Cape Peninsula University of Technology

Estimating population changes in humpback whales (*Megaptera novaeangliae*) migrating past Cape Vidal, South Africa

by

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I, Christopher Wilkinson, declare that the contents of this thesis represent my unaided work and that the thesis has not previously been submitted for academic examination towards any qualification. Furthermore, it represents my own opinions and not necessarily those of the Cape Peninsula University of Technology.

Chapters 2 and 3 are constructed in readiness for submission in different journals. The student is the first author in all the chapters and had the main responsibility for designing the study, fieldwork collection, data analysis and manuscript writing while the supervisors helped with the conceptualising of ideas, planning, and commenting on the manuscript drafts.

This thesis contains a single bibliography to minimise duplication of referencing across chapters.

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ABSTRACT

Southern Hemisphere humpback whales, *Megaptera novaeangliae,* migrate annually from summer Antarctic feeding grounds to winter breeding grounds in coastal tropical waters, including South Africa. Given changing climatic conditions and population recovery from whaling, there may be changes in migrating whales' distribution, numbers, densities, and migration characteristics (speed, bearing, and distance offshore) over the last few decades. This research aimed to calculate a relative abundance estimate and a population rate of increase of humpback whales migrating past Cape Vidal, KwaZulu-Natal, South Africa, part of the so-called C1 sub-stock of the species. Shore-based surveys were performed from two 70 m-high independent platforms located 22 m apart in 2018 and 2019 (from 27th June to 7th August each year) to compare with previous data collected in the same area between 1988 - 1991 and 2002. Observed whale groups (within timed daily observation effort) were tracked by position-fixing on surfacing bouts using survey theodolites. The numbers of whales observed (or projected at tracked speeds) to cross the midline of the survey area within the observation period each day were tallied in each of three distance bins and adjusted to account for daily sighting effort. The proportions missed by distance offshore and sighting conditions were calculated using the mark recapture-based estimates of missed groups between independent platforms. The counts allowed daily sighting rates to be aggregated across the season to result in annual relative abundances. Relative abundances of 11,098 (2018) and 13,485 (2019) individuals were estimated, and an annual increase rate of 7 - 8% over the 31 years from 1988 was estimated. These results represent a slowing of the population's rate of increase, as previous studies indicated an annual increase rate of 11% between 1988 to 2002. Such a decrease in the rate could suggest that the population is approaching the pre-exploitation numbers on their summer Antarctic feeding grounds. However, anthropogenic factors could influence various environmental factors driving humpback whale ecology and impact the species' recovery. Recommendations on further studies at Cape Vidal on humpback whales are provided.

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DEDICATION

This thesis is dedicated to my parents Peter and Meg Wilkinson, who always nurtured my interest in conservation, whales, and Antarctica from an early age.

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Appendix D: Matching resolutions between north and south towers for 2019, considering data unstratified, stratified into distance bins and weather bins and stratified by both. Nn = number of humpback whale sightings from the north tower, Ns = number of humpback whale sightings from the south tower, M = number of matches, N = total number of whales calculated by Chapman's estimation, SD= standard deviation

GLOSSARY

Term	**Definition / Explanation**
Carrying capacity	The carrying capacity of a biological species in an environment is the maximum population size of the species that the environment can sustain indefinitely, given the food, habitat, water, and other necessities required by the species (Hin, 2015).
Fix	Placing the theodolite crosshairs onto a target, resulting in horizontal and vertical angle read-outs (allowing the geographical position of the target to be estimated), often associated with time.
Mark - recapture methodology	In mark-recapture experiments, animals are captured, marked, released, and recaptured many times by repeated sampling. In this study, animals are "captured and marked" by the south tower as sightings for the first sample and "captured" as the second one. Animals sighted in both samples are recaptured animals. The result is a set of capture histories, one per observed animal, providing information on survival, recruitment, and population size.
Modern commercial whaling	The hunting of whales on a commercial scale from 1904 (in the Southern Hemisphere), with the use of motor-driven ships (catcher vessels and factory ships) and cannon-fired explosive (propulsion and impact) harpoons. These modern techniques allowed the whaling industry to travel further, be more efficient and hunt larger species of whales (IWC, 2011).
Oceanography	The study of the physical and biological aspects of the ocean, which covers a wide range of topics, including ecosystem dynamics; ocean currents, waves, and geophysical fluid dynamics; plate tectonics and the geology of the seafloor; including fluxes of various chemical substances and physical properties within the ocean and across its boundaries.
Rate of Increase	The rate at which the number of organisms in a population increases. This is calculated by dividing the change in the number of organisms from one point to another by the amount of time in the interval between time points (Hin, 2015).

Shore-based survey For this study's purpose, shore-based surveys refer to surveying from fixed shoreline points (in this case, platforms) with known coordinates and altitude. From these positions' whales are located, plotted, and tracked during such surveys.

Theodolite A surveying instrument with a rotating telescope for measuring horizontal and vertical angles (Pearsall and Hanks, 2001).

ABBREVIATIONS AND ACRONYMS

ANOVA	Analysis of variance
BS	Breeding Stock
GPS	Global Positioning System
iSimangaliso	iSimangaliso World Heritage site as well as iSimangaliso Wetland Park
IWC	International Whaling Commission
Krill	Antarctic krill *(Euphausia superba)*
M	The number of matches between towers
MPA	Marine protected area
mtDNA	Mitochondrial Deoxyribonucleic acid
Nn	Numbers of humpback whale groups sighted from the north tower
Ns	Numbers of humpback whale groups sighted from the south tower
NT	North Tower
Pn	The proportion of the humpback whale groups missed by the north tower
Ps	The proportion of the humpback whale groups missed by the south tower
ROI	Rate of increase
ST	South Tower

CHAPTER 1: INTRODUCTION AND LITERATURE REVIEW

1.1 MIGRATIONS

1.1.1 General background

Migrations are a diverse, fascinating phenomenon that link seasonal movements to resource availability. They are adaptive life-history events, generally seasonal and highly predictable (Colwell, 1974) that are often highly visible and can occur on a large geographical scale (Barendse, 2011). Migrations occur in the life of numerous taxa. For example, five Pacific salmon species (*Oncorhynchus spp*.) migrate up the rivers in Alaska from the sea to their spawning grounds (Kovach et al., 2015). Arctic terns (*Sterna paradisaea*) migrate annually from Arctic breeding grounds to the Southern Ocean (Egevang et al., 2010). Land mammals, such as wildebeest (*Connochaetes taurines*) in the Serengeti-Mara region migrate a round trip of 800 km to search for the best seasonal grazing and water resources (Holdo et al., 2009), while the caribou (*Rangifer tarandus*) of North America and Canada constantly migrate between their winter ranges and calving grounds in Alaska (Joly et al., 2019). Investigations of why animal species migrate contribute to understanding the structuring of ecosystems while raising a host of ecological and evolutionary questions and conservation issues (Joly et al., 2019).

Unfortunately, there remain few places on earth where these migrations continue unhindered and resemble their past range. For example, the historic springbok herd *(Antidorcas marsupials)* (also known as *trekbokke)* could migrate unhindered through the Karoo until the late 19th century to search for better grazing. By 1987, farming had divided the land, and livestock disease (rinderpest) diminished and segregated the mega herd (Roche, 2008). In contrast to the terrestrial environment, migratory corridors in the world's oceans may be less physically fragmented by human activities, so animals may continue their migrations in a way resembling those of the past. However, intense human activities in certain areas and climate change impacts in the marine ecosystem, for instance, are expected to influence the migration of some species, such as those exhibited by baleen whales (Meynecke et al., 2020).

1.1.2 Whale migrations

Annual migrations are well-known amongst baleen whales (Order Cetacea, Suborder Mysticeti). Most species migrate seasonally between high latitude summer feeding grounds and medium to low latitude breeding grounds, where they are observed mainly during winter months (Kellog, 1929; Norris, 1967). Such migrations include some of the longest annual migrations by any mammal globally (Stone et al., 1990; Rasmussen et al., 2007). For example, the gray whale (*Eschrichtius robustus*) migrates over 22,000 km, a roundtrip from the tropical Baja California to the Bering Sea in Alaska and back, over 172 days (Mate et al., 2015). Furthermore, Rasmussen et al. (2007) documented seven humpback whales

(*Megaptera novaeangliae*), including one cow/calf pair, that migrated from their Antarctic feeding grounds, approximately 8,300 km north to 11° N of the Equator (off Costa Rica).

In the case of baleen whales, migrations are generally a trade-off on the species' breeding and feeding requirements, and Corkeron and Connor (1999) summarise several hypotheses to explain their migration behaviour, as described and discussed below.

(i) Brodies theory hypothesises that the whales' energy budgets are optimal when migrating to warmer waters during winter when their prey are relatively scarce, and temperatures are lowest in the polar waters.

(ii) The evolutionary "tradition" hypothesis suggests migration was an ancient behavioural legacy, when the continents were closer together, assuming no intense selection pressures favour breeding in equatorial waters (Evans, 1987). However, the fact that some baleen whales do not migrate every year allows us to dismiss this hypothesis, such as humpback whales on the west coast of South Africa that take up temporary residency during summer months (Best et al., 1995).

(iii) Resource tracking may also play a role in the migration of these animals, and it is suggested that whales might reduce their period without food by feeding on plankton in mid-latitudes. An example of this is the seasonal mass feeding events of humpback whales in low latitude waters off the west coast of South Africa, whereby humpback whales suspend their southwards migrations to polar waters, remaining for extended periods in these productive temperate waters (Best et al., 1995; Barendse et al., 2011; Findlay et al., 2017). However, although resource tracking applies to some species of baleen whales, it seems less probable for others, such as the gray whale, which rarely feeds on or near the breeding grounds (Nerini et al., 2009).

(iv) The calf growth and survivorship hypotheses assume that parturition drives migration. There are two benefits for females to calve in warm low latitude waters. One is related to calf thermoregulation; as calves are not born with a thick blubber layer, energy would be expended for heat production instead of growth in cold water. The humpback whale calves' ability to conserve energy in warmer water during the first few months, therefore devoting that energy into further growth and development, provides a severe advantage over calves developing in colder water (Clapham, 2001). The early development months spent in warmer water led to a larger size in adulthood, which results in greater reproductive success; larger females have a greater ability to bear offspring, and larger males have increased competitive success (Clapham, 2001). The other is linked to predation, and the authors suggest a reduced predation risk from killer whales (*Orcinus orca*) in shallow, calm sheltered waters of the low latitudes. However, there is still evidence of predation at low latitudes, for example, the Pitman et al. (2015) observations of predation by killer whales on the migratory corridor off Western Australia. Additionally, Pitman et al. (2017) observed that humpback whales with calves took longer and more coastal routes than non-breeders to reduce the risk of killer whale attacks on the calves. Also, in low latitude waters, predation pressure from sizeable pelagic shark species such as tiger *(Galeocerdo cuvie*r) and great white sharks *(Carcharodon carcharias),* which scavenge and attack humpback whale calves with the hunting killer whales, has been reported (Pitman et al., 2015). Clapham (2001) refutes predation as the primary reason why baleen whales migrate.

Much of what is known of the migrations and seasonal abundance of whale species have been identified from the severe whaling pressure through the past centuries. Knowledge built up from whaling and the associated research, resulted in the need to manage whale stocks for whaling purposes (e.g., the *Discovery* Investigations). Consequently, it is prudent to provide a succinct overview of whaling and whaling pressure before introducing humpback whale migrations in detail.

1.2 WHALING

1.2.1 General overview

The history of whaling is essentially one of sequential discovery, over-exploitation, and the ultimate collapse of most the major stocks of baleen whales (Gambell, 1976). Whaling in Europe came to a rise as long ago as the twelfth century, with North Atlantic right whales (*Eubalaena glacialis*) hunted by the Basques in the Bay of Biscay (Gambell, 1976). In South Africa, shore-based whaling officially began a few centuries later, in approximately 1792, with open-boat whaling lasting until 1917 (Best and Ross, 1986), after the arrival of pelagic open boat whalers from North America, Britain, and France to the region. During this time, shore-based stations could be found at St Helena Bay, Table Bay, Robben Island, Simons Bay, Fish Hoek, Kalk Bay, Gordons Bay, Mossel Bay, Plettenberg, and Algoa Bay (Best and Ross, 1986). In general, this hand-harpoon and open-boat technology depleted many coastal stocks of baleen (mainly right) whales, and whales were killed faster than their populations could grow (Gambell, 1976). Low numbers of humpback whales were reported to have been taken by shore-based efforts in the Cape Colony before 1917 by open-boat whalers (Best and Ross, 1986), because they sank after death and therefore were not considered worthwhile to hunt.

Modern whaling included more industrial techniques such as motorised catcher vessels, floating factories, and harpoon cannons. In the Southern Hemisphere, modern whaling commenced in South Georgia in 1904 and lasted until a pause in commercial whaling was introduced by all Member Nations of the International Whaling Commission, effective from the 1986 whaling season (Gambell, 1993). Modern whaling can be further subdivided into shore and pelagic operations, with shore stations operating from 1904 and pelagic operations operating from 1923.

1.2.2 Humpback whaling in the Southern Hemisphere

The pre-exploitation size of the Southern Hemisphere humpback whale population was estimated at 90,000 – 100,000 (Chapman, 1974). Based on information on the catches of humpback whales in the Southern Hemisphere and the number of catcher vessels operating on the whaling grounds, (Best and Ross, 1986; Findlay, 2001; Baker and Clapham, 2004), total catches of humpback whales in the Southern Hemisphere amounted to > 220,000 and can be divided into four different sources:

(i) Pre-1917 coastal whaling from shore stations and floating factories operated at both high and low latitude localities, targeting the feeding grounds, migration streams and breeding grounds,

(ii) Between 1923 and 1963, approximately 25,393 humpback whales were taken by pelagic whaling fleets according to Antarctic and low latitude catch data that were reported to the Bureau of International Whaling Statistics (Findlay, 2001). However, due to declining population numbers, catch trends became affected by regulations soon after their initiation (Tonnessen and Johnsen, 1982). Between 1938 and 1949, humpback whales south of the 40° parallel were protected by the International Agreement for the Regulations of Whaling (now known as the International Convention for Regulation of Whaling) (Findlay, 2001). Although some grace period (4 days) was given in the subsequent year, Tonnessen and Johnsen (1982) noted that yields after the 1953 season were variable, and humpback whaling in the southern hemisphere officially ceased after October 1963.

(iii) Post-1942 coastal catches, focused on New Zealand and Australia, were subject to annual quotas, which for the west coast for Australia were met until 1957 and the east coast up until 1961. Yablokov (1994) estimated that 12,312 humpback whales were taken off the Australian west coast, and 8,307 were taken off the east coast. This excludes the "illegal Soviet catches", which are credited as the reason the east coast stations did not reach their whaling quotas in 1961 (591 of a quota of 660 humpback whales) and 1962 (68 of out of a quota of 600) (Chittleborough, 1965; Yablokov, 1994).

(iv) Other catches, including the *Olympic Challenger* and the "Illegal Soviet catches", were made outside the Bureau of International Whaling Statistics (BIWS) or IWC reporting system. The Soviet Union operated four Antarctic Whaling fleets between 1946/1947 and 1986/1987 (Findlay, 2001). The catches of humpback whales reported by these fleets (2,700 humpback whales) were unreliable for 1948/1949 to 1971/1972 (Yablokov, 1994). Actual catches (48,724 humpback whales) were presented by Zemsky et al. (1994) to the IWC in 1997, highlighting the differences between reported and actual catches. It is important to note that some of these catches were made in the Northern Indian Ocean (or north of 40° S) (IWC, 1997).

1.2.3 Humpback whaling in Southern Africa

The Norwegian Johan Bryde initiated modern whaling in South Africa in 1908 in Durban, after reports of abundant whales off the coast were received in Norway (Findlay, 2001). By 1909, floating factory ships were in operation off Saldanha Bay on the west coast of South Africa. The success of these first whaling companies between 1908 and 1910 resulted in a whaling boom across southern Africa (Gabon to Mozambique), with 17 land stations and 11 floating factories in operation by 1913. In Mozambique, a floating factory and a land-based station were operating from Bazaruto in 1910, two floating factories operated independently at Linga (Inhambane), one between 1911 and 1915, and one between 1912 and 1923 (Findlay et al., 2011). In Delagoa Bay (Maputo), a land station operated between 1912 and 1913, and floating factories operated at Qulelimane and Angoche between 1911 and 1912 (Tonnessen and Johnsen, 1982; Findlay et al., 2011). Best (1994) estimated that 7,263 humpback whales from Mozambique and South Africa were processed in these initial years. Up to 1963, it is estimated that 47,134 humpback whales were taken by modern land-based stations and moored floating factories off the Southern African coast, including 19,094 off the west coast and 28,040 off the east coast (Findlay, 2001).

1.3 HUMPBACK WHALE MIGRATIONS

1.3.1 General information

The humpback whale is considered a cosmopolitan species (Clapham and Mead, 1999), making extensive annual migrations. The first evidence of the migration of the species was derived from whaling activities (see above), based on the seasonal abundance patterns recorded as catch per unit effort on the whaling grounds (Findlay, 1994). A single peak in catches at a particular latitude each year suggests that the location is at the northern or southern limit of the migration (the destination), while a bimodal trend in catches per year indicates that a location is in the path of the northern and southern migrations. The seasonality in whale catches at different latitudes provides an understanding of the migrations between summer presence in high latitudes and winter presence in low latitudes and the identification of such areas as breeding grounds feeding grounds, and migratory corridors.

In more recent years, the ability to individually identify humpback whales provided more detail about their movements within the migrations. Early attempts to understand movement patterns began with the *Discovery* marks, a physical marking experiment initiated in 1932 whaling season to track individuals between different areas by using stainless-steel tags applied into the body of some individuals (Mackintosh, 1942). Later, photographing and identifying individual whales by their unique naturally-occurring marks (photo-identification) was used to better understand the species movements (Katona and Whitehead, 1981; Hammond et al., 1990). More modern techniques, such as mitochondrial and nuclear DNA investigations (Palsbøll et al., 1997) and carbon and nitrogen isotope analysis (Eisenmann et al., 2016), allow researchers to confirm and refine the annual migration routes while satellite telemetry of individuals makes it possible to track individual whales in real-time (Zerbini et al., 2006; Cerchio et al., 2013). Nonetheless, much of what we currently know about humpback whale migrations is derived from vast amounts of data collected by the commercial whaling industry.

1.3.2 Feeding grounds

Whaling information on the distribution of baleen whale species was used to identify five Antarctic feeding grounds, which expanded to six and then seven as further information arose (Area I to Area VI, including Areas IIIW and IIIE) (Hjort et al., 1932; Mackintosh, 1942; 1965; Donovan, 1991; IWC, 1998). These included six proposed Management Areas for humpback and other baleen whales:

(i) **Area I:** 120° W to 60° W.
(ii) **Area II:** 60° W to 0°.
(iii) **Area III:** 0° to 70° E.
(iv) **Area IV:** 70° E to 130° E.
(v) **Area V:** 130° E to 170° E.
(vi) **Area VI:** 170° E to 120° W.

The seventh feeding ground in the west of Area III (then named Area IIIW) was identified by releasing the illegal Soviet catch data in 1997 (IWC, 1998; Jackson et al., 2015).

Feeding grounds were first linked with breeding grounds by Mörch (1911) and Kellog (1929) and later by Mackintosh (1942) and others, providing the concept of discrete whale stocks within the Southern Hemisphere population.

