercepts where TF were photographed (73.84 min ± 3.88 SE, n=146) and where it was not (83 min ± 11.14 SE, n = 31) (t = -0.93, df = 175, p = 0.35). The probability of recording a dorsal fin image (right or left) of an individual whale, every time it was encountered was high (Figure 4.6). This was not the case for TF, where for individual whales the probability of recording this feature during all, half, or none of encounters was very similar (28, 25 and 23 % respectively) (Figure 4.6).

Double-mark models

For the selected capture periods used for CMP estimates, the models where TF was used for recapture (m_2) and the second sample (n_2) invariably resulted in lower abundance estimates than when the alternative features were used (Table 4.9). The highest estimates were calculated with RDF as the alternative mark, while LDF and MS yielded very similar estimates. Those in which TF were used for n_2 were 0.31, 0.39 and 0.43 of those using RDF, LDF and MS respectively for n_2.

DISCUSSION

Sighting database, resightings and migratory links

The distribution over space and time of contributions to the sighting database and resulting resighting rates reflected the generally low and often inconsistent collection effort. This makes it difficult to interpret the observed resighting rates relative to other capture-recapture studies with greater geographic coverage and higher sampling effort, such as is obtainable during dedicated survey cruises (e.g. Larsen & Hammond 2004; Wedekin *et al.* 2010) or simultaneous surveys from multiple platforms or sites (e.g. Smith *et al.* 1999; Calambokidis and Barlow 2004). Resighting rates are known to be much higher at feeding sites (some >50%) compared to breeding grounds (10% or less) (Herman *et al.* 2010). Our between-year resighting rate of 15.65% seems relatively high given the low effort, limited extent of sampling, and that it is neither a breeding nor typical feeding area, and could be indicative of strong site fidelity or a small 'population', or both. There is strong historic evidence for severe depletion of this assemblage of humpback whales: during the five years immediately prior to protection of the species in 1963, annual catches from the Donkergat whaling station at Saldanha Bay averaged only five whales taken during a six-month season (IWS 1964), compared to catches of 208-244 humpback whales a season over the first three years of whaling from Donkergat (Best 1994).

Long-term site fidelity is supported by the majority of individual resightings occurring at annual or biennial intervals, and on six occasions, up to a decade apart. While most of these whales were seen only twice, others were seen in three or more different calendar years up to a maximum of six different years; again, the *ad hoc* collection effort probably confounded the ability to detect more returns of known animals. Returns over such time scales may confirm fidelity to the area but do not necessarily identify it as anything other than a migratory corridor. However, this is challenged by sequential resightings of the same individuals on the same day, or within a week of the first sighting, suggesting that they were not merely moving through the area as expected during a typical migration. This confirms the phenomenon of temporary residency first observed during the 1993 study at Cape Columbine (Best *et al.* 1995) when the same 10 humpback whales were seen on average 2.4 times during a month-and-a-half long period. It is thus not inconceivable that whales resighted in the same year or breeding season at periods of 1 – 6 months apart could be moving around locally and remain in the general area for days, weeks, or even months. Continuous occupancy cannot be proven however, and it should be equally feasible for animals to depart from, and return to the area in such time-spans. Here, the matches with the two other regional catalogues shed more light on the possible nature of such movements. The resightings off Cape Town detected through the AHWC matches confirm the occurrence of local movements beyond the core study area, and a net southward movement during summer. The three matches between Gabon and WSA independently confirm evidence from genotypic matches (Carvalho *et al.* 2010) that showed exchange of individual whales between these two proposed 'sub-stocks'. All three records indicate movement between winter (August, September) in Gabon and late spring/summer (November – February) in WSA, with the movement occurring in both directions but with the fastest transits from north to south. The monthly distribution of animals that were seen on more than one occasion (both within- and between-region resightings) suggests that humpback whales that engage in feeding during late spring, and in particular, summer months of the west coast of South Africa (as discussed in Chapter 2) are also likely to be encountered repeatedly during these months in other years. Furthermore, some of these whales were present off Gabon during August/September, so presumably overwintered there. On the other hand, the paucity of resightings of any of the animals identified off WSA during June to August (mid-winter) during which 11.38% of all whales identified were seen (based on combined features) suggests that whales present in the region at that time might belong to a different component of the population. If, as suggested by other evidence (see Chittleborough 1965; Dawbin 1966) this corresponds to the timing of an expected northern migration, it would appear that animals utilising the study area as a spring/summer feeding ground on their southward migration do not necessarily take the same route moving north to the breeding grounds.

The lack of any matches with the few available Namibian animals does not preclude the occurrence of a 'typical' coastal migration from headland to headland (Chittleborough 1965; Dawbin 1966) from WSA through Namibia to a more northerly destination, and back, on the southern migration. However, historical evidence does not support this in that off Namibia catches showed a sign of 'recovery' in 1925-30 after initial depletion while off WSA they remained very low (Best & Allison 2010). Possibly the coastal migration stream is cumulative rather than unitary, with northward-moving animals progressively converging on the coast with decreasing latitude, and southward-moving animals leaving the coast with increasing latitude. At Walvis Bay there were some sightings during late summer, but most humpback whale sightings were in winter (June, July, August) (Simon Elwen, unpublished data); however, there was no research effort after these months to allow detection a later peak, as observed off WSA, although whale and dolphin watching operators did encounter some humpback whales during September and October. Furthermore, historical catches (Best & Allison 2010) showed strong bimodality at Walvis Bay, with a peak in June/July and another in October/November.

Abundance estimates

The available capture-recapture data were very limited in terms of sample sizes and number of recaptures detected between sampling periods: especially for TF that was apparently under-represented in the database at only 121 individuals (after correction for survival), while the similarly lower number of whales identified by MS could be partly attributed to its implementation (as means of identification) a decade later than photo identification. The higher numbers of whales identified by dorsal fins may reflect that they are more easily photographed: unlike TF, they are always exposed during surfacings (but see later), while biopsy sampling requires the closest approach of all sampling methods and may be difficult to achieve for boat-shy individuals that otherwise can be photographed. The CMP estimates for N^* during the first sampling periods more or less reflect this relative representation of features in the sighting database, i.e. dorsal fins the highest and TF the lowest at an improbable 67 individuals. For the remaining features, the estimates for N^* ranged between 122 (MS) and 265 (RDF) after error correction. That the TF estimate is an order of magnitude lower than for any other feature and is comparable to the adjusted catalogue size for TF at this time (69), suggests that the ability to capture a whale using TF may be affected by an additional factor (see later).

The generally poor (or non-) performance of the POPAN open-population models when capture probability (p) and probability of entry (β) were fixed, again suggests considerable variation in these parameters between capture periods; perhaps not surprising, given the low effort, the differences in sampling strategy (with or without a land watch) and location of sampled areas (Saldanha vs. St Helena Bay) between j_1 - j_2 and j_3 - j_6. For the most successful model variants apparent survival (ϕ) was fixed at 0.96 and both β and p were fully time-dependent (model 2), or β time-dependent and p fixed (model 3). Before looking at the magnitude of the estimated values for N (the super-population) by the POPAN models, it is worth considering it in the context of what was sampled. This parameter provides an estimate for the total number of animals, both captured or not, available in a (hypothetical?) super-population (GC White, Program MARK Help files). For example, in a study on bottlenose dolphins, Reisinger & Karczmarski (2010) using POPAN concluded that the N there potentially represented the dolphin population along a considerable segment, or even the entire South African coastline, while in other studies it has been taken to represent a full population of right whales (Wade *et al.* 2011), a sub-population of whale sharks (Meekan *et al.* 2006) or feeding assemblage of humpback whales (Larsen & Hammond 2004). From this it is apparent that N as estimated by POPAN is likely to represent more than simply the size of the feeding assemblage at Saldanha and St Helena Bays during any given season, but probably also includes whales that migrated through the area, or whose utilisation of the area varied between years and should probably be treated as an upper sub-population limit.

The abundances obtained from the open population models were larger than those from other methods. Similar to the other assessment methods, the dorsal fin estimates were twice as high as those for other features, most likely as a result of the occurrence of false negative errors (see later). Although a correction parameter for photographic and genotypic mismatches is not available in the POPAN model, estimates that include such errors would most likely still fall within the wide confidence intervals obtained, especially for dorsal fins. Tail fluke estimates were lower than for other features (but not as dramatically as with the CMP model) with the exception of model 2 where the estimate was very similar to that for MS, albeit with a much higher CV. The MS capture-recapture data yielded the most credible estimates with the lowest variation between models, and tightest confidence intervals for individual variants. The model-averaged estimate of N for this feature (calculated from all three variants in MARK) was 510±143 SE (230 - 790 95% CI's).

Biases as a result of different identification features

There are numerous known issues associated with the use of natural markings for abundance estimates (see Hammond 1986 for review), but (physical) loss of marks is not considered a major problem with humpback whales. Although dorsal fins are commonly used by researchers in the field to distinguish between different whales in a group while collecting data during boat encounters, and have been proposed as a potentially even more stable identification feature than ventral tail fluke pigmentation (Blackmer *et al.* 2000), this is, to our knowledge, the first time they have been used for an abundance estimate for the species. While false positives are probably rare in photo identification studies (we detected none), false negatives are thought to be more common, with a higher error rate the poorer the quality of pictures (Stevick *et al.* 2001). This is more likely to apply to dorsal fins, as they are smaller and have fewer distinguishing features than tail flukes. Although dorsal fin photographs (of sufficient quality) were not collected during all intercepts, there were no resighted individuals for which dorsal fin pictures were unavailable. There may be differences in the ability of researchers to obtain good quality images of these different identification features: during a typical approach from the rear, chances are good of obtaining a TF picture (provided that they are adequately exposed, see below). For dorsal fins, a considerable amount of manoeuvring of the boat is required to position the photographer at a right angle to the whale, while still at the surface. The angle between the camera and the whale affects the quality of dorsal fin pictures to a greater extent than for TF (J. Barendse pers. obs.) and poor photo quality can be the source of substantial heterogeneity in capture probability when using dorsal fins in other species e.g. northern bottlenose whales *Hyperoodon ampullatus* (Gowans & Whitehead 2001). The application of some quality control (e.g. removal of photos with incomplete subjects and those of low quality) has been shown to adequately reduce error rates when using TF (Friday *et al.* 2008), but it is unknown to what degree this is applicable to dorsal fins, and we were unable to test this with our small sample sizes.

Assuming the microsatellite identifications were error-free, dorsal fin photographs when used alone as an identification feature resulted in 9-14% missed matches, whereas this does not appear to apply to the same extent for TF or MS. If left uncorrected, this may result in a substantial over-estimation (up to 30%) of abundance when using closed population models, and produce high estimates of low confidence in open population models. This conclusion however may be case-specific, depending to a large extent on data collection protocol, photographic quality, laboratory procedures, and the size of the catalogue. The differences between abundance estimates for RDF and LDF (although less pronounced compared to TF) suggests that there may have also been a difference in the ability of photographers to obtain useable images from both sides of an individual. The reason for this is not immediately apparent, although individual behaviour could contribute to such a bias. Clapham *et al.* (1995) reported strongly lateralised behaviour by humpback whales that apparently favoured their right-side during feeding and flippering behaviour; it is possible that whales could preferentially present their right side to the boat. However, we are unable to test this with the available data.

Relative to other identification features (even after they had been corrected for missed matches) TF yielded the overall lowest abundance estimates. This suggested that fluking as an individual behavioural trait could affect the probability of an individual being sampled, and was supported by the finding that for resighted whales, the probability of collecting TF pictures during all, half, or none of the intercepts was nearly equal. The fact that for all resighted whales, over 20% had no TF image collected at all during intercepts of similar mean duration, and that in the majority of cases (65%) flukes were photographed during the first intercept, suggests that fluking is an idiosyncratic feature for humpback whales in this area. The frequency of exposure of the ventral surfaces of the flukes is a behaviour known to vary with sex (Rice *et al.* 1987), age, reproductive and behavioural class, and group size, with fluking rates ranging from <10 per 100 dives for cows, calves and principal escorts, to 46.5 per 100 dives for single animals (Smith *et al.* 1999). If some whales consistently fluke less often than others, or do not fluke at all, such individual variation in behaviour may introduce capture heterogeneity that would impact on population estimates calculated from capture-recapture models (Barlow *et al.* 2011) using this identification feature such as is strongly suggested by these data. In West Greenland such (downward) bias was estimated at 10 – 20 % of the population size (Perkins *et al.* 1984), but presumably can vary with area, season, or photographic protocol. Based on the CMP abundance estimates for the double- marked whales, those using TF recaptures and identifications during the second sampling period were 57 - 69 % lower than those when using an alternative feature. While this conclusion about the effects of individual fluking behaviour on population estimation may only be valid for the whales observed in some areas (such as WSA) as individual humpback whale behaviour may differ (and sampling protocol vary) in different parts of its range, the potential effects shown here are certainly large enough to warrant similar investigations in other areas. It is however more difficult to quantify (and thus correct for) heterogeneity attributable to individual behaviour compared to other sources of error (e.g. photographic quality) (Barlow *et al.* 2011).

Genotypic abundance estimates may be considered independent from those obtained from photo identification (as suggested by Gubili *et al.* 2009) with a lesser degree of bias from sampling heterogeneity applicable to photographs of natural marks (i.e. image quality and fluking behaviour). On a broader scale, because genetic and photographic sampling took place simultaneously and from the same platform, both could be considered subject to the same potential biases caused by non-representative sampling effort. The abundance estimates derived from MS recaptures were lower than those from dorsal fins, but more similar (but higher) to those obtained for TF, though more recaptures were made with MS. Heterogeneity of obtaining a biopsy (i.e. capture probability) cannot be excluded, given that it requires a closer approach than obtaining a TF image, for example, and recognising that for 20% of resighted whales no biopsy was collected. This could be as a result of a different individual behavioural response to boat approaches, as has been tested for whale watching boats (e.g. Scheidat *et al.* 2004; Stamation *et al.* 2010): the whales could exhibit boat avoidance (i.e. 'trap shy' animals) or be boat friendly ('trap-happy'), both of which will cause capture heterogeneity and bias in abundance estimates. However, there are certain issues relating to methodology and laboratory procedures that are specific to the use of molecular tags and may bias abundance estimates downward (Mills *et al.* 2000; Waits & Leberg 2000) or upward (Lukacs & Burnham 2005; Wright *et al.* 2009).

CONCLUSION

The consolidated photographic and genotypic sighting database for humpback whale from WSA contributes to a better understanding of residency rates and long-term attendance patterns to the region. It reveals that some whales routinely visit the coastal waters of the St Helena/Saldanha Bay region, showing high fidelity to a geographically limited area to participate in feeding during spring and summer. While acknowledging the effects of the sampling approach, low effort and small sample sizes on capture probability, possible structuring of the population would further contribute heterogeneity to individual capture, and the notion that there may be a strictly migratory (or 'transient') component is supported by the high number of once-off sightings, especially during winter. The situation is probably fairly complex, but similar to that observed off California where whales that share a wintering region show strong fidelity to specific feeding areas, with limited exchange between these, although whales from different sub-areas may make use of the same migratory corridors (Calambokidis *et al.* 2001). Given the limitations of the data, and violation of closure, the estimates from the closed-population model are likely to be underestimations of the total number of humpback whale found here on a seasonal basis, although their use did allow us to explore issues related to the use of different identification features. The findings that using dorsal fins and TF can cause substantial over-estimation and under-estimation respectively are important, especially when dealing with such a small dataset, and given that the ventral TF pattern is the standard identification feature used for humpback whales. Whether humpback whale dorsal fins are distinctive enough features to use in large catalogues (or as alternative identification feature) is debatable and it may be more appropriate to only include animals that are considered adequately 'marked', similar to the practise in dolphin studies (e.g. Elwen *et al.* 2009), although this approach may violate assumptions of equal capture probability, depending on the model used (see Reisinger *at al.* 2011). The open-population models with few restrictions and using multiple capture periods fitted the capture-recapture data better, although there was considerable variation between different identification features and model variants used. The most consistent estimates (and those with the tightest confidence intervals) were obtained from the microsatellite data, putting the number of humpback whales that visited the area during the study period at about 500 animals, a value that falls within the confidence intervals for dorsal fins (lower range), and tail flukes (mid to upper range). The geographic extent of this estimate is not clear, nor whether all these animals feed in the region of Saldanha every season, or how they relate to whales along the rest of the West African coast. Although this assemblage does not exist in isolation from the greater Breeding Stock B (given the photographic matches), it does seem to represent a previously undescribed situation in the Southern Hemisphere, although the possibility cannot be excluded that such behaviour, or similar assemblages may occur at other localities where comparable oceanographic conditions (i.e. wind-driven upwelling) are present For example, some Namibian localities such as Lüderitz (Hutchings *et al*. 2009) may provide similar feeding opportunities to those off WSA. For a better understanding of the population structure in the region, research effort and photographic and genetic data collection need to cover more seasons, and include more sites within WSA and the rest of West Africa, including farther offshore, similar to some of the long-term ocean-basin wide identification studies such as the SPLASH (Structure of Populations, Levels of Abundance, and Status of Humpbacks) program in the North

Pacific (Calambokidis *et al.* 2008), or YoNAH (Year of the North Atlantic Humpback, Smith *et al.* 1999). The strategic deployment of satellite tags off WSA may offer a more short-term solution to elucidate potential migratory routes and locations of unknown breeding or feeding areas (e.g. Hauser *et al.* 2010; Zerbini *et al*. 2006) and would help inform whether the current IWC management units are relevant to humpback whales in this region.

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TABLES

Table 4.1. Photographic and genetic contributions to west South Africa (WSA) humpback whale database from various projects and sources. Total number of individuals identified by matching using combined identification features (including microsatellites). [*Indicates projects by the Mammal Research Institute (MRI); **These numbers include all images and biopsies collected and incorporated into the database. It does not take photo quality or matches into consideration].

Project description*	Study years	No. of images/biopsies collected**					Individuals identified
		Total	TF	RDF	LDF	Biop.	
Miscellaneous contributions	1983-2007	143	96	30	17	1	32
Cape Columbine humpback *	1993	104	30	37	37	6	9
West coast Heaviside's dolphin*	1997,1999-2001, 2008	98	19	33	46	13	18
Saldanha Bay humpback whale*	2001-2003	739	173	294	272	104	135
Saldanha Bay / St Helena Bay southern right whale*	2003-2007	736	192	300	244	92	95
	Entire database	1820	510	694	616	216	289

Table 4.2. Annual collection effort of photo identification and genetic data that contribute to the WSA humpback whale database, expressed as number of days on which at least one identification image or biopsy was collected or 'collection days'. [* numbers in brackets indicate total days on which boat was deployed, when known; 'x' indicates months with no boat effort during dedicated MRI studies. Months within dashed outline indicate west coast Heaviside's dolphin study period; Light-gray shading indicates dedicated humpback whale study at Saldanha Bay (with shore-based observations); dark-gray shading indicates boat-based study on southern right whales at St Helena Bay. Italicised numbers in different typeface in 2001-2007 show those months used for abundance estimates].

Year	Months*												Total days*
	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sept.	Oct.	Nov.	Dec.	
1983		2											2
1984		1											1
1988	1							1					2
1989				1									1
1990	1										1		2
1992					1								1
1993										6(13)	1(5)		7 (18)
1997			1						1				2
1999	x	3(13)	1(13)	x									4 (26)
2000	0(4)	4(13)	1(16)	0(6)									5 (39)
2001	0(8)	0(14)	1(15)	1(7)	x	x	1(4)	4(11)	*4(14)*	*4(9)*	*3(9)*	*4(4)*	22
2002	x	x	x	x	1(7)	1(14)	4(8)	5(11)	*3(10)*	*5(14)*	*5(9)*	*2(9)*	26
2003	*7(9)*	*2(2)*	x	x	x	x	x	x	*1(2)*	*3(11)*	*3(12)*	*0(5)*	16
2004	*3(9)*	*x*	x	x	x	x	x	x	*2(8)*	*5(15)*	*4(9)*	*3(10)*	17
2005	*2(6)*	*1*	x	x	x	x	x	x	*2(9)*	*4(18)*	*3(18)*	*x*	12
2006	*x*	*x*	x	x	x	x	x	x	*0(1)*	*1(16)*	*8(17)*	*3(7)*	12
2007	*0(2)*	*0(7)*	x	x	x	x	x	x	x	x	2	0(8)	2 (9)
2008	x	1											1
All	14	14	4	2	2	1	5	10	13	28	30	12	135

Table 4.3. Sighting histories of 44 identified humpback whales (based on combined identification features) resighted inter-annually off west South Africa, as total number of resights, number of between-year resights (in brackets), and number of sightings on different days in the same year (* indicates resightings on the same day, hyphen = no record). For example: ZAW-047 was seen in 2001 and 2003; 1, 2* in the latter year indicates that it was seen three times on two separate days in that year, and resighted on one of the days. [[1] ZAW-number, # indicates an individual matched to other regional catalogues (see Table 4.4)].

ID[1]	Resights	Year															
		1988	'89	'90	'92	'93	'97	'99	2000	'01	'02	'03	'04	'05	'06	'07	'08
038	2 (2)	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-
043	2 (2)	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-
069	2 (2)	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-
075	2 (2)	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-
091	2 (2)	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-
235	2 (2)	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-
269	2 (2)	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-
286	2 (2)	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-
292#	2 (2)	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-
295	2 (2)	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-
011	3 (3)	-	-	1	1	-	-	-	-	-	-	1	-	-	-	-	-
028	3 (2)	-	-	-	-	-	1	-	-	-	-	2*	-	-	-	-	-
029	3 (3)	-	-	-	-	-	1	-	-	1	1	-	-	-	-	-	-
070	3 (2)	-	-	-	-	-	-	-	-	2	-	1	-	-	-	-	-
082	3 (2)	-	-	-	-	-	-	-	-	1	2*	-	-	-	-	-	-
085	3 (2)	-	-	-	-	-	-	-	-	1	2*	-	-	-	-	-	-
115	3 (2)	-	-	-	-	-	-	-	-	2*	1	-	-	-	-	-	-
118	3 (2)	-	-	-	-	-	-	-	-	1	2	-	-	-	-	-	-
126	3 (3)	-	-	-	-	-	-	-	-	1	1	1	-	-	-	-	-
170	3 (2)	-	-	-	-	-	-	-	-	-	1	2	-	-	-	-	-
173	3 (2)	-	-	-	-	-	-	-	-	-		1	2*	-	-	-	-
183	3 (2)	-	-	-	-	-	-	-	-	-	2	1	-	-	-	-	-
207	3 (2)	-	-	-	-	-	-	-	-	-	-	2	-	1	-	-	-
233	3 (2)	-	-	-	-	-	-	-	-	-	-	1	2*	-	-	-	-
273	3 (2)	-	-	-	-	-	-	-	-	-	-	-		2*	1	-	-
033	4 (3)	-	-	-	-	-	-	2	-	-	1	-	1	-	-	-	-
047	4 (2)	-	-	-	-	-	-	-	-	1	-	1, 2*	-	-	-	-	-
097	4 (2)	-	-	-	-	-	-	-	-	1, 2*	-	-	1	-	-	-	-
107	4 (3)	-	-	-	-	-	-	1	-	1	-	-	-	-	2*	-	-
174	4 (2)	-	-	-	-	-	-	-	-	1	3*	-	-	-	-	-	-
204	4 (2)	-	-	-	-	-	-	-	-	-	-	3	1	-	-	-	-
210	4 (2)	-	-	-	-	-	-	-	-	-	-	3*	1	-	-	-	-
213#	4 (2)	-	-	-	-	-	-	-	-	-	-	1, 2*		-	-	-	1
240	4 (2)	-	-	-	-	-	-	-	-	-	-	-	3	1	-	-	-
089	4 (3)	-	-	-	-	-	-	-	-	1	1	2*	-	-	-	-	-
096#	5 (4)	-	-	-	-	-	-	-	-	1	1	2*	-	-	1	-	-
163	5 (2)	-	-	-	-	-	-	-	-		2, 2*	-	-	1			-
009	6 (5)	-	1	-	-	-	-	-	-	1	2*	-	-	-	1	1	-
019	6 (5)	-	-	-	-	1	-	1	2		-	-	1	-	1	-	-
036	6 (5)	-	-	-	-	-	-	1	1	1	-	1	-	2	-	-	-
015	8 (4)	-	-	-	1	-	-	-	-	2	-	2, 2*	-	1	-	-	-
017	8 (3)	-	-	-		4, 2*	-	-	-	-	-	-	1	1	-	-	-
101	8 (4)	-	-	-	-	-	-	-	-	1, 2*	2*	1	2*	-	-	-	-
006	11 (6)	1	-	-	-	-	-	2	2	1	2	1, 2*	-	-	-	-	-

Table 4.4. Details of sightings (date and position) of humpback whales involved in photographic matches between tail fluke catalogues of WSA ('ZAW') and Gabon ('Gab'), and WSA and AHWC (sex determined from biopsies), and time elapsed between sequential resightings.

WSA ID (sex)	Date (and position) photographed off West South Africa	Matched to other catalogue ID	Date (and position) photographed in other region	Time between consecutive between-catalogue resightings (and direction of movement)
ZAW-213 (F)	2003/01/13 (33.013^{O}S, 17.774^{O}E and 33.064^{O}S, 17.825^{O}E); 2003/01/14 (32.702^{O}S,17.99^{O}E) 2008/02/05 (33.03^{O}S, 17.875^{O}E)	TF-Gab-03-124	2003/09/04 (9.264^{O}S, 1.928^{O}E)	234 d (N); 4.4 yr (S)
ZAW-253 (F)	2004/11/08 (32.665S, 17.988E)	TF-Gab-04-045	2004/09/26 (9.264^{O}S, 1.928^{O}E)	43 d (S)
ZAW-096 (M)	2001/12/16 (33.021^{O}S, 17.86^{O}E); 2002/11/02 (33.005^{O}S, 17.849^{O}E); 2003/01/14 (33.031^{O}S, 17.825^{O}E and 32.674^{O}S, 17.877^{O}E); 2006/11/07 (32.674^{O}S, 17.935^{O}E)	TF-Gab-02-299	2002/08/06 (9.264^{O}S, 1.928^{O}E)	233 d (N); 88 d (S)
ZAW-290 (M)	2005/11/24 (32.551^{O}S, 18.026^{O}E)	ahwc3054	2005/12/22 (33.859^{O}S,18.278^{O}E)	28 d (S)
ZAW-292 (M)	2004/12/01 (32.703^{O}S, 17.888^{O}E); 2006/11/22 (32.973^{O}S, 17.856^{O}E)	ahwc3055	2005/12/22 (33.859^{O}S,18.278^{O}E)	386 d (S); 11.2 mo (N)

Table 4.5. Minimum photographic and genetic individual catalogue size, by year and identification feature for WSA humpback whales. Correction for apparent survival (ϕ) is 0.96 from Mizroch *et al.* (2004); correction for matching error (*e*) is calculated false-negative rates for RDF/LDF (0.09 and 0.14), and for MS the mean allelic error of 0.065 (see text).

Year		Total no. individuals identified/year/feature (no. known from previous years)			
		TF	RDF	LDF	MS
1983		2	1	1	-
1984		2	-	-	-
1988		3	-	-	-
1989		1	3	-	-
1990		3	-	-	-
1992		2 (1)	2 (2)	1	-
1993		7	9	9	3
1997		1	2	3	-
1999		3	4 (1)	6 (1)	2
2000		2	5 (2)	7 (2)	5 (2)
2001		30 (3)	59 (3)	66 (5)	39 (3)
2002		33 (6)	61 (9)	51 (7)	38 (7)
2003		24 (7)	38 (8)	35 (10)	29 (7)
2004		20 (5)	26 (5)	25 (1)	27 (7)
2005		14 (0)	32 (4)	24 (2)	27 (5)
2006		24 (4)	31 (4)	32 (4)	22 (6)
2007		11 (1)	-	-	-
2008		1 (1)	3 (1)	3 (1)	1
Totals and (correction)	(none)	154	237	230	156
	(survival)	121	189	183	127
	(survival and error)	n/a	172	156	119

Table 4.6. Abundance estimates (N^*) for humpback whales at Saldanha Bay, WSA by the Chapman's modified Petersen method using separate identification features for one pair of capture periods (j_1 = Sept 2001 - Feb 2002; j_2 = Sept 2002 - Feb 2003). Photographs with quality and orientation ratings of 'poor' and lower were excluded from the analysis. Correction factor for dorsal fins refers to calculated false negative rates (RDF = 0.091 and LDF = 0.138, see Table 7), and for microsatellite the mean allelic error rate of 0.065, applied using the method of Stevick *et al.* 2001 (see text). Percentage bias calculated relative to the uncorrected estimator. [Legend: n/a = not applicable; n_1= no. of individuals identified during j_1 and n_2 during j_2; s_1 and s_2 = no. of sampling events in j_1 and j_2 respectively; m_2 = no. of individuals seen in j_1 and resighted in j_2; SE = standard error; CV = estimated coefficient of variation; LCI = lower 95% confidence intervals; UCI = upper 95% confidence intervals.]

Feature	Treatment	n_1	s_1	n_2	s_2	m_2	N^* ± SE	CV(N^*)	LCI	UCI	% bias
TF	uncorrected	15	15	16	18	3	67 ± 23.03	0.34	35	129	n/a
RDF	uncorrected	39	42	58	65	7	294 ± 81.77	0.28	172	502	
	corrected	38.70	-	57.30	-	7.70	265 ± 69.61	0.26	160	440	10
LDF	uncorrected	39	44	49	61	8	221 ± 56.02	0.25	136	361	
	corrected	38.20	-	47.08	-	9.28	182 ± 41.57	0.23	117	283	18
MS	uncorrected	34	37	41	51	9	146 ± 32.70	0.22	95	225	
	corrected	30.58	-	40.30	-	9.63	122 ± 25.28	0.21	81	182	17

Table 4.7. Selected parameter estimates and model selection criteria for three model variants in the POPAN version of Jolly-Seber open–population model in MARK 5.1, for different identification features. Photographs with quality and orientation ratings of ‘poor’ and lower were excluded from the analysis. The model estimates the super-population (*N*) for humpback whales that feed during spring/summer off west South Africa, as derived from capture-recapture data from six successive capture periods in 2001-2007 (j_1 – j_6, see Appendix 4.1). Notations used: SE = standard error; CV = coefficient of variation; LCI = lower 95% confidence intervals (UCI = upper 95% confidence intervals); $QAIC_c$ = Quasi-Akaike Information Criterion value; Mod. likel. = model likelihood; NP = number of parameters. Models are sorted according to ascending $QAIC_c$.