1.3.3 Breeding grounds

The terminology associated with humpback whale populations and stocks and the areas where they breed and feed can be confusing, mainly as ground and stock names are terms that are easily interchanged. For this species, a population refers to all humpback whales within a hemisphere (e.g., the Southern Hemisphere population), while regions in the Southern Ocean are called feeding (Areas I – VI, as presented in 1.3.2) or grounds (Donovan, 1991). A population migrates from feeding grounds to breeding grounds in the broad ocean basins; this typically occurs during winter months. The individuals using this ocean-basin delineated breeding grounds (of which there may be multiple within an ocean basin) are known as that region's Breeding Stock (BS). As described below, seven breeding stocks are currently recognised in the Southern Hemisphere population, named from A to G (IWC, 1998; Figure 1.1). As indicated, some of these BSs have been further stratified into sub-stocks, based on the breeding grounds occupied by the individuals (Figure 1.1).

(i) Breeding Stock A (BS A): migrates along the eastern side of South America to breeding grounds off Brazil. Currently, it is accepted that this is a single BS connecting with a single feeding ground, Area II (IWC, 2011).

(ii) Breeding stock B (BS B): is divided into B1 and B2 sub-stocks. The first of these migrates along the west coast of southern Africa to a breeding ground off Gabon (BS B1), while the second uses the coast of South Africa and Namibia (BS B2) during the breeding season to pause migration and feed (IWC, 2011). Some satellite-tagged humpbacks from BS B1 migrated past Walvis Ridge, and ended up in the vicinity of Bouvet Island (ca 54° S, 03° E), while others from BS B2 continued to the ice edge and were shown to be feeding on the boundary of Area II and Area III (IWC, 2011).

(iii) Breeding stock C (BS C): migrates along the east coast of Africa and divides into four sub-stocks: off South Africa to Kenya (C1), off the islands of the Mozambique Channel (C2), the coastal water of Madagascar (C3), and off the Mascarene Islands (C4) (Best et al., 1997, 1998; IWC, 2006; Cerchio et al., 2013) (see Chapter 1.3.3). The C1 sub-stock has been further divided into C1 South (hereafter C1S), using the breeding ground off Mozambique, and C1 North (hereafter C1N), which concentrates on the coasts of Tanzania and Kenya (IWC, 2006). The IWC agrees that the C1S is considered a separate breeding sub-stock from C2, C3 and C4, which show some genetic links, but refers to them as one single breeding sub-stock for management purposes (IWC, 2011). This BS C1S is the focus of the current study. BS C has been shown through Discovery Marks to range over a broad feeding ground area of Area III.

(iv) Breeding Stock D (BS D): migrates along the western coast of Australia to a breeding ground in the region of northern Western Australia and Northern Australia (*ca* 21°50' S, 114°10' E). It is accepted that this is a single breeding stock linked to Area IV (IWC, 2011).

(v) Breeding Stock E (BS E): migrates along the east coast of Australia to breeding grounds off the Great Barrier Reef and Chesterfield Reef (E1), New Caledonia (E2) and Tonga (E3). This breeding stock is linked to Area V; this area is notable because it is the minimum distance from the feeding ground compared to any other breeding ground (Jackson et al., 2015).

(vi) Breeding Stock F (BS F): migrates directly from the South Pacific islands to the Southern Ocean; unfortunately, due to the remoteness of these islands, there remain significant gaps in the data; it is believed that BS F is linked to Area VI (Jackson et al., 2015).

(vii) Breeding Stock G (BS G): migrates the furthest from the Antarctic feeding grounds, along the west coast of South America to breeding grounds off Columbia and Ecuador. BS G is linked to Area I off the west coast of the Antarctic Peninsula, including the South Shetland Islands (Jackson et al., 2015).

Sub-stocks should generally be genetically isolated to be identified as such (e.g., C1S and C3 sub-stocks) (Rosenbaum et al., 2009), and the fact that sub-stocks may visit several breeding grounds (e.g., C2, C3 and C4 sub-stocks) (Rosenbaum et al., 2009) means that breeding grounds not always adequate measures of sub-stock delineation. Such sub-stocks could be merged (to form, for example, a breeding sub-stock C2,3,4 that appears genetically isolated from C1S). There is also considerable mixing of breeding stocks on the feeding grounds; for example, BS B and BS C share Area III, making it essential to note that feeding grounds do not constitute stocks; but are areas in which whales from respective breeding grounds aggregate to feed. Unfortunately, the vernacular often refers to whales on different breeding grounds as breeding stocks or breeding sub-stock, and whilst by no means incorrect it can lead to confusion if multiple breeding grounds are visited by more than one stock or sub-stock.

Modern research methodology, particularly in regional-scale genetic sampling and analysis of mitochondrial and nuclear DNA markers, strengthens the connectivity between feeding areas and breeding grounds (e.g. Rosenbaum et al., 2009; Barendse, 2011). Of relevance to this study, BS B (South African west coast humpback whales) and BS C (South African east coast humpback whales) share a feeding ground (Area III). Genetic research indicates that while a significant mtDNA stock structure exists between the BS B and BS C, the magnitude of this structure is relatively weak concerning the other stocks (Rosenbaum et al., 2009). Area III is the geographically considered feeding ground for BS C; however, there is much complexity around the linking of breeding and feeding grounds, and boundaries appear to be more blurred than previously thought. The development of catch position models has led to discussions around the allocation of feeding ground individuals into "core" and "fringe" overlap and naïve model areas (IWC, 2011)

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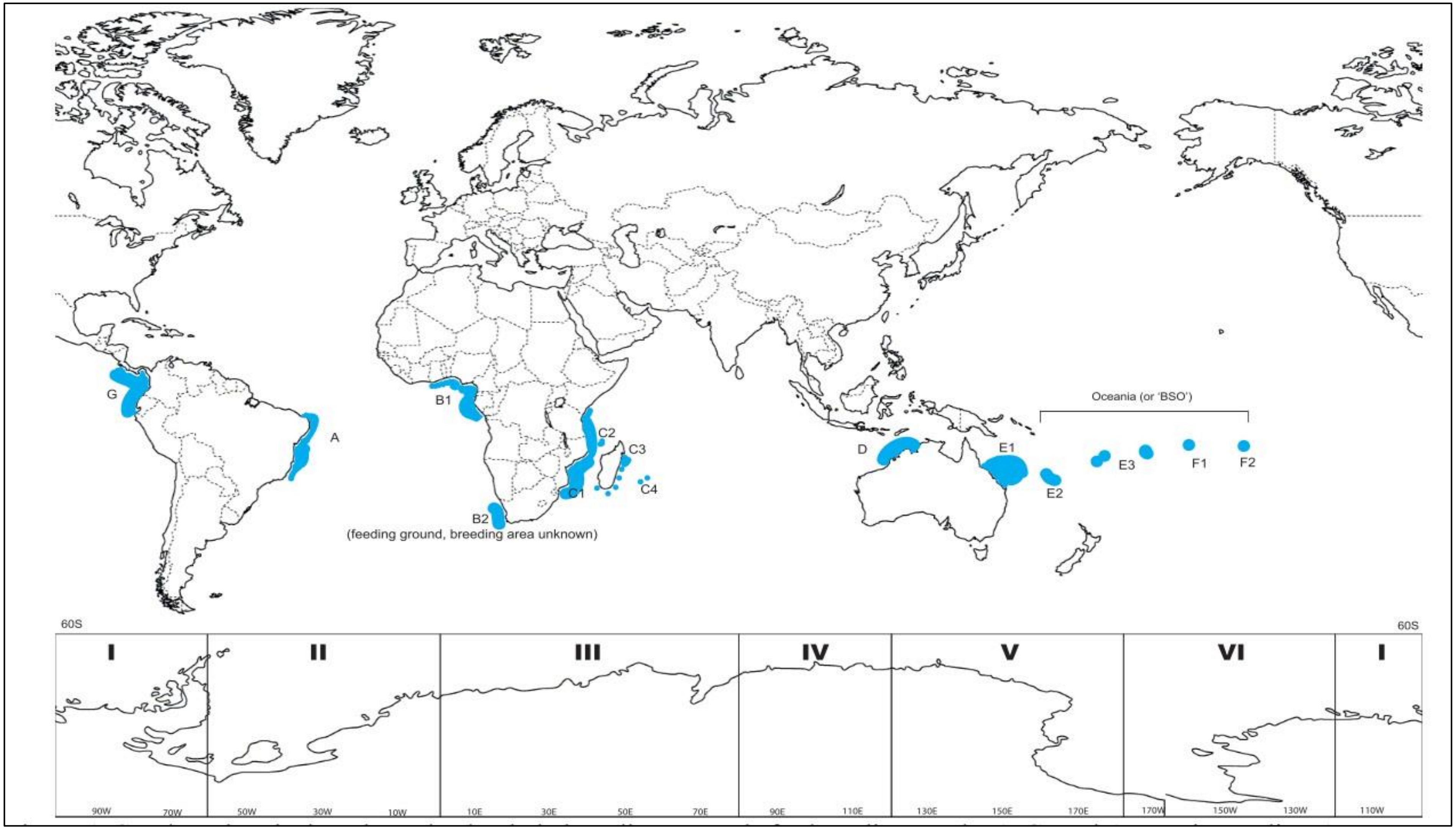


Figure 1.1: The Southern Hemisphere humpback whale feeding grounds and corresponding Breeding Stocks in summer and winter, respectively (from Jackson et al., 2015).

1.3.4 Migration streams

The annual migration between summer feeding grounds and winter breeding grounds gives rise to migration streams or corridors in coastal waters of the Southern Hemisphere continents that are linked to oceanographic and bathymetric features. Best et al. (1998) used a combination of shore- and boat-based sightings, acoustic monitoring, historical catch data, and abundance indices (from spotter aircraft and catcher boats) attached to the Durban whaling station, to propose three migratory routes used by humpback whales in the South Western Indian Ocean. The western-most route strikes the coast in the region of Knysna (34 ° S, 23° E) and continues as far as central and northern Mozambique with a possible extension to the north of this. Best et al. (1998) proposed the eastern-most route that arrives at Madagascar directly from the south, along the Madagascar Ridge. The third migration stream was proposed to travel up the centre of the Mozambique Channel towards the Comoros Islands (BS C2) and the Seychelles Archipelago. Cerchio et al. (2013), through the satellite tagging of 12 whales, identified that the BS C3 stock migrates along the Madagascar ridge and continues east up the islands of the Mascarenes group. A BS C4 sub stock has been proposed more recently due to the influx of humpback whales in the Mascarene Island group in recent years (IWC, 2011). Given the high connectivity of the C2, C3 and C4 sub stocks identified through photo identification, it is plausible to treat these three as merged sub stocks.

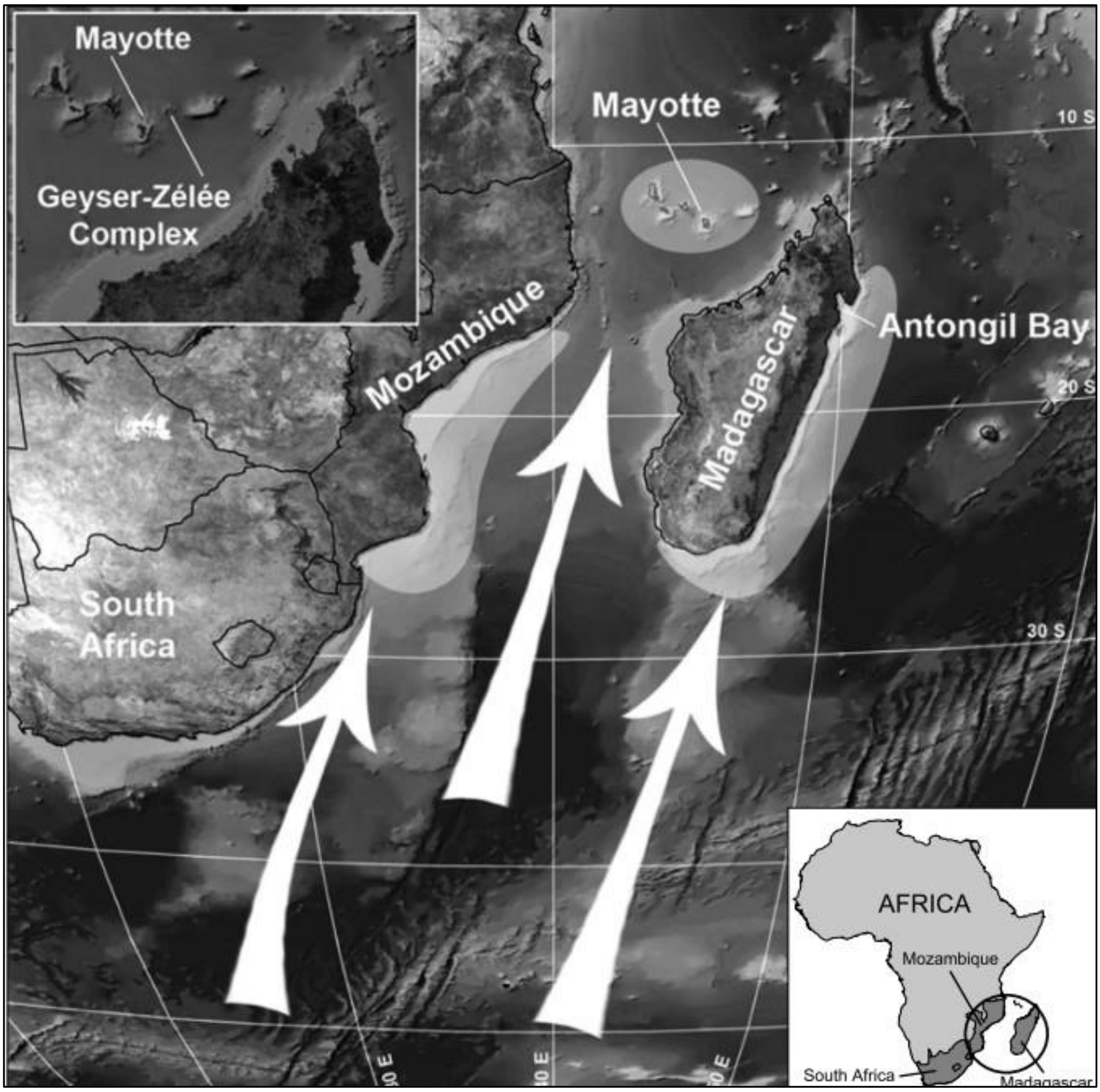


Figure 1.2: Migratory routes (white arrows) proposed by Best et al. (1998) and the general extent of the initial Western Indian Ocean breeding grounds (IWC, 2000)

The regular bimodal migration streams of most humpback whale BSs, including the C1 sub-stock, close to the shore resulted in the severely impact on this species by land-based whaling along its migration path, and means that humpback whales are well-suited to be monitored using shore-based surveying techniques.

1.4 SHORE-BASED SURVEYS

1.4.1 Advantages to shore-based surveys

Although posing a severe threat to whale populations, whaling provided important information on the ecology and biology of many cetacean species. With the cessation of whaling, non-lethal techniques of studying these animals arose, including dedicated visual surveys. However, observing these free-ranging cetaceans at sea present many challenges as these animals underwater for extended periods, move rapidly, cover vast distances (Piwetz et al., 2018), and visibility over the ocean can compromise observations. Furthermore, research approaches on the sea or from the air are expensive and can introduce a degree of potential disturbance which alter the behaviours of marine mammals during the research.

Shore-based survey methodology, where observers can study marine mammals from a distance and on land, provides a disturbance-free and cheap alternative. These techniques range from basic count surveys where the numbers of whales that pass by a specific point within a certain time frame are enumerated, often from an elevated vantage point and with use of visual aids such as binoculars, to dual operating independent platforms with the use of digital theodolites attached to laptops (Dudgeon et al., 2018; Noad et al., 2019). Shore-based survey methodology has developed considerably since it was first employed for gray whale migration surveys in the 1950s, including the methods for tracking and measuring of migration characteristics.

1.4.2 Shore-based methodology and equipment

The tracking of whales is of prime importance in shore-based methodology. The early use of clinometers started to be used from the shore to gauge the angle to the whales' abeam of the stations and therefore observers could more accurately estimate distance from the shore. Herzing and Mate, 1989 used clinometers to investigate gray whale migrations off the eastern Pacific coast of North America (1978 - 1981). Techniques progressed to single analogue land-surveying theodolites to study marine mammals from land (Piwetz et al., 2018). Theodolites measure the vertical angles relative to the zenith (directly above being 0° or 360°) and horizontal angles relative to a known location. Theodolites have a monocular eyepiece that can magnify up to 30x (magnification may vary relative to the model) and can lock in place to take an accurate reading (known as a fix) on the positions of surfacing bouts of whale groups. Measured angles are used to calculate the position of an object on the earth’s surface in the form of geographical co-ordinates. When multiple co-ordinates (or tracks) of the observed whale group are combined, the groups heading and bearing of the group and its average distance offshore can be calculated. The speed of the whale groups can by calculated when the tracks are taken in conjunction with accurate recording of the times of fixes. The measurement of migration speeds, heading, distance offshore, and group size are integral components of the relative abundance estimation methodology and require the tracking of groups by using theodolites to determine the accurate hourly passage of migrating whales.

Although Roger Payne has been credited with pioneering theodolite tracking of marine mammals (Piwetz et al., 2018), it was Würsig and Würsig (1979) who first published a description of the use of such instruments when tracking movements of bottlenose dolphins *(Tursiops truncates)* in the South Atlantic. Theodolites became an essential piece of equipment for a shore-based investigation of cetacean species, being used in several other studies over the last decades, during which it has been modernised.

Modern shore-based survey methodologies have become more complex and involve twin-platform monitoring and use digital theodolites connected to laptops running positioning software, to track migrating whales. This facilitates the direct transfer of data to a digital device, allowing less time entering data and more time to observe. The simultaneous observations from two independent observation platforms allows for simultaneous monitoring of whales, and calculations of sighting matches between platforms, and the proportion of whales missed by towers to be estimated.

1.4.3 Review of relevant past shore-based studies

Shore-based surveys have primarily been carried out on three migratory baleen whale species. These are reviewed by Findlay (1994):

1: Californian gray whales (*Eschrichtius robustus*)

Some of the first shore-based surveys were described by Reilly et al.(1983), who used binoculars and a compass to take the bearing of whales whilst conducting regular shore-based surveys to assess the population of migrating gray whales between 1967 and 1980 off California and Baja Mexico. Importantly these authors investigated five critical aspects that require inclusion when extrapolating recorded counts to total abundance estimates, namely:

(i) What proportion of the population passes beyond the sight of observers? How does the observer accuracy in estimating the distance to a whale vary? Does this change with time and experience?
(ii) Are there diel variations in migration rate? Can daylight counts be used to estimate whales at night?
(iii) How does weather (sightability) condition affect results?
(iv) Does the observer's ability to count to the number of individuals within a group vary with group size?
(v) Are the initiation and terminations of the migration fully represented in the data?

Poole (1984) also undertook shore-based count surveys (with binoculars) of migrating gray whales six days a week for 12 weeks in 1980 and 16 weeks in 1982 and found that northward migrating gray whales utilised two distinct corridors off the central Californian coast. The whales without calves moved offshore and avoided bights in the coastline, while later whales with calves travelled closer to shore following the coastal contours.