Model	*N* ± SE	CV(*N*)	LCI	UCI	$QAIC_c$	$\Delta QAIC_c$	Mod. likel.	NP
Tail flukes								
2 - $\{\phi_{0.96}\,\beta_t\,p_t\}$	531 ± 346.7	0.65	192.22	1771.18	106.399	0	1	8
3 - $\{\phi_{0.96}\,\beta_t\,p_.\}$	301 ± 99.95	0.33	171.55	587.82	106.587	0.188	0.9103	4
1 - $\{\phi_t\,\beta_t\,p_t\}$	233 ± 112.7	0.48	116.14	620.00	112.112	5.7127	0.0575	11
Microsatellites								
2 - $\{\phi_{0.96}\,\beta_t\,p_t\}$	528 ± 143.4	0.27	332.14	921.92	230.686	0	1	9
3 - $\{\phi_{0.96}\,\beta_t\,p_.\}$	400 ± 65.01	0.16	300.52	561.31	234.518	3.8323	0.1472	2
1 - $\{\phi_t\,\beta_t\,p_t\}$	496 ± 145.0	0.29	304.87	906.65	235.006	4.3198	0.1153	11
Right dorsal fins								
2 - $\{\phi_{0.96}\,\beta_t\,p_t\}$	1035 ± 374.8	0.36	551.72	2116.89	198.517	0	1	7
1 - $\{\phi_t\,\beta_t\,p_t\}$	955 ± 495.1	0.52	419.87	2604.19	206.221	7.7041	0.0212	11
3 - $\{\phi_{0.96}\,\beta_t\,p_.\}$	681 ± 139.1	0.20	472.24	1032.05	231.399	32.882	0	3
Left dorsal fins								
1 - $\{\phi_t\,\beta_t\,p_t\}$	1232 ± 773.8	0.63	454.61	3950.49	141.953	0	1	11
2 - $\{\phi_{0.96}\,\beta_t\,p_t\}$	1013 ± 497.8	0.49	449.43	2612.07	146.357	4.4036	0.1106	7
3 - $\{\phi_{0.96}\,\beta_t\,p_.\}$	760 ± 194.1	0.26	481.12	1269.69	178.347	36.394	0	2

Table 4.8. False negative rates (number missed matches as % of total number of matching opportunities) detected for humpback whale photographic identification features, west South Africa, using microsatellite matches as a control. Only pictures of quality and orientation > ‘poor’ were used (as for abundance estimates).

ID feature	Sample occasions	Matching opportunities	Confirmed matches	Missed matches	False negative rate (%)
MS (control)	88	32	-	-	-
LDF	58	29	25	4	13.8
RDF	49	22	20	2	9.09
TF	30	13	13	0	0

Table 4.9. Abundance estimates (N*) for WSA humpback whales from the Chapman’s modified Petersen estimator for various model configurations using double marked (TF plus alternative mark) humpback whales identified during first sampling period, and recaptures based on TF or alternative mark during second sampling period. SE = estimated standard error, CV = estimated coefficient of variation, LCI and UCI = lower and upper 95% confidence intervals. * An error correction of 0.065 for MS, 0.091 for RDF, and 0.138 for LDF was applied for n_2 and m_2 using method of Stevick *et al.* 2001.

Model	n_1	n'_2*	m'_2*	N*	SE(N*)	CV(N*)	LCI	UCI
{n_1 = TF&RDF,n_2 = RDF, m_2 = RDF}	10	57.30	3.30	148	48.65	0.33	79	277
{n_1 = TF&RDF, n_2 = TF, m_2 = TF}	10	16	3	46	14.58	0.32	25	84
{n_1 = TF&LDF, n_2 = LDF, m_2 = LDF}	11	47.08	3.48	128	41.47	0.32	69	238
{n_1 = TF&LDF, n_2 = TF, m_2 = TF}	11	16	3	50	16.28	0.33	27	93
{n_1 = TF&MS, n_2 = MS, m_2 = MS}	9	40.30	2.14	131	51.50	0.39	62	275
{n_1 = TF&MS, n_2 = TF, m_2 = TF}	9	16	2	56	21.51	0.39	27	116

FIGURES

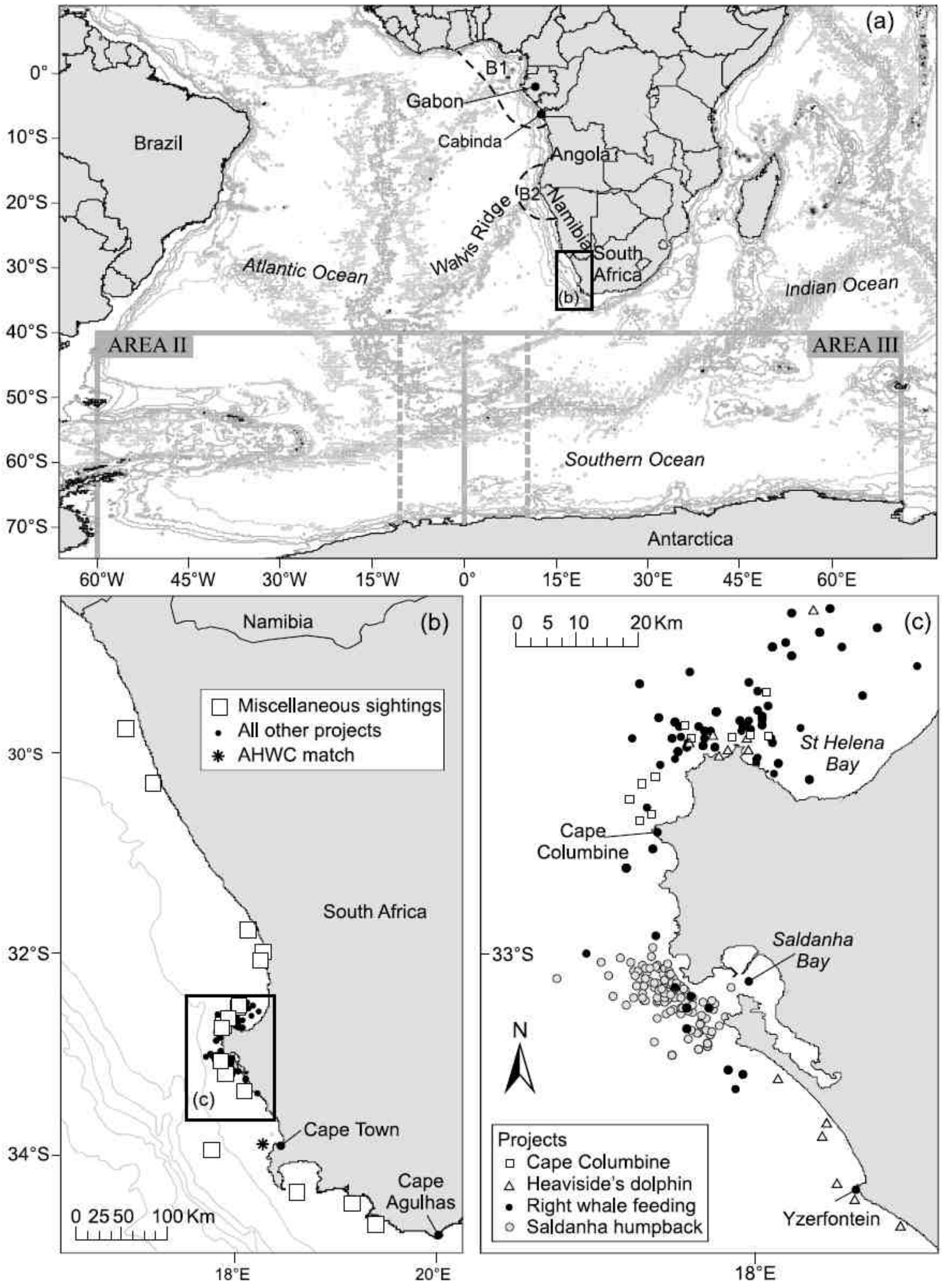

Figure 4.1: (a) The SE Atlantic-, SW Indian-and Southern Oceans showing bathymetry (to 4,000 m), areas of relevance to Breeding Stock B (B SB) southern hemisphere humpback whales, the speculated locations of sub-stocks B1/B2, Antarctic Feeding Areas II/III and suggested nucleus feeding area for B SB whales (10^{O}W – 10^{O}E, shown by dashed grey lines), and collection areas for regional photo-ID catalogues; (b) Detail of WSA and extent of collection effort from various sources; (c) Detail of Saldanha/St Helena Bay area where the majority of data were collected during four major research projects, 1993 - 2007 (also see Tables 4.1 and 4.2).

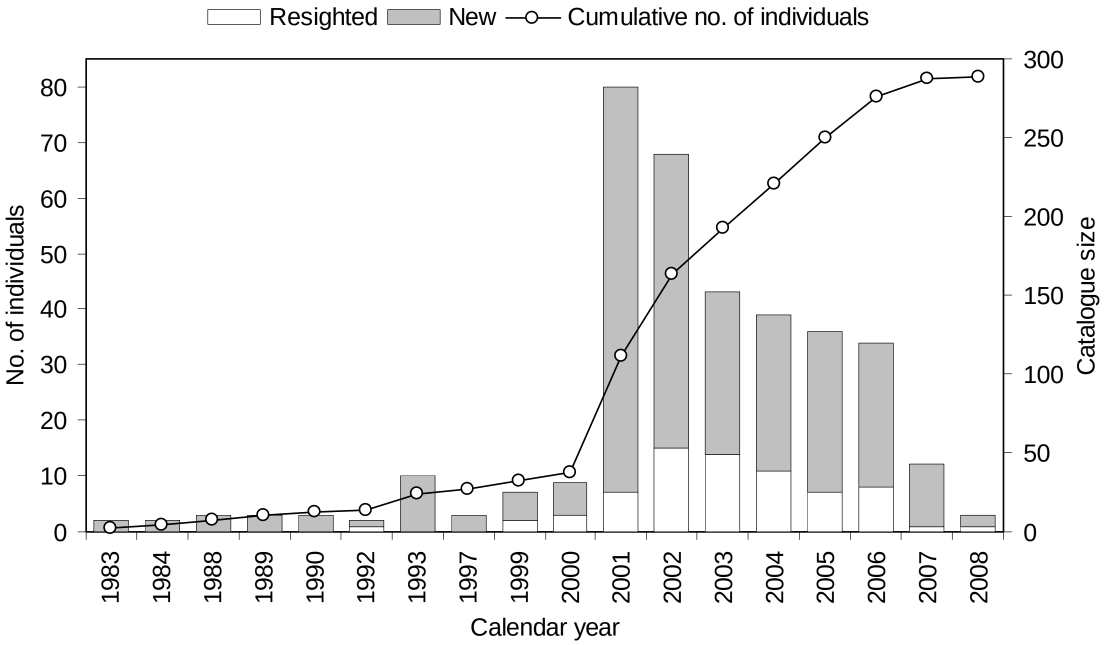

Figure 4.2. Total number of new and resighted individually identified humpback whales seen per year (1983 – 2008) off the west coast of South Africa, based on combined identification features (photographic and microsatellite), and cumulative number of individuals in the database (unadjusted for mortality).

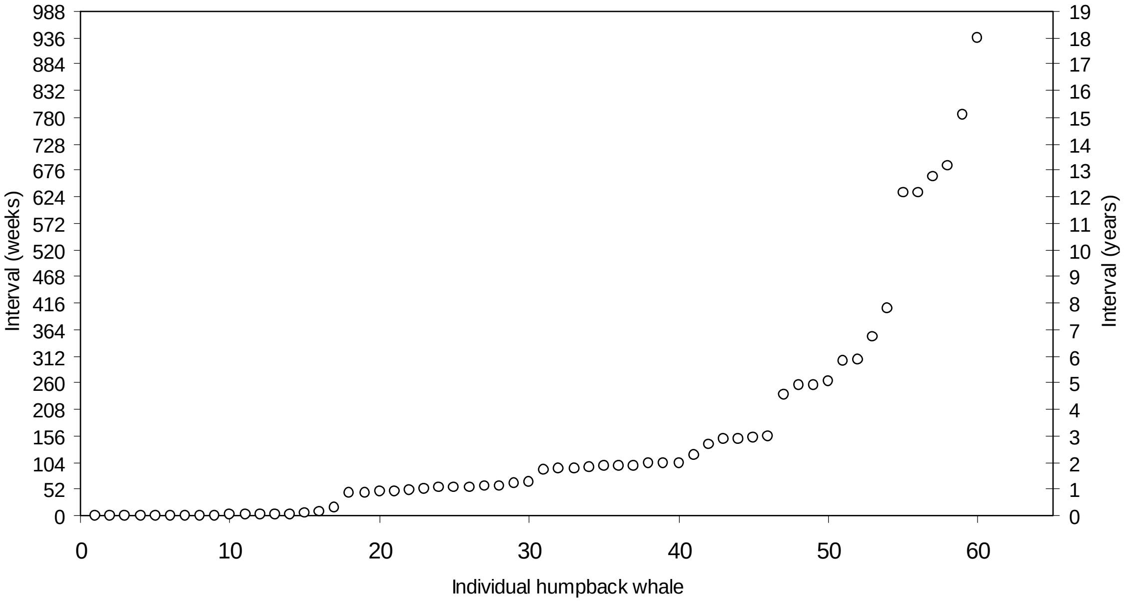

Figure 4.3. Intervals (in weeks and years) between the first and last sighting events for 60 humpback whales resighted on different days, off west South Africa.

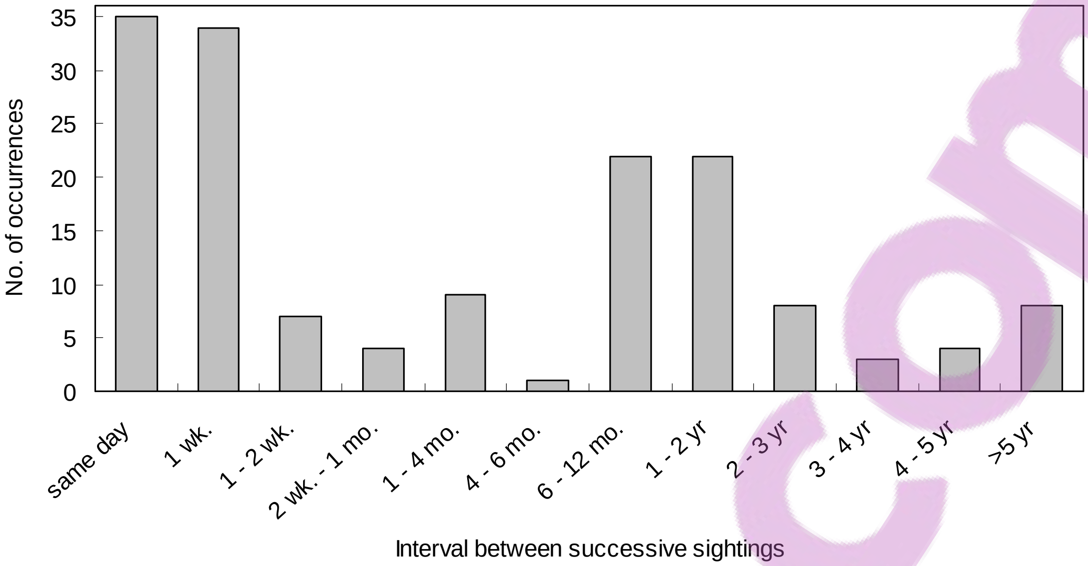

Figure 4.4. Frequency occurrence of time interval between successive sightings of 67 individually identified humpback whales off west South Africa (*n* = 157 sighting records).

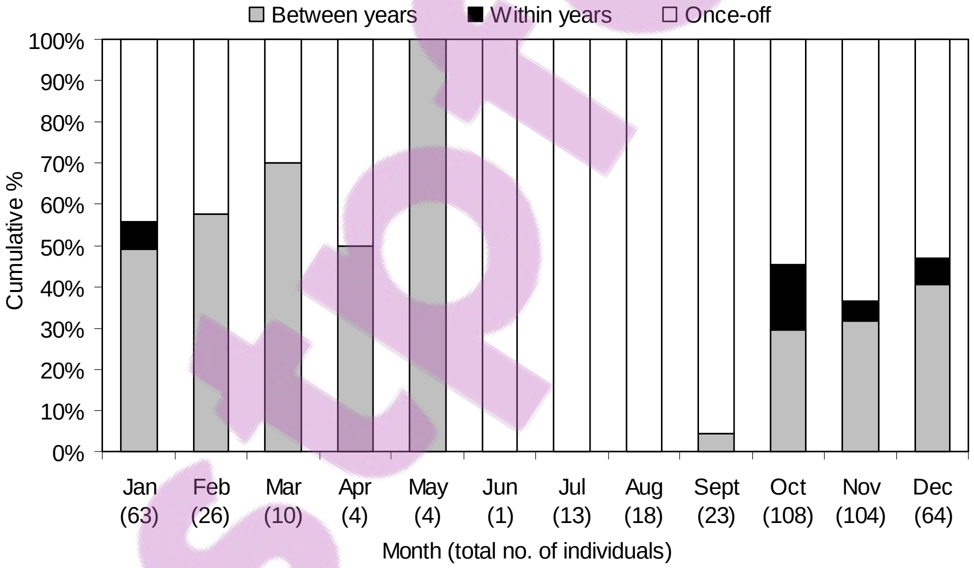

Figure 4.5. Time of year (month) off west South Africa during which humpback whales with different resighting histories (resighted within the same year only, resighted between years, and never resighted , i.e. once-off sightings) were recorded during 438 sighting events of 281 individual whales, based on combined identification features (1983 – 2008). Total number of unique individuals identified during a month is shown in brackets.

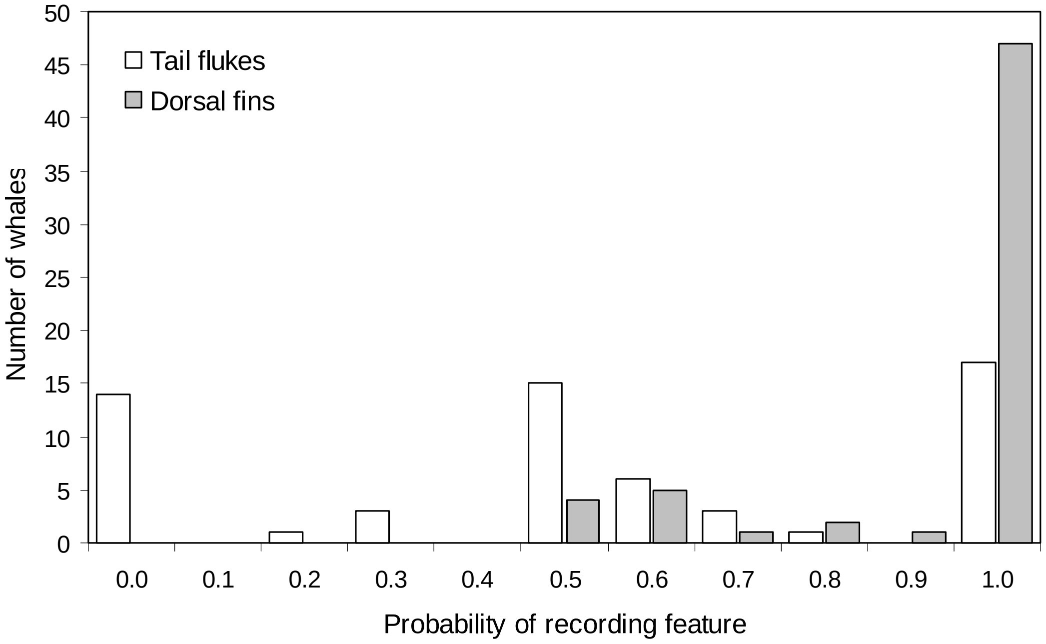

Figure 4.6. Probability for recording a photographic identification feature for 60 individual (resighted) humpback whales off WSA, calculated as the number of times a feature (tail fluke or dorsal fin) was recorded as proportion of the total number of times that the whale was intercepted.

APPENDIX 4.1: SUMMARY CAPTURE-RECAPTURE STATISTICS

Summary capture-recapture statistics for individual identification features of humpback whales off west South Africa, and all features combined for six selected sampling periods, and used in CMP and JS abundance estimates. [j = sampling period; n = total whales identified per j; m = total recaptures per j; u = new identified whales; M = number of new whales before j]. Sampling Periods: j_1 = Sept 2001 - Feb 2002; j_2 = Sept 2002 - Feb 2003; j_3 = Sept 2003 - Feb 2004; j_4 = Sept 2004 - Feb 2005; j_5 = Sept 2005 - Feb 2006; j_6 = Sept 2006 - Feb 2007.

Tail flukes

m_j

	j_1	j_2	j_3	j_4	j_5	j_6
j_1	x	3	1	0	0	0
j_2	-	x	0	1	0	1
j_3	-	-	x	1	0	0
j_4	-	-	-	x	0	0
j_5	-	-	-	-	x	1
M	0	3	1	2	0	2
N	15	16	10	7	9	16
U	15	13	9	5	9	14
M	0	15	28	37	42	51

Right dorsal fins

m_j

	j_1	j_2	j_3	j_4	j_5	j_6
j_1	x	7	1	2	1	2
j_2	-	x	0	4	1	1
j_3	-	-	x	0	0	0
j_4	-	-	-	x	1	0
j_5	-	-	-	-	x	0
m	0	7	1	6	3	3
n	39	58	14	20	25	27
u	39	51	13	14	22	24
M	0	39	90	103	117	139

Left dorsal fins

m_j

	j_1	j_2	j_3	j_4	j_5	j_6
j_1	x	8	1	0	1	0
j_2	-	x	0	0	0	1
j_3	-	-	x	0	0	0
j_4	-	-	-	x	0	1
j_5	-	-	-	-	x	1
m	0	8	1	0	1	3
n	39	49	11	16	13	28
u	39	41	10	16	12	25
M	0	39	80	90	106	118

Microsatellites

m_j

	j_1	j_2	j_3	j_4	j_5	j_6
j_1	x	9	2	3	1	1
j_2	-	x	0	4	0	1
j_3	-	-	x	0	1	1
j_4	-	-	-	x	1	2
j_5	-	-	-	-	x	1
m	0	9	2	7	3	6
n	34	41	20	27	22	22
u	34	32	18	20	19	16
M	0	34	66	84	104	123

Chapter 5 - Group composition and individual associations between humpback whales (*Megaptera novaeangliae*) resighted in a coastal feeding ground off the west coast of South Africa

"I have seen whales in the distance from boats, and I have seen them stuffed in museums, but I have never felt for the gigantic carcase as one usually feels for proper warm-blooded animals, for example a horse or an elephant. Biologically, indeed, I had accepted the whales as a genuine mammal, but in its essence it was to all intents and purposes a large cold fish. We had a different impression when the great whales came rushing towards us, close to the side of the raft. One day when were sitting as usual on the edge of the raft, having a meal, so close to the water that we just had to lean back to wash out our mugs, we started when suddenly something behind us blew hard like a swimming horse, and a big whale came up and stared at us, so close that we saw a shine like a polished shoe down through its blowhole. It was so unusual to hear real breathing out at sea, where all living creatures wriggle about silently without lungs and quiver their gills, that we really had a warm family feeling for our old distant cousin the whale, who like us has strayed so far out to sea. Instead of the cold, toadlike whale shark, which had not even the sense to stick up its nose for a breath of fresh air, here we had a visit from something which recalled a well-fed jovial hippopotamus in a zoological garden, and which did breathe – that made a most pleasant impression on me – before it sank into the sea again and disappeared".

Thor Heyerdahl – *The Kon-Tiki Expedition* (1950)

INTRODUCTION

In general, humpback whales *Megaptera novaeangliae* display very low levels of social organisation, limited to the formation of small, unstable groups (Clapham 1996, 2000). On feeding grounds in the Northern Hemisphere there are examples of larger groups that temporarily associate and cooperate when feeding on herring off Alaska (Clapham 1993, 2000; Sharpe 2001), while in the Gulfs of Maine (Weinrich 1991) and St. Lawrence (Ramp *et al.* 2010) some individuals have been found to display relatively stable and longer term associations, sometimes between different feeding seasons. Despite these associations, and exceptional cases of 'team' work (Anderson & Franks 2001), no conclusive proof of social structure has been found in either their summer feeding, or winter breeding grounds (e.g. Pomilla & Rosenbaum 2006) and kinship is not thought to be the determining factor for specific associations when engaging in cooperative foraging (Clapham 1993, 1996). During migration, social behaviour relating to breeding, such as 'mate guarding' (Brown & Corkeron 1995) has been described, but again no genetic evidence for social structure has been found (Valsecchi *et al.* 2002).

In terms of associations between individual males and females and their direct descendants, there is no known paternal care in humpback whales, or association between pairs after conception (Clapham & Palsbøll 1997). Humpback whales on average reproduce every 2 – 3 years (Barlow & Clapham 1997) although annual calving intervals have been recorded in the North Pacific (Glockner-Ferrari & Ferrari 1990; Straley *et al.* 1994) and North Atlantic (Weinrich *et al.* 1993). Calves associate closely with their mothers after birth (Szabo & Duffus 2008), wean at about six months of age (Clapham 1996) and normally become independent by the end of their natal year (Baraff & Weinrich 1993; Clapham & Mayo 1987, 1990; Clapham *et al.* 1993; Steiger & Calombokidis 2000). Some so-called 'yearling' calves are known to accompany their mothers for at least another year after their birth (Baker *et al.* 1987). The experience gained over the period of cow-calf association during nursing and weaning is thought to be critical in determining the choice of migratory route (Rendell & Whitehead 2001; Valsecchi *et al.* 2002), prey (Baker *et al.* 1994), and feeding area (Weinrich 1998) by the calf after independence. Such maternally directed site fidelity has been confirmed by annual returns of calves to the same feeding grounds (e.g. Weinrich *et al.* 1993; Steiger & Calombokidis 2000). Return to the same feeding area may not necessarily offer detectable reproductive or survival benefits for individuals (Rosenbaum *et al.* 2002), nor provide evidence for kin-selected associations (Weinrich *et al.* 2006) but it may effect reproductive segregation (Baker *et al.* 1986; Stevick *et al.* 2003) that in turn, could account for the sub-structuring seen in some breeding stocks based on mtDNA, sometimes in the absence of differences in nuclear DNA (Baker *et al.* 1990, 1998; Rosenbaum *et al.* 2009; Pomilla 2005; Carvalho *et al.* 2010).

Southern Hemisphere humpback feeding grounds (for the original demarcations see Figure 1a in General Introduction, and Donovan 1991), due to their oceanic nature and remote locations away from human habitation have not enjoyed the same levels of research coverage as their northern counterparts, with the possible exception of the Antarctic Peninsula (Dalla Rosa *et al.* 2008). Although direct links between low latitude breeding grounds and Antarctic feeding areas have been established in many cases (e.g. Stevick *et al.* 2004; Rock *et al.* 2006; Zerbini *et al.* 2006), there is no detailed information on the return of individually identified whales to specific feeding localities, or on possible associations or social structure during feeding. The west coast of South Africa, based on its geographical position and trends in historical catches has been viewed as coastal migration corridor (Best *et al.* 1995), but more recently has also been recognised as a near-shore feeding area utilised during spring and summer, apparently by a small component of the greater Breeding Stock B (BS B) population of humpback whales (Chapter 2, Barendse *et al.* 2010). A examination of the resightings of individually identified humpback whales here has shown long term fidelity to the area as suggested by multiple annual returns, while sojourns of longer than a month in the same year appears to indicate temporary residency (Chapter 4). These resighted humpback whales thus provide a unique opportunity to study some aspects of feeding ground utilisation, such as individual association patterns and matrilineal directed return, which have thus far only been described for Northern Hemisphere locations.

MATERIAL AND METHODS

Sighting database, group information and within-season attendance patterns

A sighting database for individually identified humpback whales was compiled from photographic and genetic data collected during boat intercepts off the west coast of South Africa (south of the Orange River mouth at about 29^{O} S, and west of Cape Agulhas at 20^{O} E) during various projects between 1983 and 2008. Full details of the collection area, effort and photographic matching procedures are described in Chapter 4. In brief: matching within and between calendar years was carried out separately by two independent matchers for the three different photographic identification features, *viz.* ventral tail flukes, and left and right views of the dorsal fin and caudal peduncle. All images of usable quality were considered and matching results were verified by a third person. Furthermore, some individuals were identified and re-identified through microsatellite genotyping of skin biopsies; this also allowed for sex determination of sampled animals (methods are described in Chapter 4 and in Carvalho *et al.* 2010). All sightings (a combination of the date and daily group number) of each individual were retrospectively linked using all available identification features recorded at each event; the resulting combined ID-feature database contains 289 individually identified whales seen during 225 different sightings. An additional sighting of two whales was included that involved known individuals (one not previously resighted) found through tail fluke matches to the Antarctic Humpback Whale Catalogue (AHWC), but actually seen within the west South Africa study area (details in Chapter 4).

A group was defined as one or more animals in close proximity (<100 m) to each other that displayed similar or visibly co-ordinated movement or behaviour (Whitehead 1983; Corkeron *et al.* 1994). Cow-calf pairs were defined as two closely associated whales (sometimes accompanied by other individuals), one of which was visually judged to be about 50% or less of the length of the other. Where genetic material was available for such pairs, maternity was verified by comparison of their genetic profiles, i.e. sharing of the same mtDNA haplotype and at least one allele in each 10-microsatellite locus (Inês Carvalho personal communication, Sackler Institute for Comparative Genomics). Some characteristics such as group size, behaviour, sex composition, the presence of calves, etc. at Saldanha Bay (33^{O}02'S, 17^{O}55'E) are described in Chapter 2 (Barendse *et al.* 2010).

Within-season attendance patterns of individual whales were based on the definitions of Clapham *et al.* 1993; however, because of the known summer presence in the region and the low relative abundance observed in autumn to early winter (see Chapter 2, Barendse *et al.* 2010), a 'seasonal offset' of three months was introduced to capture the presence of over-summering animals. Thus, the time unit used for this analysis was not a calendar year, but rather a period of 12 months spanning from the first of April of one year to 31 March in the following year. Throughout this chapter (in this context) this unit will be referred to as a 'full season', while 'year' will indicate a calendar year. Thus, *occurrence* indicates the number of separate days in any given full season, on which the same whale was seen. *Occupancy* refers to the number of days recorded between the first and last sighting dates within a full season, counted from the day after the first sighting; i.e. the whale had to be sighted on at least two separate days in the same season. It follows that occurrence and occupancy could only be calculated for time periods where there was relatively high effort with relatively continuous coverage within the defined seasons; that is 1993 – 2006 (Chapter 4, Table 4.1), although there were some months with no coverage during all years.

Information on the sex of individual whales was used in two ways. First, by comparing the sex-ratio of samples from resighted and non-resighted animals, it should indicate whether one sex was more likely to be resighted than the other. Second, an 'operational' sex ratio (OSR), although not entirely true to the definition of Emlen & Oring (1977) – "the number of fertilizable females to sexually active males", in the sense that not all whales were sexed, and that sexual maturity could not be determined (only known nursing calves were excluded), could be calculated for whales available on a daily basis in the study area, and seasonal patterns examined. While the seasonality of such a sex ratio using all biopsies collected had been previously reported in Chapter 2 (Barendse *et al.* 2010), the identity of individual whales (except on the same day, when duplicate biopsies were excluded) was then not taken into account, in keeping with other studies that examined similar ratios (e.g. Brown & Corkeron 1995). Because calculation of this ratio (in Chapter 2) depended on the collection of a biopsy, non-biopsied animals of known sex would therefore not have contributed to the reported ratio. This could be improved on by including individuals of known sex, every time they were identified (but not necessarily biopsied) using the full sighting histories available by employing all available ID features. This should be more fully represented of the OSR present in the area on any given day, although by giving more weight to resident (resighted) than transient (once-off sighted) individuals it would not be equivalent to sex ratios calculated from catches, for instance. The same seasonal groupings as in Chapter 2 are used (late autumn to mid-winter = May, June, July; late winter = August; early spring = September; mid-spring = October; late spring = November; early summer = December; mid- to late summer = January/February), and resightings in the same month in different years were added to obtain a single seasonal sample.

Individual associations

Resighting data were available for 68 humpback whales, including those only seen on the same day. These were inspected to identify any short or long term associations that occurred between individuals and for any evidence of social structure (Table 5.1). Association patterns were examined at the sighting level, i.e. an association was regarded as an occasion where two or more individuals were recorded together during the same intercept, which assumes direct association between individuals seen during such an encounter, bearing in mind that not all individuals in a group were necessarily identified (photographed or biopsied) and some associates in a group may not have been resighted. A 'sighting' (or intercept) was also used as the sampling period, so that short-term (same day) associations known to occur at other feeding grounds (e.g. Weinrich & Kuhlberg 1991) would not be concealed by selecting a longer sampling period (e.g. a day), whilst still allowing detection of longer term associations (between different days). This means, however, that multiple sightings of the same animal on the same day, or replicate associations on a day, could affect the overall weight of individual associations between different days. While data from multiple groups on the same day may not necessarily be independent (see Karczmarski *et al.* 2005), we believe that the small group sizes, few identified individuals, and generally sparse data warranted this approach.

Thus: to qualify for inclusion in this analysis, an individual had to be identified during two or more sightings, at least once with another resighted individual. For such individuals their full sighting histories were included, i.e. even when sighted alone. These criteria were met by 60 individuals involved in 122 sightings on 77 different days, and the truncated dataset imported into SOGPROG 2.4 compiled version (available at http://whitelab.biology.dal.ca/index.html) in 'group mode' format (Whitehead 2009). The half-weight association index (HAI) was selected as it is the most commonly used index to describe cetacean associations (e.g. Lusseau *et al.* 2003; Ramp *et al.* 2010) and displays less bias when not all associates are identified (Cairns & Schwager 1987; Whitehead 2008a). The HAI between two individuals (*a* and *b*) was calculated using the following formula:

$$\mathrm{HAI}_{a,b} = \frac{X}{X + 0.5(Y_a + Y_b)} \qquad (5.1)$$

Where, X is the number of sightings during which *a* and *b* were seen together, Y_a is the number of sightings when *a* was seen without *b*, and Y_b is the number of sightings when *b* was seen without *a* (from Lusseau *et al.* 2003). Note that the term X_{ab} (the number of times *a* and *b* were seen within the same sampling unit, but not together) that is normally added to X below the division, does not apply with 'sighting' as a sampling unit, and is therefore omitted. The mean and maximum HAI per individual were calculated, and individual associations between duos were visually represented as sociograms generated in SOCPROG (Whitehead 2008a).

RESULTS

Group characteristics and attendance patterns of resighted whales

The mean overall group size (n = 226) was 2.2 ± 0.12 (SE). The mean size for groups with resightings ('resighted' groups) was 2.5 ± 0.17 (SE) (n = 134, range 1-20), significantly larger than the 1.7 ± 0.15 (SE) (n = 92, range 1-14) of groups with none recognised (referred to as 'non-resighted' or 'once-off' sightings) (t-test, t = -3.5815, df = 224, $p < 0.001$). Both resighted and non-resighted groups had an outlier group with 20 and 14 individuals respectively (Figure 5.1); however the result remained the same when these groups were excluded, so they were retained in the sample. Nevertheless, all but one of the 13 groups larger than three whales contained resighted individuals (Figure 5.1). Of the groups containing resightings, all individuals were known animals (100% identification rate) in 63 groups and 50% or less were known individuals in 59 groups (Figure 5.2). For these groups, there was no significant relationship (r = 0.0759, $p < 0.2569$) between the identification rate (the number of resighted or 'known' individuals in a group as decimal fraction of group size) and the size of the group (Figure 5.3).

The mean overall occurrence (number of days on which a whale was seen in the same full season) for the selected period (1993 – 2006) was 1.19 times (range: 1 - 5); single occurrences in a full season were most common (n = 255), followed by twice (27), three (8), four (3), and five times (1). Mean occupancy for whales that were resighted within a full season during all seasons combined (n = 39) was 31.44 days ± 9.05 (SE), ranging from one to a maximum of 245 days. For individual full seasons in which more than one individual was resighted, the 2002 season (i.e. 1 April 2002 to 1 April 2003) had the highest mean occupancy (53.2 days): this season also had the most whales identified. The season with highest mean occurrence was 1993 where whales were seen 2.4 times (Table 5.2).

Sex was determined for 152 individually identified whales (100 once-off sightings and 52 resightings); these included 12 different females identified as cows (8 were resighted individuals, some seen more than once, see Table 5.4), and 10 calves (3 resighted with their mothers). Assuming that the presence of a calf is not independent from that of its mother during its first year, the calves (3 females and 7 males) were excluded when analysing sex ratios of samples. The overall sample sex ratio excluding calves (n = 142) was 1 female to 0.89 male; for samples from non-resighted individuals (n = 93) it was

0.94 female to 1 male and for those from resighted groups (n = 49) 1 female to 0.63 male. None of these ratios differed significantly from parity, and the sex ratio in resighted and non-resighted groups also did not differ significantly (z = -1.457, two-tailed, p = 0.1451). This suggests that neither of the sexes was more likely to be resighted. Excluding cow-calf pairs, sex was determined for both members of 20 other pairs (excluding resightings of the same pair on the same day). Most contained a female and male (11), while there were five all-female, and four all-male pairs (Table 5.1): these agree almost exactly with the proportions that would be expected under binomial sampling theory, i.e. 10 groups with both sexes, 5.5 groups containing only females and 4.5 groups containing only males. This indicates that the pairs represented a random association of sexes.

The seasonal representation of the OSR allows comparison of both the relative contribution of the two sexes, overall, and for resighted and non-resighted whales separately (Figure 5.4). During autumn to late winter, the whales seen were predominantly once-off sightings, mostly male. The relative contribution of once-off sighted males decreased steadily as the season progressed, after a peak in late winter. This seasonal pattern was virtually identical for once-off sighted females, although during the first three and last two seasons, the males outnumbered the females, while this was not the case in mid- and late spring. In mid-spring, resighted females predominated and the sex-ratio varied significantly from parity both for all animals (2.2F:1M, X^2 = 8.35, df = 1, p < 0.0039), and resighted only (3.7F:1M, X^2 = 10.94, df = 1, p < 0.0009). This was also the case for mid-to late summer (3.2F:1M, X^2 = 11.52, df = 1, p < 0.0007 for resighted whales, 2.5F:1M, X^2 = 9.0, = 1, p < 0.003 for all). The ratio did not deviate significantly from parity in any other season. Very few resighted whales were seen before mid-spring, while their relative contribution (for both sexes) increased from mid-spring onwards. Resighted males from mid-spring to late summer showed virtually the opposite trend to that of resighted females, in that the proportion of males increased between mid- and late spring, and that of females decreased. Males decreased again after early summer, while resighted females was the only group to increase sharply after early summer, making up nearly two-thirds of all sightings (Figure 5.4).

Resightings, individual associations and social structure analyses

The frequency distribution of total number of associates (Figure 5.5) with which individual whales were seen with (during all sightings), and the raw group resighting data (Table 5.1) reveal a number of patterns. The majority of animals were associated with only two other known animals, followed by one and three; only 15 individuals associated with more than four other known animals (Figure 5.5). The number of associates may be influenced by several factors, such as the total number of times an individual was resighted, and the number of known animals in a group, with larger groups potentially containing more possible associates. Furthermore, recurring associations (i.e. with the same individual in more than one group) would reduce the total number of associates. For example ZAW-006 was seen 11 times and associated with six other whales (Table 5.1) over a period spanning a decade and a half, but never with more than two at a time and often the same ones (see later), while ZAW-100 was associated with 10 known whales in three groups over just two days (16/17 December 2001) (Table 5.1). There was a significant relationship between the total number of times seen and total number of associates (r = 0.3590, p = 0.0049).

The sighting rates and number of resightings were too low to allow the calculation of a confidence interval (CI) for the measured association indices (a minimum of 15 observations per duo is required to calculate reasonable values, Whitehead 2008b) or measures of preferred/avoided companionship. Without CI's, very limited inferences can be made from the magnitude of the mean HAI value, although it should provide a relative indication of the number and recurrence of associations, i.e. a higher mean may indicate that some of the HAI values between duos were high, or that an individual associated with many others. The mean HAI values ranged from 0.0043 – 0.0633 with the majority (49 out of 60) below 0.03 and only 11 at or above 0.04 (Figure 5.6); these included seven females, three males and one whale of unknown sex (Table 5.3). Only three individuals had a mean HAI > 0.06. The lowest maximum HAI value was 0.25 and the highest 1, the latter indicating that some individuals were always seen together. Most maximum HAI values were in the 0.3 – 0.5 range (35), with only 20 individuals involved in associations stronger than 0.5 (Figure 5.7). Mean HAI values of females and males were the same (0.02) although sample sizes are small.

The HAI between a duo highlights the strength of that specific association, bearing in mind that this index is influenced by both the number of times seen together, and sighted separately (Equation 5.1). It is therefore helpful to look at individual cases to put the HAI values into perspective. For example, the HAI between ZAW-017 and ZAW-036 was 0.13 (one association on 29 October 2005, Table 5.1); they associated with 6 and 2 other individuals, and their mean HAI values were 0.03 and 0.01 respectively. ZAW-017 recorded a maximum HAI of 0.5 with ZAW-23 (seen together twice in 1993), and a HAI of 0.4 with ZAW-016 (also twice in the same year). ZAW-036 had the strongest HAI (0.36) with ZAW-107; these animals were seen together twice, once on 10 February 1999 and again on 17 December 2001 (Table 5.1). Compare this to ZAW-181 and ZAW-183 both with a mean HAI of 0.02 and maximum of 0.8, but only seen twice (on 30 and 31 October 2002), both times together, once accompanied by another whale (ZAW-118). From this it appears that any HAI between duos of whales over 0.3 is worth a closer examination, but that it needs to be interpreted in conjunction with the sighting histories (Table 5.1).

A sociogram with all HAI values included (Figure 5.8a and b) shows numerous 'weak' (≤ 0.2) associations. Also featured are 'isolated' pairs of individuals with much stronger associations sometimes not associated with other known whales - some of these were confirmed cow-calf pairs that were sighted on multiple days such as ZAW-204 and 205 (see below). Also noteworthy are several clusters made up of a number of joined individuals that represent the occurrence of multiple groups on the same day or consecutive days, where some individuals were seen in more than one group (sometimes together) or where individuals from smaller groups joined to form larger ones, e.g. 17 October – 5 November 1993, 16 – 17 December 2002, 17 October 2002, 13 – 14 December 2002, and 21 November 2004 (Table 5.1). These clusters of multiple associations are better visible on the sociogram with lower HAI values excluded (HAI ≥ 0.3, Figure 5.8c). During such 'episodes', some individuals associated and re-associated in different groups (e.g. ZAW-101 and 102 on 16/17 December). Although these associations generally did not last longer than a few days they account for some of the stronger associations visible between duos (HAI ≥ 0.4, Figure 5.8d) and also some of the highest mean HAI values (Table 5.3). Furthermore, some of the same individuals appeared during more than one of these episodes in different years, sometimes within a few days of the same day and month. For example, the male ZAW-101 was seen on 16 and 17 December 2001, and the following year three days earlier (14 December) during a similar episode (of more than one group on the same day); it was again seen on 25 November 2003, and in 2004 on 29 November (Table 5.1). ZAW-082 and 085 were seen on 3 November 2001 in a feeding group, and again on 17 October 2002 (Table 5.1).

Cow-calf pairs and recurring associations

Among the resighted individuals, 13 different pairs were identified as mothers with a calf of the year (i.e. nursing) of which the cows and some of the calves were resighted (Tables 5.3 and 5.4). Genetic samples were available for both mother and calf in six cases, although the sample for the calf was sometimes collected at a later occasion during a resighting. Four of the cow-calf pairs were resighted together on more than one day, sometimes on consecutive days, e.g. ZAW-019 and 039 were seen on 14 and 15 February 2000, or, within a few days, e.g. ZAW-204 and 205, first seen on 10 January 2003, and subsequently resighted on the 17th and 18th of that month. Incidentally, this calf (a male) was one of the smallest to be observed and associated very closely with its mother during these intercepts. The calf had a prominent, somewhat indented, light patch, on its left side below the dorsal fin which may have been the result of a recently unfurled dorsal fin, a known neonatal trait (Cartwright & Sullivan 2009). Similar markings were observed on a few other calves.

One female provided examples of both short term associations with her calf (as described above), and much longer periods of association. This was the oldest known individual in the database, ZAW-006: a closer examination of the full sighting histories of this female (named '*Ampersand*'), her offspring and other associates reveals significant information (Table 5.4, Figure 5.9). First identified on 15 January 1988, she was sighted 11 times over a period of 15 years (up to 26 January 2003) in groups that ranged in size from 1 – 4. During this time she was observed three times with three different calves, and associated with four other resighted animals. The first time she was seen with a calf (ZAW-033) was on 6 and 13 February 1999; the calf was identified from left and right dorsal fin, and tail fluke pictures. The following year *Ampersand* was seen again on 20 and 22 February with a calf ('A') of which the left and right dorsal fins were photographed and did not match those of the previous calf (ZAW-033). On the first occasion she was accompanied by another female (ZAW-036) also with a calf ('B') (Table 5.4). Unfortunately neither of these calves was biopsied and there are no subsequent resightings. On 10 November 2001, *Ampersand* was sighted with a third new calf (ZAW-089), that was biopsied and left and right dorsal fins photographed (that did not match those of the previous two calves); they were resighted together six months later on 26 May 2002. Eight months later, they were seen again, in separate groups associated with other individuals, but also together in a group on 26 January 2003. At this time they were not identified as a cow-calf pair (Figure 5.9). Both her calves ZAW-033 and ZAW-089 were resighted in post-natal years, either on the same day (and group) or within a day of their mother, and in close proximity to her sighting (Table 5.4). There was a similar example of a confirmed calf (ZAW-292, a male) being seen two years after its natal year (2004), three days after its mother (ZAW-286) was seen (Table 5.4) although these sightings were about 30 km apart. This calf was seen in its second year (22 December 2005) with ZAW-290 off Cape Town (about 100 km south of Saldanha Bay) (see Chapter 4). ZAW-286 was seen again with a different calf in 2006 (Table 5.4).

One more female (ZAW-269) was seen with two different calves in successive years although neither of the calves was resighted; while females ZAW-286 and -295 were seen with calves at two and three year intervals respectively (Table 5.4).

The only other example of a recurring 'stable' association between years (not by a cow-calf pair) was by the female ZAW-036. On 10 February 1999 she was seen with a male (ZAW-107) as part of a trio, and they were resighted as a pair nearly two years later on 17 December 2001, a day on which one of the feeding episodes occurred. ZAW-107 was subsequently resighted during another feeding episode (Table 5.4) and was one of the individuals with a higher mean HAI of 0.04 (Table 5.3). ZAW-036 had previously associated with *Ampersand* (on 20 February 2000), when both were accompanied by calves – in the year before she had been seen three days before *Ampersand*, and again seen in her near vicinity on 26 January 2003 (Figure 5.9).

Four pairs, of which one of the animals was noticeably smaller, were identified in the field as cows with 'yearling' calves. Genetic comparison of the 'mothers' and 'calves', and in some instances sex determination (two of the 'cows' were found to be male!) ruled out maternity in all but one case. This pair was identified as a cow with yearling calf on 4 March 1999, and later confirmed to be mother and offspring by genetic comparison. The cow (ZAW-019) was seen with a new calf the following year, and was one of only two of the animals from the 1993 Cape Columbine study (Best *et al.* 1995) to be resighted in later years.

Record of known mortality

One female (ZAW-126) biopsied once before on 17 December 2001 was matched by microsatellite to an animal that was seen floating dead in Yzerfontein harbour 28 January 2004, and came ashore the next day 1.5 km north of Yzerfontein town (see Figure 5.9 for locality). The carcass was in poor condition, with most of its skin off. The rostrum was not visible and skull may have been lost; the tongue washed up 100 m down the beach. The cause of mortality could not be established. While still alive, this whale had been resighted on 16 November 2002 and 31 January 2003 (Table 5.1), matched by dorsal fin pictures. It was also one of the individuals with the highest mean HAI (Table 5.3).

DISCUSSION

The first study to suggest the presence of 'non-migratory' humpback whales during spring off the west coast of South Africa was at Cape Columbine in 1993 (Best *et al.* 1995), when individual photo identification revealed that 11 out of the 12 groups sighted over a 3-week period consisted of resightings of the same 10 humpback whales. Both the unusual seasonality and the apparent 'temporary residency' associated with feeding have been confirmed during two seasons of shore-based observations at Saldanha Bay (Chapter 2). Resightings of individual whales between years (based on the entire sighting database) showed that the same whales return to the Saldanha/St

Helena Bay area during spring and summer, while no whales identified during winter months were ever resighted (Chapter 4). Individual resightings during the months of October to January in later years (2001 – 2006), when sufficiently continuous collection effort allowed, shows a similar pattern of fluid associations between different groups on the same day (or successive days) to that seen at Cape Columbine, where a limited number of the same individuals would form and re-form groups in different combinations, sometimes over a number of days. The larger mean size of groups including resighted individuals may be a reflection of this rather than an actual demographic feature, e.g. the group of 20 seen on 17 December 2001 was composed of an amalgamation of several individuals seen in smaller groups earlier on that day and the previous day. However, smaller groups and a higher incidence of singletons during late winter had been reported for the area (Chapter 2; Barendse *et al.* 2010) and may reflect the fact that most non-resighted humpback whales were seen alone.

The timing of migration for humpback whales is known to relate to the age, sex, and reproductive state of the individual whale (Chittleborough 1965; Craig *et al.* 2003; Dawbin 1997). Furthermore, it has been suggested that the migration functions as a behavioural continuum with breeding grounds, since social behaviours normally associated with breeding such as singing (Clapham & Mattila 1990) and ‘mate guarding’ by males have been recorded *en route* (Brown & Corkeron 1995). However, it is difficult to assess how the availability of feeding opportunities may influence the actual migration, i.e. when does it cease to be a migration? Despite more of the resighted animals being female, the sample sex-ratios for resighted and once-off sighted whales did not vary significantly from parity. However, the seasonal changes in approximate OSR (i.e. the proportions of males and females available based on full resighting histories of animals), confirmed some of the trends reported previously (Chapter 2; Barendse *et al.* 2010) and could lead to the following interpretation.

During mid-spring (October), there were significantly more females available, with very few cows with calves. Females without calves and juvenile whales are known to depart first from breeding grounds, and thus should appear first on the migratory route, followed by mature males and then cows nursing a calf (Craig *et al.* 2003). The influx of non-lactating females would explain the observed female bias in mid-spring, while juveniles of both sexes presumably also contribute to the numbers. However, the gradual change from a female dominated sample to one of parity (as opposed to a male dominated one, see Brown *et al.* 1995) from October through to December may be explained by the later arrival of (more) males, but also the failure of many of the females (the resighted component) that arrived earlier, to leave the area and continue with their migration. This, along with the late arrival of cow-calf pairs, could contribute to the significant peak of resighted females in mid-to late summer.

We do not know whether all humpback whales sighted during spring and summer off west South Africa actually feed there. However, both males and females participated in the feeding aggregations, and both sexes were involved in multiple associations. The within-season occupancy when separated by sex (and excluding calves), showed that females (n = 19) had the longest mean occupancy of 36.73 d ± 13.47 (SE) compared to males (n = 8, 22.75 d ± 10.41 SE) and unsexed animals (n = 9, 9.56 ± 3.96 SE). The considerable number of non-resighted individuals of both sexes in spring and summer suggests that we may be observing both migratory and non-migratory components, a notion first suggested by seasonal variation in the directionality and speed of movement as tracked from land (Chapter 2; Barendse *et al.* 2010) and here reinforced by the diminishing numbers of all groupings except the resighted females. It remains difficult to explain temporal overlap of these different groups of animals as it should be equally feasible to resight animals during migration if they make use of the same route every year, or visit the same feeding ground, although the capture probabilities for these would be different. Furthermore, it may also reflect insufficient sampling effort, both within large groups where not all individuals were identified, or where effort was discontinuous. The rapid decline of males in general and once-off sighted males in particular, towards the later seasons does suggest that there may be a difference in the way the two sexes utilise this area. This idea is supported by recent findings in the western South Pacific (Valsecchi *et al.* 2010), suggesting that male humpback whales may carry out much more extensive latitudinal and longitudinal movements than females, *inter alia*, making use of different migratory routes in different seasons presumably to optimise mating opportunities. In contrast, females would be expected to favour movements and behaviours that would improve reproductive success, i.e. minimise energy expenditure and utilise any available feeding opportunities (Valsecchi *et al.* 2010).

The sighting data were not specifically collected to examine social structure but did confirm the occurrence of short-term and relatively unstable groupings that are considered typical for humpback whales on feeding grounds in the Northern Hemisphere (Clapham 1996, 2000). Furthermore, the mean occupancy of about 30 days in the same feeding season in a specific area and evidence that some individuals move between different sub-areas, albeit in different years (e.g. the same whales seen at both Cape Columbine and Saldanha Bay, or at Saldanha and St Helena Bay) is reminiscent of recent observations from the Antarctic Peninsula (Dalla Rosa *et al.* 2008). Satellite tagged humpback whales feeding there were shown to travel 32 km.d^{-1} on average although a mean travel rate of 75 km.d^{-1} was recorded for one individual. Various foraging strategies were used by different individuals, such as short residency times of up to 10 days in specific areas, fluid movements between areas, foraging between adjacent patches (or ‘commuting’), and movements between more distant areas with different oceanographic conditions (‘ranging’) (Dalla Rosa *et al.* 2008).

Although singletons were the most frequently encountered group size overall (Chapter 2; Barendse *et al.* 2010), the resighted component contained higher number of duos (as opposed to singles) than the non-resighted one. Singles have also been found to be most prevalent on Northern Hemisphere feeding grounds (Weinrich & Kuhlberg 1991; Ramp *et al.* 2010) while a majority of duos is in common with trends observed during migration (Valsecchi *et al.* 2002); the prevalence of male-female duos agrees with observations from both. One of the male-female duos was confirmed to be a mother with her yearling calf; these have been shown to accompany their mothers (Valsecchi *et al.* 2002), but associations beyond the second year have not been documented, although juveniles are known to follow the migratory routes of their mothers. This was confirmed by the two calves of *Ampersand* that were resighted and known to have survived beyond their natal years. The first (ZAW-033) was seen three years after being sighted as a calf, only one day before and within 10 km of where her mother was sighted. The case provided by the third calf (ZAW-089) is interesting in that we observed an association of at least six months, independence by 10 months, and then a re-association at a known age of 14 months, a time by which associations of close-proximity should have ceased (Szabo & Duffus 2008). Whether this was simply a case of a yearling travelling in the general vicinity of its mother (and briefly re-associating) is unclear.

Calving intervals of one year were established on three occasions by two different individuals: for one female both calves survived to at least three months, while all three calves of the other female survived to at least six months: these are the first recorded annual calvings for southern humpback whales. The production of three calves by a humpback whale in three successive seasons has only been reported three times before (Weinrich *et al.* 1993; Straley *et al.* 1994), all in the Northern Hemisphere. Straley *et al.* (1994) suggested that older females (9-14 yr) were more likely to achieve a successful annual calving interval than younger animals. They concluded that while postpartum ovulation may be common in humpback whales, only some of the females can successfully maintain the pregnancy, and that this success may be dependent on the availability of adequate prey resources in the season preceding the pregnancy, during the period when the cow is both pregnant and lactating, and during the lactation period for the second calf. All of these criteria were met by *Ampersand*: she had a known age of at least 11 years when first seen with a calf and made use of an additional food source that was available much earlier in the season than would be the case at an Antarctic feeding ground.

Apart from *Ampersand*, it was noticeable that several of the ‘older’ individuals identified in 1993 and earlier were not only resighted in multiple years, but were often involved in many associations, or were present during summer feeding aggregations (e.g. ZAW-009, -011, -015, -017 and -019). Furthermore, these included two males. Such associations could represent examples of ‘cultural transfer’, in this case, the use of a specific migratory route and feeding area. It has been demonstrated for southern right whales (*Eubalaena australis*) that fidelity to feeding areas may be maternally transferred over several generations (Valenzuela *et al.* 2009). The return of at least three known calves to the Saldanha Bay area seems to represent site fidelity at a relatively small spatial scale that was derived from their mother, as suggested by Weinrich (1998).

Previously, the presence of male-female dyads on feeding grounds has been interpreted as males seeking potential mating opportunities (Clapham 1993; Valsecchi *et al.* 2002), and also during migration (Brown & Corkeron 1995), although statistically a prevalence of mixed-sex pairs would be expected even if associations were random with regards to gender. In the only study to date to examine social structure in humpback whales in detail (Ramp *et al.* 2010) some evidence was found for long-term associations between mature males and non-lactating females that lasted up to six years. We found one example of such a recurring association between the female (ZAW-036) and the male (ZAW-107, confirmed not a calf of this female) on 10 February 1999, and a re-association nearly three years later. Although this may have just been a chance event, this female was seen almost exactly a year after the first encounter accompanied by a calf, indicating that conception must have occurred some six months prior to the initial sighting with ZAW-107. Incidentally, when resighted with the calf, ZAW-036 was associated (in the same group) with the female *Ampersand* (also with a calf); these two were sighted on two other occasions in close proximity, once three days apart (in February

1999) and once by less than three hours (26 January 2003). While such sightings do not necessarily prove direct association, they do show strongly corresponding temporal and spatial overlap, with the potential for interaction.

CONCLUSION

No persuasive evidence for long-term social association of humpback whales was found in the St Helena Bay/Saldanha Bay area of the South African coast. However, the types of short-term associations and movement patterns recorded confirm this to be a feeding area that is utilised by humpback whales of both sexes in mid-spring and summer. Females that are apparently not migrating, contribute to a significant female bias during October and January/February, and appear to make use of the feeding opportunities till later in the season than males. The observed associations may simply be a result of groups of animals making use of the same prey resource in an area of limited spatial extent, rather than any co-operative feeding behaviour as has been seen primarily for fish prey (Weinrich 1991) - in fact, humpback whales feed mainly on euphausiids in the area (Chapter 2; Barendse *et al.* 2010), a prey that is not thought to necessarily require feeding cooperation (Clapham 2000). Records of post-weaning returns of individuals, and extended associations between mothers and calves seem to confirm maternally derived site fidelity. The records of post-partum ovulation and successful pregnancy during lactation are the first for the Southern Hemisphere, and may be an indication of the possible nutritional and reproductive advantages that a mid-latitude feeding area offers for females. Although mature males also occurred in feeding aggregations, it appears that their attendance in the region may be a combination of more conventional migratory patterns, with some opportunistic feeding included, rather than the exploration of potential mating opportunities. This may explain the departure of most males during mid-to late summer when more lactating females are expected. The question of how many humpback whales make regular use of this coastal feeding ground remains an important one, as the differential utilisation of such an area by both males and females from a greater breeding stock may account for the genetic differences reported between animals west South Africa and Gabon (Carvalho *et al.* 2010; Pomilla 2005; Rosenbaum *et al.* 2009).

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TABLES

Table 5.1. Details of date, sighting number, time closed with, best estimate of group size, and catalogue number (ZAW-###) of all 134 groups containing resightings of 68 individual humpback whales intercepted off West South Africa (including one stranding of a known individual). [Legend to notation: * = groups reported to feed or defecate in Chapter 2; ** = summary of 11 intercepts at Cape Columbine (Best *et al.* 1995); *** group in AHWC; [1] = only resighted individuals are shown; subscript shows sex, if determined (M=male, F = female); cow-calf pairs in bold and joined by +, non-resighted calves shown by 'C' – see also Table 5.4; italics indicate individuals not used in social analyses.]