Rugh (1989) began using a clinometer in 1977 and 1978 to help gauge distances offshore while counting gray whales at the Unimak Pass in Alaska. He mentions that because it was only used with one eye, it allowed for quick readings; however, it provided a range of angles where the animal was sighted and had an accuracy limit of 3.7 km offshore. In 1979, a theodolite was installed in the glass shell used to house a Coast Guard beacon at Cape Sarichef, which provided precisely calculated positions of the passing gray whales. With the new theodolite installed, the distance offshore of the migrating whales was accurately calculated to be between 0.03 km to 1.53 km offshore; additionally, an extent of 3.7 km of coastline could be monitored on either side of the observation platform.

Buckland et al. (1993) reanalysed a portion of the data (the 1987-1988 seasons) collected from the work of Reilly et al. (1983) on migrating Californian gray whales when independent counts were made from two observation platforms. A score based on distance offshore, pod size, and time the pod was abeam the observation platform were assigned to each sighting. The average swimming speed of 6 km/h (Buckland et al., 1993) was used to estimate when pods were abeam of the station if the whales were no longer visible for the observers. A computer program was used to print out scores lower than a threshold value, and matching whale groups between platforms was then done manually.

2: Bowhead whales (*Balaena mysticetus*)

A twin-platform shore-based survey protocol was implemented from 1978 to 1988, and again in 1992, 1993, 1999, 2000 and 2001 to assess the abundance and population trend of bowhead *(Balaena mysticetus)* whales migrating past Barrow, Alaska (Zeh et al., 1991; George et al., 2004). The authors also conducted aerial surveys to estimate the proportion of whales beyond visual range. In 1984 and 1985, systematic acoustic surveillance was in used in conjunction with these aerial surveys and produced more precise results. During these experiments, the counts of whales were corrected by calculating the whale groups missed by observers and were estimated as a function of visibility, number of observers and distance from shore (George et al., 2004). These counts were also adjusted for time of day when there was no watch under acceptable conditions (George et al., 2004). These revised estimates were summed to provide a total number of whales passing within visual range for a season. An annual rate of increase (ROI) of 3.4% was calculated for the Arctic bowhead whale through these methods.

3: Southern right whales (*Eubalaena australis)*

Lundquist et al. (2004) used theodolite fixes to gauge behavioural responses of the southern right whales *(Eubalaena australis)* in a swim-with-whales tourism assessment at Península Valdéz (Argentina) from September to November 2005 and July to October 2006. Fixes were taken on focal southern right whales, on boats approaching animals, and on swimmers in water as frequently as possible to ascertain behaviour responses. The study used a digital theodolite, attached to a laptop, which recorded all the information into the *Pythagoras* software program, which the same person operated for the entire survey.

1.5 PROJECT RATIONALE

Anthropogenic activities are impacting global oceans at a rapid pace, resulting in ocean acidification, pollution, overexploitation and rising temperatures (Fabry et al., 2008; Branch et al., 2013; McCauley et al., 2015; Waters et al., 2016; Cheng et al., 2017; Bindoff et al., 2019). One of the most significant changes affecting the Southern Ocean is the decline in sea ice (Fraser and Hofmann, 2003; Cotté and Guinet, 2007). A predicted 33% decrease in the Antarctic sea ice is expected by the end of this century (Bracegirdle et al., 2008). The direct relationship between sea ice coverage and the recruitment of Antarctic krill *(Euphausia superba,* hereafter known as krill) is of great concern for the Southern Ocean baleen whale populations that are dependent on krill as a primary food source (Fraser and Hofmann, 2003). This is the case for Southern Hemisphere humpback whales, as they rely on an abundance of krill during the summer months to fuel their activities, including migrations and reproduction (Seyboth et al., 2021). Therefore, it is critical to monitor humpback whale populations to identify the possible effects of Southern Ocean ecosystem change on these whales' population parameters and health.

Data presented in this study can be helpful in the ocean governance and oceans economy sectors. Information on the whales' spatial and temporal occurrence is of value when planning coastal and ocean use zones, including, e.g., where to place shipping lanes to avoid whale collisions or conducting seismic surveys off the coast. Furthermore, the results will assist in managing, developing, and planning the South African whale-watching industry, whether from boat or land. Such industry is vital to enhance the economy of some parts of the country (Findlay, 1997), and its potential conscious expansion could bring benefits for new areas.

1.6 PROJECT AIMS

The main aim of this study was to estimate the annual rate of increase of the Southern Hemisphere humpback whale C1 sub-stock land-based observations (at Cape Vidal) on the east coast of South Africa through further measurement of relative abundances.

1.7 PROJECT OBJECTIVES

The specific objectives of the study were to:

(i) Update and refine the migration characteristics (timing of migrations, speed, the width of migration path, group size, and heading) of humpback whales migrating past Cape Vidal to the C1 sub-stock breeding grounds.

(ii) Provide updated relative abundance estimate of humpback whales of BS C from the humpback whales migrating past Cape Vidal to the BS C1 sub-stock breeding grounds; and

(iii) Estimate the current rate of increase of the humpback whales of BS C from the humpback whales migrating past Cape Vidal to the C1 sub-stock breeding grounds.

CHAPTER 2: STUDY AREA

2.1 STUDY SITE INFORMATION

Shore-based visual monitoring of the northward migrations of humpback whales was undertaken from Cape Vidal (28° 07' S, 32° 33' E) on the north-eastern coast of South Africa within the iSimangaliso World Heritage site (hereafter referred to iSimangaliso) in 2018 and 2019 (Figure 2.1). This area was chosen as it is a headland, has a high vantage above sea level, and the orientation of the coastline relative to the general south to north migration results in the congregation of whales into a migratory corridor. Adequate infrastructure was also available at Cape Vidal as this camp forms part of the iSimangaliso World Heritage site, managed by the iSimangaliso Wetland Park Authority and Ezemvelo KZN Wildlife. This site was previously used in 1988, 1989, 1990, 1991 and 2002 for similar investigations of the migrations of whales along the east coast of Southern Africa (Findlay and Best, 1996a; b; Findlay et al., 2011) so that the results of this study allow for population trend analysis over an extended period.

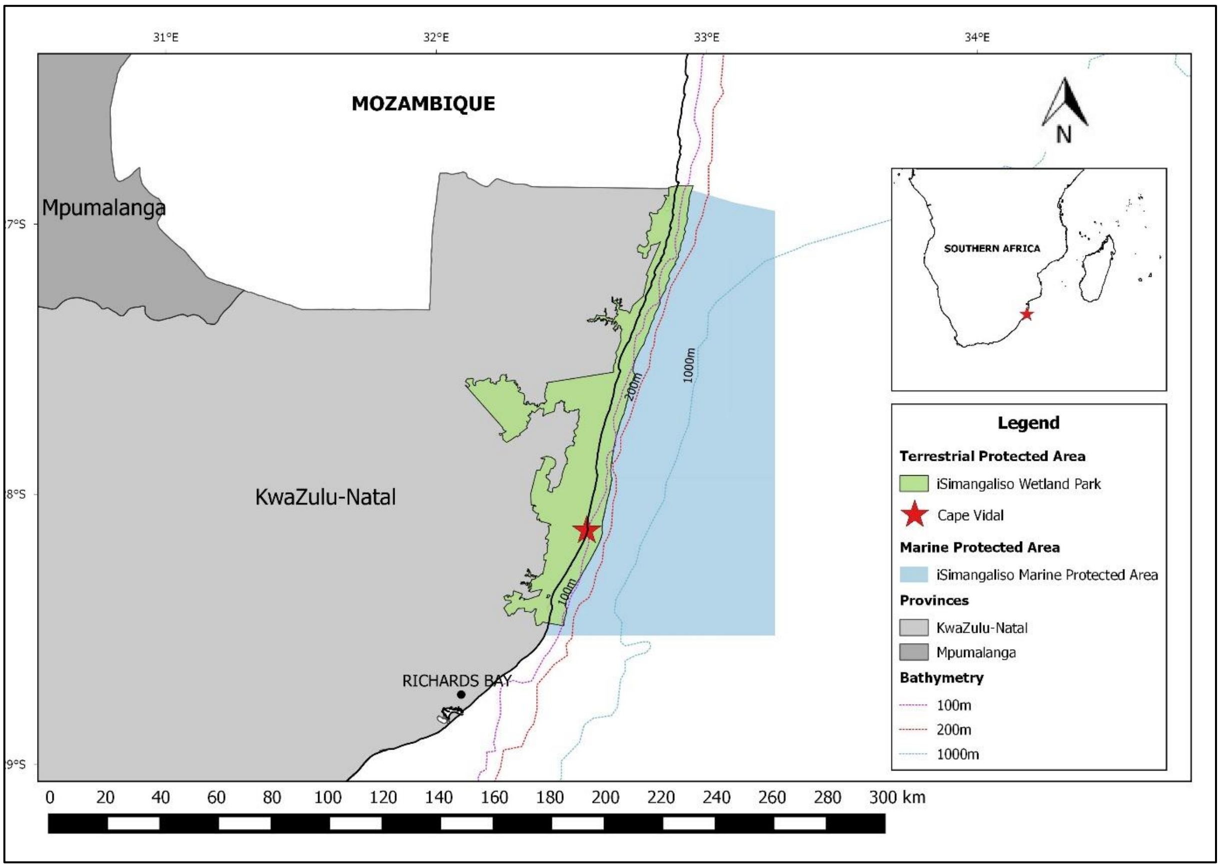


Figure 2.1: Map of the study area, encompassing the coastal area around Cape Vidal, South Africa. The blue polygon around the study area is the iSimangaliso Marine Protected Area

Cape Vidal falls within the subtropical climatic zone of Africa and experiences both tropical (summer) and warm-temperate (winter) weather systems. The average sea surface temperature (SST) during the year is 24.1° C, with maxima in February at an average of 27.3° C and minima in August at an average of 21.1° C (Ezemvelo KZN Wildlife 2018 – 2019) (Figure 2.2).

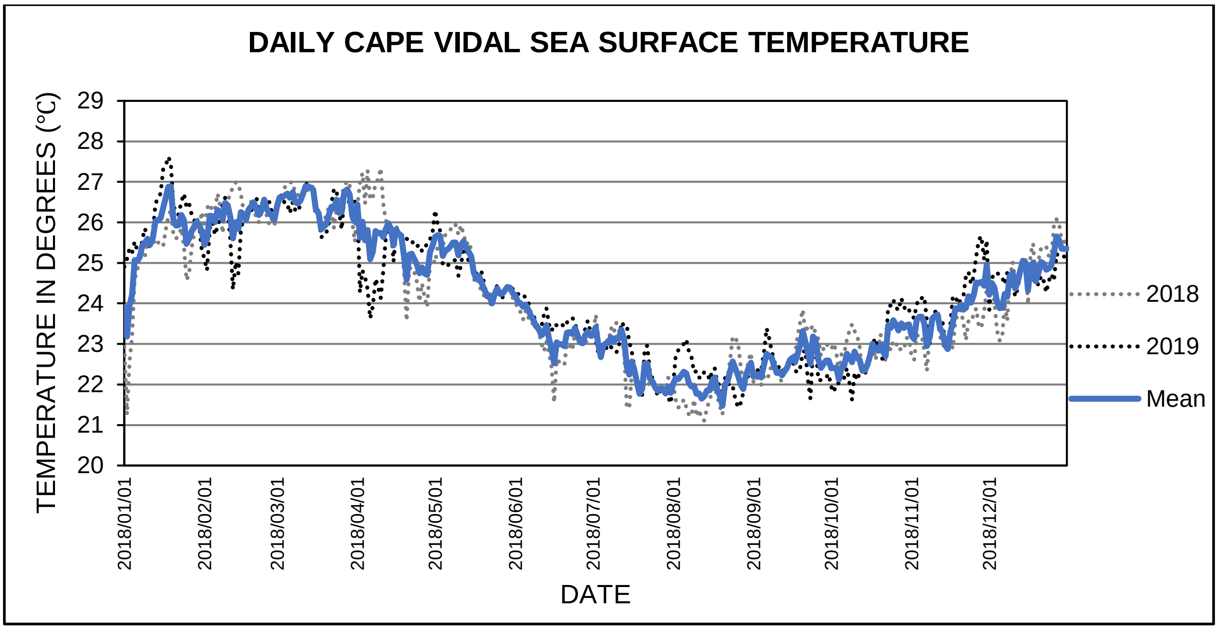


Figure 2.2: 2018 and 2019 daily sea surface temperatures (dotted line) and the average daily sea surface temperatures across both years (solid line) (Ezemvelo KZN Wildlife unpublished data)

The seasonal rainfall is highly variable; about 60% of the rain occurs during the spring and summer months from September to March, with a mean annual rainfall of 1,200 mm per year (Kelbe, 2021). The wind directions are dominated by north-easterly winds in the summer months and south-westerly in the winter months. During the winter months from May to September, cold fronts sweep across the subcontinent bringing cold air from the Southern Ocean and widespread light rainfall that may last for several days (Kelbe, 2021). Cold fronts are preceded by north-westerly winds, which swing to strong south-westerly winds blowing at over 20 knots with rain. Such weather condition reduces the ability to detects whales, as their blows are quickly dispersed, and the wavelets (white caps or white horses) obstruct views of surfacing whales.

The most influential oceanographic feature in the vicinity of Cape Vidal is the Agulhas Current, the primary western boundary current in the region. Lutjeharms (1972, 1996) identified that the current is driven by the intense sub-gyral circulation of the Southwest Indian Ocean with smaller and discontinuous inputs from the Mozambique Channel and the East Madagascar Current around the southern tip of Madagascar. Lutjeharms (1996) noted that from 28° S (the latitude of Cape Vidal) the Agulhas Current is well developed and continuously present, flowing with a mean speed of 1.4 m/s in a southerly direction, the core flows are on average seaward of the 200 m isobath, that is some 9 km offshore (Lutjeharms 2000a) but meanders approximately 15 km either side of the isobath north of Richards Bay. The current location is stable compared to other western boundary currents globally, such as the Gulf Stream and the Kuroshio Current (Lutjeharms and De Ruijter, 1996). The stability is due to the very narrow shelf along the coastline and the steep continental slope, limiting any meandering effect of the current.

At Cape Vidal, the water depth drops sharply from 50 m to 1,000 m within less than 5 km from the shore (Photopoulou et al., 2011). Although there is no current monitoring directly off Cape Vidal, current measurements (speed and direction) taken in the general vicinity (100 km north of Cape Vidal at Sodwana Bay) in 2002 range between 0.50 m/s and 0.75 m/s at a 26 m depth (Photopoulou et al., 2011). Strong northward (counter-current) conditions are experienced after periods of stable weather, suggesting the current direction is not wind-driven (Photopoulou et al., 2011). The presence of a mesoscale cyclonic eddy south of Cape St. Lucia in 2004, which as a possible mechanism for this current reversal, has been reported (Roberts et al., 2006). Off the continental shelf edge, the current speed is 0.8 m/s north to south at a depth range of 100 – 140 m at Sodwana Bay (Roberts et al., 2006); in the absence of current speed measurements at Cape Vidal, such values are regarded as the most relevant for the study area.

It has been long assumed that humpback whales use the inshore counter currents / eddies to facilitate their northern migration (Findlay, 1994) and the strong southerly current to return to the Southern Ocean. Humpback whale migration linkages between Plettenberg Bay, on the South African south coast, and the Mozambique breeding grounds have been identified, indicating that the southward migration path is maintained westwards within 20 km of the coast from well south of Cape Vidal.

2.2 STUDY PERIOD

Fieldwork was conducted from Cape Vidal from 27th June to 7th August in both 2018 and 2019. This period coincides with the peak of the northward migration of the humpback whales along the east coast of southern Africa, based on historic whaling data from the Durban Whaling Station and studies of the species in the area (Findlay and Best, 1996b; Findlay et al., 2011). **OBSERVATIONS SITES**

Observations were conducted from two timber observation towers (termed the north (NT) and south towers (ST)), each with a 3 m x 3 m covered work platform, on the vegetated dunes south of the Cape Vidal campsite. These towers stand 70 m above sea level and are 22 m apart (Figure 2.3). They provide a view through 190° (south tower) and 180° (north tower) and have an overlapped view of 160° (Figure 2.4). The distance to the horizon from this vantage is approximately 20 km. The south tower was constructed in 1988, whilst the north tower was erected in 1990 (Findlay and Best, 1996b; Findlay et al., 2011).

Figure 2.3:a) North tower observation platform and (b) South tower observation platform at Cape Vidal, South Africa

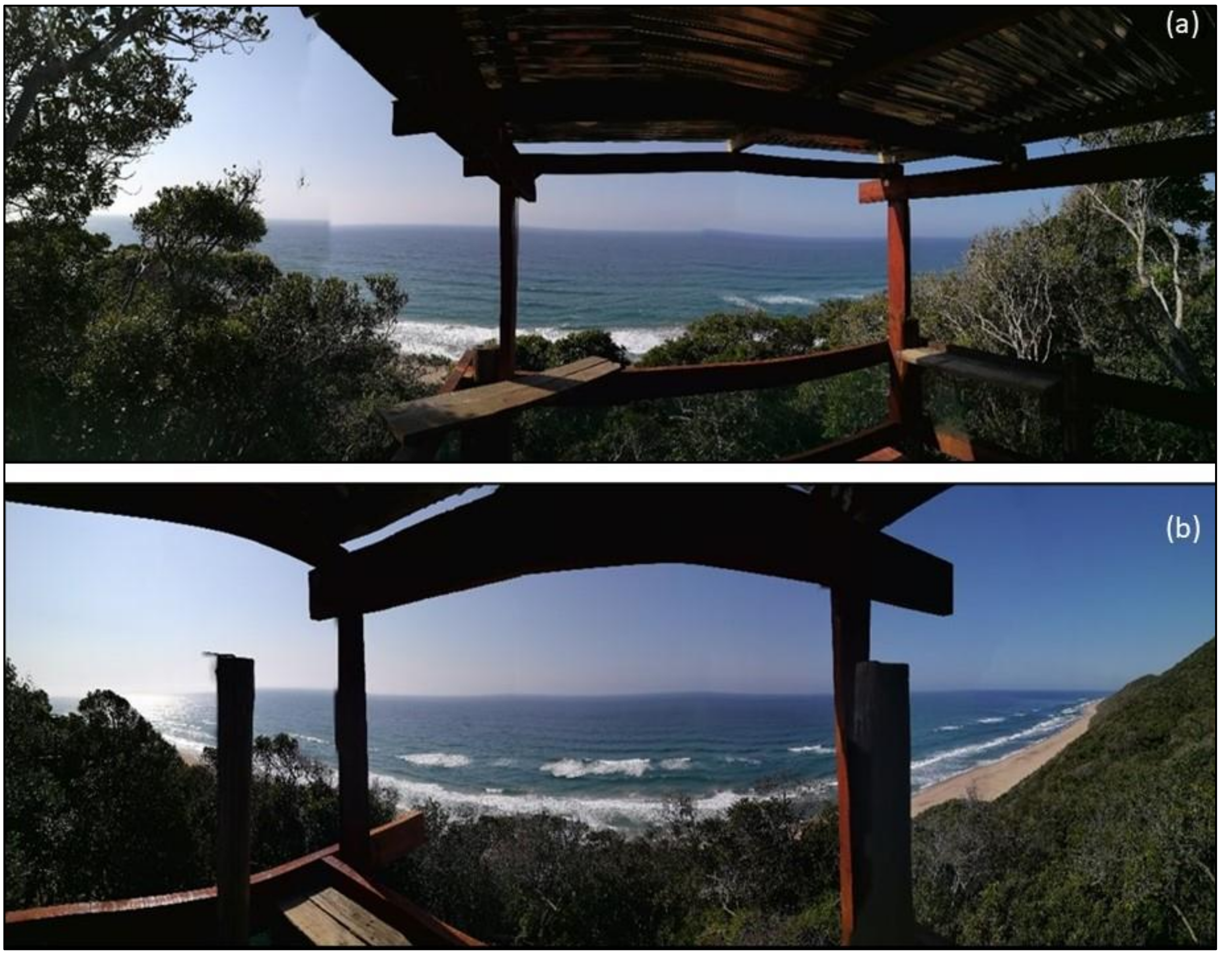


Figure 2.4: (a) Panoramic 180° field of view from the north tower and (b) Panoramic 190° field of view from the south tower, at Cape Vidal, South Africa

The two towers were visually and acoustically isolated from each other to ensure observer independence between towers.

Using the mark-recapture methodology, the rationale for using two independent observation towers was to be able to ascertain the total number of groups passing the study area and determine how many groups of whales were potentially missed by observers .The groups detected by the south tower being the initial (marked) sample, the groups the north tower made for the second sample, and those groups seen by both towers (determined through timed theodolite positional tracking) being the marked-recaptured component.

Before the 2018 field season, both towers were restored with new wooden supports, stairs, and roofing. The path to the towers was refurbished, and new stairs up the dunes were installed to minimise any potential future erosion. In 2019, new PVC (60%) roof sheets were installed to allow lighter conditions on the work platforms. Some trees were trimmed in 2018, allowing for the 160° uninterrupted overlapped view to the horizon, while no additional trimming was required for the 2019 field season.

CHAPTER 3: DENSITY AND MIGRATION CHARACTERISTICS OF HUMPBACK WHALES MIGRATING ALONG THE EAST COAST OF SOUTH AFRICA

3.1 INTRODUCTION

Shore-based surveys of humpback whales have been conducted from 1978 onwards on the east coast of Australia (Chittleborough, 1965; Bryden, 1985; Paterson and Paterson, 1989; Paterson, 1991; Brown 1996; Noad et al., 2008; Noad et al., 2019). Different projects took observations from two prominent headlands at the northern ends of the North Stradbroke and Moreton Islands, 42 km apart (Paterson and Paterson, 1989). Various authors have monitored population abundance and rates of increase throughout the years. In 1987 the abundance estimate for humpback whales was 790 with an ROI of 14.4% (Bryden et al., 1990), this increased in 1992 to 1,896 and ROI of 9.7% (Paterson et al., 1994), continuing to 2,099 and an ROI of 10% by 1996 (Brown, 1996). In 2015 the most recent survey was conducted with an absolute abundance estimate 24,545 and a long term average ROI of 10.9% per annum (Noad et al., 2019).

Studies that incorporate theodolites from twin observation platforms were undertaken in Queensland, eastern Australia, by Dudgeon et al. (2018) and Noad et al. (2008), which built on work by Brown (1996). The authors identified heterogeneity in detection probabilities from two vantage points on land, using digital theodolites connected to laptops, in conjunction with aerial surveys. A negative relationship with detection whales was observed when multiple whales were being tracked simultaneously. In addition, the effect of group size was explicit; the bigger groups had an increased chance of being "recaptured" across both platforms.

In Western Australia, off Shark Bay, Hedley et al. (2020) used twin platform theodolite surveys to estimate an abundance estimate of the BS D stock. Unfortunately, they only completed one of the two survey weeks planned, due to logistical issues. However, this shore-based work was performed in conjunction with 26 successful survey flights, and the land based estimates were used to calibrate the aerial survey estimates (Hedley et al., 2011). It was found that observer team and group size caused significant heterogeneity in sighting probabilities (Dudgeon et al., 2018).

Barendse et al. (2010) undertook shore-based surveys from Saldanha Bay on the West Coast of South Africa, using a Wild T1 manual theodolite (equipped with a 22x telescope) to monitor the movement patterns of humpback whales offshore. They observed a significant reduction in actual swimming speed and increase in “non-directional” movement during mid-spring compared with other times of the year. They also found the distribution of whales to be farther offshore during mid-spring.

James (2014) employed shore-based theodolite tracking to investigate spatial use, seasonality and movement patterns related to anthropogenic factors that could influence the cetacean species in both Mossel Bay and Vleesbaai. She used the theodolite to obtain spatial data from the cetaceans, while another researcher collected their behaviour data from observations through binoculars. Levy (2017) used the same methodology when examining the underlining environmental variables that could potentially affect five cetacean species in Mossel Bay.

In South Africa, the first study using theodolites to study humpback whales was Findlay (1994) on the east coast between 1989 and 1991 (more detail to follow). Findlay recorded and tracked all cetacean species during his study, and latter Photopoulou et al. (2011) analysed all the bottlenose dolphin *(Tursiops aduncus)* sightings recorded. She ascertained the dolphins' heading and travel distance from shore in the study area through this previously collected data.

Findlay and Best (1996a; b) conducted dedicated daily observations from platforms specifically built for shore-based whale monitoring at Cape Vidal, South Africa during June, July, and August from 1988 to 1989 (south tower). The authors introduced a second tower during the 1990 and 1991 surveys (north tower), and simultaneous observations were introduced to determine observer efficiency through independent mark-recapture analyses of sightings. In 2002, the shore-based surveys were repeated by Findlay et al. (2011), using the same tower platforms, equipment and sampling protocol.

3.2 METHODS

3.2.1 Field methods

Observations were conducted by teams of two observers on each tower between 07h00 and 17h00 each day (weather and observation conditions permitting). Team changes were carried out at 09h00, 12h00 and 15h00 so that each team carried out a total of 5 hours of observation per day (one shift of two hours and one shift of three hours with alternations between shifts each day). Both observers searched each platform's entire field of view, with one observer searching the area with 8 x 50 Nikon wide-angle binoculars while also scribing and searching for new groups of approaching whales. The second observer operated the theodolite (as described below) while also searching with the naked eye (Figure 2.5). The observers chose the role that they were most comfortable with, and they were not rotated for the duration of their study period. Most of the teams were not altered between years; this ensured the most consistency, thus providing the collection of more accurate data.

Analogue, one-second resolution survey theodolites (model Wild TM 1 A) were used exclusively throughout the study. These theodolites were preferred as Findlay et al. (2011) used them at Cape Vidal, thus making the datasets more comparable. Additionally, the observation platforms would not allow the calibration of digital or total station systems. Observers received training on setting up, calibrating, and operating the theodolites before each survey and whenever necessary thereafter. Observers were supervised every morning and checked throughout the day to ensure calibrations of reference angles were correct; whenever the theodolite was adjusted, these reference angles were calibrated again (e.g., on a shift change).

Once sighted, whales were tracked using the theodolite as positional fixes of horizontal and vertical angles of successive bouts of surface-active behaviour. A group of whales was defined as having animals within five body lengths of each other. Vertical angles to groups provided the radial distance between them and the observers on towers, while horizontal angles provided the bearing from the north. Positions were immediately plotted on charts (adjacent to the datasheet), which permitted checking possible errors in the fixes obtained (see Appendix A). Discrimination between closely migrating groups also provided a vertical reference as to where the animals may surface next. Time was measured to the nearest second using synchronised timepieces in both towers.

Search activity was planned to occur seven days per week during daylight hours, although this was weather-dependent. The time when searching began and ceased were recorded daily. Additional information was also recorded, such as observer team changeovers, sightings of dolphins (species, group size), or when boats or ships entered the field of view.

Collected data can be divided into search effort data, sighting data combined with the theodolite tracks measuring whale behaviour, weather conditions (see below) and sightability data. These can be divided into abundance parameters (frequency of sightings by effort), behavioural parameters (speed and direction of migration, distance offshore, and group size) and environmentally dependant parameters (time of day, wind speed and direction, distance offshore and depth and sightability) determined from the weather records.

Weather conditions recorded hourly, on the hour, included:

(i) Wind (speed and direction).
(ii) Cloud cover (rating out of 8^{ths} cover).
(iii) Sea state (in the Beaufort scale).
(iv) Swell height (in m).
(v) Visibility (maximum distance offshore the theodolite could accurately record a vertical angle, in km); and
(vi) Sightability (an overall rating of combined weather conditions considering the probability of a whale to be detected in the conditions; 1 = poor to 5 = good).

Findlay and Best (1996a) noted that heterogeneity in sighting probability arises from four factors: whale behaviour, distance from the observer, sighting conditions, and group size. Heterogeneity in sighting probabilities is best measured by stratification of the data into bins as follows:

(i) The mean daily sightability conditions were averaged throughout the day and again between the two towers to give a mean sightability of the study area for the day. Data were stratified into poor (≤ 3), fair (3 - 4), and good (> 4); and
(ii) Distance offshore data were stratified into < 3 km, 3 - 6 km and > 6 km bins.

Stratification of group size and behaviour were precluded because:

(i) evaluation of behaviour can be highly subjective, and
(ii) (ii) some groups were recorded by both towers as having different group sizes (given the distances of observers from the whale groups).

3.2.2 Data analyses

Data were digitised and analysed through custom Python coded applications, using the Anaconda Spyder console version 3.8 (Spyder-IDE.org). Initial analyses converted the horizontal and vertical theodolite angles into distances and bearing from the platform, taking both a refraction correction factor and the curvature of the Earth into consideration. These were subsequently converted into GPS coordinates on a cartesian plane (as position fixes).

Additional Python code applications were used to calculate migration speed and heading of groups with more than two fixes. Groups with only one fix were given the mean speed and bearing of all groups observed in that same survey period. However, groups with three or more theodolite fixes were used to calculate mean speed, group size, and heading. Distance offshore was calculated as the distance between the mean position of the group and the shoreline directly west.

As observations can only occur during daylight hours, and whales are assumed to continue migration at night, the daily densities of migrating whales (over 24 hours) needed to be extrapolated by the number of groups sighted during the watch periods each day. Such extrapolation requires an assumption that whales' migration speeds are constant across the 24 hours (Findlay and Best, 1996b). This assumption of constant diel migration has been confirmed by Zerbini et al. (2006), Cerchio et al. (2013) and Riekkola et al. (2019) through satellite tagging and telemetry tracking of migrating humpback whales.

For a group to be included in the daily density estimations, the group must have crossed the midline of the observation area within the observation period, otherwise daily densities would be inflated. Groups not seen crossing the midline of the observation area were projected forwards or backwards using their measured speed and bearing to calculate their projected time of midline crossing. Further coding was developed to accomplish this. Such groups were included in the analyses only if the projected time of their projected intersection fell within the observation period.

3.2.3 Statistical analysis

Data collected in this project were categorised into:

(i) Observer effort: the time spent in towers observing whales daily and survey tallies.

(ii) Sighting frequencies: the number of whales observed per migration parameter, such as the number of whales per hour or the number of whales per offshore distance bin.

(iii) Migration characteristics: the mean of different migration parameters, such as mean speed of whale groups and mean whale group size; and

(iv) Weather and observation conditions: the mean daily sightability conditions used to explain the estimated proportion of whale groups missed by observers in each tower per day.

Whereas only observations with three or more fixes from the theodolite (maximum accuracy) were used to analyse the mean group size, speed, and headings, in contrast, all sightings were used in estimating the distance offshore and the number of groups per day. All data were further filtered to ensure that implausible speeds of over 20 km/h and distances from the shore over 20 km were disregarded from analyses. Such values were likely a product of inconsistent tracking with the theodolite.

As the sample sizes is between 0 and 2000 a Shapiro Wilk normality test will be run to indicate if the data were distributed normally, and a parametric test could be used. If the data is found to be skewed and non-parametric tests would be used. Testing will be done using the same methodology, between the years to measure any differences in the population migration characteristics, and we will be comparing one variable at a time. In that regard the parametric test to be used be a T – Test, and the non-parametric test will be a Wilcoxon signed rank test.

Additionally, the data will be divided in to four ten- day periods (27/06 – 06/07; 07/07 – 16/07; 17/07 -26/07; 27/07 -05/08). The mean of these data will be analysed with linear regression and plotted on to a graph to understand the impact of any changes over the time periods.

A Spearman rank correlations matrix is used to investigate correlations between the migration parameters (for example, if the whales were further offshore depending on the group size or migrating faster/slower depending on their distance from shore).

3.3 RESULTS

3.3.1 Observation effort

A total of 289 and 312.5 hours of independent surveying was conducted from each tower in 2018 and 2019, respectively, over a monitoring period of the same 42 days each year (Figure 3.1).

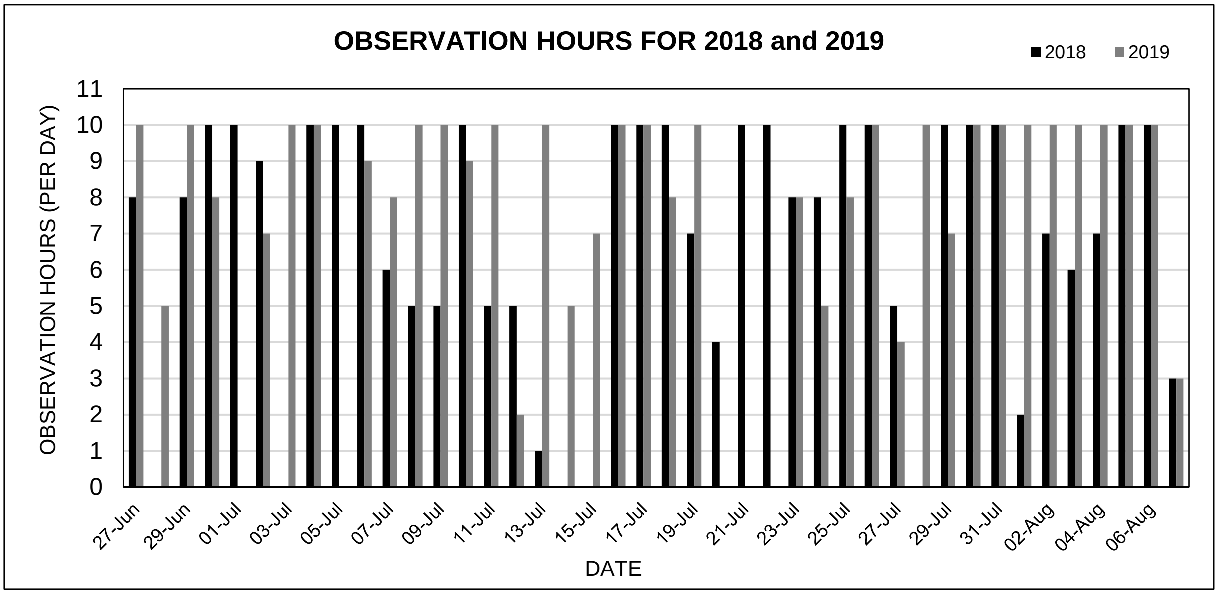


Figure 3.1: Distribution of observation daily effort (hours) carried out during independent surveys in 2018 and 2019 at Cape Vidal, South Africa

The number of hours of surveying per day varied from zero to ten hours due to the variable weather conditions (Figure 3.1). During the 2018 season, only five days (12%) had no observation effort, while 19 days had over nine hours of observations (45%) (Figure 3.2). It was similar in the 2019 survey when there were also five days of no observation effort (12%), but 23 days (54%) of observation days were for more than nine hours (Figure 3.2). Shapiro Wilks test for normality found the data to skewed ($p < 0.05$). A Wilcoxon signed rank test revealed that there was no significant difference in survey effort in 2018 (*Md* = 8, *n* = 42) when compared to 2019 (*Md* = 9.5, *n* = 42), *T* = 335 z= -0.977, *p*= 0.329.

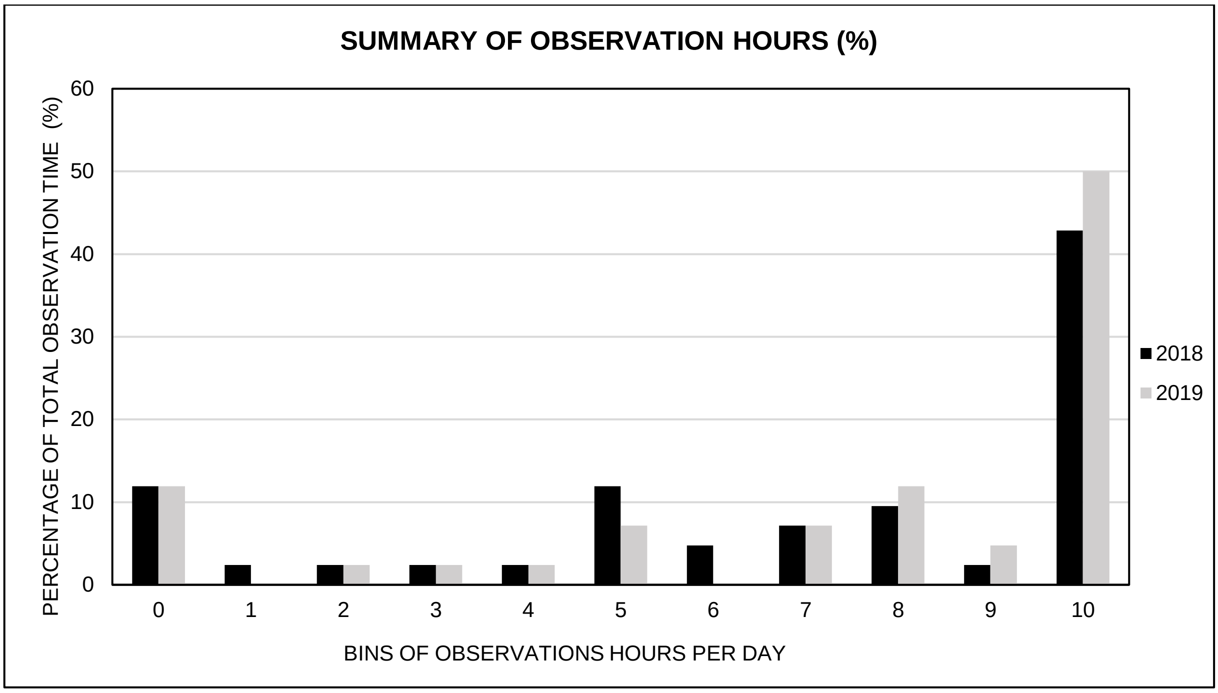


Figure 3.2: The percentage of the total observation effort (hours) carried out per day during the 2018 and 2019 surveys in Cape Vidal, South Africa

3.3.2 Sightability conditions

In both study years (Figure 3.3), the general weather patterns experienced on the survey comprised cycles of five days of north-westerly winds, starting from calm (Beaufort scale 1 or 2) in the morning and ending with strong breezes (Beaufort scale 4 or 5) in the evening (acceptable sighting conditions). This period would be followed by two days of south-westerly wind and eventual rain squalls (unacceptable sighting conditions). For most days, sightability was rated "good" (55% in 2018 and 45% in 2019), followed by "fair" (24% in 2018 and 38% in 2019) and "poor" conditions (21% in 2018 and 17% in 2019) (Figure 3.4). Shapiro Wilks test for normality found the mean sightability data over the survey period to skewed ($p < 0.05$). A Wilcoxon signed rank test revealed that there was no significant difference in mean sightability conditions in 2018 (Md = 4.14, n = 42) when compared to 2019 (Md = 3.96, n = 42), T = 391 z = -0.512, p= 0.609.