Date	Sight.	Time	Size	Individuals[1]	Date	Sight.	Time	Size	Individuals[1]
				1988-97					
15 Jan 88	1	-	2	006$_F$	05 May 92	1	-	2	011$_M$, 015$_F$
11 Apr 89	1	-	3	009$_M$	17 Oct – 05 Nov 93 **	-	-	10	016, 017$_F$, 018, 019$_F$, 022, 023, 024
17 Jan 90	1	19:05	3	011$_M$	18 Mar 97	19	12:01	2	028$_M$, 029
				1999					
06 Feb	10	-	2	**006$_F$+033$_F$**	13 Feb	1	-	2	**006$_F$+033$_F$**
10 Feb	9	-	3	036$_F$,107$_M$	04 Mar	4	-	2	019$_F$, 038$_M$
				2000					
14 Feb	4	-	2	**019$_F$+039**	22 Feb	4	-	2	**006$_F$+C**
15 Feb	7	-	2	**019$_F$+039**	27 Mar	8	-	2	043$_F$
20 Feb	2	-	4	**006$_F$+C, 036$_F$+C**					
				2001					
29 Mar	2	-	2	009$_M$	10 Nov*	1	08:00	2	**006$_F$+089$_M$**
05 Apr	9	-	1	047		3	12:55	2	091$_M$
24 Oct	1	08:51	2	069$_F$, 070$_F$	16 Dec*	2	08:54	2	096$_M$
24 Oct	2	11:34	2	072$_M$		4	11:10	2	015$_F$, 097$_M$
06 Aug	*3*	*16:57*	*1*	*050*		6	12:40	2	100$_F$, 101$_M$
	4	*17:24*	*3*	*050*		7	14:01	3	102$_M$, 174$_M$
*31 Oct**	*4*	*15:25*	*2*	*075$_F$*	17 Dec	1	08:12	2	036$_F$, 107$_M$
	6	16:59	3	038$_M$, 080$_F$		3	09:53	4	097$_M$, 100$_F$, 101$_M$, 115$_F$
03 Nov*	1	07:57	3	085$_M$		4	11:05	20	015$_F$, 029, 070$_F$, 080$_F$, 097$_M$, 100$_F$, 101$_M$, 102$_M$, 115$_F$, 118$_F$, 126$_F$
	2	11:17	3	072$_M$, 082$_F$					
				2002					
26 May	1	13:30	2	**006$_F$+089$_M$**	30 Oct	1	10:13	6	118$_F$, 181, 183$_F$
27 Sep	*4*	*16:27*	*2*	*075$_F$*		2	12:55	2	162$_F$
11 Oct	1	16:34	2	033$_F$	31 Oct	1	08:31	2	181, 183$_F$
12 Oct	1	12:04	1	006$_F$		*2*	*09:18*	*2*	*176*
	3	17:20	2	162$_F$, 163$_M$	02 Nov	4	13:02	2	096$_M$
17 Oct*	1	13:06	3	170$_F$		5	17:07	1	029
	2	13:57	2	085$_M$, 172$_M$	06 Nov	2	16:51	2	115$_F$
	3	14:34	2	082$_F$, 174$_M$	15 Nov	2	11:55	2	118$_F$
	5	*16:28*	*3*	*176*	16 Nov	1	11:16	1	126$_F$
	6	17:10	2	082$_F$, 172$_M$	13 Dec	3	16:38	2	163$_M$
	7	17:29	3	174$_M$	14 Dec	1	10:20	1	009$_M$
	8	17:29	7	085$_M$, 172$_M$, 174$_M$		2	11:02	2	101$_M$, 163$_F$
						3	12:19	4	009$_M$, 091$_M$, 101$_F$, 163$_F$

Table 5.1 continued:

Date	Sight.	Time	Size	Individuals[1]	Date	Sight.	Time	Size	Individuals[1]
2003									
10 Jan*	1	09:05	2	**173_F+C**	18 Jan	1	09:41	2	**204_F+205_M**
	3	12:35	2	**204_F+205_M**		3	11:55	1	047
13 Jan	*1*	*09:37*	*2*	*207_M*		*4*	*14:20*	*2*	*207_M*
	2	09:51	2	210_F		7	17:53	2	069_F, 170_F
	3	09:57	2	210_F, 211	26 Jan*	2	09:45	2	028_M, 089_M
	4	12:09	2	015_F, 213_F		3	11:22	3	006_F, 028_M, 089_M
	5	13:21	2	210_F, 211		7	14:29	2	036_F
	6	14:49	2	015_F, 213_F	31 Jan	8	18:08	3	015_F, 126_F
14 Jan	1	12:51	3	015_F, 047, 213_F	06 Feb	1	16:17	2	011_M, 170_F
	2	13:02	2	006_F, 096_M		3	12:46	2	070_F
	3	14:28	3	006_F, 047, 096_M	15 Oct	2	12:48	2	183_F
17 Jan	1	09:03	2	**204_F+205_M**	27 Oct	3	12:32	3	233
					25 Nov	12	13:30	1	235
						14	15:14	2	101_M
2004									
11 Jan	*3*	*12:29*	*2*	*240_F*	21 Nov	1	14:15	2	233, 254
	5	*14:38*	*2*	***295_F+C_M***		2	14:20	2	033_F, 235
15 Jan	*4*	*09:46*	*2*	*240_F*		3	14:42	8	097_M, 233, 254
24 Jan	*1*	*11:53*	*2*	*240_F*	29 Nov*	6	10:15	2	101_M, 173_F
28 Jan	*Stranded at Yzerfontein*			*126_F*		7	11:57	2	101_M, 173_F
12 Oct*	4	11:11	2	043_F, 243_F	01 Dec	3	09:06	3	**286_F+292_M**
25 Oct	2	09:03	2	204_F	02 Dec*	5	11:22	2	019_F, 243_F
08 Nov*	4	10:50	2	017_F, 210					
2005									
19 Jan	1	09:26	5	163_M	*21 Nov*	*5*	*11:01*	*3*	***269_F+C_F***
20 Jan	1	09:02	2	015_F	24 Nov*	2	10:15	3	273_M
23 Mar*	1	13:49	2	036_F		3	11:08	3	019_F, 273_M, 290_M
06 Oct	*4*	*12:27*	*1*	*240_F*	*26 Nov*	*1*	*08:45*	*1*	*207_M*
29 Oct	4	12:01	8	017_F, 036_F	22 Dec***	1	-	2	290_M, 292_M
2006									
12 Oct*	1	09:20	2	273_M	19 Nov*	3	13:13	5	107_M, 281, 288_M, 291_F
	2	10:58	3	281		4	15:25	2	107_M, 291_M
01 Nov	*5*	*14:16*	*1*	*282_F*					
07 Nov	22	12:40	1	096_M	22 Nov*	2	12:30	2	292_M
09 Nov	*5*	*10:55*	*1*	*282_F*	*23 Nov*	*2*	*08:51*	*3*	***295_F+C***
19 Nov*	1	11:38	2	**286_F+C**	29 Nov*	5	10:49	2	009_M
	2	12:26	1	288_M	*16 Dec*	*3*	*12:57*	*3*	***269+C***
2007/08									
13 Nov ‘07	6	12:21	4	009_M	05 Feb ‘08	1	-	3	213_F

Table 5.2. Seasonal occurrence (number of different days on which an individual is seen) and occupancy (number of days between the first and last sightings in the same season[1]) of humpback whales in west South Africa resighted on different days during selected seasons (1993 – 2006). [[1] = not calendar year, but from 1 April of the year indicated to 31 March the following year; [2] = minimum occurrence is always one; [3] = of individuals seen on more than one day].

Season[1]	No. identified	Occurrence[2]		Occupancy[3]		
		Mean	Max	*n*	Mean ± SE	Range (min – max)
1993	10	2.4	5	5	10 ± 2.92	4 - 19
1998	7	1.29	2	2	7 ± 0	7
1999	10	1.3	2	3	1.33 ± 0.33	1 - 2
2001	78	1.1	2	8	17.86 ± 7.86	1 - 54
2002	90	1.27	4	17	53.24 ± 19.25	1 - 245
2003	22	1.09	3	1	n/a	13
2004	43	1.02	2	1	n/a	51
2006	34	1.06	2	2	23 ± 15	8 - 38

Table 5.3. Details of number of associations, sex, and maximum half-weight association index (HAI) of individual humpback whales with mean HAI at or above 0.03 († = known mortality).

Individual	Date first seen	Date last seen	Nickname	Sex	No. associations	Max. HAI	Mean HAI
ZAW-097	16 Dec. 01	21 Nov. 04	*James blunt*	M	12	0.57	0.06
ZAW-080	31 Oct. 01	17 Dec. 01	*Curly*	F	11	0.50	0.06
ZAW-100	16 Dec.01	17 Dec. 01	*Chopped*	F	10	0.67	0.06
ZAW-102	16 Dec. 01	17 Dec. 01	*Rounded*	M	11	0.50	0.06
ZAW-115	17 Dec. 01	06 Nov. 02	*Leading edge*	F	10	0.67	0.06
ZAW-118	17 Dec. 01	15 Nov. 02	*Whistler*	F	12	0.40	0.06
ZAW-101	16 Dec. 01	29 Nov. 04	*Plain Jane*	M	14	0.55	0.05
ZAW-070	24 Oct. 01	06 Oct. 03	*Delphine*	F	11	0.40	0.05
ZAW-029	18 Mar. 97	02 Nov. 02	*Kilimanjaro*	-	11	0.40	0.05
ZAW-126 †	17 Dec. 01	28 Jan. 04	*Rakes*	F	10	0.40	0.05
ZAW-015	05 May 92	20 Jan. 05	*Jagged*	F	13	0.50	0.04
ZAW-017	17 Oct. 93	29 Oct. 05	*Columbine*	F	7	0.50	0.03
ZAW-018	17 Oct. 93	31 Oct. 93	*Type one*	-	6	0.44	0.03
ZAW-022	27 Oct. 93	31 Oct. 93	*Nine stripe*	-	4	1.00	0.03
ZAW-024	27 Oct. 93	31 Oct. 93	*Big knuckle*	-	4	1.00	0.03
ZAW-107	10 Feb. 99	19 Nov. 06	*Omega*	M	4	0.67	0.03

Table 5.4. Details of cow-calf pairs of which all the mothers and some calves (in post natal years) were resighted off West South Africa, with an indication of whether maternity confirmed genetically. [*nursing calves not seen again after natal year are numbered A-H].

Date	Group size	ID of mother	ID of calf (sex)*	Position	Comments
6 Feb. 1999	2	ZAW-006	ZAW-033 (F)	32.685 S, 17.987 E	Maternity confirmed
13 Feb. 1999	2	ZAW-006	ZAW-033 (F)	32.680 S, 17.938 E	Maternity confirmed
04 Mar. 1999	2	ZAW-019	ZAW-038 (M)	32.701 S, 17.960 E	Confirmed yearling calf
14 Feb. 2000	2	ZAW-019	ZAW-039	33.361 S, 17.144 E	
15 Feb. 2000	2	ZAW-019	ZAW-039	33.401 S, 18.212 E	
20 Feb. 2000	4	ZAW-006 ZAW-036	Calf-A Calf-B	33.248 S, 18.104 E	Two pairs in one group
22 Feb. 2000	2	ZAW-006	Calf-A	33.182 S, 18.033 E	
10 Nov. 2001	2	ZAW-006	ZAW-089 (M)	33.071 S, 17.897 E	Maternity confirmed
26 May. 2002	2	ZAW-006	ZAW-089 (M)	33.117 S, 17.917 E	Maternity confirmed
10 Jan. 2003	2	ZAW-173	Calf-C	33.093 S, 17.957 E	
10 Jan. 2003	2	ZAW-204	ZAW-205 (M)	33.040 S, 17.869 E	Maternity confirmed
17 Jan. 2003	2	ZAW-204	ZAW-205 (M)	33.061 S, 17.877 E	Maternity confirmed
18 Jan. 2003	2	ZAW-204	ZAW-205 (M)	33.042 S, 17.885 E	Maternity confirmed
11 Jan. 2004	2	ZAW-295	Calf-D (M)	32.682 S, 17.893 E	Maternity confirmed
01 Dec. 2004	3	ZAW-286	ZAW-292 (M)	32.703 S, 17.888 E	+ male escort
21 Nov. 2005	3	ZAW-269	Calf-E (F)	32.529 S, 18.096 E	Maternity confirmed, + male escort
19 Nov. 2006	2	ZAW-286	Calf-F	32.690 S, 17.902 E	
23 Nov. 2006	3	ZAW-295	Calf-G	33.109 S, 17.900 E	+ female escort
16 Dec. 2006	3	ZAW-269	Calf-H	32.694 S, 17.924 E	+ escort of unknown sex

FIGURES

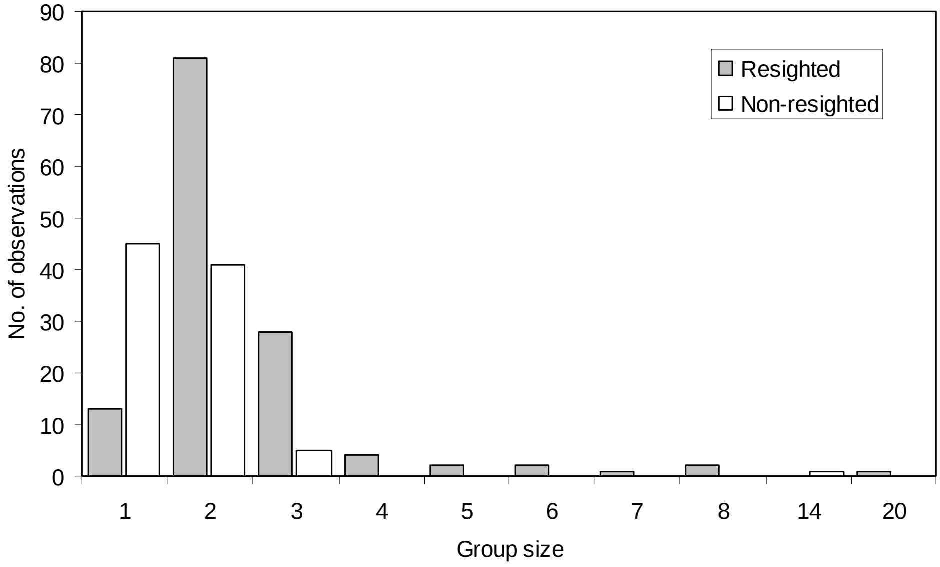

Figure 5.1. Frequency distribution of group sizes recorded for sightings with and without resighted individuals.

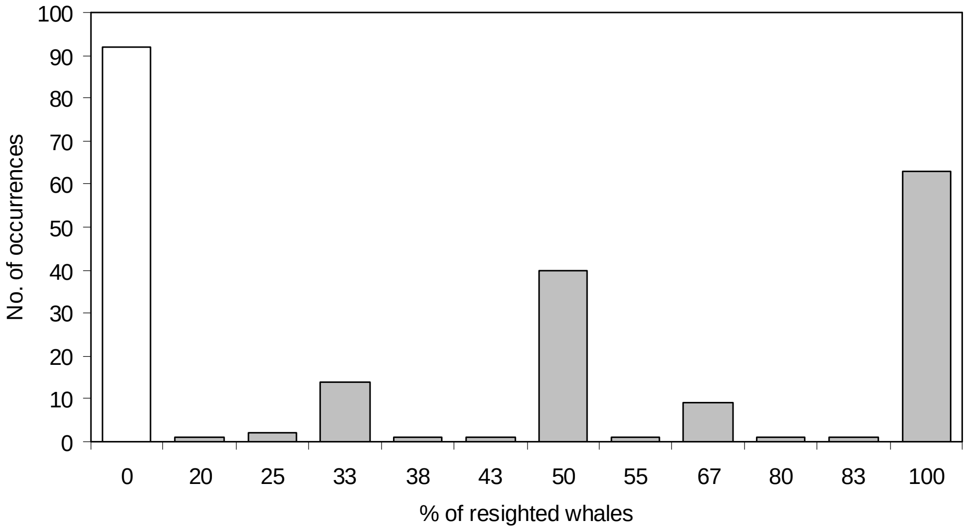

Figure 5.2. Distribution of proportion (%) of resighted individually identified humpback whales making up the total group size of intercepted groups (*n* = 226); i.e. 0% means no resighted individuals in a group while 100% means all were ‘known’ whales.

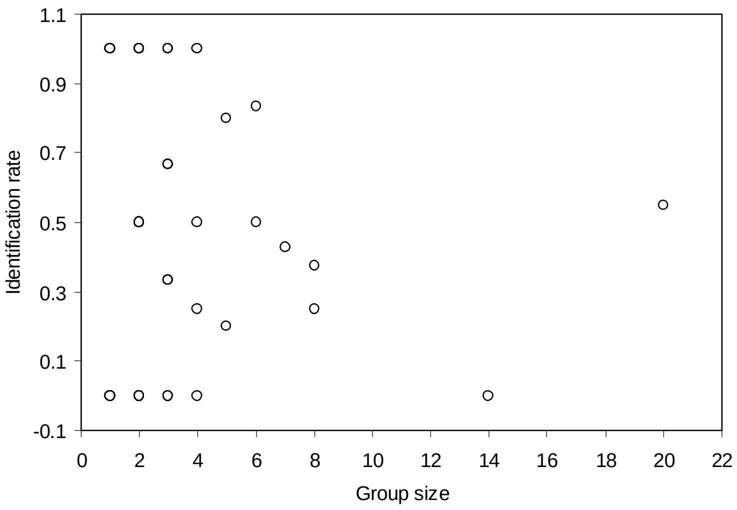

Figure 5.3. Comparison of identification rate (number of known individual humpback whales as a fraction of group size) to total size of the group.

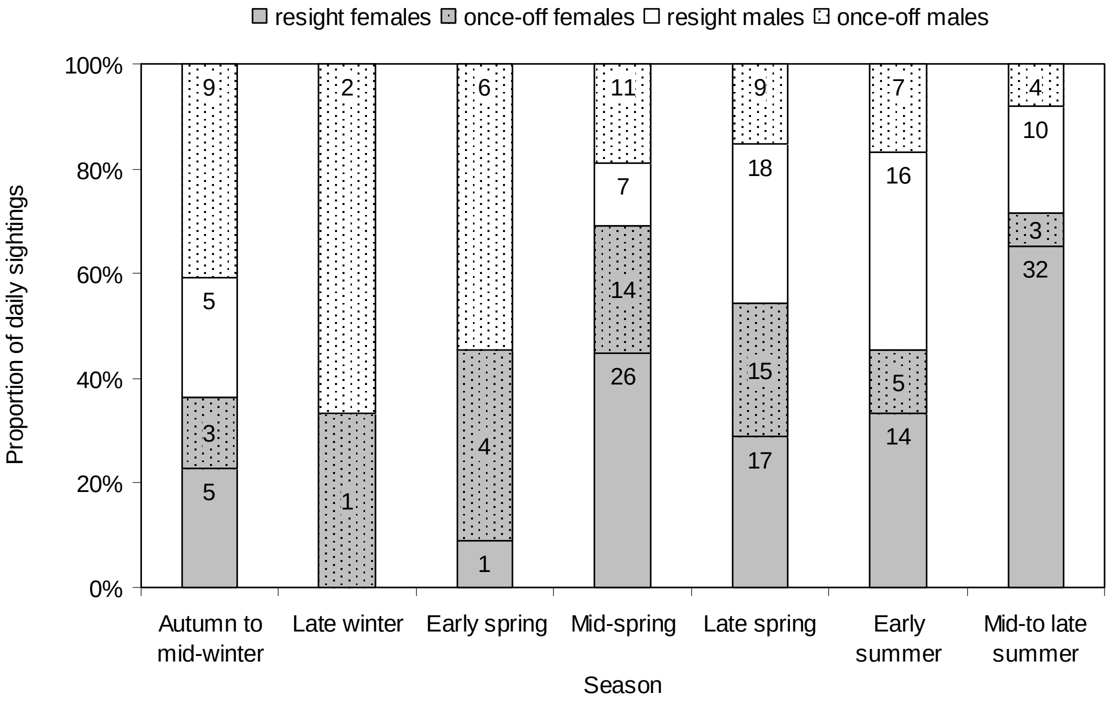

Figure 5.4. ‘Operational’ sex ratio per day in humpback whales identified (from all features combined) during boat intercepts off the west coast of South Africa. Data shown for both those whales only seen once (*n* = 93) and those resighted (51 individuals in 151 sightings); nursing calves excluded.

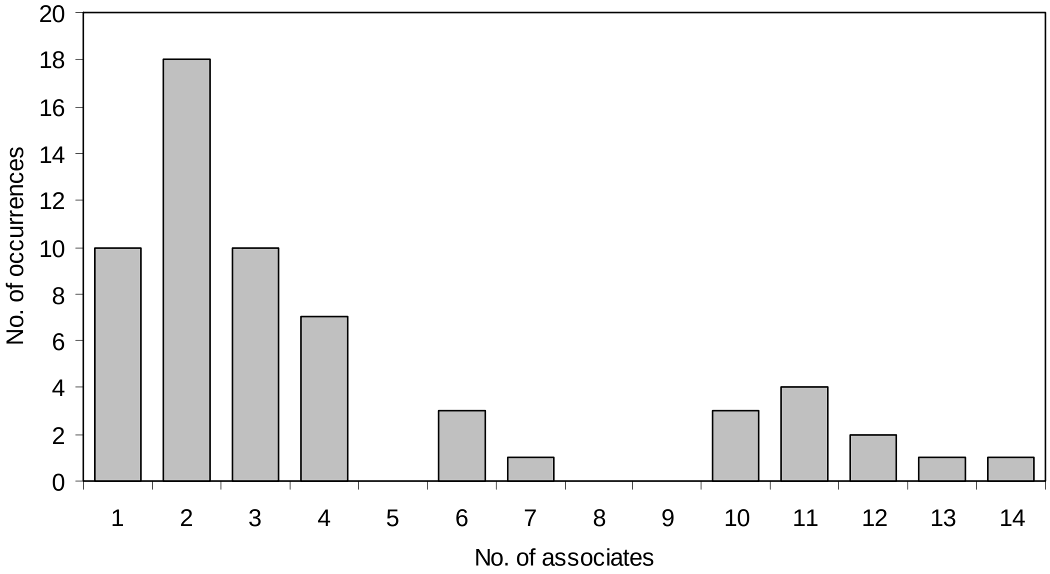

Figure 5.5. Total number of other resighted whales (= associates) that individually identified humpback whales were associated with throughout their sighting histories.

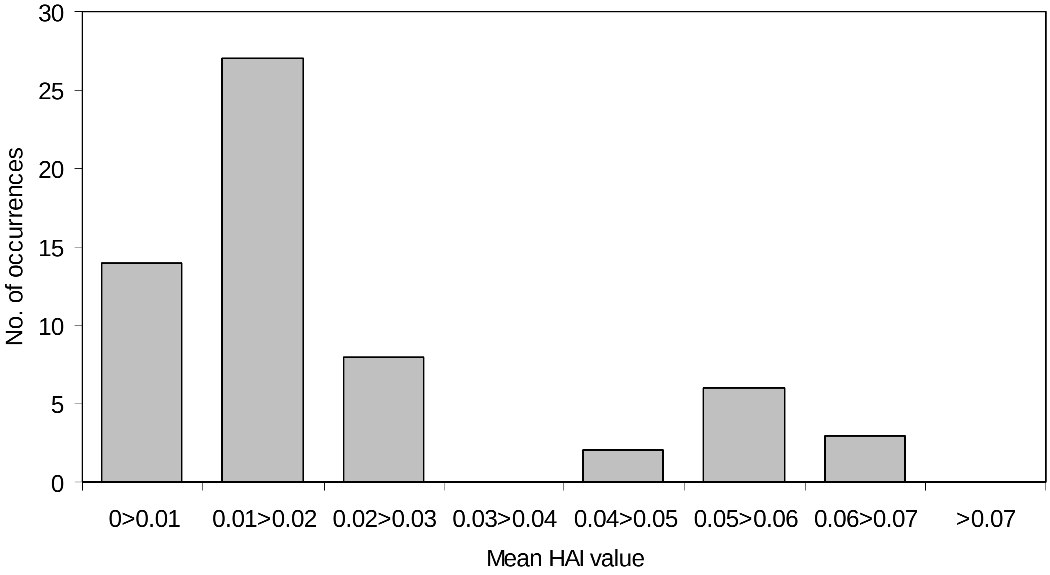

Figure 5.6. Distribution of mean half-weight association indices (HAI) for resighted individual humpback whales at the sampling scale of sighting.

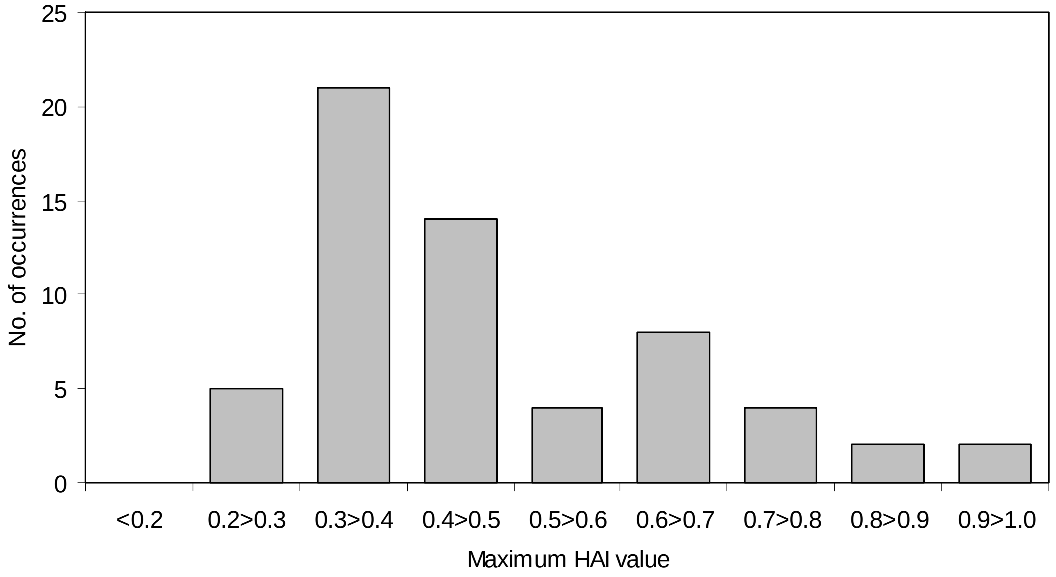

Figure 5.7. Distribution of maximum half-weight association indices (HAI), rounded to the nearest decimal, between duos of resighted individual humpback whales at the sampling scale of sighting.

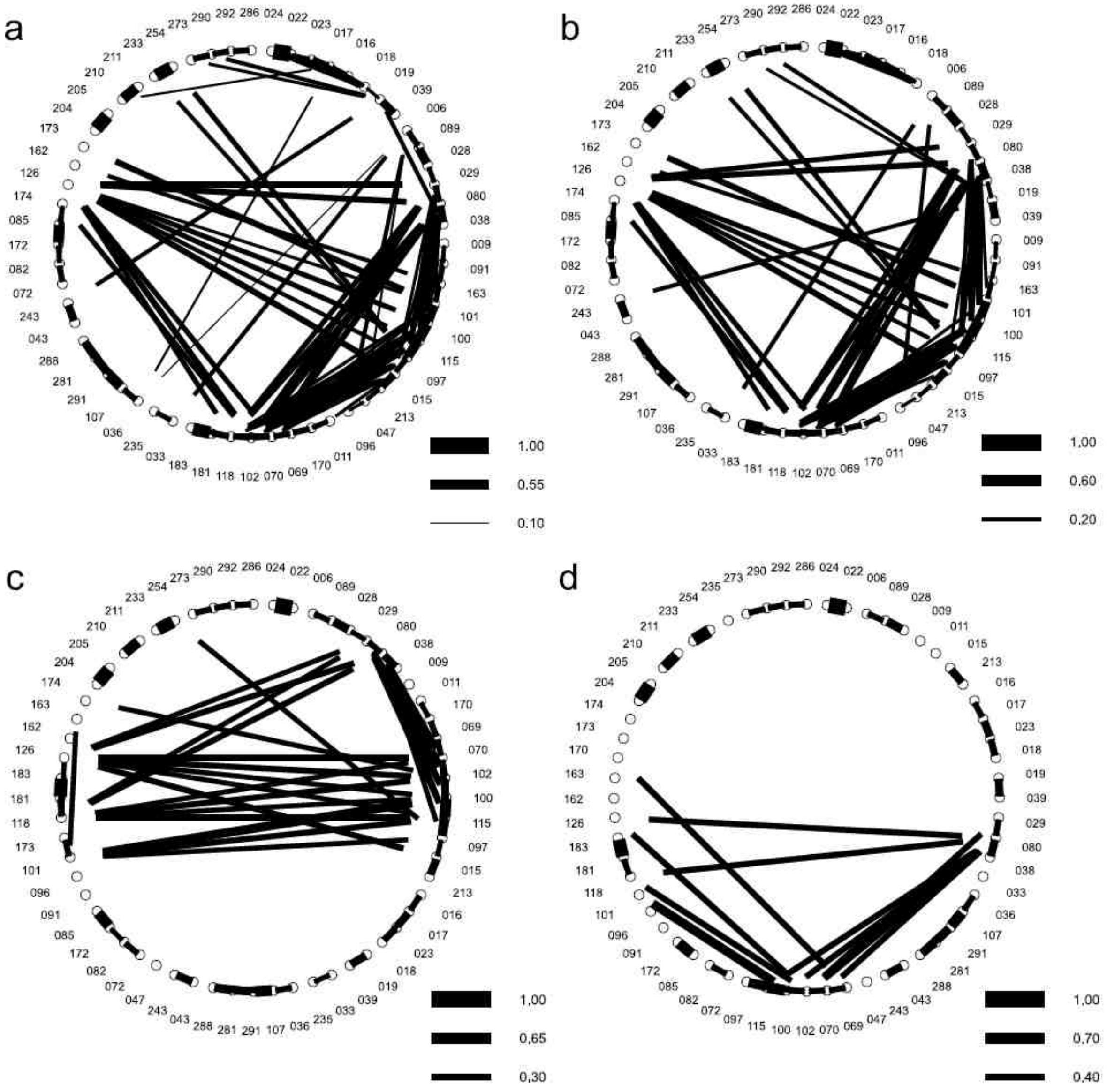

Figure 5.8. Sociograms based on half-weight association index (HAI) values calculated between duos of individually identified humpback whales (*n* = 60) at the sampling scale of sighting. Three-digit numbers are individual catalogue numbers (ZAW-###); thickness of lines scaled according to HAI values; (a) includes all values, (b) from 0.2, (c) from 0.3, and (d) from 0.4. Note that the order of the individuals is determined by SOCPROG in order to optimize display of associations.

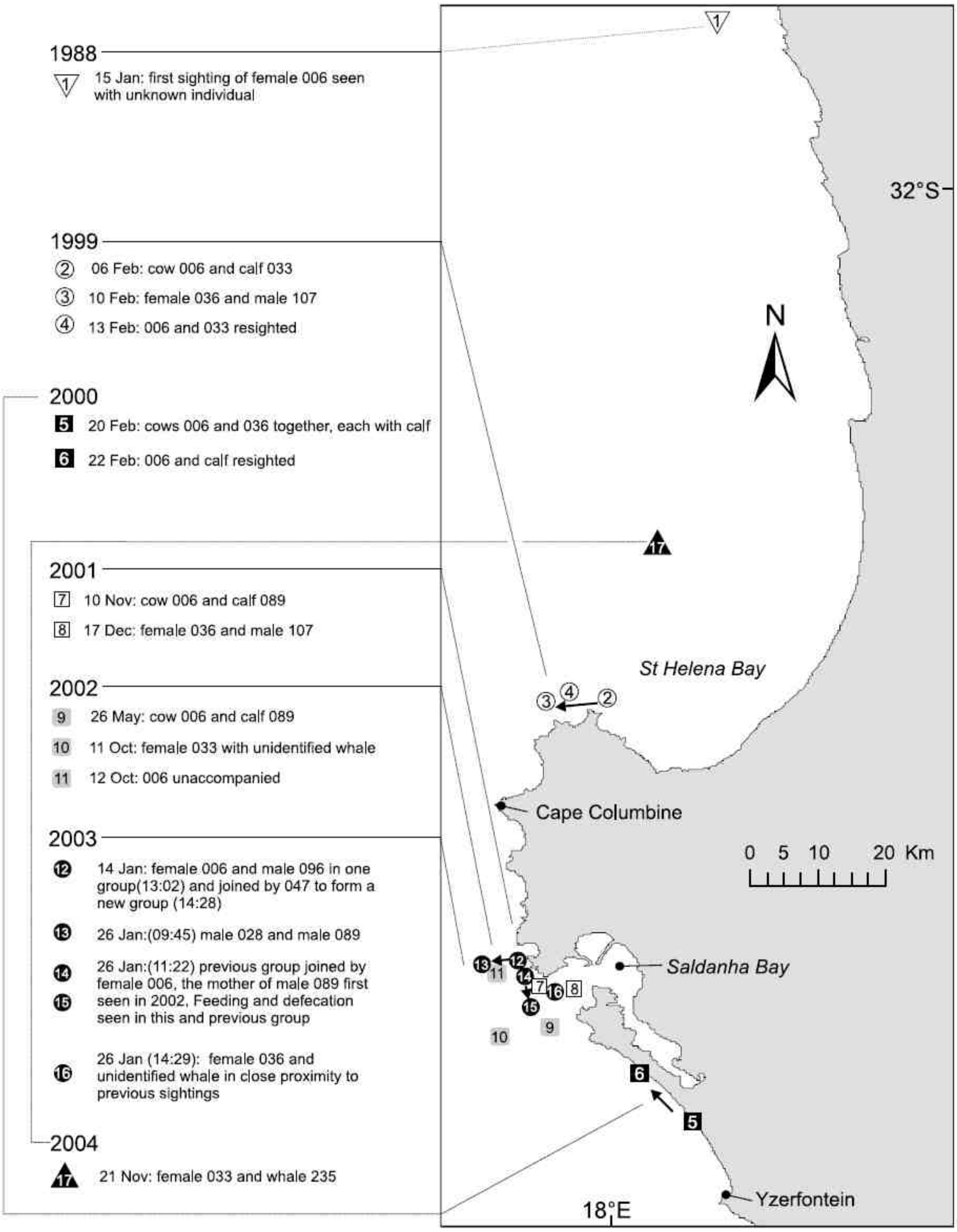

Figure 5.9. Spatial and temporal distribution of boat intercepts that involved the female *Ampersand* (ZAW-006), her offspring, and associates off west South Africa. Sightings are numbered in chronological order, and each calendar year has a unique symbol. Direction of movement (where possible to infer) is indicated by arrows between sightings of the same individual/s in the same year.