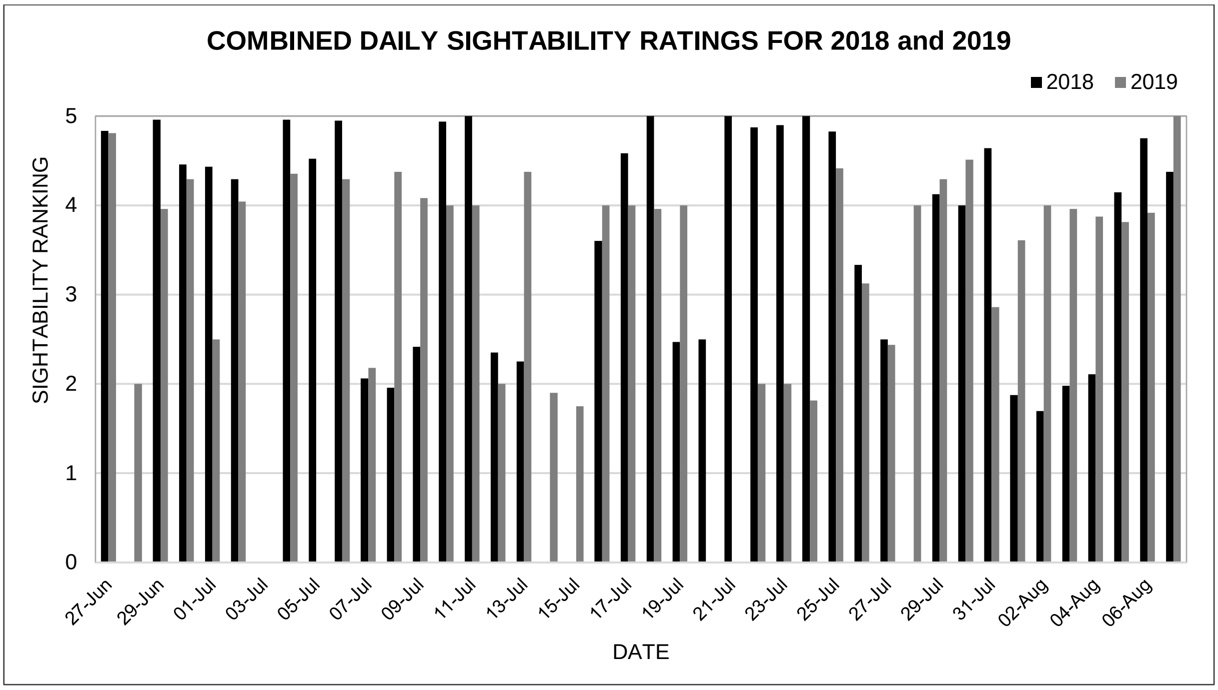


Figure 3.3: Distribution of mean north and south tower daily sightability ratings over the surveys in 2018 and 2019 at Cape Vidal, South Africa

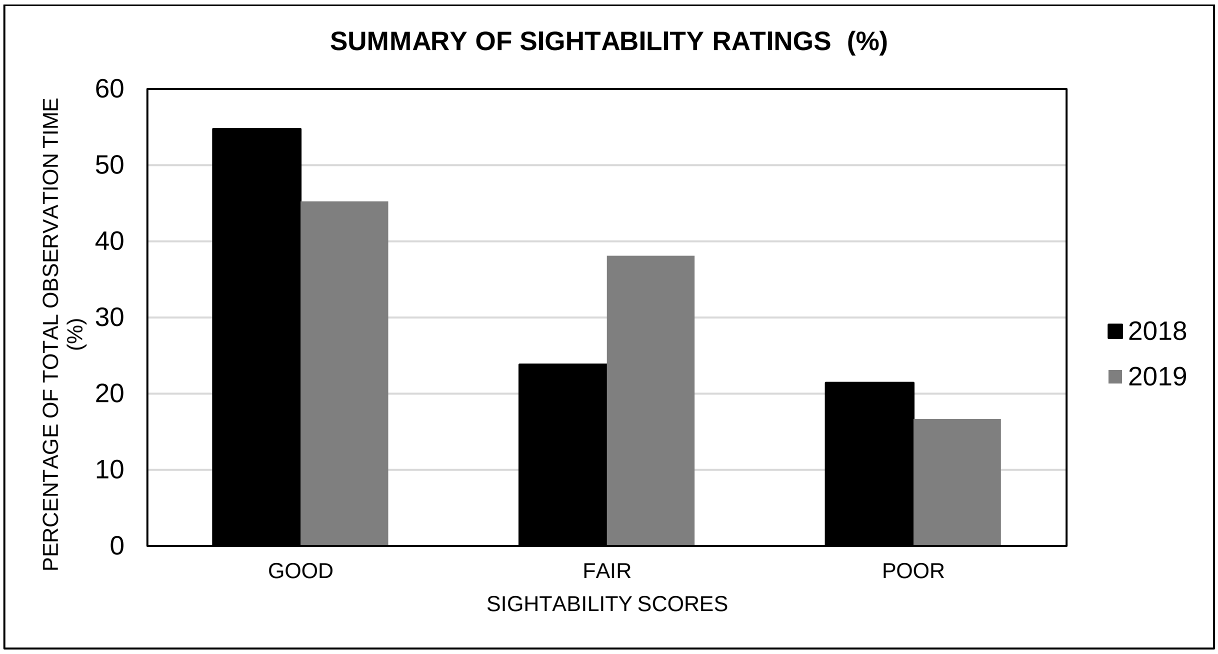


Figure 3.4: Percentage of observation hours per mean sightability score in the 2018 and 2019 surveys at Cape Vidal, South Africa

3.3.3 Densities

In 2018, 1,281 humpback whale groups were tracked from the north and 1,100 from the south tower. In 2019, 1,271 groups were recorded from the north and 1,306 from the south tower, respectively (Table 3.1).

Table 3-1: Summary of the observation effort and the number of humpback whale groups observed during shore-based surveys undertaken at Cape Vidal, South Africa, during 2018 and 2019

Year	Observation effort (h)	Number of humpback whale groups observed	
		South tower	North tower
2018	289.0	1,100	1,281
2019	312.5	1,306	1,271

Daily densities (whale groups per hour per day) of migrating humpback whale groups observed during the study period are shown below in Figure 3.5 and Figure 3.6. In both 2018 and 2019, densities peaked during the week from 28th July to 3rd August. The highest number of whale groups per hour was seen during 2018 in a single day was on 31st July 2018, with nine whale groups per hour (90 groups in 10 hours effort). In 2019 it was on the 7th of August 2019, with 12 groups per hour (36 groups in 3 hours) were counted.

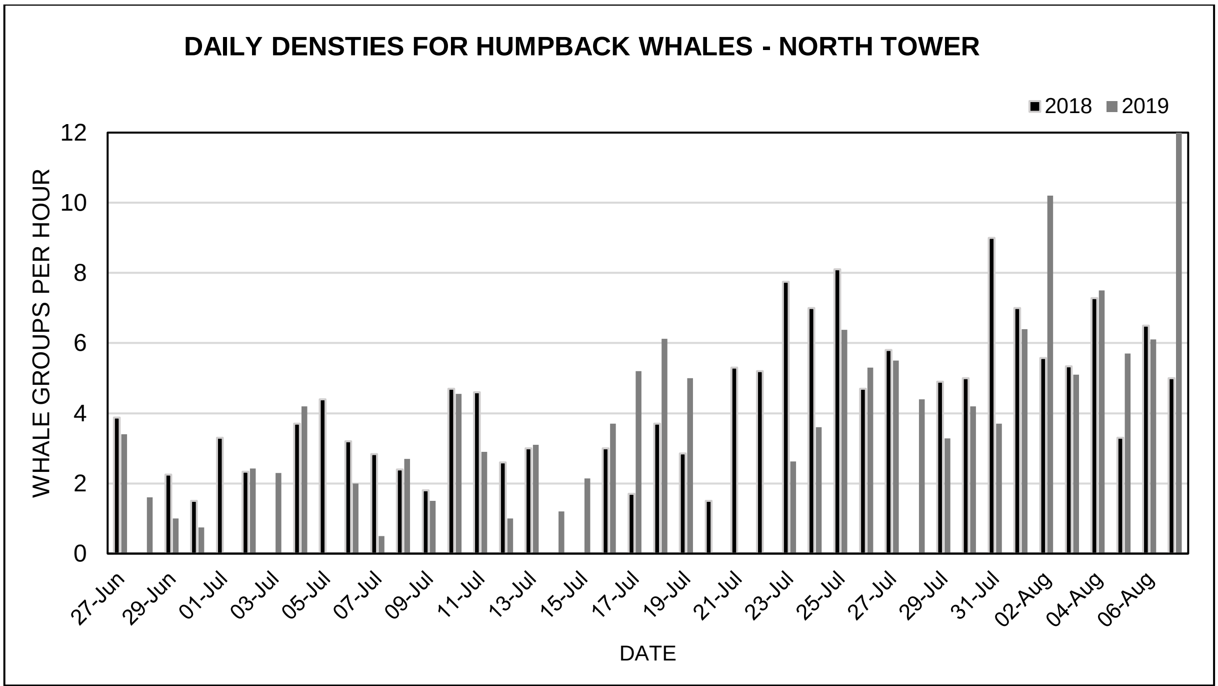


Figure 3.5: Daily densities of migrating humpback whale groups per day passing Cape Vidal, South Africa, observed from the north tower

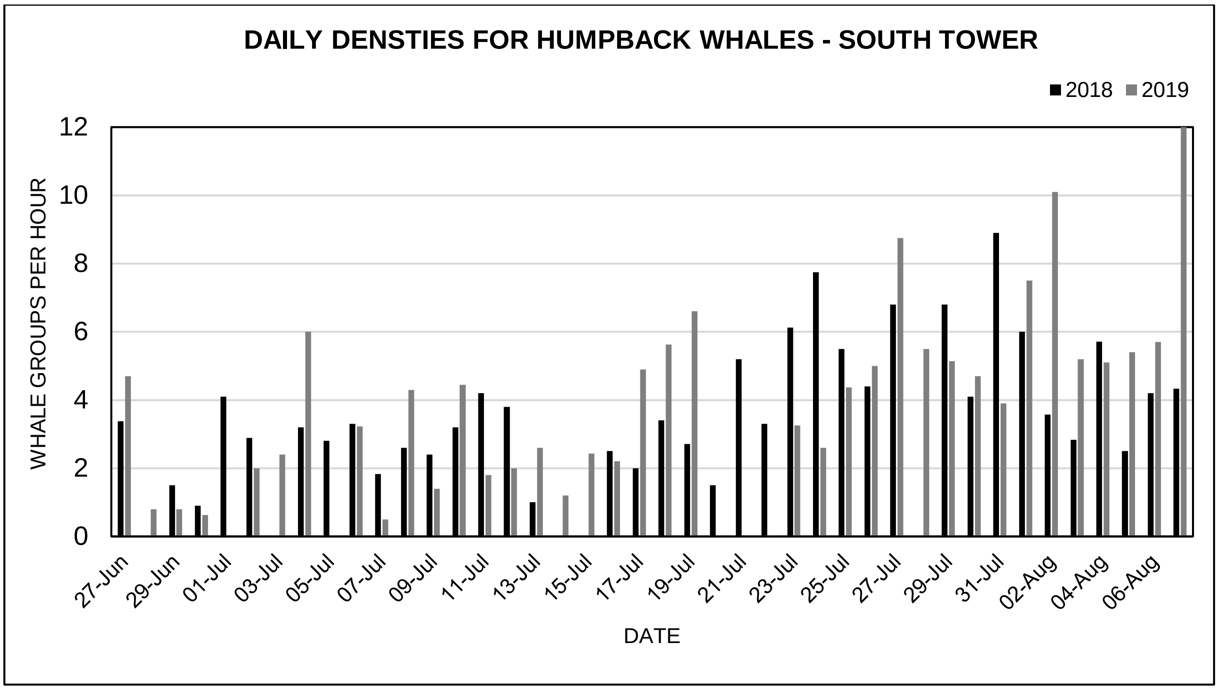


Figure 3.6: Daily densities of migrating humpback whale groups per day passing Cape Vidal, South Africa, observed from the south tower

A Shapiro Wilks test for normality found the data to distributed normally for the north tower in 2018 (p = 0.397) and 2019 (p = 0.016) and are therefore suitable for parametric testing. A paired-samples t – test was conducted to compare the whale group densities in 2018 and 2019 from the north tower. The number of whale groups per hour seen from the north tower in 2018 (M = 3.856, SD = 2.333) and 2019 (M = 3.555, SD = 2.692) were not statistically significantly different between the years t (42) = 0.718, p = 0.477). The south tower data was also tested as normally distributed (Shapiro Wilks test) in both 2018 (p = 0.218) and 2019 (p= 0.018). The number of whale groups per hour seen from the south tower in 2018 (M = 3.363, SD = 2.151) and 2019 (M = 3.689, SD = 2.814) were also not statistically significantly different between the years t (42) = 0.714, p = 0.480).

Whale groups increased in numbers throughout the survey in both years and according to the observations from each tower (Figures 3.7 and 3.8) A linear regression was used to analysis the trend in whale group densities in the north tower (Figures 3.7) and in the south tower (Figures 3.8) between 2018 and 2019 across the same ten-day periods. All the comparisons indicate an increase in whale group densities throughout the season with the highest densities being in the last ten-day period in late July, early August.

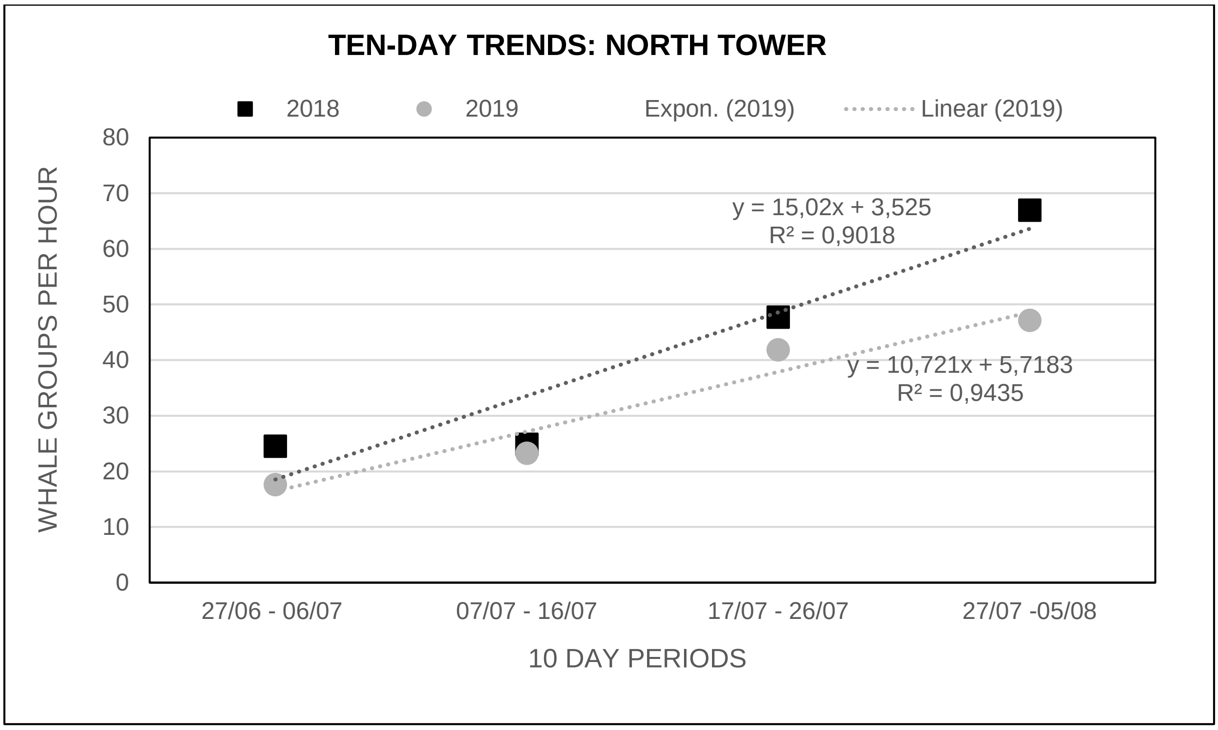


Figure 3.7: Trend in the number of humpback whale densities (groups observed per hour) passing Cape Vidal per 10-days periods in the 2018 and 2019 field seasons, as observed from the north tower

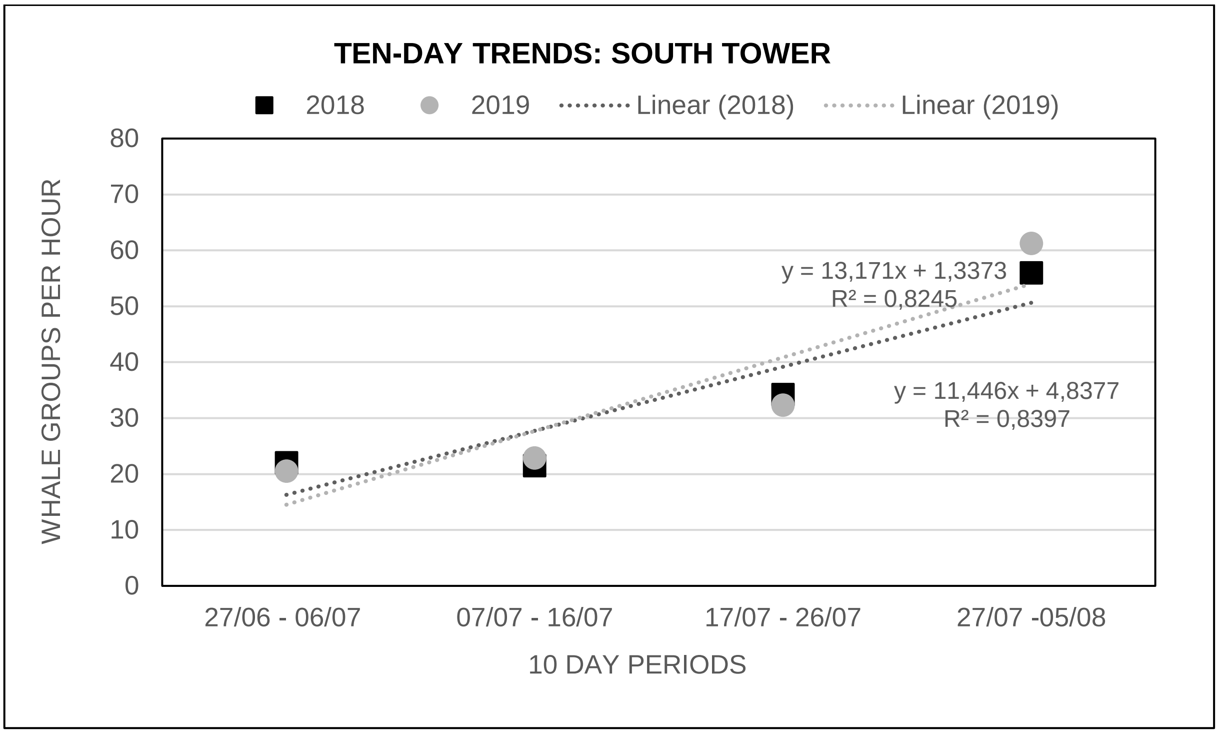


Figure 3.8: Trend in the number of humpback whale densities (groups observed per hour) passing Cape Vidal per day in the 2018 and 2019 field seasons, as observed from the south tower

3.3.4 Migration characteristics

3.3.4.1 Group sizes

Group sizes varied from one to nine animals (Figures 3.9 and 3.10), a median group size of 2.00 was observed for the north tower in 2018 and 2019 as well as the south tower in 2018 and 2019 (see figure

3.11). Group sizes of one to two individuals were the most common, comprising 71% and 85% of all the sightings in 2018 and 2019, respectively.

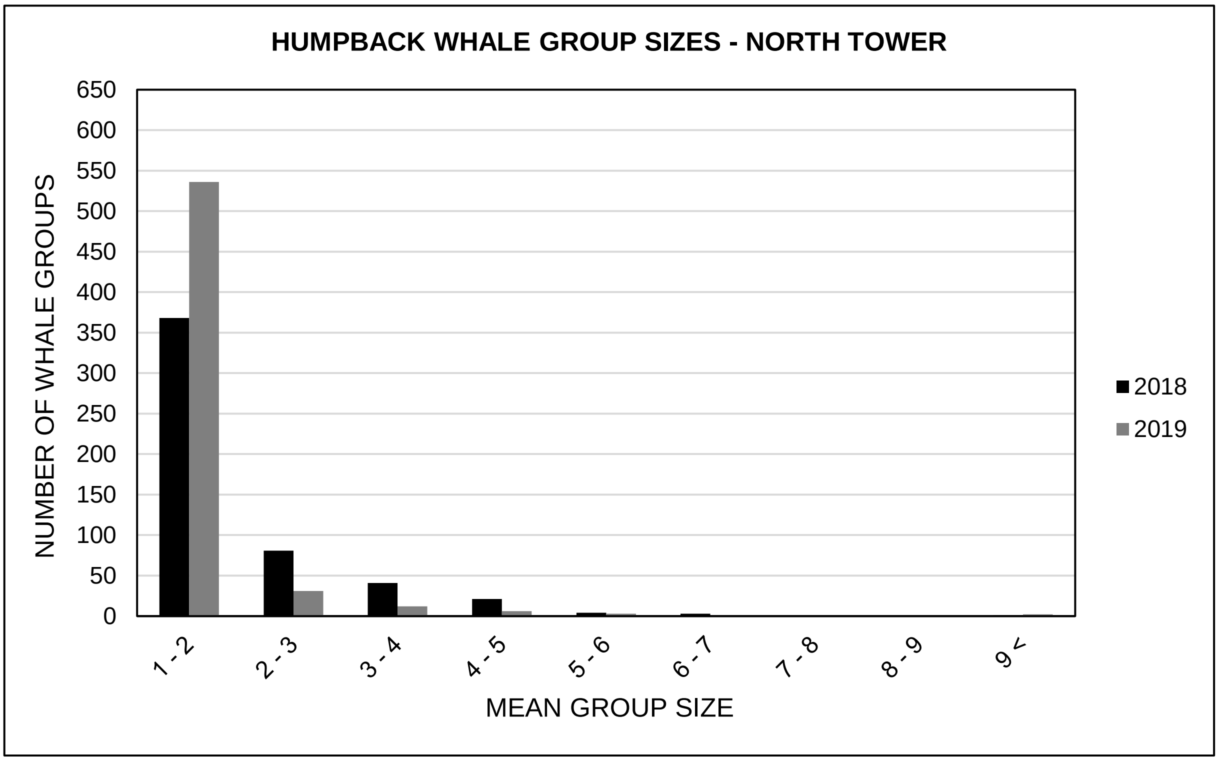


Figure 3.9: The frequency of mean group sizes of humpback whales sighted from the north tower in 2018 and 2019 surveys from Cape Vidal, South Africa

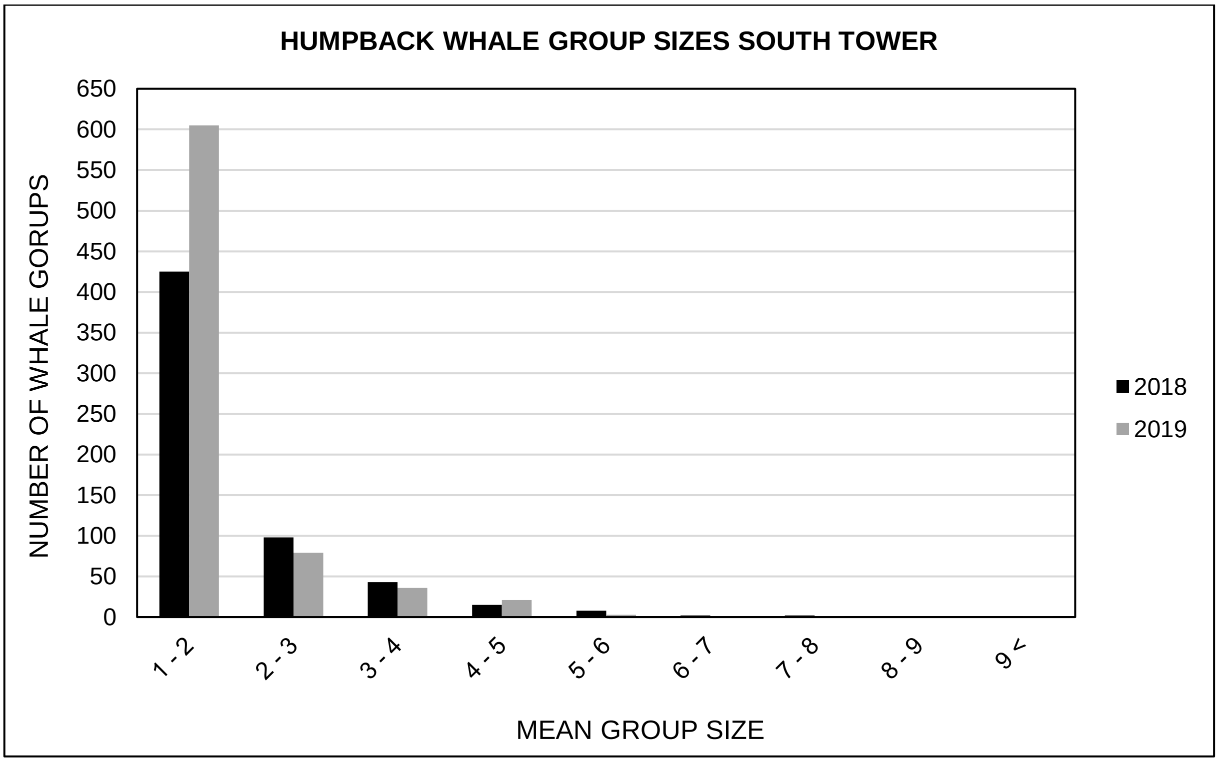


Figure 3.10: The frequency of mean group sizes of humpback whales sighted from the south tower in 2018 and 2019 surveys from Cape Vidal, South Africa

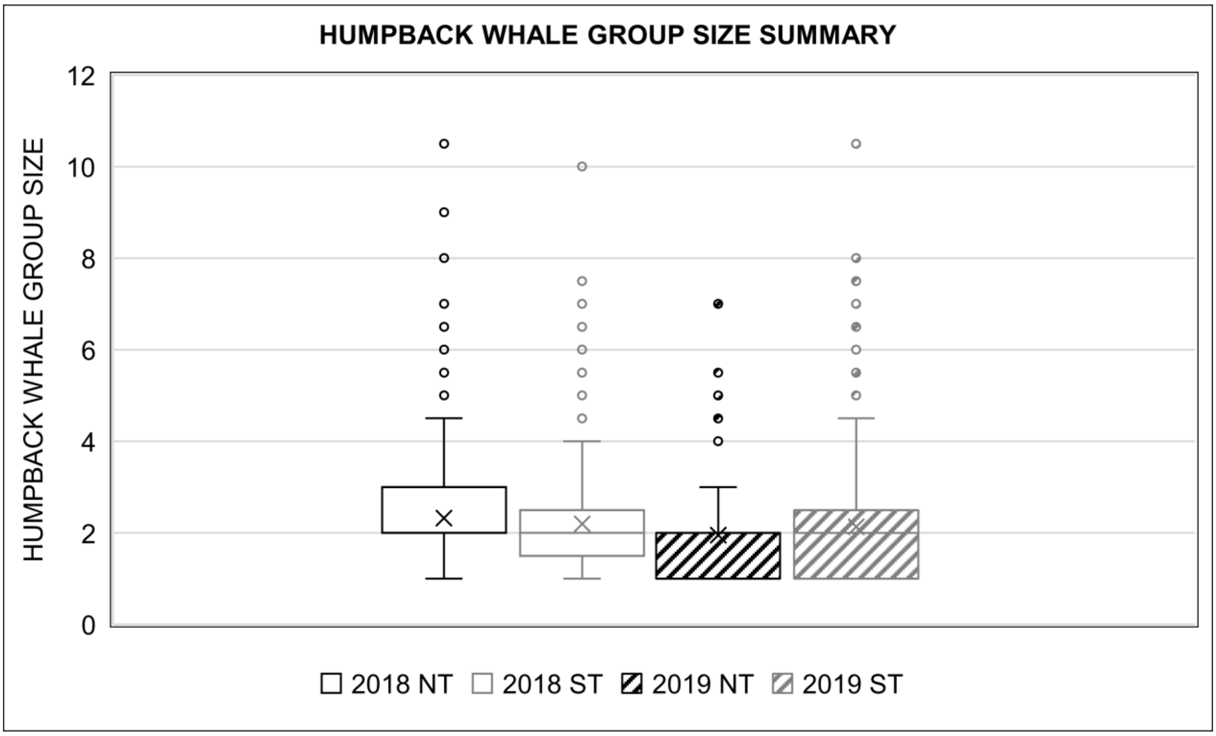


Figure 3.11: A box whisker plot summarising the mean, median, upper, and lower quartile as well as the extreme maximums of the humpback whale group sizes observed from both towers during the 2018 and 2019 surveys at Cape Vidal, South Africa

A Shapiro Wilks test for normality found the data to skewed for both towers in 2018 (p < 005) and 2019 (p < 0.05) and therefore suitable for non-parametric testing. The whales' groups size passing the north tower recorded a median of 2 whales per group in both 2018 (*MD* = 2, *SD* = 1.142) and 2019 *(MD* = 2, *SD* = 0.948), however a Wilcoxon signed rank test indicated that the group sizes between the two years are statistically significantly different, *T* = 11739.50, *z* = -6.456 *p* < 0.05. In contrast the south tower (also a median of 2 whales per group in 2018 (*SD* = 1.180) and 2019(*SD* = 1.230)) illustrated that there was no statically significant difference between group sizes between years, *T* = 69366, *z* = -1.090 *p* = 0.276. This result may reflect the larger sample size that the north tower contributed to the dataset.

Linear regressions were used to illustrate trends in the mean group size over the various ten-day periods of the surveys (see figures 3.12 and figure 3.13). In 2019 both the north and the south tower noted an increase in mean group size during the third ten-day period (17 July to the 26 July). That observation aside, the group sizes remained consistent across both surveys in both towers.

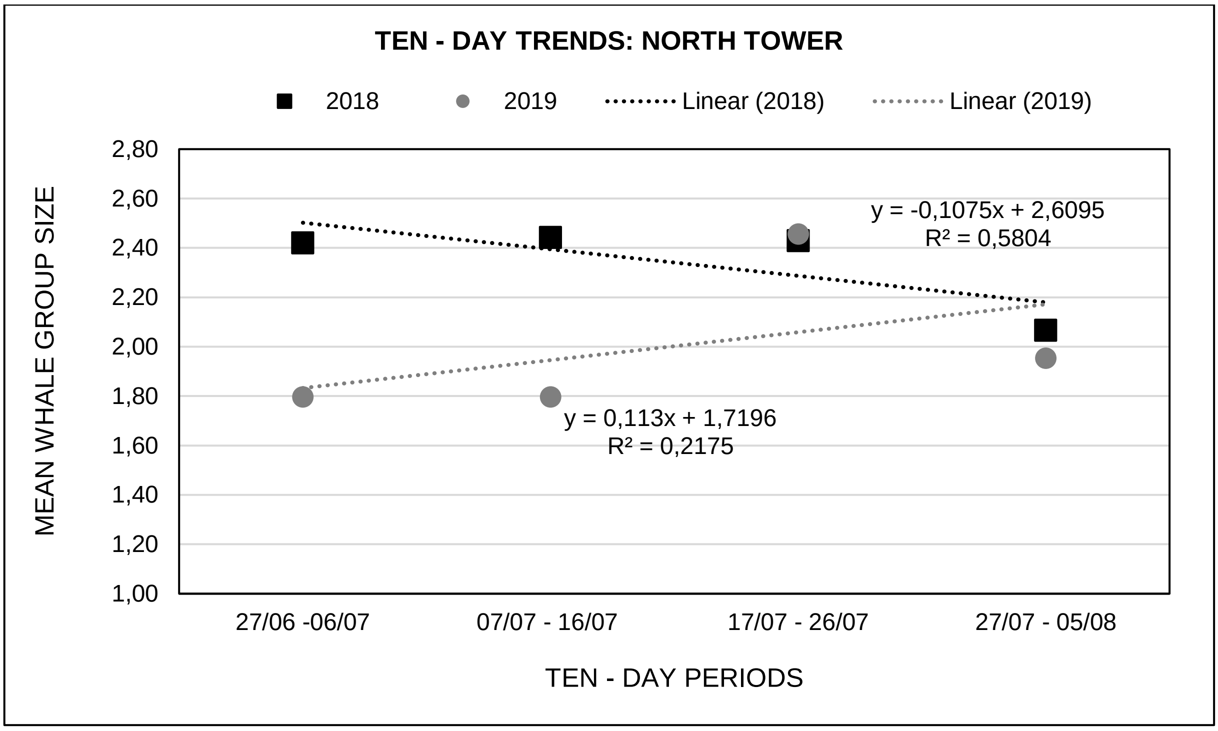


Figure 3.12: Trend in the mean humpback whale group size passing Cape Vidal per day in the 2018 and 2019 field seasons, as observed from the north tower

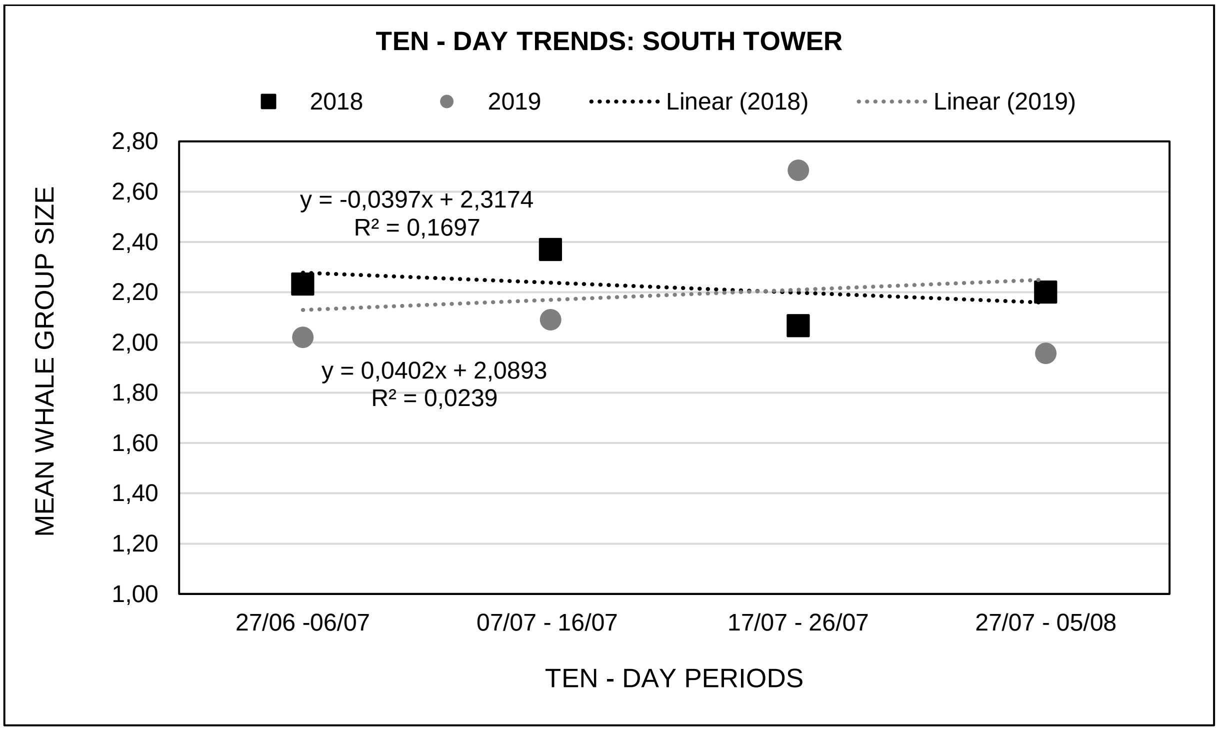


Figure 3.13: Trend in the mean humpback whale group size passing Cape Vidal per day in the 2018 and 2019 field seasons, as observed from the north tower

3.3.4.2 Distance offshore

The distances from the shore of the recorded groups varied from 0.1 km to 20 km, covering depths that ranged from 10 m to over 1000 m (Figure 3.14 to Figure 3.17).