General conclusion

"I think it is perhaps the most remarkable thing about the sea: its power to invest all that lives and moves upon it with a wonder that nothing on land can equal. Its authority over our imagination seems to me final, as if it is at our beginning as it will be at our end".

Laurens van der Post - *The Hunter and the Whale* (1967)

The work presented in this thesis represents the largest research effort with the greatest seasonal coverage on large whales to date, to be carried out in the waters off west South Africa. It relied on the use of a combination of standard research and survey approaches, such as shore-based tracking (Chapter 2) and photo identification (Chapter 4) to describe present-day seasonality of humpback and southern right whales at Saldanha Bay, and how the humpback whales may relate to the breeding population that occurs of the rest of the coast of West Africa. Prior to the few contemporary studies (e.g. Best *et al.* 1995) and new data mentioned or described here, all knowledge about the migratory patterns of humpback and southern right whales on this coast was based on whaling data and a few historic observations (Chapter 1). Many of the historically observed patterns, such as seasonal catch rates for humpbacks, when viewed in isolation, did not reveal fully the atypical nature of the migration. However, certain data such as the sex ratios of humpback catches and reproductive condition of individual whales, when interpreted together with the recent findings and some of the descriptions by historic observers (e.g. Olsen, 1914), can now be viewed in an improved context. This suggests that localised productivity associated with the Southern Benguela upwelling system, and the seasonal availability of prey may influence the migratory pattern of both species examined. The importance of predictable oceanographic features such as upwellings has been the subject of a number of recent studies, e.g. blue whales have been observed to feed on masses of euphausiids linked to the higher primary production from a wind-driven coastal upwelling off California (Croll *et al.* 2005; Tynan *et al.* 2005) and the occurrence of four rorqual whale species (including humpback and blue whales) was found to be highly correlated with the presence of thermal fronts in the Gulf of St Lawrence (Doniol-Valcroze *et al.* 2007). What makes the results presented here of particular interest is that the study area is located outside of the 'traditional' feeding grounds for these species in the Southern Hemisphere: humpback whales feed at much higher latitudes south of the Antarctic Polar Front (APF) at 50^{O}S and nearer the ice edge (Dawbin 1966; Murase *et al.* 2002), while right whales feed from around and south of the subtropical convergence, at about 40^{O}S as well as the APF (Mate *et al.* 2011). From the recorded observations it is apparent that the area around St Helena and Saldanha Bays has been functioning as a supplemental feeding ground for at least the duration of the last two centuries, but most likely for as long as these feeding opportunities have been available to whales. It is possible that, due to the depletion of the numbers of whales (for both species) that participate in feeding here, their unseasonal occurrence has gone relatively unnoticed, a phenomenon also observed in the Northern Hemisphere for North Atlantic right whales *Eubalaena glacialis* (Smith *et al.* 2006) and humpbacks (Reeves *et al.* 2004).

Although both species have been studied elsewhere along the South African coast: right whales along the south coast using aerial surveys (see Chapter 3) and humpback whales at Cape Vidal on the east coast (Findlay 1994), the results again highlight the importance of adequate seasonal and regional coverage when studying large whale species, and the value of examining historical data when interpreting more recent findings. An important result was that historic data (Chapter 1), movement patterns observed from land (Chapter 2), and patterns in resightings (Chapter 4) all suggest that humpback whales seen here are not necessarily representative of a discrete or entire breeding stock (B2), and that some whales join and leave the African coast north of the SW Cape, using mid-oceanic migratory routes. Other noteworthy findings included:

- The significantly female-biased sex ratio during mid-spring and summer (Chapters 2 and 5), the first such recorded for any region.
- Feeding on euphausiid prey by humpback whales and the estimation that about 500 individuals may be participating in this activity during spring and summer months (Chapters 2 and 4).
- The presence of right whales virtually throughout the study period, with the highest sighting rates recorded in summer, also associated with feeding behaviour (Chapter 3).
- The confirmation of humpback whale migratory links between west South Africa and the breeding ground off Gabon through three photographic matches (Chapter 4).
- The record of a humpback cow that produced calves in three consecutive years, each of which survived to at least six months of age, providing the first observations of successful post-partum ovulation for this species in the Southern Hemisphere. Also, the return of three known calves to the same area, sometimes on the same day as their mothers, which is strongly suggestive of maternally derived site fidelity (Chapter 5).

These findings suggest that our current understanding of the stock-structure of the humpback whale Breeding Stock B remains inadequate, despite the conclusion of its assessment at the Scientific Committee of the International Whaling Commission (IWC), held in Trømso, Norway from 30 May – 11 June 2011. The recommendations in the report from that meeting (IWC 2011) highlight future research needs that are equally applicable to the west South Africa region, and the region as a whole (adapted from the report):

- More extensive genetic and photographic data collection over wider range, and coordinated amongst regions (i.e. SPLASH, YONAH type studies) (see Chapter 4).
- Long-term study of targeted populations for estimates of trend.
- Determine movement patterns and connectivity through strategic implementation of satellite tagging effort throughout the region.
- Surveys and sampling (genetic and photographic identification) of lesser studied areas where humpback whale aggregations are known or suspected to occur, especially Angola, Namibia, São Tomé and Príncipe, Gulf of Guinea, and Bight of Benin, to characterise the potential importance of these areas (see Hazevoet *et al.* 2011; Carvalho *et al.* 2011; Weir 2011).

- Passive acoustic monitoring to help characterise the distribution of humpback whales in less well-studied parts of their range (e.g. Cerchio *et al.* 2010).
- Extension of coastal surveys and sampling into offshore areas, beyond the continental shelf and territorial waters of coastal African states.
- More genetic sampling in the Antarctic to help improve allocation of catches (for assessment purposes), dependent upon further understanding of the stock structure from low-latitude breeding grounds.
- A more comprehensive evaluation of the models and approaches to stock assessments (e.g. multi-stock assessments) that is:
    - Informed by new data collected above;
    - Considers a wider range of possibilities to ensure compatibility of models with data;
    - Takes account of information on whales seen in more than one region.

More specific to the west Southern Africa region, it would be interesting to determine the geographical extent (e.g. does it include other centres of upwelling, including in Namibia) of the feeding grounds for both humpbacks and southern right whales and to examine how their primary prey species (euphausiids and copepods respectively) respond to changes in oceanographic conditions and primary production, as could be derived from remote sensing and other physical environmental data (e.g. Tynan *et al.* 2005; Croll *et al.* 2005). A better understanding of this may be important in the light of biological regime shifts and climatic changes that have been recorded in these marine systems over the last few decades (see Cury & Shannon 2004; Roualt *et al.* 2010), as such changes are known to affect the distribution of cetaceans (Benson *et al.* 2002). Furthermore, it would be interesting to examine whether there are any interactions between the two species studied on such a mutual feeding ground, or with other species of whale that may utilise the same prey sources (e.g. blue, fin, sei or minke whales).

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Afterthought

"Before leaving whaling science, I must report the major scientific discovery I made in the south, which was in the science of nutrition. It is that whale meat not only is edible, but, properly cooked, is delicious and infinitely preferable to the meat of the ox. Properly cooked, I say! And, as it is now appearing in New York restaurants, where it is variously described by the customers as tasting like cod-liver oil and long-dead hippopotamus, I will end my chapter on science in the south by reporting on detail the manner of cooking it.

Take a ten-pound cut from the rump of a finback whale, just aft of the dorsal fin.(It must be a fin whale or, if you can find one, a humpback. If any New York waiter offers you blue whale, take it in preference to beef, but complain about the absence of fin from the menu; and, if any man tells you he has eaten sperm whale, or that any stomach could tolerate what even the Cape pigeons and the killer whales spurn, give him the lie, even though his name may be Melville.) Hang your cut of fin rump steak up on a hook, preferably in a fairly warm spot exposed to the sun. Leave it there for three days. The horrid black mess you will see when you return at the end of that period may put you off whale meat for the rest of your days, but do not be deceived or discouraged. Hold your nose, cut away all the black crust and bury it deeply far away from your house. In the centre of the cut you will find about two pounds of fresh, juicy, oil-free, fatless steak. Put this under a scorching broiler and char it quickly on both sides. Then put it on the table and cut from it the finest pound of medium-rare steak you ever ate in your life. Bury it under a mountain of fried onions and eat it with roast potatoes".

R.B. Robertson – *Of Whales and Men* (1956)

INTRODUCTION

In addition to data collection and scientific research, the extended periods of fieldwork at Saldanha Bay also provided me with an opportunity to observe the activities of fishing industry based there, interact with locals that belong to fishing communities, get to know new varieties of fish, catch rock lobsters (on misty days) and hone my cooking skills on a captive audience of unsuspecting volunteers and colleagues. All of this probably sowed the seeds for my 'parallel' career – my involvement in the Southern African Sustainable Seafood Initiative (2004 – 2009) during the extended writing-up phase of my thesis. It also contributed to my love for cooking and food. Cooking is not unlike scientific research, and requires the correct equipment, much experimentation and sufficient sample sizes. I was never tempted to eat whale meat, even from the freshest stranding. I therefore include here the recipe for 'braai-ing' (= to barbeque) snoek *Thyrsites atun* with a 'traditional' West Coast style basting sauce (although many variations exist).

MATERIAL AND METHODS

To feed 6-8 volunteers you will need:

- 1 freshly flekked[1] snoek of about 3 kg, salted to taste; 1 hot wood fire with fairly hot coals (light about 50 min before estimated lunch time); splash of olive oil.

For the basting:

- 1/2 cup of apricot jam; 1/2 cup of butter; juice of 1 lemon; 2-3 cloves of finely chopped garlic; 1 tablespoon of chopped parsley; 1 tablespoon of fennel seeds (optional); ground black pepper to taste.

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[1] Flekking is a manner of butterfly-cutting a fish from the dorsal side, so that the belly remains intact. Genuine West Coast fishermen can do this in a matter of seconds. See Wilkinson, A. 2005. The Complete South African Fish and Seafood Cookbook. Struik Publishers, Cape Town.

- Place all of the above in a small metal pot or enamel cup and place near heat of fire so that all ingredients melt, stirring occasionally. Do not boil.

How to braai:

- Rub the olive oil over the skin side of the snoek, and place into a closable braai-grid ('toeknyp-rooster') of adequate size, with the skin on the top flap of the grid. Close the grid.
- Spread the coals out evenly when ready.
- With the skin side down, place the grid over the coals at a reasonable height (25 – 30 cm), depending on how hot the coals are. Leave for a short while, turn over, open the grid carefully so that the skin does not stick to the grill, and re-place over coals, again skin down.
- Baste the flesh side of the snoek with the melted sauce using a spoon or a brush. Allow the snoek to braai like this for at least 5 minutes, and then turn over. Remember to baste the small strip of flesh along the backbone that is visible on the skin side. Braai on flesh side for about 2 min, turn over, and baste again. The flesh should start to turn opaque-white; take note of any areas that may start to show signs of charring, especially on the stomach – this may indicate that the coals are slightly too hot.
- Alternate braai-ing the skin and flesh side, while liberally applying the rest of the basting. Be careful not to overcook the fish. When ready, the skin should be crispy with small bubbles forming, but not black, and the flesh side should start to turn golden brown. Check with a fork, if necessary; the meat should flake easily but still be moist. Total braai time should not exceed 20-25 min.
- Remove from heat, turn grid upside-down (i.e. skin down) and slide snoek into a serving dish.
- Serve with traditional (sweetened) sweet potatoes, Cape seed-loaf bread and grape jam, accompanied by a crisp *Chenin-* or *Sauvignon Blanc* from the region.

DISCUSSION

A braai-ed snoek is probably one of the most cost-effective and simple ways to feed a large number of volunteers. It is generally very popular, even with people who do not eat garlic. There are however some caveats. Snoek caught in autumn and early winter tend to be fatter and better eating than those available in summer. In addition, some snoek may suffer from a parasitic infection of the muscle that, although harmless, can give the flesh an unpleasant floury consistency. This is known as 'pap' snoek. Although one can sometimes spot this when buying a snoek, you can never be 100% certain that your snoek is not pap. It is therefore recommended that you 'test' your snoek before braai-ing, by cutting a small piece of flesh off and frying it in a pan. Or, have handy a 'back-up' snoek or other fish (such as an angelfish *Brama brama*) in case your snoek is pap. This can help you avoid bitter disappointment around the braai fire. A pap snoek has very little use, except perhaps in a snoek-pâté.

Addendum: Published paper and popular article

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Migration redefined? Seasonality, movements and group composition of humpback whales *Megaptera novaeangliae* off the west coast of South Africa

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The migration of Southern Hemisphere humpback whales *Megaptera novaeangliae* between their feeding and breeding areas has thus far been considered a highly predictable and seasonal event. However, previous observations on the humpbacks that pass through the nearshore waters of the west coast of South Africa have revealed deviations from the behaviour and seasonality expected during a typical migration. This 'anomaly' is hypothesised to be associated with prey availability in the region. Shore-based observations between July 2001 and February 2003 from North Head, Saldanha Bay, in the Western Cape province, yielded relative abundances that again did not support a classical migration pattern, with the highest sighting rates from mid-spring through summer. Movement parameters (actual swimming speed, direction and linearity) of humpback groups tracked by theodolite showed mid-spring to be a turning point in their behaviour, after which we observed a significant reduction in actual swimming speed, an increase in 'non-directional' movement, and a distribution farther from shore than in other seasons. Additional data on group composition and sex collected between 1993 and 2008 showed a significantly female-biased sex ratio during mid-spring, the first such recorded for any region. Direct observation of feeding on crustacean prey during spring and summer further supports the notion that humpbacks may have more flexible foraging habits than previously appreciated, and that the southern Benguela upwelling region may function as an important feeding area for these whales.

Keywords: Benguela upwelling, Breeding Stock B, feeding, group composition, humpback whale, migration, Pythagoras software, seasonality, sex ratios, shore-based survey, South Atlantic, theodolite tracking

Introduction

Humpback whales *Megaptera novaeangliae* in general are believed to undertake extensive and predictable migrations from polar feeding grounds in summer to tropical overwintering areas, displaying high fidelity to the same breeding and feeding areas (Clapham et al. 1993, Clapham 2000, Stevick et al. 2003, Rasmussen et al. 2007). These migrations frequently follow nearshore migration corridors in the Southern Hemisphere (Dawbin 1966, Bryden 1985). Although behaviour associated with reproduction, e.g. male–male competition (Brown and Corkeron 1995) and singing (Clapham and Mattila 1990), is often observed during migration, feeding behaviour during transit is only seen occasionally, and very rarely in the Southern Hemisphere (Best et al. 1995, Stockin and Burgess 2005, Stamation et al. 2007). The bulk of feeding is thought to occur in the areas of high productivity at high latitudes where the whales spend their summers (Clapham and Mead 1999) with the exception of the unique Arabian Sea population that is apparently resident year-round (Mikhalev 1997, Rosenbaum et al. 2009, Minton et al. in press).

The division of different populations of humpback whales in the Southern Hemisphere reflects their associated feeding and breeding areas and has been based on their previously assigned summer feeding regions or Antarctic Areas numbered I–VI (Donovan 1991) and the more recently designated Breeding Stocks labelled A–G (IWC 1998). Whales from Breeding Stock B (BSB) found off the west coast of Africa are thought to feed in Areas II (60° W–0°) and III (0°–70° E). In some Breeding Stocks there has been some evidence for substructuring of stocks based generally on ongoing mitochondrial DNA analyses (e.g. Rosenbaum et al. 2009). In the case of BSB, the stock has been separated

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into B1 and B2 (IWC 2001) with the former located in the Gulf of Guinea (north of 18° S), whereas the humpback whales that migrate past the west coast of South Africa are presumably part of B2, found south of 18° S (see IWC [in press] for details of most recent BS subdivisions).

Historical catches from shore-based whaling stations in the Saldanha Bay region have hinted that the whales there conform more or less to a classic migration pattern with two distinct seasonal peaks of abundance, thought to correlate with the northward (July/August) and southward (October/November) migrations (Olsen 1914, Harmer 1931). On the other hand, Olsen (1914), based on his observations from 1912 to 1913, commented that the whaling season at Saldanha Bay was relatively long, lasting till mid-December. More recent and mounting evidence has added further support that this area does not function as a typical migration corridor, and that there may be other contributory factors that influence the timing and duration of visits of humpback whales to this region (Best et al. 1995, Findlay and Best 1995).

This study was conducted to examine trends in humpback whale relative abundance, occurrence, and movement across seasons in the Saldanha Bay region, based mainly on shore-based observations. As such, it represents the most extensive research effort to date on the species in this region, and, apart from a six-week long pilot study in 1993 (Best et al. 1995), the first since the *Discovery* investigations of the 1920s (Matthews 1938). Furthermore, data on group composition were obtained from the most comprehensive genetic collection available for the region, collected during boat intercepts of humpbacks between 1993 and 2008.

Material and methods

Description of study area and study period

The study was carried out from North Head, Saldanha Bay (33°02′ S, 17°55′ E), located on the west coast of South Africa, approximately 100 km north of Cape Town (Figure 1). This is some 30 km south of Cape Columbine, the westernmost headland in the Western Cape province of South Africa, and the site of an earlier pilot study (Best et al. 1995). The region has a Mediterranean-type climate (Kruger 2004) with an average rainfall of 298 mm per annum recorded mostly during winter (Zucchini et al. 2003, Zucchini and Nenadić 2006). The wind blows from a predominantly southerly direction in summer and westerly in winter. Saldanha Bay was the site of two modern whaling stations, Donkergat and Salamander, which operated sporadically between 1909 and 1967 (Best 1994, Findlay 2000).

The highly exposed coastline has an approximate north-westerly/south-easterly orientation (330°–150° True) and is characterised by a rocky shore, broken by a number of small bays with sandy or boulder beaches, and a few small nearshore islands and rocks. The tidal cycle is semi-diurnal with an average tidal range of about 1.2 m. The bathymetry of the area is shown in Figure 1.

In an attempt to gather data across all seasons, a shore-based watch was kept from North Head during two periods of fieldwork: the first for five months, from 24 July to 20 December 2001, and the second for nine months, from 6 May 2002 to 15 February 2003.

Observations of environmental and sighting conditions

A number of environmental observations were made at the lookout every hour in order to assess the sighting (searching and tracking) conditions. The following variables were recorded:

(a) Surface windspeed (in knots) and direction (magnetic bearing): measured with a hand-held anemometer (analogue at first and digital from 25 August 2001 onward) and compass
(b) Cloud cover: expressed as a fraction of eight (0/8 = no cloud, 8/8 = complete cover) over observation area only (i.e. over the sea)
(c) Sea-state: judged according to the Beaufort Scale over the entire observation area
(d) Glare: magnetic bearing and estimated extent of reflection of sun off the water, expressed as percentage of total search area affected
(e) Swell: estimated by judging the height of the average swell rising against a rocky islet (Schooner Rock) with a known height of 9 m above sea level (ASL)
(f) Visibility at the midline: the midline was set perpendicular to the coastline, at a bearing of 240° True from the lookout. The visibility at this line was the radial distance from the tower to the fix, calculated from the maximum vertical angle at which individual wavelets could clearly be distinguished through the theodolite eyepiece. This distance was assumed to be equivalent to the distance at which a whale could still be accurately tracked. This measurement was not made when the theodolite was being used for tracking whales
(g) Sightability: a subjective index on a scale of 1–5 (1 = very poor, 5 = very good) that summarised how good overall conditions were for spotting whales, and taking into account factors (a)–(f) above

Search effort was classified into one of three categories, based on prevailing sighting and weather conditions:

(a) Optimal watch: full search effort during suitable conditions over the entire search area, with at least one person searching with binoculars and another with naked eye
(b) Suboptimal watch: equivalent to whale vessel surveys where masthead watch discontinued. Conditions were considered suboptimal at average windspeeds >20 knots for extended periods, Beaufort sea-states of 5 or more, or when more than one half of the search area was obscured by mist or clouds. In practice, this was when the sightability was estimated to be 2 or less (poor to very poor). During a suboptimal watch, searching would be carried out as described above, but sightings would only really be possible within the visible area or within a certain distance from shore. Both optimal and suboptimal efforts were considered in the calculation of sighting rates
(c) Standby: this mode was entered into under the following conditions: when a suboptimal watch continued for longer than two hours with no visible signs of improvement; at the sudden onset of extreme weather conditions, e.g. continuous rain, thick mist, windspeeds >30 knots, swell height >7 m; or where such extreme conditions already existed at the start of a day. During standby, the team would remain at the lookout for some time to assess whether conditions were improving to acceptable levels

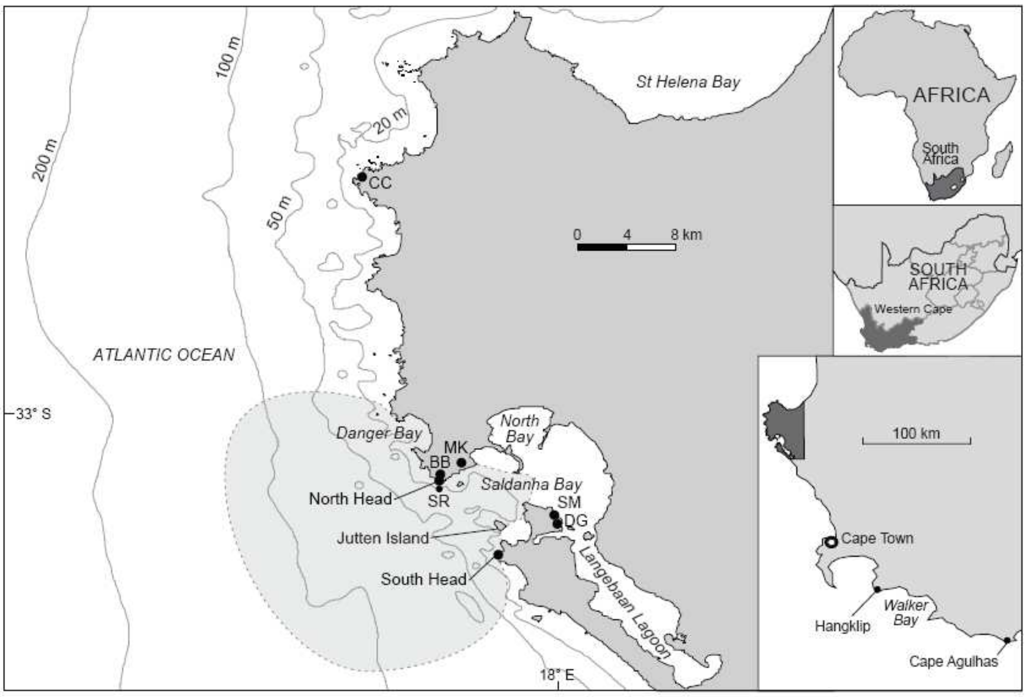

Figure 1: Location of the study area on the west coast of South Africa (BB = Baviaansberg, MK = Malgaskop, CC = Cape Columbine, DG = Donkergat, SM = Salamander, SR = Schooner Rock). Approximate extent of the search area is indicated by lightly shaded area

or not. No searching with binoculars was attempted and any whales sighted during this time were regarded as incidental sightings and excluded from trackline analysis

Climatic data

Further environmental measurements (daily minimum and maximum air temperatures [°C], twice daily air pressure [kPa]) were obtained from the South African Weather Services as recorded at the nearest coastal weather station, Cape Columbine lighthouse (32°49′36″ S, 17°57′30″ E, 68 m ASL). Hourly tidal measurements (m), as recorded by a tide meter situated in Saldanha Bay, were obtained from the South African (SA) Naval Hydrographer's Office (http://www.sanho.co.za). These were all required for calculating the correction for the effect of refraction during trackline analysis (see below).

Data collection: shore-based observations

The primary lookout (or tower) was at Baviaansberg, a hill 72.8 m ASL about 700 m (at 240°) from the shoreline on the North Head of Saldanha Bay. The lookout position was located within a military small-arms firing range, and on the rare occasion when the range was active, a secondary observation post at Malgaskop (111.8 m ASL), another hill set 2.65 km farther inland, was used (Figure 1).

The search area was defined as the area of open ocean to the south, west and north of the lookout, stretching as far as visibility allowed (Figure 1). Although Saldanha Bay, Danger Bay and visible parts of Langebaan Lagoon were also searched from time to time, they were not considered as part of the primary search area, but groups of whales that entered these bays were still tracked. Only small sections of the search area were obscured by land, e.g. behind Jutten Island or extremely close inshore.

Teams of 2–4 observers searched for whales for alternating two-hour shifts, starting approximately one hour after sunrise and ending an hour before sunset, weather permitting. Half of the team searched by the naked eye and the other half with 7× or 8× wide-angle binoculars, alternating roles every 10 minutes. At least one experienced observer (who could also operate the theodolite) was always included with novices. The entire search area was searched by all on watch, regardless of the number of observers.

When a whale or group of whales was spotted, the first cue (i.e. blow, body, splash, breach, slick) was recorded, the species identified if possible and the group size estimated. The most experienced observer would then track the group, using a Wild T1 manual theodolite (equipped with a 22× telescope) that was mounted and levelled on a fixed base. The height of the focal plane at each lookout was calculated through triangulation using a geographically referenced orthophoto (1:10 000) produced by the South African Chief Directorate: Surveys and Mapping, and two reference points of known height and position in the field of view: a trigonometric beacon situated at North Head Lighthouse, and the highest tip of Schooner Rock. The latter was also used as the fixed reference point of known position and bearing on which the horizontal azimuth was calibrated every day. The aim of the tracking was to obtain an accurate 'fix' on the group on at least three different surfacing events, where an event was defined as a number of short-spaced surfacings bracketed by a longer submergence. A fix consisted of the recorded behavioural cue (body, blow, breach, splash or slick), an estimate of group size, the time (to the nearest second) and the vertical and horizontal angles (to the nearest second) as measured by the theodolite. A series of such fixes was termed a 'track'. Searching would resume once a reliable fix was made on the group being tracked. Although groups were tracked for a minimum of three fixes, tracking could continue for several hours if no other groups were seen, or up to an interception by the boat (see below). Revised group size estimates were made as tracking progressed. The group size recorded at the first fix was considered the minimum estimate, whilst the number at the final fix (excluding any feedback from the boat if the group was intercepted) was taken as the best group size estimate available. In the event of a group splitting, the two resultant groups would be treated as new groups. During tracking, the search area was still scanned for new sightings by watchers not operating the theodolite, and although the search effort during this time could be considered somewhat reduced, it was assumed during analyses that search effort remained constant during both searching and tracking.

Spatial analyses

Tracks were inspected and for each surfacing event a single fix was selected based on the type of cue recorded at the fix, in the following order of priority: body, splash, and blow. In the few instances where no fixes on such cues were available, a fix on a breach or slick would be used. The horizontal and vertical angles and time recorded at the selected fixes were imported into and analysed using the software program Pythagoras (Gailey and Ortega-Ortiz 2000, 2002). The algorithm used is based on the work of Lerczak and Hobbs (1998), and takes into account tidal height (in m, measured at the nearest hour) and a refraction correction (G Gailey, Department of Wildlife and Fisheries Science, Texas A&M University, pers. comm., Leaper and Gordon 2001); the latter was based on the air temperature (°C) and pressure (kPA) measured daily at 14:00 at Cape Columbine. The refraction correction was applied to all fixes from both tracks and midline visibility measurements.

The coordinates (latitude and longitude) of each fix were calculated by Pythagoras, and these positions along with associated sighting data were imported into a global information system (GIS) (ESRI® ArcMap™ 9.2 and ESRI® Arcview™ 3.3). Accurate digital versions of the coastline, depth soundings and depth contours of the study area were obtained from the SA Naval Hydrographer's Office (as used for marine navigational chart SAN 117, scale 1:150 000). Due to its irregular nature, it was necessary to create an 'idealised' version of the coastline before calculating the distance of a fix from the shore. This was done by joining the heads of bays within the search area, thus essentially 'removing' these bays to provide a more accurate estimate of the distance from this 'smoothed' coastline. In the few cases in which whale groups were inside these bays, the distance from the shoreline would be indicated as a negative measurement. At least one reliable fix was taken for 259 groups of humpback whales and the position of this first fix (in some cases the only reliable fix) was used to calculate the distance of the group to the nearest shoreline in a GIS, using a Transverse Mercator Projection with central meridian set at 17.9° E.

Seasonality

Conventional austral seasons, viz. autumn (March–May), winter (June–August), spring (September–November) and summer (December–February) were considered. The prefixes 'early', 'mid-', or 'late' were added to the season name for the first, middle and last month in a season respectively (e.g. mid-spring = October). Where observations were carried out in the same month in different years, these duplicate months were combined into a single seasonal sample, e.g. October 2001 and 2002 formed the mid-spring sample. Sample sizes of tracked whale groups varied considerably between months due to the timing of study periods, variability in sighting rates, and associated effort. Some months/seasons with very low sample sizes (<15) were therefore combined in order to increase the available sample size, resulting in seven seasonal groupings: late autumn to mid-winter = May 2002, June 2001/2002, July 2001/2002 ($n = 23$); late winter = August 2001/2002 ($n = 25$); early spring = September 2001/2002 ($n = 16$); mid-spring = October 2001/2002 ($n = 55$); late spring = November 2001/2002 ($n = 31$); early summer = December 2001/2002 ($n = 36$); mid- to late summer = January 2003, February 2003 ($n = 26$). The term 'season' is used herein to refer to these seasonal groupings, unless stated otherwise.

Trackline analysis

Three or more reliable fixes at different surfacings could be obtained for 212 groups and these were used in trackline analyses in Pythagoras (Gailey and Ortega-Ortiz 2002), and separated according to the seasons described above.