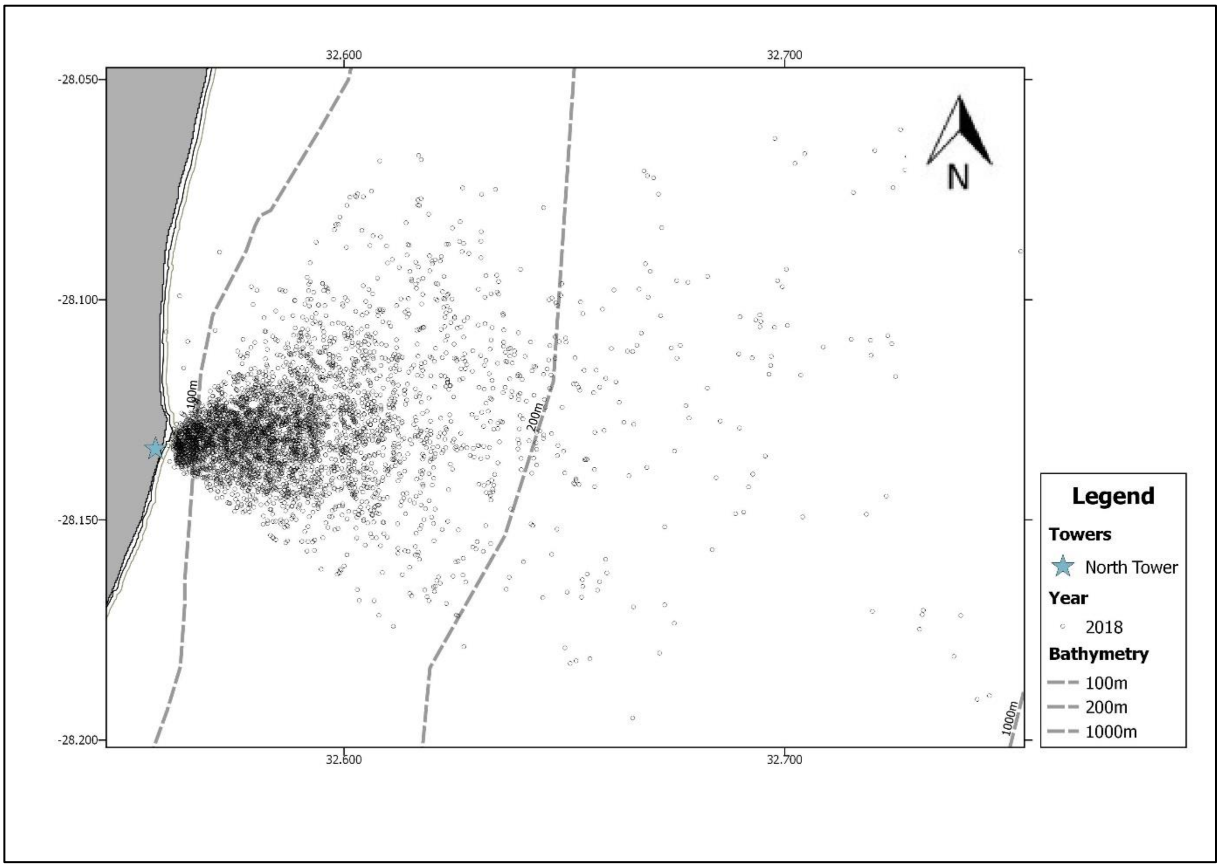


Figure 3.14: Position of all groups of humpback whales observed from the north tower, in 2018, during surveys from Cape Vidal, South Africa

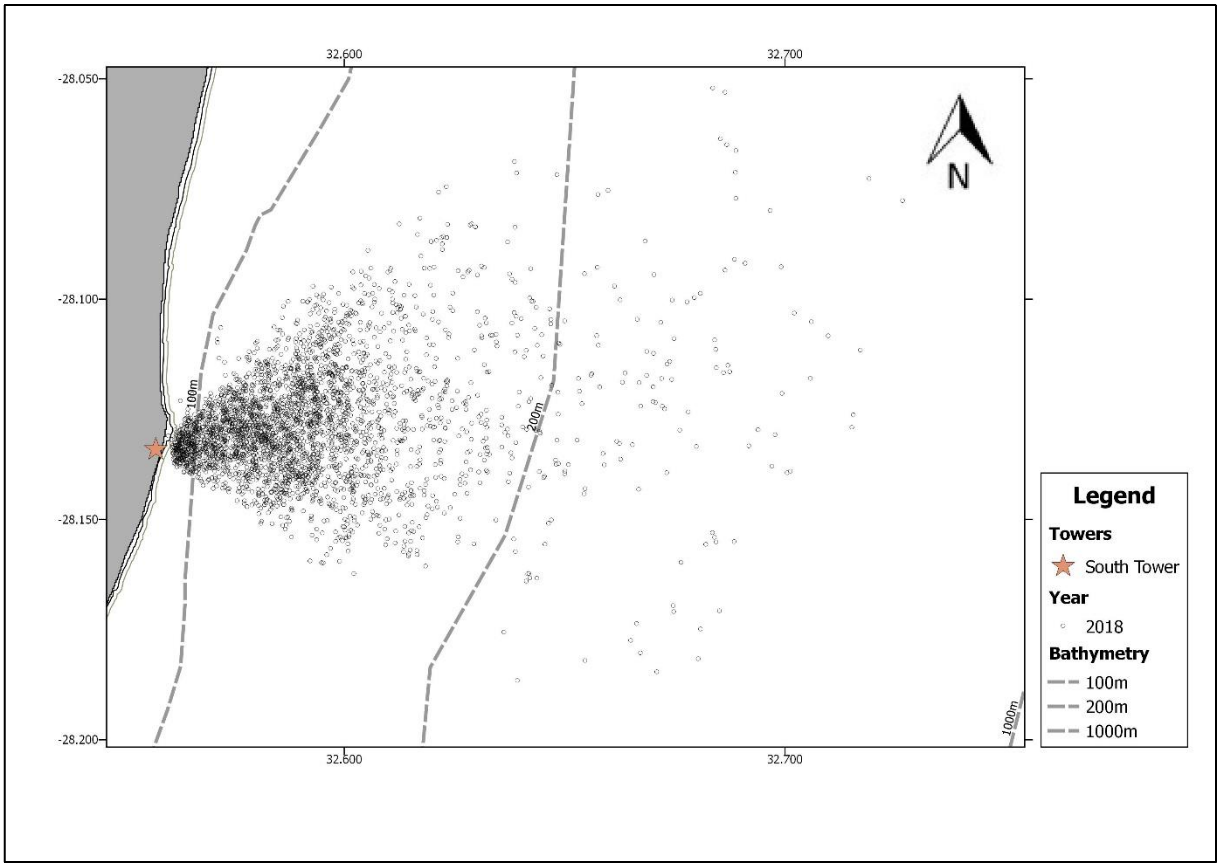


Figure 3.15: Position of all groups of humpback whales observed from the south tower in 2018 during surveys from Cape Vidal, South Africa

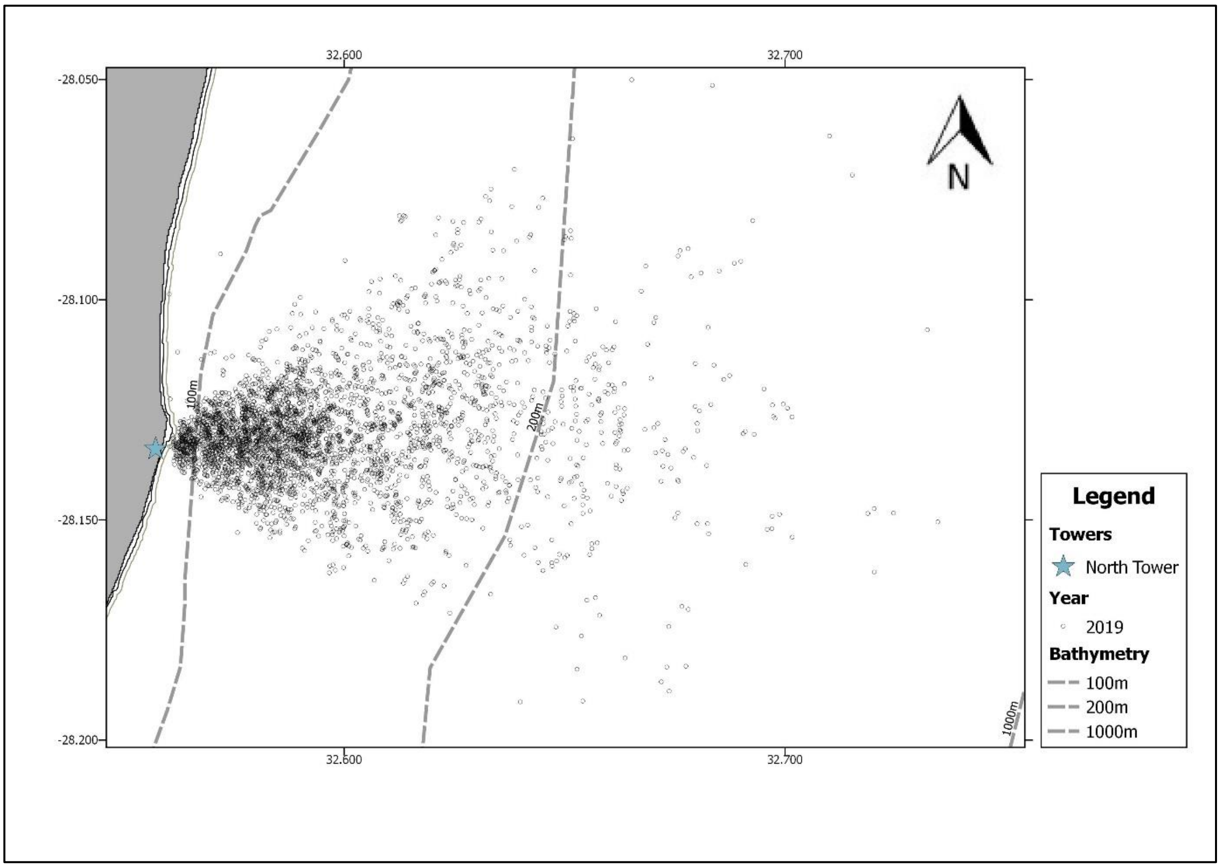


Figure 3.16: Position of all groups of humpback whales observed from the north tower, in 2019, during surveys from Cape Vidal, South Africa

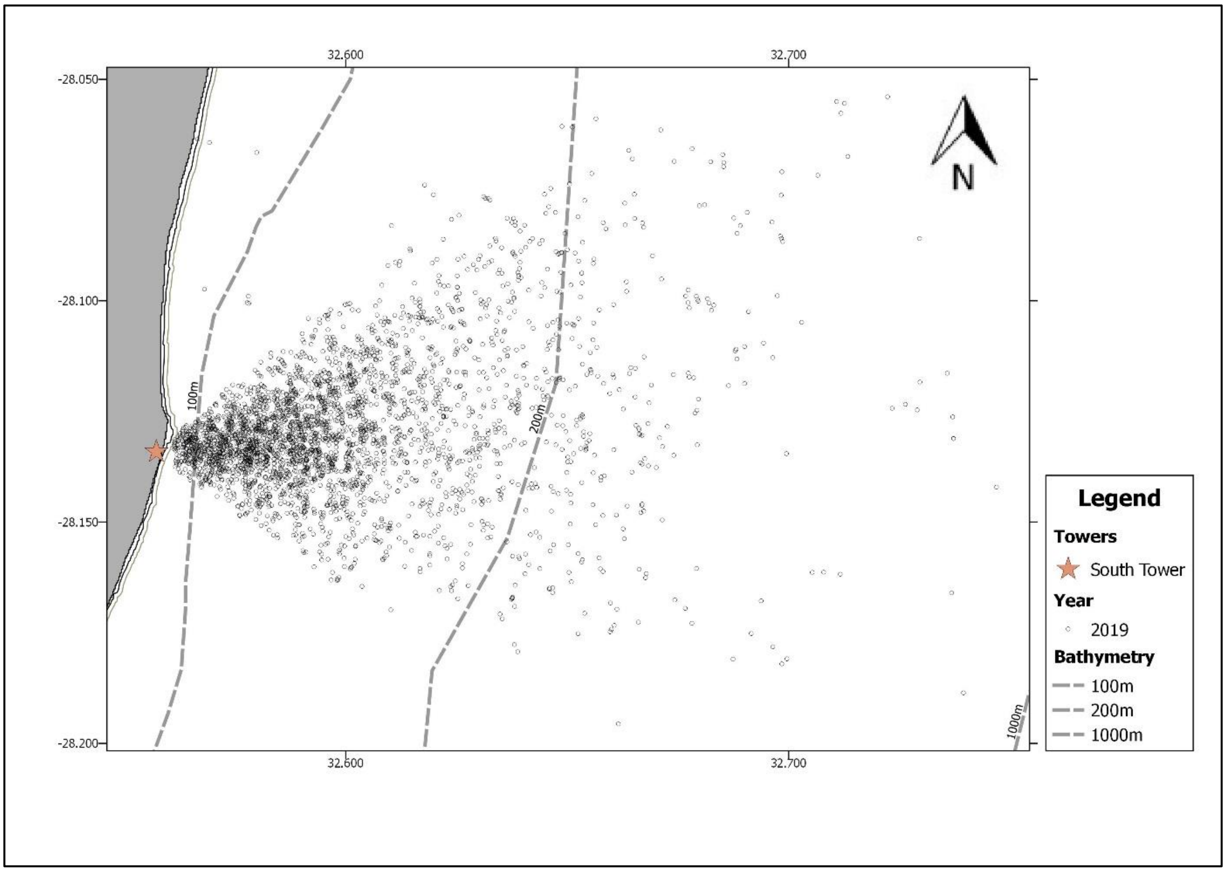


Figure 3.17: Position of all groups of humpback whales observed from the south tower, in 2019, during surveys from Cape Vidal, South Africa

Figures 3.18, 3.19, 3.20 and Table 3.4 indicate that distances offshore were similar between the towers; however, the variances are considerable due to many whales distributed over an extensive range of distances. From the north tower, the mean distance offshore was 3.26 km (± 0.16 km) in 2018, while in 2019, it was 3.71 km (± 0.18 km). Similarly, the mean distance offshore from the south tower was 3.43 km (± 0.17 km) in 2018 and 4.19 km (± 0.2 km) in 2019.

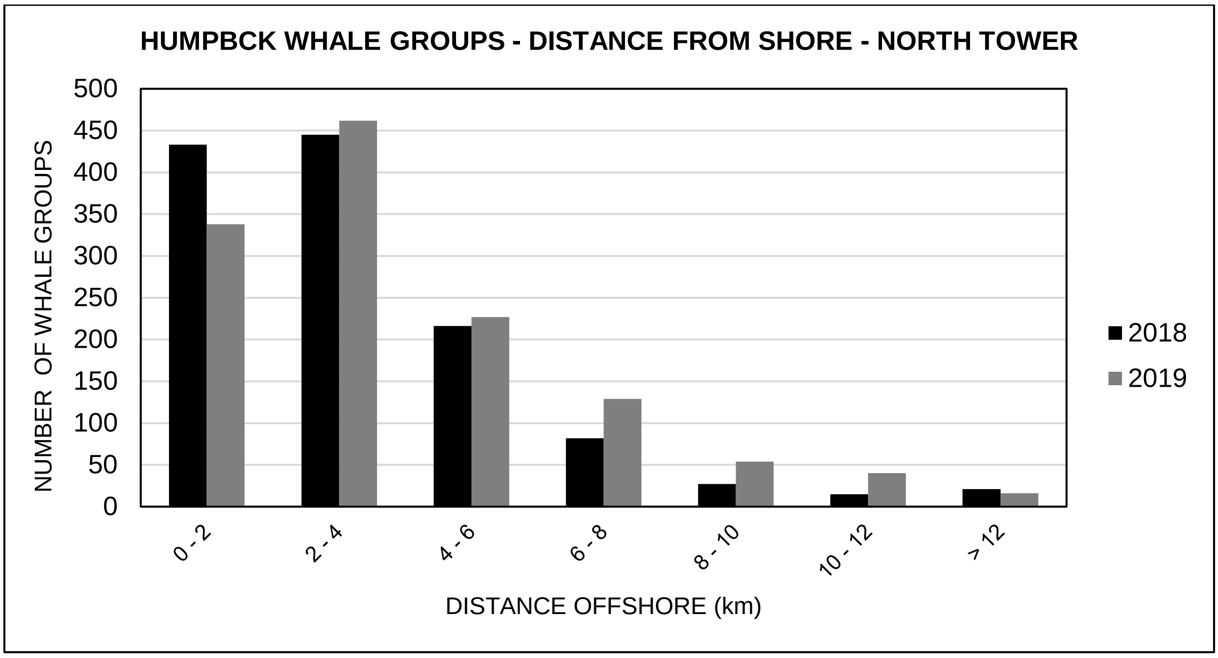


Figure 3.18: Number of humpback whale groups per distance interval offshore from the north tower in 2018 and 2019, off Cape Vidal, South Africa

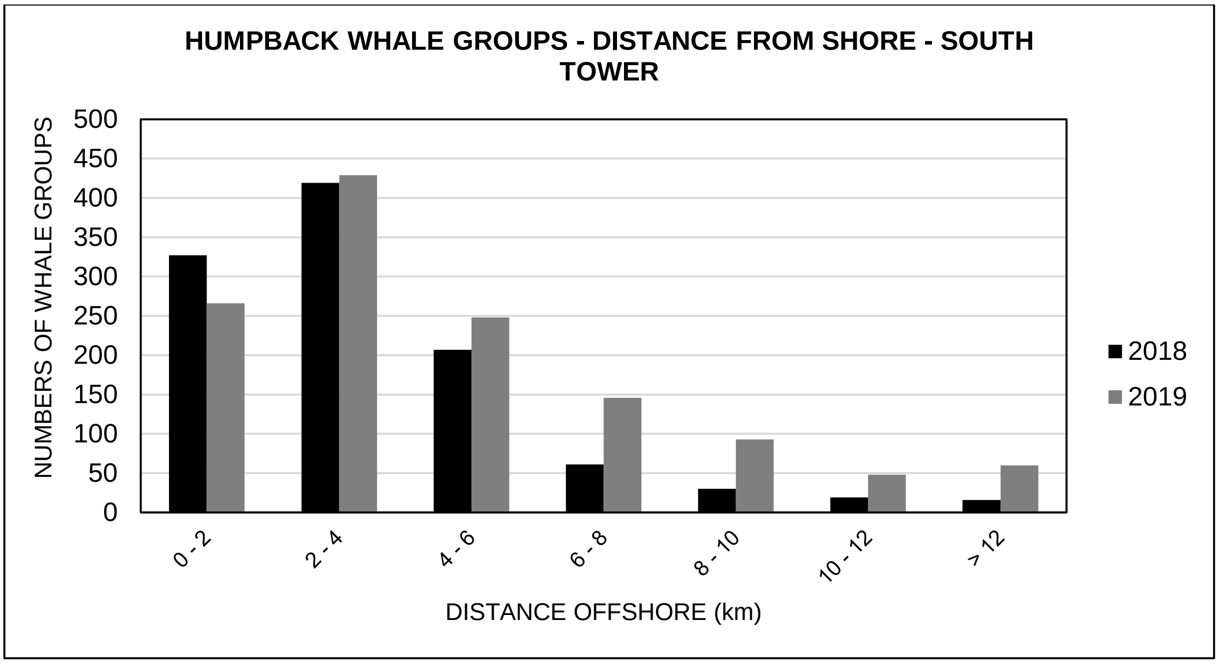


Figure 3.19: Number of humpback whale groups per distance interval offshore from the south tower in 2018 and 2019, off Cape Vidal, South Africa

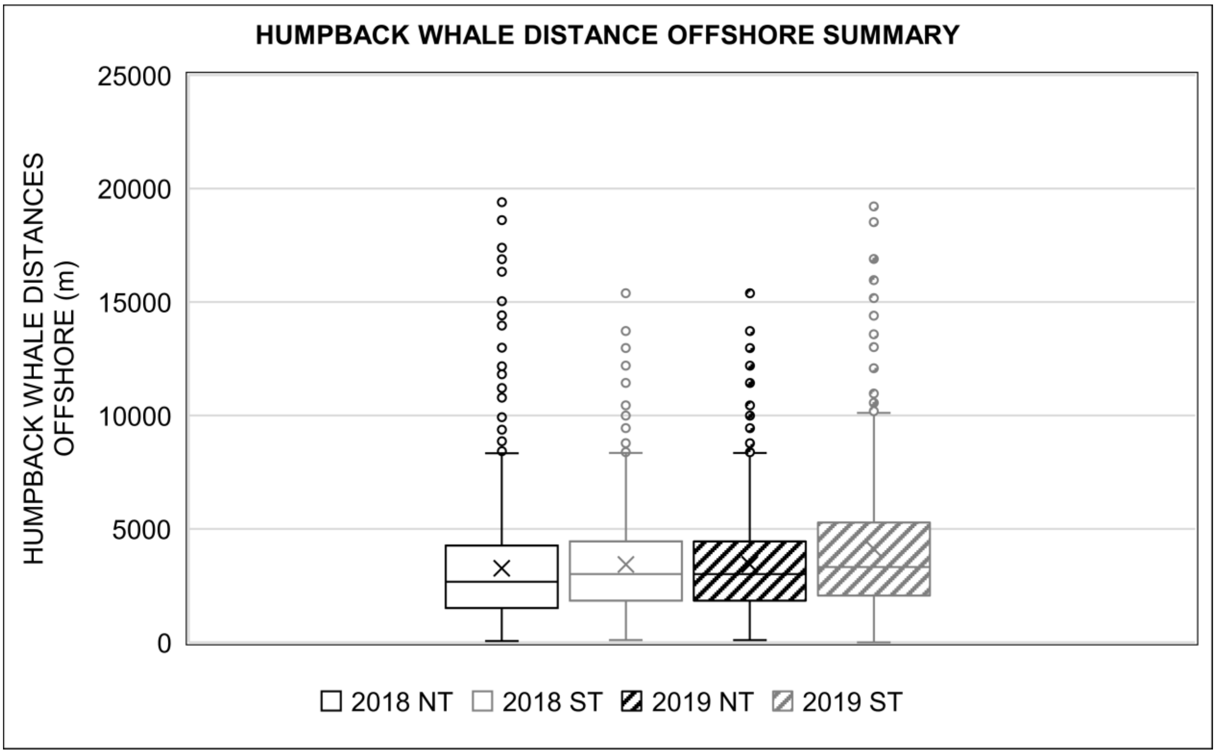


Figure 3.20: A box whisker plot summarising the mean, median, upper and lower quartile as well as the extreme maximums of the humpback whale distances from shore observed from both towers during the 2018 and 2019 surveys at Cape Vidal, South Africa

A Shapiro Wilks test for normality found the data to skewed for both towers in 2018 (p < 005) and 2019 ($p < 0.05$) and were therefore suitable for non-parametric testing. The north tower recorded a median migrating distance offshore of 2956.862 m (2.956 km) (*SD* = 2472.347*)* for humpback whales in 2018, while in 2019 this was 3184.774 m (3.184 km) (*SD* = 2623.562). A Wilcoxon signed rank test indicates that the difference is statically significant between the years, $T = 176812.00$, $z = -3.964$ $p < 0.005$ and whales were observed to migrating further offshore in 2019 from the north tower. Likewise, when analysing the data from the south tower, in 2018 the median distance offshore was 2890.021 m (2.890 km) (*SD* = 2185.83) in 2018 and 3241.200 m (3.241 km) (*SD* = 2924.793) in 2019. The difference between the medians is similar to what was observed in the north tower, the Wilcoxon rank test indicates that the two years are also statistically significantly different $T = 134679.00$, $z = -5.386$ $p < 0.05$. Therefore, the humpback whales were observed to be migrating slightly further offshore in 2019 when compared to 2018.