For each trackline the following parameters were calculated:

(a) Actual swimming speed (= 'leg' speed): the unweighted mean of the swimming speeds calculated for each leg (the distance travelled between two consecutive fixes in a track) by dividing the distance covered between a pair of fixes, by the time it took to travel between them

(b) Linearity: a form of migration index, calculated by dividing the net distance covered by a track (i.e. the direct measurement between the first and last fix) by its cumulative distance (the sum of all legs). Linearity values range between 0 and 1, with values close to 1 representing a straight track-line, whereas a value close to 0 represents a track with no constant direction

(c) Net course: the true bearing in degrees of a track, calculated between the first and last fixes

(d) Net speed: calculated by dividing the linear 'distance made good' between the first and last fixes of a track by the time it took to travel between them (i.e. total duration of track)

Data collection: boat-based observations

For the duration of the study, when weather and personnel availability permitted, whale groups were intercepted using a 6 m semi-rigid inflatable boat powered by twin outboard motors. The boat was directed from its mooring inside Saldanha Bay to whale groups by the land-based observers via VHF radio, as soon as they had made an accurate fix on the group. The boat was dispatched to any sighting that appeared to be within reasonable range of a small boat (about 15 km) and that, based on its direction and speed, would not disappear from the search area or field of visibility before the boat could reach it. Groups would generally be intercepted in the order of being spotted; in the case of simultaneous sightings, priority would be given to groups that were most likely to be lost (i.e. farther away or faster moving). If other groups were spotted by the boat crew during an intercept, these groups would be visited after data collection was completed.

Intercepts were used to confirm group size, take individual identification photographs and collect skin biopsies using a Paxarms biopsy rifle (Krützen et al. 2002). Skin samples were placed into individual cryogenic tubes filled with a NaCl-saturated, 20% dimethylsulfoxide (DMSO) solution. At the end of each day all skin samples were stored in a domestic freezer (–5 °C) until they could be transferred to a –15 °C freezer at the laboratory in Cape Town.

At periodic intervals while the boat was at sea during or between humpback sightings, a hydrophone would be deployed and an acoustic watch maintained for approximately 10 minutes at a time.

Group composition and behaviour

A group was considered to be one or more animals that displayed noticeable coordinated movement or behaviour and where individuals were no further than an estimated 100 m from each other (after Whitehead 1983, Corkeron et al. 1994). Cow–calf pairs were defined as two whales, one of which was less than half the length of the other.

All humpback whale groups from which genetic skin and photo-identification samples were collected during other boat-based cetacean studies of the Mammal Research Institute (MRI) in the same region (between 1993 and 2008) were included in the group composition analyses.

Total genomic DNA was extracted from the epidermal layer of biopsies using proteinase K digestion followed by a standard phenol/chloroform extraction method (Sambrook et al. 1989) or using DNAeasy tissue kit (Qiagen). Sex determination was carried out by polymerase chain reaction (PCR) amplification followed by *Taq*I digestion of the ZFX/ZFY region of the sex chromosomes (Palsbøll et al. 1992), or using multiplex PCR amplification of the ZFX/ZFY sex linked gene (Bérubé and Palsbøll 1996).

Behavioural observations made from the shore were limited to estimating group size and recording overall group behaviour (such as travelling, milling, surface activity, breaching, and possible feeding). Group size, behaviour and composition were also recorded during all boat intercepts. Any incidents of defecation were noted and a faecal sample was collected when possible.

Results

Sightings, search effort and sighting conditions

Shore-based observations were carried out on 102 (or 68%) of the available days between 24 July and 20 December 2001 and on 177 (61.9%) of the available days between 6 May 2002 and 15 February 2003 for a total of 1 802.18 hours. A total of 1 197 groups of baleen whales was sighted, the majority being southern right whales *Eubalaena australis* (669) followed by humpback whales (289), four mixed species (humpback and right whale) groups, and a single blue whale *Balaenoptera musculus*. Positive species identification was not possible for 234 other groups of large whales, although 15 of these were recorded as 'like-humpback', 16 as 'like-right whale' and 12 as Bryde's *B. brydei* or minke *B. bonaerensis* whales. Only groups that were positively identified as comprising solely humpback whales were considered in the analyses.

Effort during both field seasons was very discontinuous, with gaps of up to seven days with no watch, mainly due to poor sighting conditions. In order to create approximately equivalent subsamples to calculate mean sighting rates and measures of variance during a month or season, daily search effort for days 1–7, 8–14, 15–21 and 22 to month end were summed; this resulted in four subsamples in a full month. Sightings per unit effort (SPUE) was calculated by dividing the number of whale groups seen by the total number of hours watched (including both optimal and suboptimal effort) in a subsample, and transformed to groups per 10 hours of searching (Figure 2). The SPUE, as calculated here, is not an absolute measure of humpback whale abundance, because *inter alia* it includes all sightings within the search area, not only those that crossed the midline during the watch period, and does not exclude the possibility that a group may have been resighted on more than one occasion on or between days. Furthermore, the number of groups passing through the search area when there was no search effort, or at night, is unknown. A between-season comparison of the mean daily sightability index (calculated by dividing the sum of hourly sightability estimates by the number made on that day) showed a slight decrease in mean sightability from autumn/mid-winter (2.95 ± 0.102 SE) through to late summer (2.46 ± 0.14 SE), although this difference was not significant (ANOVA, df = 6, $F = 2.69$, $p = 0.0163$). Sightability therefore appeared to be constant enough across seasons to allow the use of SPUE as an index of relative abundance.

In general, effort levels were higher and more consistent during the first part (autumn and winter) of both study periods, but the SPUE was low with only slight peaks in late July/August. During both study periods, search effort became more variable from September onwards, mainly due to the frequent occurrence of unfavourable weather conditions that interrupted or prevented searching. Prominent peaks in SPUE occurred at the end of October in both years (peaks A and C in Figure 2), and both times these stretched into November. The highest overall SPUE was recorded during the fourth week of October 2002 (peak C) when at least one group was seen per hour. Other above-average peaks in SPUE occurred in December 2002 (peak B), and at the end of January/beginning February 2003 (peak D) despite low and very discontinuous search effort (Figure 2).

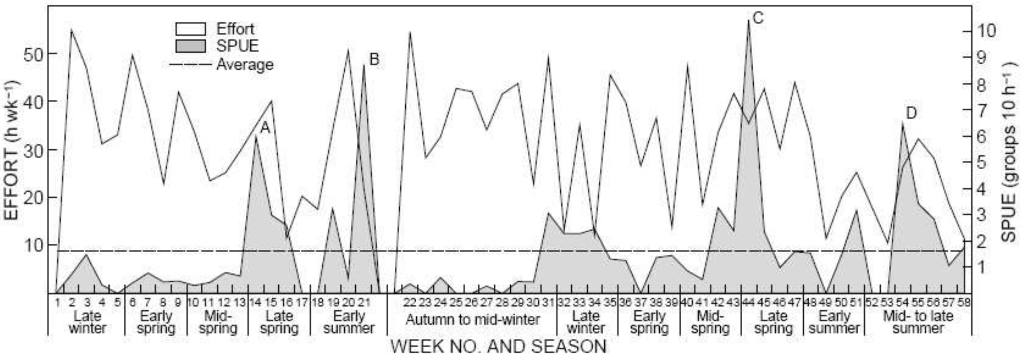

Figure 2: Sightings per unit effort (SPUE) of humpback whale groups and search effort per week for two field seasons 24 July–20 December 2001 (weeks 1–21) and 6 May 2002–15 Feb 2003 (weeks 22–58). Dashed line is average SPUE (1.63) over the entire study period. Peaks marked A–D are referred to in the text

Table 1: Summary of mean sightings per unit effort (SPUE, whale groups per 10 h of search effort), range and search effort by seasonal grouping based on monthly subsamples (four per month)

Season	*n*	Mean SPUE (groups 10 h⁻¹) ± SE	Range SPUE (min–max)	Total hours on watch	Days on watch	Daily hours on watch
Late autumn to mid-winter	12	0.69 ± 0.28	0–3.06	459.08	69	6.65
Late winter	8	1.19 ± 0.32	0–2.46	293.30	46	6.38
Early spring	8	0.71 ± 0.18	0–1.45	260.80	38	6.86
Mid-spring	8	3.07 ± 1.25	0.43–10.46	242.23	42	5.77
Late spring	8	1.51 ± 0.40	0–2.99	238.63	35	6.81
Early summer	7	2.46 ± 1.16	0–8.73	180.95	32	5.65
Mid- to late summer	6	2.59 ± 0.92	0–6.48	127.18	20	6.36
All seasons	57	1.63 ± 0.28	0–10.46	1 802.18	282	6.35

The mean SPUE by season showed an apparent increase in whale availability from mid-spring onwards, despite a strongly decreasing trend in total hours watched from winter to summer (Table 1). There were fewer suitable watching days from late spring onward. All seasons, with the exception of mid-spring, experienced weeks with no sightings (min SPUE = 0), and despite higher mean sighting rates in mid-spring and summer (Table 1), no significant difference was detected between seasons (Kruskal-Wallis statistic = 10.05229, n = 57, p = 0.1225). Given the small and variable sample sizes and the large difference in range between minima and maxima of the seasonal groupings (Table 1), the median may be a more appropriate measure of central tendency than the mean (Zar 1996), and the multisample median test showed a significant difference between seasons (χ^2 = 12.62920, df = 6, p = 0.0493). When samples were combined into only two seasonal blocks, namely autumn/winter (mean SPUE = 0.96 ± 0.22 SE, n = 20) and spring/summer (2.03 ± 0.40 SE, n = 37), a t-test showed a significantly higher SPUE for the latter grouping (p = 0.0477, t-value = −2.0252).

Visibility at midline and spotting distance of whale groups

Overall, 1 834 hourly theodolite readings were taken at the midline as indicative of the theoretical maximum visibility during periods of optimal and suboptimal watch. The average visibility from the tower over the entire period was 8.21 ± 0.08 km (SE) ranging from 1.29 to 26.46 km. The average distance from the tower (the 'sighting distance') for all 251 humpback groups on which a reliable fix was made (excluding the eight sighted and fixed inside Saldanha Bay) was 7.24 ± 0.26 SE and ranged between 1.24 and 25.11 km (Table 2). A comparison of the frequency distribution of all midline visibility measurements and radial sighting distances to all humpback groups (placed in 0.5 km bins) showed similarly shaped distributions, with the highest number of visibility observations recorded in the 7.5–8.0 km bin, although there was an extended peak from about 5.5–8.5 km (Figure 3). The distribution of whale sighting distance showed a much flatter peak with a wider range of 2–8.5 km, the 5–5.5 km bin containing most groups. Whale groups, in general, appeared to be seen at shorter distances from the tower than the recorded visibilities (Figure 3), with a fairly abrupt fall-off of sighting distances beyond 8.5 km, whereas visibility measurements showed a much steadier decrease from 8.5 km and farther. To determine whether the theoretical visibility limited our ability to spot and track whales, we compared the distance at which a group was sighted with the visibility taken at the nearest hour to the time of the fix at which the group distance was calculated (the 'prevailing

Table 2: Seasonal mean radial sighting distance from the tower to humpback groups on which a reliable theodolite fix was made (n = 251, shaded columns), and mean hourly visibility measured at the midline. Eight whale groups sighted within bays were excluded from this analysis

Season	Mean ± SE (km)		*n*		Minimum (km)		Maximum (km)	
	Whales	Visibility	Whales	Visibility	Whales	Visibility	Whales	Visibility
Late autumn to mid-winter	7.46 ± 0.74	8.20 ± 0.16	27	496	2.68	1.28	18.98	23.46
Late winter	8.61 ± 0.74	9.22 ± 0.21	25	293	2.16	2.02	16.62	26.46
Early spring	5.29 ± 0.82	8.94 ± 0.26	16	256	1.77	2.98	11.46	25.00
*Mid-spring	8.67 ± 0.55	8.18 ± 0.22	71	237	1.24	2.14	23.28	21.51
Late spring	6.40 ± 0.60	8.18 ± 0.22	32	233	1.34	2.50	13.89	23.80
*Early summer	6.18 ± 0.56	7.20 ± 0.27	49	185	2.21	1.50	25.11	19.63
Mid- to late summer	6.22 ± 0.59	6.20 ± 0.23	31	134	2.25	2.18	17.47	14.68
All seasons	7.24 ± 0.26	8.21 ± 0.08	251	1 834	1.24	1.29	25.11	26.46

* Seasons between which sighting distances from tower to whales were significantly different ($p < 0.05$, Tukey's HSD test for unequal sample sizes)

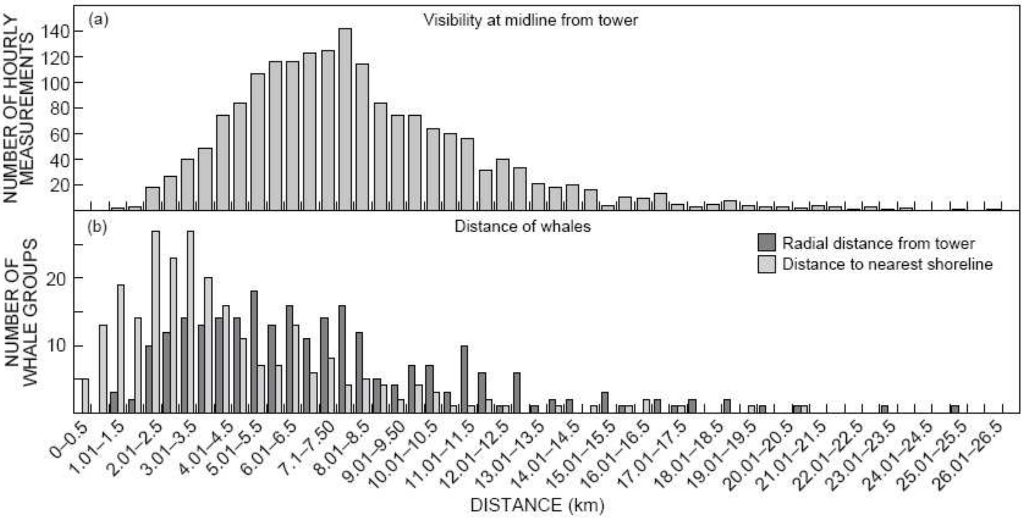

Figure 3: Frequency distributions of (a) all hourly midline visibility measurements (n = 1 834) and (b) all radial sighting distances from tower, and calculated distances to nearest shoreline, of whale groups fixed by theodolite (n = 251, excluding eight groups sighted within bays)

visibility'). These measurements were sorted into 1 km bins according to the prevailing visibility, and the mean distance from the tower for whale groups within each bin calculated. A plot of mean sighting distance against prevailing visibility showed that up to about 7 km from the tower, sighting distances were on average higher than the visibility, but beyond this, whale groups were seen at distances well below the prevailing visibility (Figure 4). However, the mean distances of whale groups to the nearest shoreline (i.e. perpendicular distance) at prevailing visibility were considerably less compared with prevailing midline visibility (Figure 4).

Seasonal variations of visibility at the midline were tested and showed a highly significant difference (ANOVA, df = 6, F = 14.4918, $p < 3.24 \times 10^{-16}$) with significant differences in mean visibility between a number of seasons shown by Tukey's HSD test for unequal n (Table 3). The best visibility was measured in late winter with a clear decreasing trend in visibility from late spring to late summer; the poorest mean visibility being recorded in mid-late summer (Table 2).

Distance distribution of whales from the shore

Whale groups were seen beyond 15 km from the shore on only six occasions, once in both late winter and early summer, and four times in mid-spring. For all seasons, except late winter and mid-spring, groups were closer to shore than the overall mean (Table 4). Between-season ANOVA showed a highly significant difference of distance of groups from shore (df = 6, F = 4.41, $p < 0.0003$) and Tukey's HSD test for unequal sizes indicated that this difference was between mid-spring (highest) and early summer (lowest) ($p < 0.004$). A quarter of the number of whale sightings was within 2 km from the shore, including the eight sightings within Saldanha Bay (negative distances). More than half the groups were seen in the range 2–6 km and the remaining

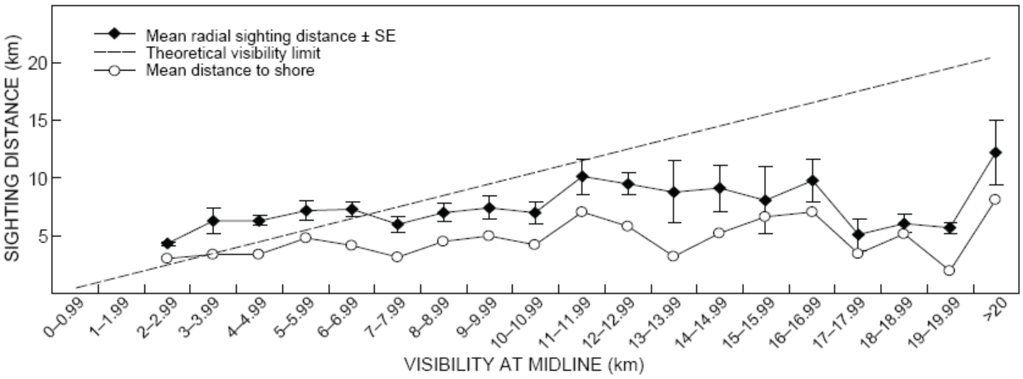

Figure 4: Mean radial sighting distances (km ± SE) from tower, and calculated distances to nearest shoreline, of whale groups at prevailing visibility at the midline (per 1 km bin) as measured by theodolite. Dotted line indicates theoretical visibility limit

Table 3: Between-season comparison of visibility measurements at midline using Tukey's HSD test for unequal sample sizes (shading indicates $p < 0.05$)

Season	Autumn/ mid-winter	Late winter	Early spring	Mid-spring	Late spring	Early summer	Mid- to late summer
Autumn/mid-winter		0.010203	0.592470	0.999879	1.000000	0.091302	0.000111
Late winter			0.752770	0.010471	0.025587	0.000026	0.000026
Early spring				0.409064	0.581084	0.000538	0.000026
Mid-spring					0.999984	0.186617	0.000309
Late spring						0.113501	0.000147
Early summer							0.259254
Mid- to late summer							

Table 4: Seasonal mean distance from position of first reliable theodolite fix on whale groups to nearest the coastline and minimum and maximum distances of whales from shore

Season	Mean ± SE (km)	*n*	Minimum	Maximum
Late autumn to mid-winter	3.69 ± 0.35	27	0.48	9.34
Late winter	5.58 ± 0.75	25	1.34	15.65
Early spring	3.35 ± 0.58	16	0.58	9.93
*Mid-spring	5.81 ± 0.48	71	0.37	19.01
Late spring	3.74 ± 0.43	32	0.37	7.73
*Early summer	3.36 ± 0.45	49	0.04	20.75
Mid- to late summer	3.86 ± 0.56	31	0.58	14.55
All seasons	4.42 ± 0.21	251	0.37	20.75

* Seasons when groups were seen at significantly different mean distance from shore ($p < 0.05$, Tukey's HSD test for unequal sample sizes)

25% farther than 6 km and up to a maximum of 20.75 km. There was a rapid fall-off in number of sightings from 10 km onward with only about 6% of groups recorded in this zone (Figure 3b). When groups were sorted into four distance zones, viz. inside bays to 5 km, 5–10 km, 10–15 km, and farther than 15 km, a seasonal pattern in distance offshore became evident (Figure 5). The majority of groups were seen within 5 km from the shore in all seasons, and the hypothesis that the proportion of groups within and beyond 5 km did not differ significantly (χ^2 test) was rejected for all except late winter, mid- and late spring (Figure 5).

Group size and composition

The size of 289 groups observed from shore ranged between one and six, with the notable exception of the maximum group size recorded of 15 individuals, and another of 10. These apparent outliers were probably loose association of several smaller groups rather than single groups. The most frequent group size ($n = 122$) was two animals (10 of which were identified as cow–calf pairs by the boat crew) followed by singletons ($n = 83$). The mean group size based on these best estimates was 2.2 ± 0.08 SE ($n = 289$) and excluding the outliers mentioned above, 2.12 ± 0.06

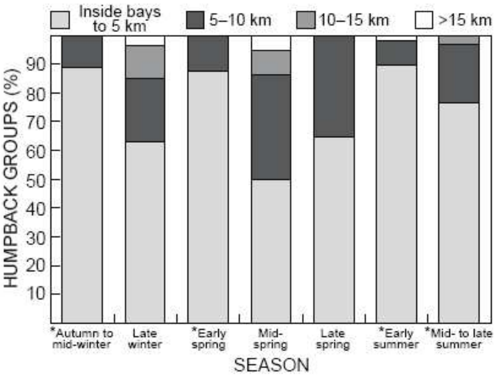

Figure 5: Seasonal breakdown of distance from shore of humpback groups (n = 259). Seasons where numbers of groups within and beyond 5 km zones differ significantly (χ^2, $p < 0.05$) are indicated by an asterisk

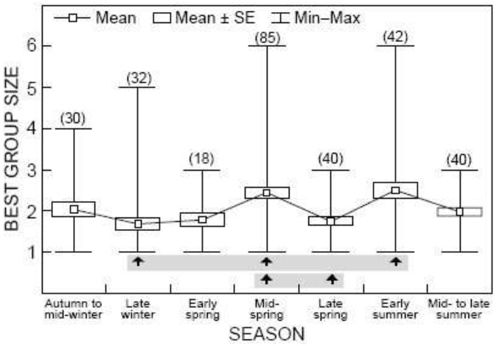

Figure 6: Seasonal mean (range = whiskers and SE = boxes) of best estimates for group size (sample sizes in parentheses) as observed from land, excluding two outlier groups (n = 287). Shaded rectangles below plot summarise significant results from multiple comparison *post hoc* test with arrows indicating significantly different seasons

(n = 287). The largest mean group sizes were recorded in mid-spring (2.44 ± 0.12) and early summer (2.5 ± 0.19) and the smallest in late winter (1.69 ± 0.15) and late spring (1.75 ± 0.11), with an overall significant difference between seasons (Kruskal-Wallis H = 25.5825, df = 6, p = 0.0003). Dunn's multiple comparison *post hoc* test showed late winter (August) to have a significantly smaller mean group size than both mid-spring (z = 3.540, $p < 0.0084$) and early summer (z = 3.1402, $p < 0.036$), whereas the mean of mid-spring was also significantly higher than late spring (z = 3.1903, $p < 0.03$) (Figure 6).

Group sizes recorded during the 116 boat intercepts ranged from one to seven, except for one grouping recorded as 20, which in reality was a dynamic aggregation of several smaller groups. Excluding this grouping, the mean group size encountered was 1.97 ± 0.084 SE (n = 115). Group size was recorded for the same group by both shore observations and boat intercepts 85 times; of these 61 were identical, in six cases boat estimates were higher than corresponding land estimates and in 18 cases land estimates were higher than boat-based ones. Although the mean size of these groups estimated from land (2.09 ± 0.12) was larger than that made during boat intercepts (1.85 ± 0.086), the difference was not significant (t-test, independent variables, two-sided, df = 168, t-value = −1.7145, p = 0.08843).

Genetic analysis

Sex determination was attempted for 216 skin biopsies collected between 1993 and 2008. The majority of samples (104) were taken at Saldanha Bay during the principal study, followed by 92 taken during a St Helena Bay study on southern right whale feeding (2003–2006). The balance was made up of six samples collected at Cape Columbine in 1993, a single sample from Walker Bay (1999) and 13 taken during boat transects for Heaviside's dolphins *Cephalorhynchus heavisidii* along the coast (1999–2000, 2008). Overall, 119 females and 91 males were identified but six samples did not yield results. Three duplicate samples of the same individual on the same day and/or from the same sighting were identified from genotyped individuals (using 10 microsatellite loci) (Pomilla 2005, Carvalho et al. 2009) and these were removed, leaving a total of 207 sexed samples. The overall female (56.5%) to male (43.5%) ratio, including cow–calf pairs, did not vary significantly from parity (n = 207, df = 1, χ^2 = 3.521739, $p > 0.06057$). A total of 32 groups was identified as cow–calf pairs and, from these, 20 cows and 12 calves were biopsied: the calves were comprised of nine males and three females. A possible bias may exist towards the sampling of cow–calf pairs due to their generally slower movement (Noad and Cato 2007) and more time spent at the surface. Cows and calves that were sampled (32 out of 64 animals) were therefore removed from the overall sample to test this, but the remaining female (53.7%) to male (46.3%) ratio still did not deviate significantly from an 1:1 ratio (n = 175, df = 1, χ^2 = 0.965714, $p > 0.32575$). Following this, the 20 cows were retained in the sample, but the 12 calves were excluded. The reasons for this were that the presence of calves was presumably dependent on their mothers, and that whaling data on gender included only mature whales. This resulted in a significant female bias in the overall sex ratio (1.407 females:1 male, n = 195, χ^2 = 5.584615, $p < 0.01812$).

Other possible biases in selection of intercepted groups

Cows with calves have also been shown to prefer areas closer to shore in a breeding area (Ersts and Rosenbaum 2003), perhaps introducing another source of bias, although this has not been illustrated during migration. To test this, we compared the mean distance from shore of all cow–calf pairs to other groups intercepted by boat between 1999 and 2006 at Saldanha Bay/St Helena Bay, during months when cow–calf pairs were sighted (Figure 7). Distance (calculated using a GIS) was measured between the GPS position of the boat at the time of the intercept, and the nearest coastline. The mean distance to shore of cow–calf pairs (n = 30; 3.49 ± 0.713 km SE) did not differ significantly from non-cow–calf groups (n = 137; 4.98 ± 0.359 km) (t-test, independent variables, two-sided, df = 165, t-value = −1.77487, p = 0.07776).

To test whether group size affected the likelihood of being intercepted, thus introducing a bias through the selection of larger groups, the mean of the best estimates of group size made from land was compared for whale groups that were intercepted (n = 85; 2.094 ± 0.115) and not intercepted (n = 104; 2.23 ± 0.101). There was no significant difference between the means of these groupings (t-test, independent variables, two-sided, df = 287, t-value = 0.7877, p = 0.4315).

In terms of a selection bias of humpback groups intercepted during the other studies, these were all incidental sightings (excepting the six samples from Cape Columbine) during effort directed at other target species, and thus we have to assume that these encounters were random.

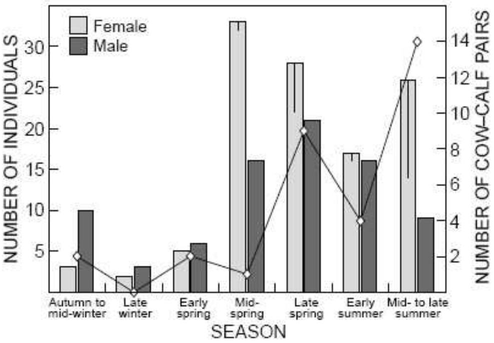

Figure 7: Numbers of male and female whales (including 20 cows, as indicated by the solid lines within the bars) per season as determined genetically (n = 195). Calves (n = 12) were excluded, but total number of cow–calf pairs seen per season is indicated by line plot

A seasonal plot of the numbers of females and males (including cows with calves but excluding the calves themselves, Figure 7) suggests that during autumn, winter and early spring, slightly more males than females were sampled, bearing in mind that sample sizes were very small. For the rest of spring and summer, more females were available, and for mid-spring and mid- to late summer, this bias was significant (Table 5). The number of cow–calf pairs seen during boat intercepts increased from late spring onwards with most seen from December to February (Figure 7).

Genetic samples of 76 complete groups of whales (132 individuals) were collected and the overall sex ratio (excluding eight calves but including cows) did not deviate significantly from parity (53 males, 71 females; χ^2 = 2.612903, p < 0.106). Identical numbers (13) of males and females were recorded for lone animals. Most pairs (excluding cows with calves) consisted of a male and female (18) followed by female-only pairs (14), and then male only (6). The eight cow–calf pairs included six male and two female calves, whereas two of the pairs were accompanied by single male escorts. Apart from these cow–calf pairs with escorts, groups of three individuals were completely sampled only another four times; one all-male, two with more males and one with more females. A seasonal breakdown of the gender composition of groups that were completely sampled (Figure 8) shows a decrease in the occurrence of single males after early spring, with none recorded in mid-spring. Female-biased groups were found in all seasons except late winter (however, note the low sample size). Male–female pairs and cow–calf pairs (including those with escorts) were only seen from mid-spring onwards. No single females were recorded after late spring. Mid-spring was the only season where there was a significant (female) biased sex ratio of 2.88:1 (Figure 8, χ^2 = 7.258, p = 0.00706).

Swimming speed

Actual swimming speed (= leg speed) ranged from 0.55 to 10.68 km h^{-1} (Table 6), with an overall mean of

Table 5: Seasonal sex ratios in humpback whales biopsied in the region of Saldanha Bay, South Africa, 1993–2008 (shading indicates p < 0.05)

Season (month[s])	Female (%)	Male (%)	n	χ^2	p
	Including cows and calves (n = 207)				
All seasons combined	56.52	43.48	207	3.522	0.06057
Autumn/mid-winter (March–July)	21.43	78.57	14	4.570	0.03251
Late winter (August)	40.00	60.00	5	0.200	0.65472
Early spring (September)	45.45	54.55	11	0.091	0.76303
Mid-spring (October)	66.00	34.00	50	5.120	0.02365
Late spring (November)	57.69	42.31	52	1.231	0.26726
Early summer (December)	51.43	48.57	35	0.029	0.86577
Mid- to late summer (January, February)	65.00	35.00	40	3.600	0.05778
	Excluding calves (n = 195)				
All seasons combined	58.46	41.54	195	5.585	0.01812
Autumn/mid-winter (March–July)	23.08	76.92	13	3.769	0.05221
Late winter (August)	40.00	60.00	5	0.200	0.65472
Early spring (September)	45.45	54.55	11	0.091	0.76303
Mid-spring (October)	67.35	32.65	49	5.898	0.01516
Late spring (November)	57.14	42.86	49	1.000	0.31731
Early summer (December)	51.52	48.48	33	0.030	0.86181
Mid- to late summer (January, February)	74.29	25.71	35	8.257	0.00406

4.6 ± 0.15 km h^{-1} SE. An examination of leg speed by season revealed a strong decrease in mean swimming speed from autumn through to late summer, and Kruskal-Wallis analysis of variance showed a highly significant difference between seasons (Kruskal-Wallis statistic = 59.21, $p < 0.0001$). Dunn's multiple comparison between the seasons showed significantly higher swimming speeds in autumn to winter compared with mid-spring to late summer ($p < 0.05$) (Table 6). Overall, net speed averaged 3.91 km h^{-1} and ranged from 0.091 to 10.47 km h^{-1} (Table 6). Seasonal mean net speed was always lower than actual swimming speed, with the smallest difference between these parameters observed during autumn to late winter, whereas the difference increased from early spring onwards, and was the greatest in mid- to late summer (Table 6).

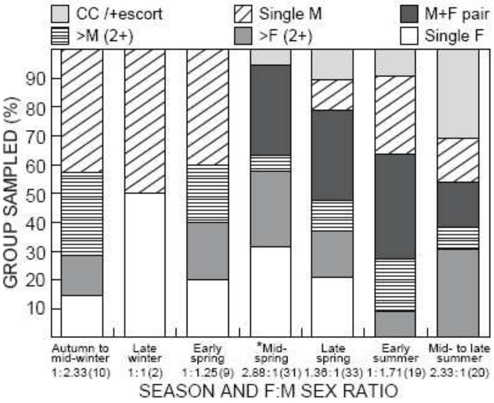

Figure 8: Seasonal composition of humpback whale groups that were completely sampled genetically, 2000–2006. Female:male sex ratio and total number of individuals (in parentheses) are indicated below each season. Asterisk = significant female bias ($\chi^2 = 7.258$, $p < 0.05$). Key to legend: CC = cow–calf pairs, including two with (male) escorts; M + F pair = male and female; >F = all-female duos and groups of three or more with female bias; >M = all-male duos and groups of three or more with male bias; single male (M) and single female (F)

Direction and linearity of movement

Net course and linearity of movement were calculated for all groups with three or more fixes made at different surfacing events ($n = 212$). A frequency distribution plot of net course (Figure 9) showed a bimodal distribution, with the larger mode at 100–200° and a second smaller peak at 280–360°. Taking into account that the orientation of the coastline is at approximately 330–150°, it may be assumed that the first mode (100–200°) represents predominantly southbound and the second (280–360°) northbound animals. For linearity, the highest number of groups observed (Figure 10) had an index in the 0.7–1.0 range (where 1 = a straight line) with a definite peak between 0.9 and 1.0. Although there was some variation between 0 and 0.7 levels, the number of observations across this range remained relatively constant and much lower than the peak. It was therefore assumed that a linearity index of 0.9 and greater indicated migration-like movement (swimming in a more-or-less straight line) whereas indices of <0.9 represented non-migrating groups.

A plot of cumulative frequency of direction of movement by season, with three directional groupings based on the two modes (north and south), and another containing all groups heading in other directions, shows predominantly southwards movement in autumn to late winter (Figure 11). The null hypothesis that mean angles of movement by groups were distributed uniformly each season (i.e. no directionality) was tested using the Rayleigh's test for circular uniformity (Zar 1996). This was rejected ($p < 0.05$) for autumn/mid-winter ($n = 23$, average degrees = 155.14,

Table 6: Mean actual swimming speed (leg speeds) and net speed by season, with Dunn's multiple comparison post-test on actual swimming speeds (shading indicates $p < 0.05$)

Season	Actual swimming speed and net speed (in parentheses) (km h^{-1})				Dunn's multiple comparison of actual swimming speeds between seasons: *z*-value (*p*-value)		
	n	Mean ± SE	Min.	Max.	Autumn/ mid-winter	Late winter	Early spring
Autumn/mid-winter	23	6.07 ± 0.35 (5.80 ± 0.42)	1.68 (0.94)	8.47 (8.55)	–	ns	ns
Late winter	25	6.53 ± 0.29 (6.04 ± 0.36)	3.46 (2.09)	9.32 (9.29)	ns	–	ns
Early spring	16	5.77 ± 0.61 (5.18 ± 0.71)	1.89 (0.64)	9.62 (10.47)	ns	ns	–
Mid-spring	55	4.14 ± 0.33 (3.30 ± 0.34)	0.55 (0.16)	10.68 (9.18)	3.19 (0.0031)	4.71 (0.53 × 10^{-4})	ns
Late spring	31	4.23 ± 0.37 (3.60 ± 0.40)	0.91 (0.091)	8.62 (8.77)	3.13 (0.0367)	3.92 (0.0018)	ns
Early summer	36	4.28 ± 0.31 (3.31 ± 0.33)	1.04 (0.41)	8.37 (7.85)	3.09 (0.0417)	3.91 (0.0019)	ns
Mid- to late summer	26	2.67 ± 0.20 (1.90 ± 0.21)	1.01 (0.13)	5.28 (4.10)	5.5 (0.1 × 10^{-5})	6.31 (0.6 × 10^{-6})	4.24 (4.78 × 10^{-4})
All seasons	212	4.61 ± 0.15 (3.91 ± 0.17)	0.55 (0.091)	10.68 (10.47)			

ns = not significant

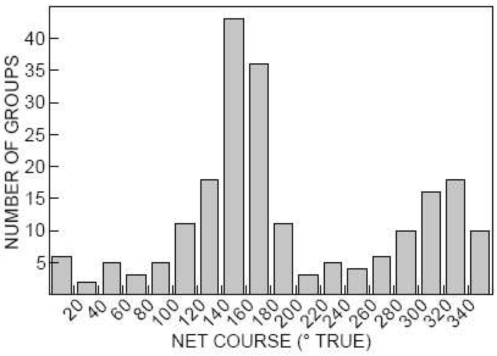

Figure 9: Frequency distribution of net course of 212 humpback whale groups tracked from North Head, Saldanha Bay

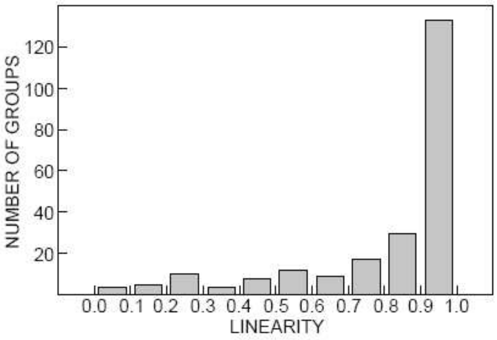

Figure 10: Frequency distribution of linearity of movement of 212 humpback whale groups tracked from North Head, Saldanha Bay

Rayleigh's $R = 19.78$, Rayleigh's $z = 17.012$) and late winter ($n = 25$, average degrees = 158.52, $R = 16.61$, $z = 11.03$) as well as late spring ($n = 31$, average degrees = 148.51, $R = 14.77$, $z = 7.04$). Thus, in these seasons, distribution of the mean angle was not distributed uniformly and there was definite directionality in a predominantly southerly direction (Figure 11). In the other seasons there were more or less equal numbers of groups moving both north and south, although there were ever-increasing numbers of groups moving in other directions from early spring onwards.

Non-directionality reached its peak in mid- to late summer, when the number of groups moving north, south or in other directions each made up roughly one-third of the total groups tracked (Figure 11). The incidence of 'migration-like' movement predominated from autumn to early spring after which there were more or less equal numbers of 'migrators' and 'non-migrators' for the remaining spring months (October/November), and a marked decline in groups moving in straight lines (Figure 11). Throughout summer, non-migrating groups predominated.

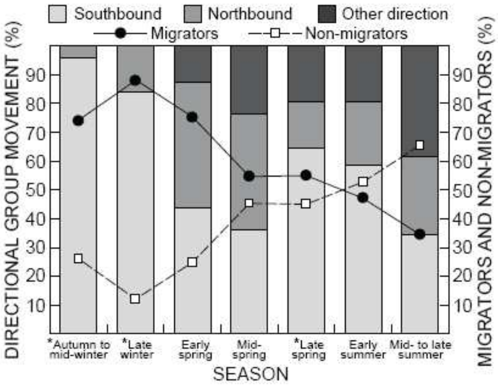

Figure 11: Directionality (net course) and linearity of movement of humpback whales groups ($n = 212$) by season. Bars show cumulative frequency of occurrence of groups that were southbound (100–200°), northbound (280–360°) or heading in other directions, based on net course (° True). Asterisk indicates seasons with significant ($p < 0.05$) directionality as determined by Rayleigh's test. Line plots show percentage of migrating (linearity ≥0.9) or non-migrating (linearity <0.9) groups seen

Relationships between trackline parameters and other variables

The relationships between the various trackline parameters (linearity, leg speed and direction) and other variables (season, distance from shore and group size) were not always clear. There was no relationship between group size and leg speed ($r^2 = 0.0059$, $r = -0.0768$, $p = 0.2655$), nor between distance from the shore and linearity ($r^2 = 0.006$, $r = 0.078$, $p = 0.258$); but there was a significant and positive correlation between leg speed and distance offshore (Figure 12a, $r^2 = 0.0433$, $r = 0.2081$, $p = 0.0023$) with groups farther offshore travelling at higher speeds. A separation of groups into nearshore (within 5 km from land and inside bays, $n = 156$) and offshore (beyond 5 km, $n = 56$) showed the latter to move significantly faster, at a mean leg speed of 4.99 km h^{-1} compared to the nearshore mean of 4.47 km h^{-1} (t-test, t-value = −1.4928, df = 210, $p = 0.04775$). Leg speed also showed a significant and positive correlation with linearity (Figure 12b; $r^2 = 0.2103$, $r = 0.4586$, $p < 0.00005$), but there was no significant correlation between speed and net course ($r^2 = 0.0076$; $r = 0.0874$, $p = 0.2049$). A significant and negative correlation between linearity and group size suggests that larger groups tended to display non-migratory movement (Figure 12c; $r^2 = 0.0228$, $r = -0.1511$, $p = 0.0278$).

Seasonal patterns in movement

Whereas the various trackline parameters considered independently showed seasonal differences between winter and summer, a movement pattern was more difficult to define for combined parameters. To test for seasonal patterns in movement, a *post hoc* multivariate approach was attempted using the software PRIMER v6 (Clarke

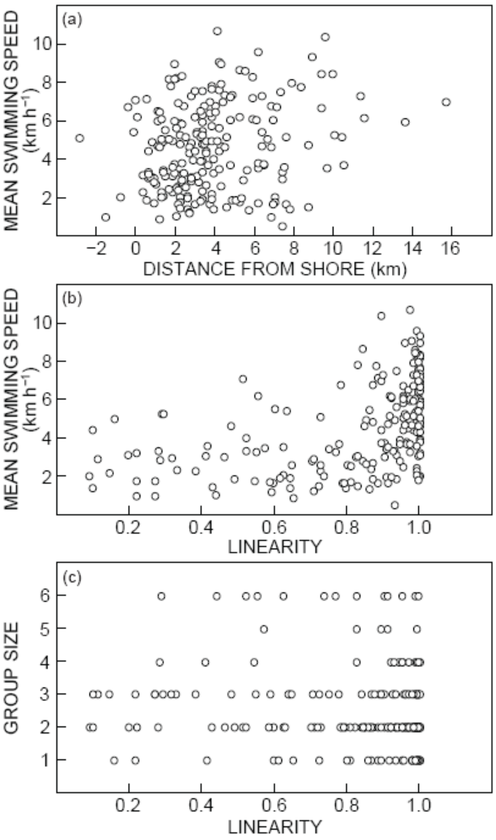

Figure 12: Relationship between mean swimming speed and (a) distance of whale groups from the shoreline, (b) linearity of movement of humpback groups and (c) relationship between size of humpback groups and linearity of movement

1993, Clarke and Warwick 2001, Clarke and Gorley 2006). Each whale group was considered a 'sample' with values for the three parameters: leg speed, course and linearity. Parameter values were normalised (the mean subtracted from each value and divided by the standard deviation) and the similarity between every pair of samples calculated based on Euclidian distance. In a non-metric multi-dimensional scaling (MDS) ordination of whale groups (Figure 13a; stress-value = 0.1 indicating a good two-dimensional representation), with season selected as the identifying feature (or 'factor', see Clarke and Gorley 2006), the first marked feature is the major grouping of samples into the top and bottom halves of the plot. The second major feature is the clustering of most autumn/winter samples into the bottom right of the lower group. Mid-spring samples are the most dispersed, and more or less equally distributed between the top and bottom clusters. While the summer samples are also found in both clusters, they are located more to the left of the plot, particularly the mid- to late summer samples (Figure 13a, all to the left of line A). A one-way analysis of similarities (ANOSIM) was applied to samples according to the seven seasonal groupings. This is a non-parametric permutation procedure applied to a resemblance (= similarity) matrix based on the rank similarity of each sample. It calculates a global *R*-value and overall *p*-value, as well as a measure of significance of similarity for pairwise tests between sample groups. The ANOSIM showed an overall significant difference (global $R = 0.055$, $p = 0.005$) between seasonal groupings. The pairwise comparison between seasons (Table 7) showed no difference between groups from the two autumn/winter seasons. Late winter and early spring stood out as the least similar to any other seasons, differing significantly from all (including each other) except mid-spring. The latter (October) was the only season that did not differ from any other season. The similarity between late spring and early summer, and the significant difference between both these seasons with mid- to late summer, is also noteworthy. To establish which of the three parameters were responsible for the groupings, a principal component analysis (PCA) was carried out on the data, and the two factors responsible for most of the patterning (in the MDS ordination) shown as an *XY*-scatterplot with the parameters overlaid (Figure 13b). From this, we can conclude that differences in course were mostly responsible for the separation of the top (northbound) and bottom (southbound) clusters, accounting for 33.1% of the variation, whereas the strong grouping of winter samples was due to speed and linearity (49% of variation).

Migrators vs non-migrators

In order to show up possible differences in the movement patterns of migrators and non-migrators according to their linearity of movement, the groups were plotted in an MDS ordination (as described above), but this time including the parameters leg speed, course and distance from shore, and using linearity as distinguishing factor (migrators ≥0.9 and non-migrators <0.9). The plot (Figure 14a; stress-value = 0.15 showing a fairly reliable two-dimensional representation, Clarke 1993) shows some degree of separation, firstly between the two groupings (group A = non-migrators, group B = migrators), and secondly within migrators (groups B1 and B2). The PCA (Figure 14b) showed distance from shore and leg speed to be responsible for the separation between migrators and non-migrators, whereas the two migratory subgroups separated out mainly due to differences in course, B1 containing northbound and B2 southbound groups (Figure 14a). Migrators and non-migrators were found to be significantly different when an ANOSIM was applied (global $R = 0.133$, $p = 0.001$).

Feeding behaviour

From land, eight groups were observed to display apparent feeding behaviour, which included milling about (slow movement of indeterminate direction) and faster erratic movement with frequent directional changes. Nine groups intercepted by boat also appeared to be engaged in feeding, although actual feeding behaviour (lunges at surface) was directly observed during only five

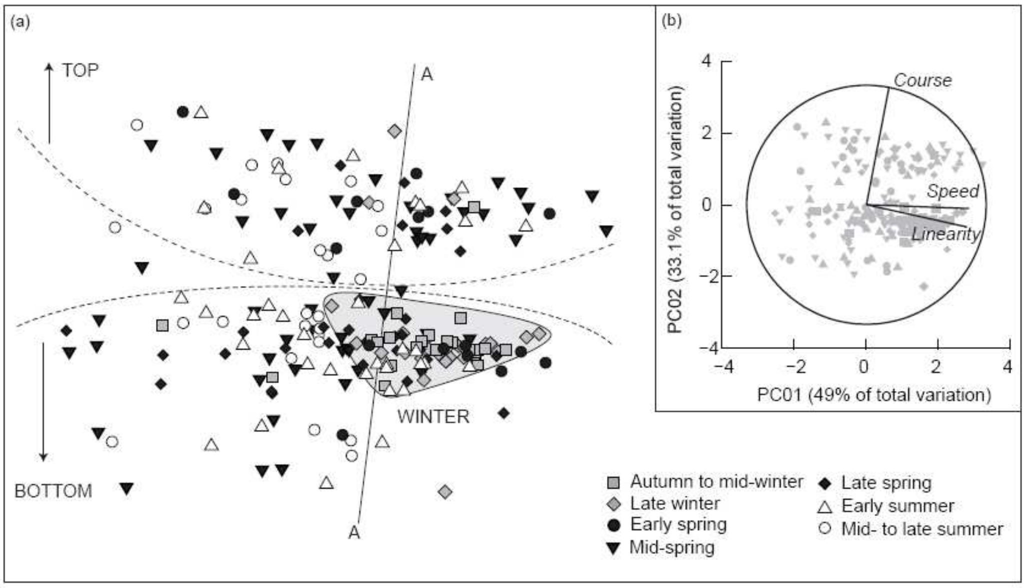

Figure 13: (a) Non-metric MDS ordination plot of seasonal samples based on the combination of movement parameters (normalised, Euclidian distance, stress-value = 0.1). Dashed lines indicate the top and bottom groupings and shaded shape encloses the majority of autumn/winter samples. Line A represents the right-hand limit of all mid- to late summer samples; and (b) PCA of seasonal samples of whale movement parameters with those responsible for most variation (speed and linearity horizontally and course vertically) overlaid onto the scatterplot

Table 7: Summary results from ANOSIM of pairwise, between-season comparisons based on the trackline parameters speed, course and linearity (shading indicates $p < 0.05$)

Season	Autumn to mid-winter		Late winter		Early spring		Mid-spring		Late spring		Early summer	
	R	*p*	*R*	*p*	*R*	*p*	*R*	*p*	*R*	*p*	*R*	*p*
Late winter	–0.023	0.937										
Early spring	0.189	0.003	0.174	0.007								
Mid-spring	0.014	0.352	0.059	0.106	0.017	0.371						
Late spring	0.061	0.054	0.115	0.003	0.188	0.038	–0.038	0.878				
Early summer	0.061	0.075	0.114	0.009	0.118	0.031	–0.014	0.681	–0.018	0.814		
Mid- to late summer	0.014	0.352	0.478	0.0001	0.256	0.005	–0.009	0.545	0.101	0.005	0.065	0.033

of these (Table 8). Fourteen groups were observed to engage in surface activity other than feeding, including repeated breaching and competitive behaviour such as flipper slapping. Defecation was observed 37 times for 23 groups intercepted during nine months from 2001 to 2006. All defecating groups were seen during the months of October 2002/04 (five times), November 2001/04/05/06 (11), December 2001/04 (5) and January 2003 (3). The total number of defecating groups seen from the boat, expressed as a fraction of the total humpback groups intercepted during these nine months (94 groups), results in a defecation incidence of 24.47%. The groups included two of the groups observed to be feeding (Table 8). The stools ranged in colour from dark/bright pink to brick red, presumably indicating crustacean prey. Most of the faecal samples collected (preserved in 95% ethanol) were highly diluted and consisted of whitish to pink paste in emulsion or as a particulate suspension. Four samples that contained slightly larger particles were examined through a stereo-microscope and yielded unidentifiable crustacean (possibly euphausiid) exoskeleton remains, with the exception of one collected on 29 November 2006 that contained fairly intact specimens of a hyperiid amphipod.

The possible relationship between observed/suspected feeding behaviour (including defecation) and whale movement patterns and distribution was explored by labelling all groups tracked on the days in which such behaviour was recorded (all groups 30 October 2001–26 January 2003 in Table 8) as 'feeding' groups, and all groups on other days as 'non-feeding'. Using the same MDS plot (Figure 14, based on the parameters leg speed, course and distance from shore), but with feeding/non-feeding as distinguishing factor, there was a strong similarity between the grouping based on linearity (Figure 14a) and feeding behaviour (Figure 14c).

Acoustic stations

In all, 33 acoustic stations were surveyed, for a minimum of 10 minutes each, from 2001 to 2003 during August, September, October, November, December and January. During a total time of 141 minutes monitored, no humpback vocalisations were detected.

Discussion

Despite variable and, at times, discontinuous search effort, the summer seasonal coverage of this study meant across-year effort was more extensive than during any previous attempt at shore-based monitoring of southern humpback whales. All seasons, with the exception of autumn, were well surveyed. This allowed us to compare whether the observation of a 'suspended migration' reported by Best et al. (1995) during spring was indeed unusual, or whether the observed whale availability and behavioural patterns were applicable to other seasons and years.

Sighting conditions, visibility and distance of whales from shore

On days when searching occurred, the mean sightability, based on the various environmental observations, appeared to have been constant enough to allow comparison of sighting rates across seasons. The significant seasonal variation of mean visibility at the midline between some seasons may raise concerns about whether whale groups were missed in the search area due to limited visibility. Such conditions were most prevalent during summer months when not only the lowest visibility was recorded but also the maximum distances at which whales were tracked exceeded visibility maxima estimates. This suggests that visibility was difficult to judge during these months, in all likelihood as a result of the frequent occurrence of coastal fog, persistent south-easterly winds, or strong refraction due to the strong gradient between high air and low sea temperatures. Despite this, some of the highest sighting rates were still recorded during summer.

Compared to the radial sighting distances to whales, the overall mean visibility was always greater, except for mid-spring and mid- to late summer. However, when the mean sighting distance was compared to the mean visibility measurement prevailing at the time of sighting, it was greater than the visibility up to about 7 km. This apparent contradiction might be the consequence of the visibility measurements being taken on the midline, whereas most sightings were made well away from the midline. If alongshore visibility should be greater than offshore visibility in times of moderate–poor visibility (for instance, owing to the majority of haze being over the sea rather than the

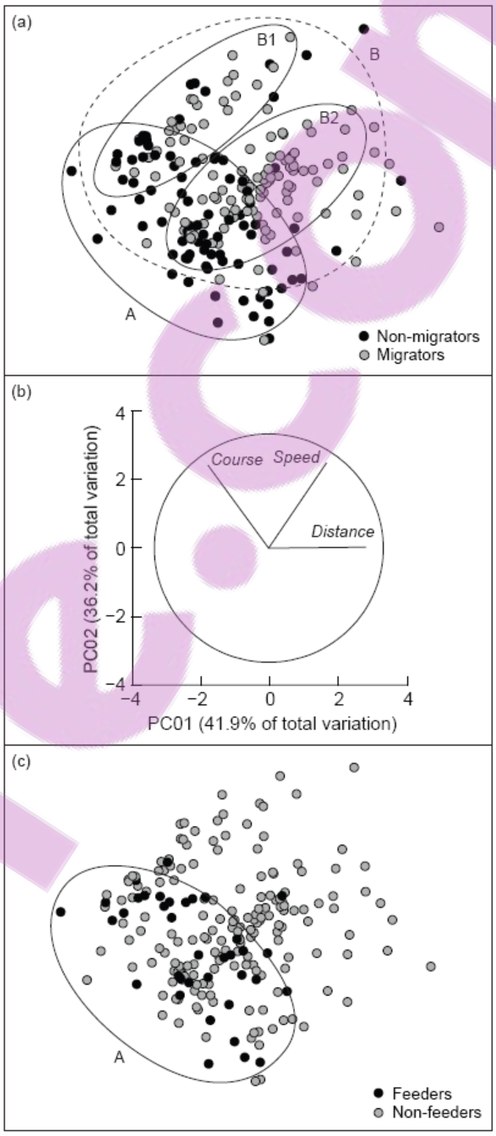

Figure 14: (a) Non-metric MDS ordination of migrators (linearity ≥0.9) and non-migrators (linearity <0.9) based on the parameters speed, course and distance from shore (normalised, Euclidian distance, stress-value = 0.15). Group A (enclosed by the solid line) indicates non-migratory grouping, and group B (dashed line) migrators; shape B1 includes the northbound (280–360°) groups and B2 the southbound (100–200°) groups; and (b) shows the PCA axes and parameters that best explain the clustering seen in (a); (c) shows the same MDS plot with feeding and non-feeding as the distinguishing factor

Table 8: Description of groups showing feeding or feeding-like behaviour seen from land and/or boat

Date[1]	Sighted from	Group size	Def.[2]	Description of behaviour
30 October 2001	Land	2	N	Milling about, apparently feeding
03 November 2001	Boat	3	Y	Dark pink defecation
10 November 2001	Boat	2	Y	Bright pink defecation
06 December 2001	Land	3	N	Slowly moving south, apparently feeding. Associated with seven dusky dolphins *Lagenorhynhcus obscurus*
16 December 2001	Boat	2 and 2	Y	Two groups seen defecating
17 December 2001	Land/boat	±20 and 3	Y	Large, loosely associated group identified as 11 smaller groups from land. Milling and suspected feeding behaviour. Defecation seen in this group and during a later sighting of three animals
19 December 2001	Land	15–20	N	At least two subgroups of animals scattered over large area, milling about
11 September 2002	Land/boat	1	N	Small animal with erratic movements, long dives, spending brief time at the surface. Cape fur seals *Arctocephalus pusillus*, seabirds and unidentified dolphins displaying feeding behaviour nearby
17 October 2002*	Boat	8	Y	Combination of seven earlier sightings. Pairs of animals doing sideways coordinated surface lunges, mouths open and ventral grooves distended. Jellies, euphausiids and mysids seen in water. Defecation seen
29 October 2002	Land	2 and 3	Y	Two separate groups, one milling and possibly feeding and the second active on the surface. Defecation seen
30 October 2002	Boat	6 and 2	Y	Defecation seen in first group that was made up of a cow–calf pair and escort, later joined by another pair and singleton. Later sighting of two, also defecated
13 December 2002*	Land/boat	2	N	Milling and feeding lunges, erratic movement in circles, apparently along thermal divide (16 °C on one side and 17 °C on the other)
10 January 2003	Boat	2 and 1	Y	Cow–calf pair and later single animal. Bright, brick-red defecation by both groups
26 January 2003*	Land/boat	3 and 2	Y	One group seen from land to be lunging, also surface active and milling about. A different group seen from boat also lunged. Bright pink defecation seen during intercept. Blue whale *Balaenoptera musculus* sighted displaying suspected feeding behaviour, swimming along a foam line parallel to shore
12 October 2004	Boat	5	Y	Two humpbacks and three southern right whales. Defecation seen
08 November 2004	Boat	2 and 2	Y	Defecation seen in two groups
29 November 2004	Boat	1	Y	Individual travelling slowly while defecating. Later resighted and defecated whilst lobtailing (five stools produced in five minutes)
02 December 2004	Boat	9	Y	Single humpback with eight southern rights, defecation by both species
23 March 2005*	Boat	2	N	Lunge feeding
24 November 2005	Boat	3	Y	One animal slightly separate from others and evasive. Defecation seen
12 October 2006*	Boat	3	N	Two humpbacks and one southern right both apparently feeding. Humpbacks made sideways lunges through 'mysid' patch. Plankton sample collected
19 November 2006	Boat	1 and 5	Y	Single animal, later resighted as part of larger group. Defecation seen both times
22 November 2006	Boat	2	Y	Defecation seen
26 November 2006	Boat	2	Y	Evasive group. Defecation seen
29 November 2006	Boat	1	Y	Evasive pair, apparently feeding. Defecation seen
14 November 2007	Boat	14–20	N	Large association of several subgroups, apparently feeding, associated with feeding seabirds

[1] * indicates direct observation of feeding
[2] Def. = defecation seen; yes (Y) or no (N)

land), this could account for the apparent discrepancy. When visibility was good, i.e. 7 km and farther, this effect seemed to disappear. Considering that the seasonal mean distance from shore of whale groups never exceeded 6 km, and was <4 km in all but two seasons (see below), and assuming that north- or southbound whales would remain at a more or less constant distance from the shore as they travel through the search area, it seems likely that the majority of whales would have passed within the visibility range at some stage. This is apparent when comparing the mean radial distance at which whales were sighted to the calculated distance to the nearest shoreline. Groups were evidently sighted well before they passed the nearest point to the tower. Visibility as measured through the theodolite is probably a conservative estimate of the distance at which whales may be sighted (but not necessarily tracked), given that cues such as blows are visible with the naked eye, and not only at a 22× magnification.

The mean distance of whales from the shore was fairly similar (at around 3.5 km) for most seasons, with the notable exceptions of late winter and mid-spring when it was about 5.5 km. Not surprisingly, these two seasons exhibited a greater proportion of groups in the 5–10 km range. Generally, the majority of whales were still seen in the 'inshore' zone (<5 km) with very few beyond 10 km, and this was unlikely to be as a result of restricted visibility offshore. This is compatible with observations by Best et al. (1995) at Cape Columbine during mid- to late spring, although the mean offshore distance of 3.1 ± 0.2 km recorded in that study was lower than both our overall mean (4.41 ± 0.21 km) and that of the same season (5.78 ± 0.48 km). This may be because Cape Columbine is situated slightly more to the west than Saldanha Bay and so possibly acts as a headland that coastally migrating whales have to navigate around.

Seasonality of occurrence and movement patterns

Mid-spring (October) stands out in more than one respect as a seasonal 'turning point'. First, the highest sighting rate was recorded at this time of year and it remained relatively high from then onwards, despite the decreased search effort and reduced visibility. Second, there were also noticeable changes in the whale movement parameters from autumn to early spring, and the remaining seasons. Mean actual swimming speed started decreasing significantly from mid-spring onwards, from more than 6 km h^{-1} in winter to <3 km h^{-1} in late summer. The corresponding mean net swimming speeds are well within the range of 'migration' speeds of humpback whales recorded off the east coast of South Africa (Findlay 1994), and elsewhere (Noad and Cato 2007, Lagerquist et al. 2008). However, the low actual and net speeds recorded in mid- to late summer certainly fall in the lower end of the range and are very similar to the low speeds recorded at Cape Columbine (Best et al. 1995).

Sightings in mid-spring were distributed almost evenly between the near- and offshore zones, recording the overall highest mean distance from shore. This was also the period when non-directionality in movement became a prominent feature and where almost equal numbers of groups either milled around or moved in near-straight lines, in all major directions. Multivariate representation of the movement variables in combination confirms mid-spring as a period where whale movement was less distinctive than in any other season, sharing similarities with both the preceding and following seasons. This is in strong contrast with groups from the winter months that all displayed movement patterns that were, with few exceptions, very alike in terms of speed, course and linearity. From this, it could be speculated that mid-spring represents a period when we observed an overlap of two behaviourally distinctive 'subgroups' of humpbacks: one component migratory, although judging by the observed direction both north- and southbound, and the other distinctly non-migratory, and each perhaps occurring at different distances from the shore. Olsen (1914) reported similar 'anomalous' behaviour off Saldanha during 1912/1913, and speculated that there may be two components to humpbacks moving past during their northern migration. One consisted of animals that moved straight to the north, and had empty stomachs when caught, while the other was seen to move 'wildly back and forth' along the coast, apparently in search of food (see later discussion on feeding).

Olsen (1914) also reported on whales frequently seen by vessels farther offshore, which presumably met the coastline north of South Africa on their northward migration. Reeves et al. (2004) made similar inferences during an estimate of historical seasonal distributions of humpbacks and blue whales from 18th and 19th century logbooks of catches in the North Atlantic. They concluded that the humpbacks migrated over an extended period making use of both nearshore and offshore routes, and that sporadic feeding took place well south of 'traditional' feeding grounds, a behaviour that may persist to the present. Our finding that groups farther offshore moved slightly faster may support this, although the distance that Olsen (1914) refers to was presumably well beyond the visibility range of our station. It therefore remains difficult to distinguish different 'components' of the population based on movement patterns alone.

Defining migrators/non-migrators

High availability or relative abundance of whales in an area, whether based on direct observations or historical catches, is not necessarily conclusive evidence of a migration peak, but could represent a local feeding aggregation. The multivariate comparison of migrators vs non-migrators did show a difference between these groupings on the basis of actual swimming speed and distance from shore. Furthermore, within the 'migratory' group, two subgroups separated out on the basis of their course; this suggests the existence of two migrational streams heading in opposite directions. Although there was a definite increase in the proportion of groups showing non-migratory (non-linear) movement from autumn through to late summer, linearity alone can thus not be considered a reliable indicator of migrational behaviour without taking into account direction of movement, and speed. For example, in early spring more groups showed linearity >0.9, but the number of groups heading south and in other directions were about equal.

Our observations in October/November (mid- to early spring) are consistent with those made earlier at Cape Columbine (Best et al. 1995) during the same months, in that the groups showed both southerly and northerly directionality. Perhaps more difficult to explain is the dominance of southbound groups, moving at higher speed during the winter, at a time when we would expect to observe at least the tail end of a northern migration (Olsen 1914). It would appear that, although groups that displayed both strong directionality and linearity were present during almost all the seasons, there was a shift in movement pattern from October/November onwards when both strong directed movement (both north and south) were observed, as at Cape Columbine, but also an increase in the 'non-migrating' and slow-swimming components. Whether the 'fast-and-straight' swimmers were actually migrating or simply moving up or down the coast, perhaps between Cape Columbine and Saldanha, in a determined manner (as suggested by Olsen 1914), remains uncertain. What is clear is that the dominant movement pattern changed between winter and summer; fast movers became fewer towards summer, especially those heading south, and by mid- to late summer almost all groups moved slowly. This is supported by the significantly low average speed of 2.9 km h^{-1} and the virtual disappearance of the fast-moving and straight-swimming component that characterised groups sighted during winter.

Other behaviours observed elsewhere during migration have included singing (Clapham and Mattila 1990) and non-acoustic means of communication such as breaching, tail-slapping and other surface behaviour (Dunlop et al. 2007, 2008). Although surface active behaviour was observed, we did not detect any vocalisations, but we received a reliable report of singing on 29 December 2003 from an observer in a steel-hulled yacht near Dassen Island, about 50 km south of Saldanha Bay (P Evans, pers. comm.).

Group size, sex ratio and composition

The changes observed in mid-spring were not limited to movement patterns alone. Group sizes recorded were larger than average, and it was the only season where the overall sex ratio varied significantly from parity, with a strong female bias of about 2:1, even when cow–calf pairs were excluded. This is in marked contrast to the findings of Brown et al. (1995) who described a migration (both north- and southward) off the eastern Australian coast from May to October that was overall highly skewed towards males. Similar apparent male-dominated sex ratios have been observed on breeding grounds (Craig and Herman 1997, Palsbøll et al. 1997). With no evidence for any stock-level deviations from an approximate 1:1 sex ratio (see discussion in Clapham and Mead 1999), it has been speculated that male bias during migration may be a result of some females possibly remaining in 'feeding' areas (presumably at high latitudes) throughout winter. On the breeding grounds, such a bias might be explained by a longer residence time of males (Craig and Herman 1997). Our discovery of a region with a significant female bias may offer a plausible explanation as to where the 'missing' females go while males complete the full migration, with mid-spring falling roughly between the northward and southward migrations. Compared to ours, the study site of Brown et al. (1995) was situated much closer to the Group V northern destination (breeding area), but unfortunately they did not provide a seasonal (monthly) breakdown of recorded sex ratios, which prevents more detailed comparisons. A number of questions thus still remain: (1) Where were these females during winter? Did they spend time in an unknown area or merely travel at a more leisurely pace from the feeding grounds, compared to males, to reach the coast of Saldanha during mid-spring? (2) Do male-biased sex ratios occur at localities farther up the west coast of Africa? Whaling data from the former Congo (now Gabon) at about 1° S indicated that, in 1949, males made up nearly 65% of all catches, 47.55% in 1950 and about 50% in 1951 (Budker and Collignon 1952), implying that the situation is not markedly different than in the breeding grounds for humpbacks. More recently, however, Pomilla and Rosenbaum (2006) reported a male-biased sex ratio at breeding grounds off Gabon, as well as Madagascar.

Apart from the sex ratio at any given site, a number of authors have commented on differential timing of migrating humpbacks based on sex, age and reproductive state (see summaries in Clapham 1996, 2000), as well as group composition (Brown and Corkeron 1995). Typically, for Southern Hemisphere humpbacks, lactating females with 'yearling' calves are believed to head north from the feeding grounds first. They are followed by immature whales of both sexes; then mature males and resting females, and finally pregnant females (Dawbin 1997). Resting and recently impregnated females are the first to leave on the southward migration, followed by immature whales and mature males. The last to leave breeding areas are cows with new-born calves (Chittleborough 1965, Dawbin 1966). Bearing in mind that we could not assess the reproductive condition of female whales, except when they were accompanied by small calves, we did observe seasonal changes in composition of completely sampled groups, suggesting some staggering in migrational timing. The proportion of singletons (both males and females) decreased from winter to summer, with single females disappearing altogether after late spring. Again, mid-spring stands out with the first appearance of male/female pairs; this was also the most commonly recorded grouping off East Australia (Brown and Corkeron 1995), especially during the northward migration. The decrease in singletons of both sexes and increase in mixed gender pairs from mid-spring may be evidence of increased breeding interactions. This may be due to 'mate guarding', as suggested by Brown and Corkeron (1995), a notion supported by Clapham's (1993) finding of male–female dyads on feeding grounds (also see discussion in Valsecchi et al. 2002). We did not test for the relatedness of pairs, so males accompanying females could conceivably include some large male yearlings not identified as calves.

From late spring onwards the number of cows accompanied by calves was highest, although some cow–calf pairs were sighted in most months. The peak birth month for Southern Hemisphere humpbacks is early August (Matthews 1938, Chittleborough 1958, 1965). Although not explicitly measured, the size of calves observed off Saldanha (estimated relative to the size of the accompanying female) ranged from about new-born size in a few instances (3.96–4.57 m) to the suggested size at independence (between 8 and 10 m; Clapham et al. 1999), with the majority falling in roughly 'half the mother's length'; or between 5 and 6 m. This suggests considerable variation in the departure time from breeding areas, and arrival at, or transit through the study area, or may reflect some yearlings or second-year animals still accompanied by their mothers. There is some support for the latter possibility from the records of adult female humpback whales accompanied by calves/juveniles, as described in a Norwegian Whaling Statistics form (obtained from S Burkett, International Whaling Commission), annotated by the manager of the Hangklip whaling station (K Bernsten) in 1913 (Table 9). Between 21 October and 19 November, eight small whales were landed that were described as being accompanied by their mothers (or whales assumed to be their mothers) at the time they were taken, seven of which were also killed and proved to be females

Table 9: Details of humpback whales accompanied by 'calves' taken at Hangklip whaling station, South Africa, in 1913 (length data converted from whole feet or inches), from notes by the manager of the station, K Bernsten

Date	Length of adult female (m)	Accompanying 'calf'		Notes on records (translated from Norwegian)
		Length (m)	Sex	
21 October		8.53	F	In company of mother that escaped
31 October	14.33	8.53	M	These two animals together so assumed to be mother and calf
01 November	14.63	7.32	M	As above
	12.80	7.01	F	As above
10 November	15.24	8.84	M	Young one shot first then the mother. Adult pregnant with 12.7 cm foetus
15 November	14.02	8.53	F	These two animals together so assumed to be mother and calf
18 November	14.02	8.84	M	As above
19 November	14.63	8.84	M	As above

of adult size (12.8–15.24 m). Six of the small whales were 8.53–8.84 m long, or about the size of humpback whales at 10–11 months of age (8–10 m, Clapham et al. 1999). These were presumable calves from the previous year. The other two were considerably smaller (7.0–7.3 m), and may represent calves-of-the-year, about three months old, a finding not inconsistent with some estimates of early growth in humpback whales (Stevick 1999).

Feeding behaviour

Humpback whales have been observed to shift their feeding areas as a response to changes in prey availability in the Gulf of Maine, North Atlantic, over a period of <10 years (Weinrich et al. 1997). At traditional feeding grounds in the Southern Ocean, Murase et al. (2002) showed that humpback whales associate strongly with high concentrations of euphausiids and that their distribution was determined by the availability and location of prey species. They suggested that humpbacks should be able to feed equally efficiently during migration in high-density euphausiid swarms. Such swarms of the dominant euphausiid species in the southern Benguela, *Euphausia lucens*, do occur periodically off Saldanha (Stuart 1986, Pillar et al. 1989, 1992), although numerous other meso- and macrozooplanktonic crustaceans (other euphausiids, amphipods, mysids) and small pelagic fish are found in the area that could be potential humpback prey (Hutchings et al. 1991, Gibbons et al. 1995, Gibbons and Hutchings 1996). Historical records of humpback stomach contents from the region (Olsen 1914) include copepods ('rodaate' in Norwegian) and fish: a stomach full of 'herrings' from a humpback whale taken at Donkergat in 1912 or 1913 was illustrated by Olsen (1914), whereas the stomach contents of four humpbacks examined there in 1926 were empty (2) or contained fish (2). One of the latter, taken on 25 June was crammed with fish noted as '?clupeoids', while the other (taken on 20 September) was filled with a pasty mass of fish scales and bones (Matthews 1938). However, four stomachs examined at Donkergat in 1962 and 1963 in June (1), July (2) and August (1) were all empty (Best 1967).

Feeding by humpbacks during migration has thus far been considered opportunistic, such as the surface feeding on small 'baitfish' by a single humpback associated with bottlenose dolphins *Tursiops aduncus* observed off Queensland, Australia (Stockin and Burgess 2005), and the more recent description of a 'supplemental' feeding ground by Stamation et al. (2007), also for the Area V stock. However, Dawbin (1956) suggested that feeding opportunities could cause deviations or interruptions in the southward migration of humpback whales past New Zealand, recently confirmed by satellite telemetry (Gales et al. 2009), and a similar situation seems to occur off the west coast of South Africa. Although we observed actual feeding only five times, defecations were observed in almost a quarter of all groups, during months when defecation was recorded. In many cases we saw movements and concentrations of whales that suggested feeding, similar to observations at Cape Columbine in 1993 (Best et al. 1995). These groups almost always consisted of two or more animals, and on several occasions these smaller 'sub'-groups formed loose aggregations of up to 20 animals that moved around in a fairly large general area. Such aggregations were first seen in December 2001, and again in October 2002 and November 2007. The strong correspondence of groups seen or suspected to be feeding (based on behavioural observations) and 'non-migratory' groups (based on movement parameters), as shown by multivariate analysis, suggests that most groups in the general area were probably engaged in feeding.

The regular incidence of defecations seems to support the fact that feeding occurred over a number of days in the vicinity (following the reasoning of Danilewicz et al. 2008). We observed swarms of euphausiids, mysids and gelatinous organisms at the surface on at least one occasion next to feeding humpback whales (17 October 2002). Massive swarms of *E. lucens* were also found washed up on the beach of North Bay, inside Saldanha Bay, during October 2002 and 2006. A plankton haul carried out near a feeding group on 26 January 2003 contained *E. lucens* and the amphipod *Themisto gaudichaudi* (Gibbons 1999). These findings, along with the amphipod remains found in one faecal sample, and an earlier record by Findlay and Best (1995) of an entangled juvenile humpback that had fed on stomatopods before its death, suggests that crustacean prey is not confined to euphausiids.

As in October/November 1993 (Best et al. 1995), an examination of humpback movement patterns off the South African west coast failed to provide strong supporting evidence for a conventional bi-directional humpback migration, this despite longer seasonal coverage and clear seasonal peaks in relative abundance during early spring and summer. These peaks, when considered in combination with the observed movement pattern, pointed to activities other than migration, in particular localised feeding. In the light of this, it seems that Olsen's (1914) observations nearly a century ago, as well as those of Best et al. (1995), were not anomalous for the region, and that a significant component of humpback whales may make use of the area as a feeding ground. This occurs at least from October to February/March, well beyond the expected peak of the southern migration. The prevalence of this behaviour during the time when the southward migration should take place may relate to the nutritional condition of the animals, as suggested by the much lower oil yields of southward migrating humpbacks compared to northbound ones off West Australia (Chittleborough 1965). Specifically, females that are either pregnant or nursing are likely to have a greater urgency to feed at the first available opportunity. Male humpbacks would presumably also have expended considerable energy in the breeding areas, as demonstrated for sei whales *Balaenoptera borealis* heading south that had significantly reduced testis mass compared to during the northern migration (Best and Lockyer 2002).

The spatial extent of this feeding/non-migratory behaviour remains unclear. If we assume it to be associated with upwelling cells of high productivity in the southern Benguela system (Weeks et al. 2006), the range could span for about 1 000 km from Lüderitz in the north to Cape Point in the south. Some historical observations in summer of humpback whales off the Namibian coast at Hollam's Bird Island (see John Keeler's 1830 account reported in Best and Shaugnessy 1979), and catches in the 19th century off Walvis Bay up to January (Townsend 1935), may support this. There are notable differences in the nature of these upwelling cells: Cape Columbine and the Cape Peninsula cells are synchronous but seasonally variable, with highest upwelling in spring and summer, whereas the Namaqua cell at Lüderitz is more perennial and extends farther offshore (Weeks et al. 2006). Movement between different cells could explain the determined northerly and southerly directionality seen from mid-spring through summer.

The movement patterns and behaviour observed in this study do not exclude the presence of a strictly migratory population component, but make it virtually impossible to identify it from these data. Grey whales *Eschrichtius robustus* that feed opportunistically in 'pockets' along their migration route in the eastern Pacific (Moore et al. 2007) are now considered to be flexible foragers. The putative migration of humpbacks appears to represent not only a continuum in terms of breeding behaviour as suggested by Brown and Corkeron (1995), but also includes a component of foraging. Based on our findings, as well as an ever-growing number of records of feeding during migration (e.g. Stamation et al. 2007), in traditional 'wintering' areas (Danilewicz et al. 2008, de Sá Alves et al. 2009) and 'rediscoveries' of previously unknown feeding grounds (Gibbons et al. 2003), 'flexible forager' is a label that seems equally appropriate for humpback whales.

It is possible that such feeding behaviour may occur at other mid-latitude locations with similar oceanographic conditions to the southern Benguela, provided that suitable prey organisms are present at sufficiently high densities. The resident population of humpback whales in the Arabian Gulf certainly proves that they are able to subsist off the monsoon- and upwelling-driven productivity found off Oman (Mikhalev 1997). A better understanding of the scale of this behaviour off the west coast of South Africa may only be achievable through satellite telemetry or a subregion-wide survey (ship or aerial) during the spring to summer peak, similar to the study by Moore et al. (2007) on grey whales.

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TEXT BY JACO BARENDSE

A HEAD OF STEAM

When Jaco Barendse embarked on his PhD thesis – a study of humpback whales off South Africa's West Coast during the summer months – eyebrows were raised. Humpbacks are one of the best-studied whale species and everyone in the whale world knows that they spend winter in the tropics and summer in the polar regions. Or do they? ▸

THOMAS P. PESCHAK

WWW.AFRICAGEOGRAPHIC.COM 41

JACO BARENDSE (2)

ABOVE A perfect pair. Two humpback whales blow in unison.

OPPOSITE An early morning wake-up call from a resident Cape spurfowl or *weskushoender* gets the show on the road on a misty West Coast morning.

PREVIOUS SPREAD Hauling out most of their 30-tonne bodies, humpback whales are known for their energetic displays at breeding grounds and while they are migrating.

The early morning sun reflecting off binocular lenses was the only clue to the presence of the otherwise well-concealed observers. Two students were systematically scanning a 270-degree view of the sea from one of a series of concrete bunkers at the summit of a low hill, some 500 metres from the shoreline. Constructed during World War II to provide fortified vantage points for Allied soldiers on the lookout for Nazi U-boats, these buildings are perfectly camouflaged against the summer landscape of South Africa's West Coast – grey, lichen-covered granite boulders interspersed with dry grass, wild sage and rosemary bushes. The submarines these observers were trying to spot on this December morning, however, had no immediate plans to annex the harbour.

At the top of the Baviaansberg hill everything was quiet. It was near the end of the observers' two-hour session and, together with a 'fresh' student, I was preparing to take over the watch. Lulled by the sound of waves breaking, the smell of kelp and the hypnotic songs of a pair of bokmakieries, concentrating on the task at hand was becoming a real challenge.

'Anything yet?' I asked, trying to sound as cheerful as possible. 'Nothing,' came the despondent reply.

Relieved to be off-duty, the volunteers handed over the stopwatch, binoculars and blank data forms. They had whiled away two weeks of their summer holidays participating in a research project that had yet to deliver any trace of a whale, and they were beginning to wonder whether they had been swindled. Whales in December? Perhaps there's a good reason that the Hermanus Whale Festival is held in September each year. To the east, sheltered behind the breakwater at Saldanha, similar thoughts were no doubt crossing the minds of four other researchers sitting on an inflatable boat moored at the jetty.

As the morning wore on, it became clear that this would be another whaleless day. Barely an hour into our watch, the southerly breeze strengthened and a grey bank of mist choked our view. Forced to abandon our post, we left to pick up the boat crew and return to our field station.

In many ways, the rationale behind my doctorate went against conventional wisdom. As one of the most well studied of all baleen whales, the humpback whale *Megaptera novaeangliae* is widely accepted to undertake annual migrations between breeding areas in tropical waters and polar feeding grounds. Like clockwork, humpback whales leave the productive waters around Antarctica and the North Pole at the onset of winter, gradually moving north or south (depending on the hemisphere they occupy) to the calmer waters off coastal equatorial countries. Here, the males sing to attract females and mating and calving takes place before the start of summer and the retreat of the ice, when the whales return to the polar areas. This means that populations in the two hemispheres are essentially out of synch, that is, always migrating in opposite directions.

One of the main reasons that humpback habits are so well known is that researchers are able to identify an individual by the unique pattern on the underside of its tail, or fluke. The fluke pattern can range from pitch black to completely white, and all variations in between. In addition, scars, nicks and spots, or the shape of the flukes and their trailing edge, can assist identification. Dorsal fins, though having fewer distinguishing features than flukes, may also be used to tell the animals apart.

The other reason that we know so much about humpbacks is that from the 1900s, with the depletion of right whale populations, they became one of the primary targets of global whaling fleets. Though less valuable than right whales in terms of the amount of oil that could be extracted, their predictable migration destinations and habit of staying close inshore, often moving from headland to headland, made them easy prey. The ensuing decimation of humpback populations was extraordinary.

Between the Cape and Gabon more than 28 000 humpbacks were killed from 1904 to 1974. Almost two-thirds of these catches occurred between 1909 and 1916, with 17 347 whales landed (1 359 of these were taken off the western Cape coast). Full formal protection for humpbacks only came in 1963, when a moratorium was placed on killing them. (Illegal Soviet catches, however, continued for almost another decade.) By then, over 200 000 humpbacks had been killed in the southern hemisphere, the bloodiness of the era evidenced by the remains of shore-based whaling stations that dot the length of the African west coast. Two of these, Donkergat and Salamander, stood less than five kilometres south of the Baviaansberg lookout.

All these observations suggest that the whales should have been engaged in more amorous activities in a tropical paradise. Why on earth was I expecting to see them here, in the middle of a migration route that they would probably only follow at the end of summer?

The next morning I awoke to the familiar cries of my resident alarm clock, a Cape spurfowl or *weskushoender* ('west coast chicken') as they are called here, outside my window. The mist from the previous evening was still evident and it took all my persuasive powers to get the volunteers out of bed. Morale had reached an all-time low and I sensed mutiny in the air.

Today I would be on boat duty, while my colleague Meredith Thornton would run the shore-based observations. Meredith and a volunteer took the first watch on what seemed to be another quintessential West Coast day. At ▶

ALL THESE OBSERVATIONS SUGGEST THAT THE WHALES SHOULD HAVE BEEN ENGAGED IN MORE AMOROUS ACTIVITIES IN A TROPICAL PARADISE

THE NOT-SO-USUAL SUSPECTS

MRI WHALE UNIT

Fluke 'fingerprints'. The ventral or underside of a humpback fluke has unique features that enable individual identification.

Photo-identification, that is, the identification of individual animals through photographs, is one of the most widely used methods available to scientists who study animal movements. Prior to the use of natural markings to enable individual identification, whale researchers had to rely on artificial markers. The first ones were 'Discovery Tags', serialised metal rods that were fired into the blubber of the whale. The information they yielded was limited in that a tag could only be retrieved once a whale was killed and slaughtered. The identification of humpback whales through photographs was pioneered in the early 1970s in the North Atlantic and, to date, the ventral fluke patterns of over 6 000 individuals have been photographed and included in the North Atlantic Humpback Whale Catalogue. This list enabled scientists to establish that the same whales returned to the same breeding and feeding areas every year. *www.coa.edu/html/nahc.htm*

MEREDITH'S VOICE CRACKLED THROUGH THE RECEIVER ... 'WE HAVE A GROUP OF HUMPBACKS GOING SOUTH IN BLOCK 134. GO, GO, *GO*!'

TIM COLLINS/WCS

A humpback whale surfaces and appears to feed near an oil platform off the coast of Gabon. Genetic sampling has, for the first time, shown that individuals move between these waters and South Africa's West Coast.

first, the mist was impenetrable, a grey cloak that concealed everything, but finally it lifted, and revealed a sea alive with whale blows. Everywhere!

'Blow! Blow! Two animals, just over Schooner rock, one-third to the horizon.' The trance-like ambience of the morning was shattered as volunteers sprang into action like soldiers preparing for an aerial raid.

The time was carefully noted. One spotter stood behind a surveyor's theodolite, an instrument for measuring both horizontal and vertical angles, while the other clutched a stopwatch, a pencil and a clipboard. The position of the whale was pinpointed by cranking the theodolite's array of metal knobs and wheels. Through its 22-times magnification telescope, the wavelets on the surface of the sea looked larger than life. Suddenly, a knobbly black shape broke through the blue-green surface, filling the entire viewfinder. 'Ready.....time...NOW!' The scribe recorded the time to the second, then jotted down the horizontal and vertical bearings. A few more surfacing events were observed, the species of whale identified and the size of the group estimated. Once satisfied that they could follow the path of the whales, Meredith grabbed the VHF-radio handset. The boat crew's day was about to get exciting.

'Balaena-Balaena-Balaena, this is Minke-Minke-Minke.' Meredith's voice crackled through the receiver on the boat. 'We have a group of humpbacks going south in block 134. Go, go, *go*!' The crew scrambled to undo the moorings and soon the two 50-horsepower four-stroke engines roared into life. I steered the *Balaena* past the mussel rafts, a few iron-ore bulk carriers and finally towards the open ocean. Saldanha Bay is big and it takes a good 20 minutes to get to the heads that are guarded by Malgas Island to the north and Jutten Island to the south.

The mirror surface of the harbour had been replaced by a tricky two-metre swell and a slight wind chop. With expert instructions from Meredith and directions from an observer perched on top of the boat's custom-made overhead superstructure, we closed in on the action. Fellow student Simon Elwen stood in the bow, camera ready, and every time the whales broke the surface to breathe, he tried to photograph each side of the dorsal fin of each individual, as well as the underside of the fluke. Reminiscent of the whale hunts of old, Simon then tried to 'shoot' the whale with a special biopsy rifle, which fires a floating dart that collects a tiny piece of skin for genetic analyses.

'Our' group of whales led us into the epicentre of several other groups, a total of at least 20 whales that had gathered in an area of about one square kilometre. With blows and splashes all around, we noticed that the water was teeming with dense swarms of a local krill species, *Euphausia lucens*, and that whales were swimming in apparent unison, mouths open and baleen blades ready, through this thick, pink soup. Several hours and many rolls of film later, an exhausted boat team docked at the jetty. Equipment still had to be cleaned, samples stored and notes checked before we could even think about going to bed. ▶

BENEKE DE WET

JACO BARENDSE (3)

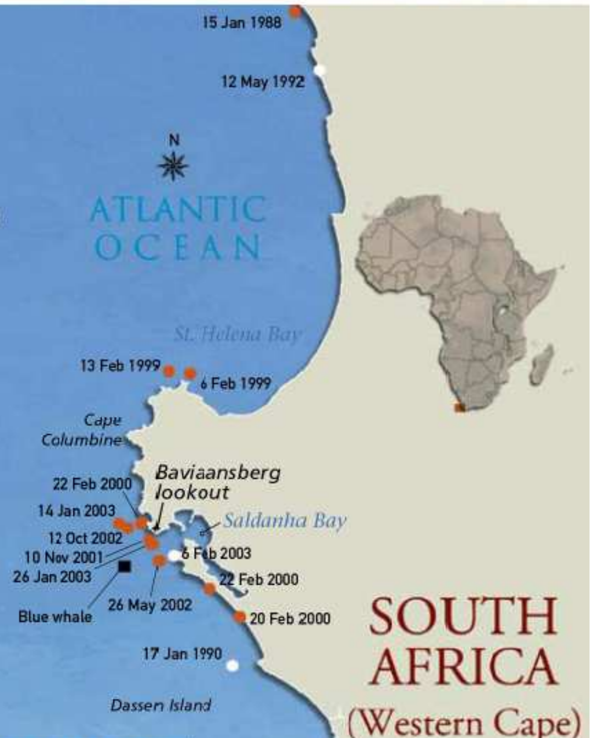
SALDANHA BAY'S SUMMER WHALES

During the summers of 2001 to 2003, researchers stationed at Baviaansberg in Saldanha Bay saw 289 humpback groups and identified 156 individuals. Subsequent photo-identification work showed that numerous individuals regularly summer off South Africa's West Coast. One whale, Ampersand, has been seen 11 times in the past decade, always between the months of October and February.

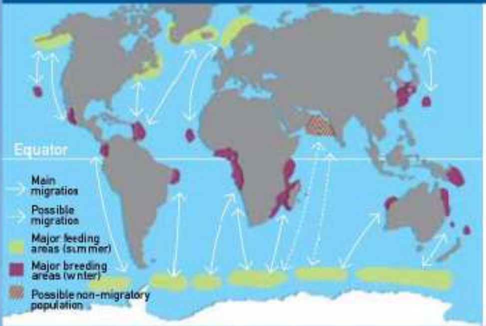
● AMPERSAND

○ FOLDFLUKE

MRI WHALE UNIT (4)



GLOBAL DISTRIBUTION OF HUMPBACK WHALES



Newborn *Four to five metres*
Adult *11.5 to 15 metres*

This map shows the major feeding and breeding areas of humpback whales, together with their possible spring and autumn migration patterns.

THESE FINDINGS SUGGEST THAT WHALES HAVE FAR MORE FLEXIBLE HABITS THAN PREVIOUSLY THOUGHT


SIMON ELWEN/MRI WHALE UNIT

OUT OF THE BLUE

The sea drives everything on the West Coast, the effect of the cold Benguela Current creating a far more interesting and unpredictable place than first impressions might suggest. The ocean can be fickle but, as we discovered, it can reward you with almost any surprise imaginable. It could be a pod of killer whales or even an inquisitive ocean sunfish scratching against your boat.

The highlight happened on 26 January 2003 during one of our whale 'hunts'. We were on the trail of a group of humpbacks when we saw another whale blow, twice as high as the average humpback spout, to our starboard. The surface in front of us was suddenly broken by a mottled blue-grey beast, with a jaw shaped like a Gothic arch. Its two muscular blow-holes opened like caverns, expelled huge columns of warm vapour and then inhaled. It started diving, revealing an extremely long, smooth body utterly unlike the 13-metre, knobbly black shape of a humpback. A tiny dorsal fin signalled the end of more than 20 metres of whale, and the sight of its huge tail, as wide as our boat, finally brought home the fact that we had just seen the world's largest living creature – a blue whale. It is the only photographically confirmed sighting of a blue whale since an individual was killed and taken to the Donkergat whaling station on 16 May 1966.

Nothing can explain the thrill of making that first photo-identification match. It was strange that our first should be of an unmistakable animal with a deformed and scarred fluke. When I first described its bizarre tail to my supervisor, Dr Peter Best, he slid open the catalogue drawer and pulled out our first clue: a single fuzzy photo from 1990 stapled to an old identification card. Normally such a poor picture would not be considered for use in matching, but this animal was so distinctive that there was very little doubt that the two images were of the same whale.

After painstakingly scanning every colour slide and black-and-white negative (digital photography was beyond the budgets of most whale researchers until 2003), and ensuring that each image was associated correctly with all the collected data, the process of matching could begin. After 16 months of intense data collection and keeping scores of volunteers happy and fed, the current catalogue now contains all known photographs taken by researchers on the West Coast. It spans a period of over 20 years and contains more than 1 300 images belonging to 260 individuals. As matches were made, so the story of the West Coast humpbacks started to unfold.

One of our champions was named 'Ampersand' ('&') for the mirror image of this typographic symbol situated on the left-hand underside of its fluke. This animal was seen no fewer than 11 times over as many years, sometimes up to three times in a single year. When we saw it accompanying a small calf, we knew that Ampersand was a cow, a fact confirmed by subsequent biopsies. She was a regular visitor to Saldanha Bay and, over the decade that we can trace her movements, covered almost 65 000 kilometres. But between October and February, it appeared that the Saldanha area was the only place for her. What was the attraction?

Before our study, there had been little reason to doubt that humpback whales off South Africa's West Coast did not conform to conventional migrations, apart from a brief pilot study that hinted otherwise. Carried out at Cape Columbine to the north of our study site during October and November 1993, the unexpectedly high number of whale sightings and their erratic movements suggested that the whales had 'suspended' their migration to attend to other matters. It formed the original motivation for my own research.

We now believe that this apparent behavioural 'anomaly' can be attributed to the climatic and oceanographic conditions of the region. In summer, the West Coast is not only known for its sunny days, but also for a less enjoyable climatic feature, a persistent south-easterly wind. At the start of September, the weather in the region changes from a rather wet winter, dominated by a north-westerly wind, to a hot and dry spring and summer, with a generous dose of very windy days. The south-easterly can blow for prolonged periods, often reaching gale-force speeds. It pushes surface water away from the coastline, thus creating an upwelling of cold, nutrient-rich water. This seasonal injection of nutrients is the engine that drives the highly productive Benguela Large Marine Ecosystem.

It is probably safe to assume that the whales stop off between St Helena Bay and Cape Point on their way back from their northern wintering grounds in response to the increased food availability at the various upwelling plumes that result from the intense bouts of south-easterly winds. Apart from feeding behaviour, we saw regular defecations by both humpback and southern right whales. Some of the stools were collected in buckets and microscopic examination revealed semi-digested bits of krill from humpbacks and copepods from southern rights, confirming our observation.

These findings suggest that whales have far more flexible habits than previously thought, and that they would not hesitate to enjoy the benefits of unexpected positive conditions. How many whales participate, how long they stay and where they go when the bonanza ends are questions that remain unanswered.

Understanding the movements between winter and summer feeding grounds and how whales from different regions relate to each other, are critical pieces of information for the

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future management and conservation of large cetaceans. Every year at the International Whaling Commission (IWC), there is mounting pressure from 'whaling nations' to resume commercial whaling on selected species. Some populations of humpback whales, such as the one that migrates past the East Coast of Australia, have shown remarkable recovery rates of some 10 per cent per annum. For other populations these estimates are more difficult to make as the numbers are still too low, or the population structure too complex.

Genetic work by researchers affiliated to the American Museum of Natural History/Wildlife Conservation Society has shed new light on movement patterns and population substructures of humpbacks from around Africa. Firstly, between December 2001 and January 2003, four females that had been biopsied off the coast of Gabon were seen and biopsied again in Saldanha Bay, conclusively linking whale populations in the two locations.

The studies also showed that there were significant similarities between nuclear DNA markers in whale samples from the African west coast, whereas mitochondrial DNA analysis revealed more subtle differences in maternal lineages. This suggests that male and female whales may be doing different things in different places. Some hypotheses propose that certain behaviours, for example making use of feeding opportunities in particular areas, may be 'taught' by mothers to their offspring, something that can only be confirmed with extensive genetic sampling and, perhaps, the use of satellite trackers on whales across the region.

South Africa may have realised and enjoyed the tourist value of live whales for many years, but other nations view whales as large and increasingly available sources of protein. The 'dead versus alive' debate will undoubtedly intensify over the next few years and, to ensure science-based and objective decision making regarding this controversial issue, research work on these large mammals remains crucial. ■

In transit. A group of humpbacks on the move. Heading for a summer snack in Saldanha Bay, perhaps?

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