The means of the ten-day periods were plotted with linear regression to illustrate the trend of the distances offshore the humpback whales were migrating throughout the survey periods (refer to Figures 3.21and 3.22). In 2019 during the third and fourth ten-day periods the humpback whales were migrating north closer to the shore later in the survey period. As these results are consistent across the year, and the density data indicates that the number of whales migrating increase over this period, this result is likely to be a product of poor weather conditions or sampler bias and will be discussed further in the discussion.

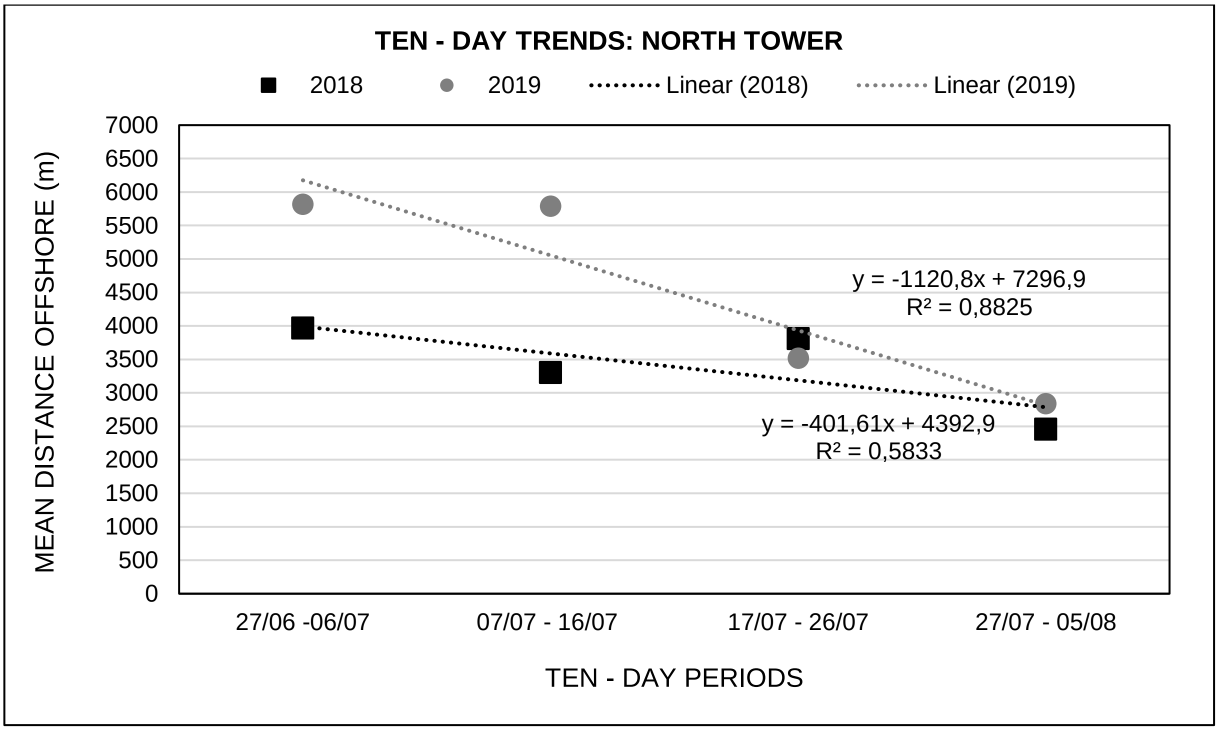


Figure 3.21: Trend in the mean humpback whale groups distance offshore when migrating past Cape Vidal per ten -day periods in the 2018 and 2019 field seasons, as observed from the north tower

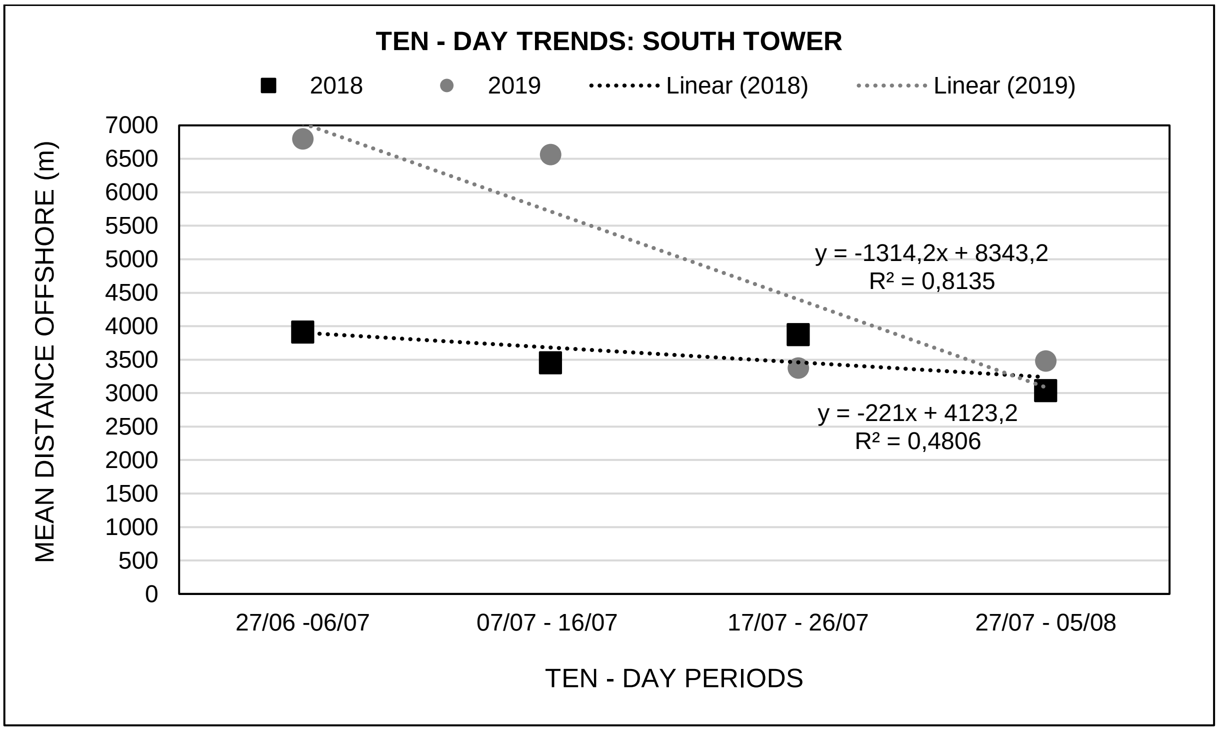


Figure 3.22: Trend in the mean humpback whale groups distance offshore when migrating past Cape Vidal per ten -day periods in the 2018 and 2019 field seasons, as observed from the south tower

3.3.4.3 Migration speed

The migration speed of the groups sighted varied from 0 km/h to 20 km/h (Figure 3.23 and 3.24). The average speed of the migrating whales in 2018 was 7.1 km/h (± 0.27 km/h), while in 2019, it was slightly slower, with the mean speed being 5.5 km/h (± 0.25 km/h) (Figure 3.25). An extensive range in speed is expected as some animals showed milling behaviour (0 km/h) while others were moving fast (at up to 20 km/h) during the survey period. As explained in the methodology, the extensive data set made it difficult to deduce any significant difference in speed statistically.

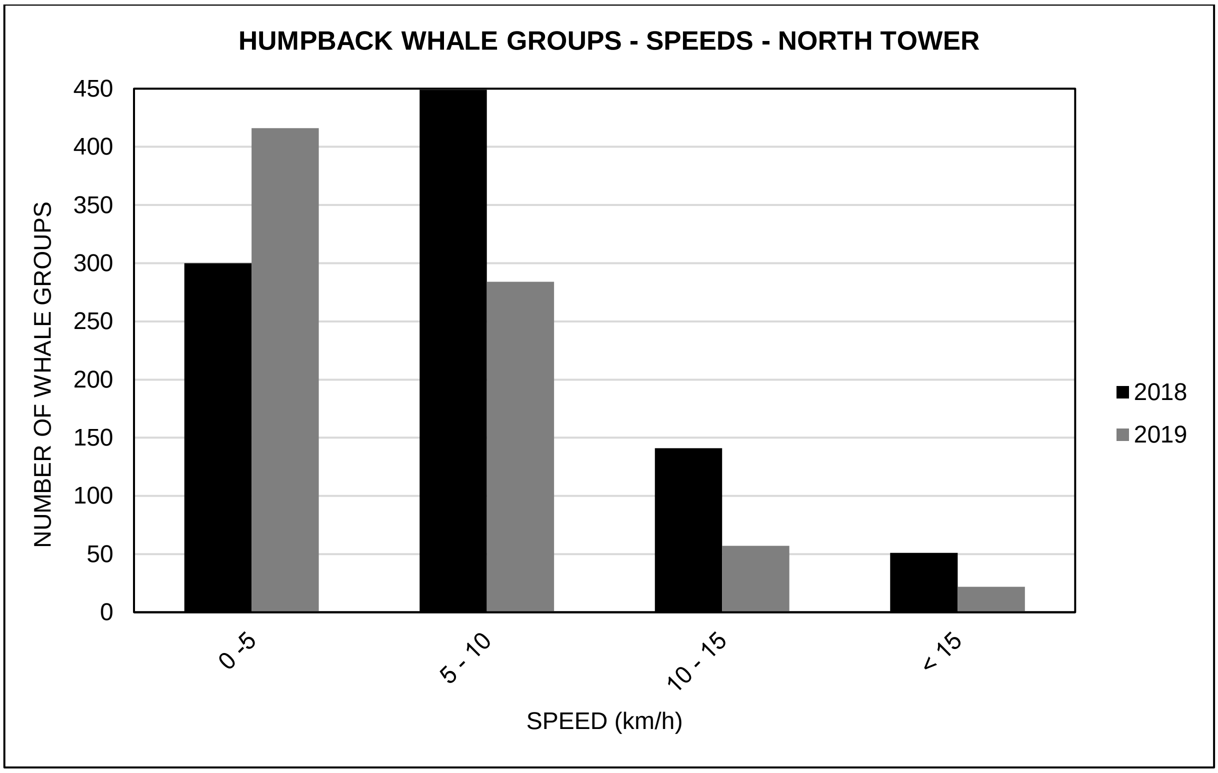


Figure 3.23: Number of humpback whale groups per speed group observed from the north tower at Cape Vidal, South Africa, during 2018 and 2019 surveys

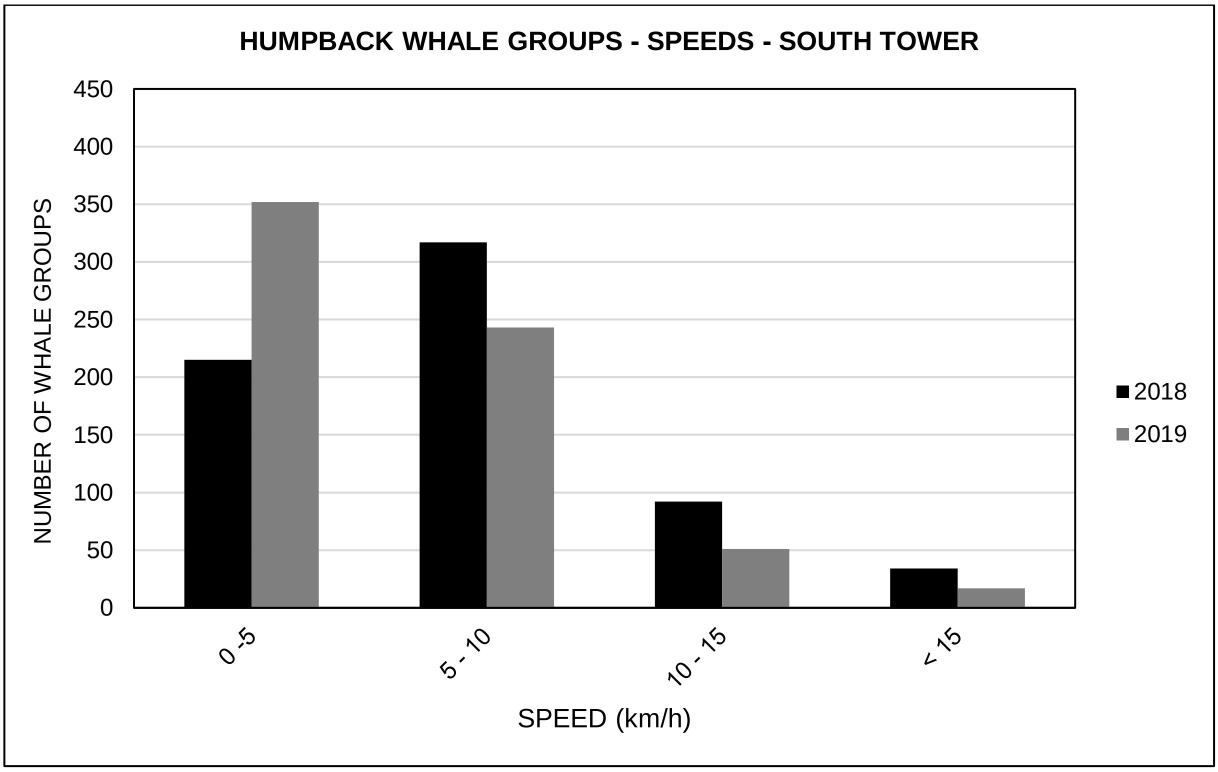


Figure 3.24: Number of humpback whale groups per speed group observed from the south tower at Cape Vidal, South Africa, during 2018 and 2019 surveys

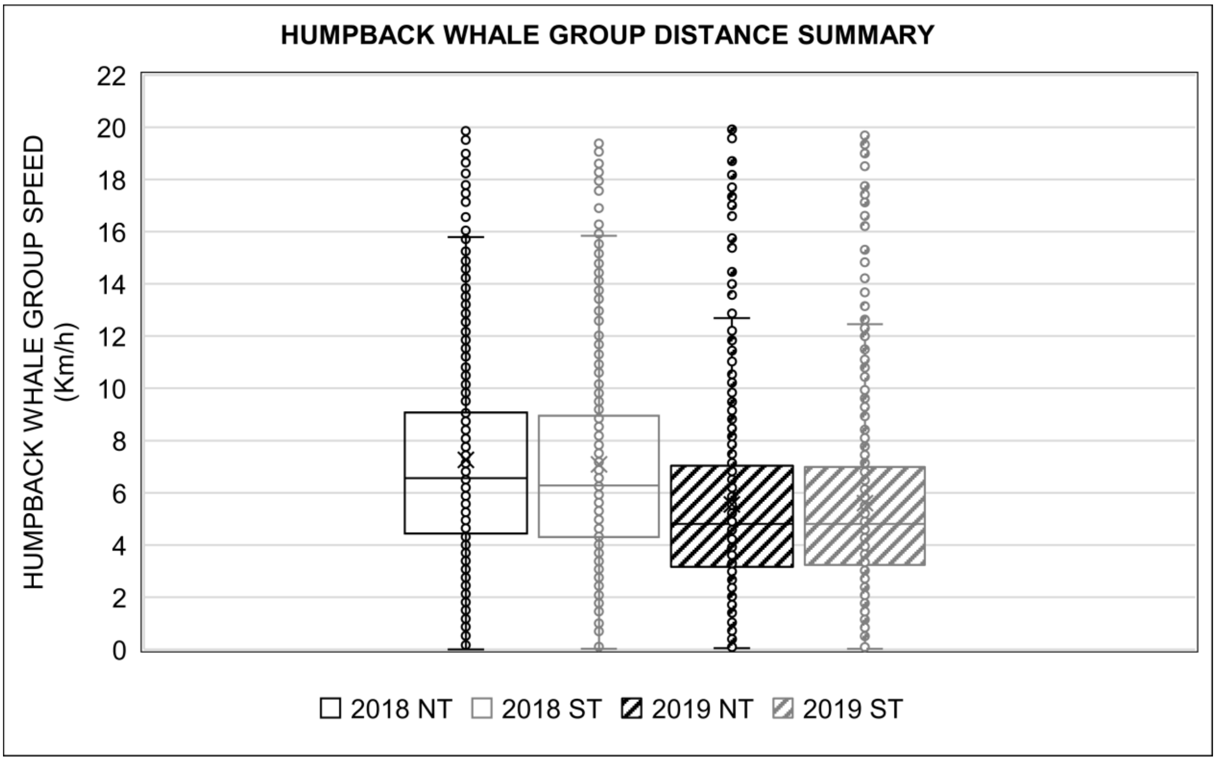


Figure 3.25: A box whisker plot summarising the mean, median, upper, and lower quartile as well as the extreme maximums of the humpback whales' group speeds measured from both towers during the 2018 and 2019 surveys at Cape Vidal, South Africa

A Shapiro Wilks test for normality found the data to skewed for both towers in 2018 (p < 005) and 2019 (p < 0.05) and are therefore suitable for non-parametric testing. The north tower recorded a median migrating speed of 6.47km/h (*SD* = 4.051) for the migrating humpback whales in 2018, while in 2019 this had decreased to a median migrating speed of 4.83km/h (*SD* = 3.657). A Wilcoxon signed rank test indicates that the difference in the north tower is statically significant between the years, *T* = 95703, *z* = -8.901 *p <0.05*. Similarly, when analysing the data from the south tower, in 2018 the median migrating speed was 6.27km/h (*SD* = 3.901) and 4.81 km/h (*SD* = 3.464) in 2019.The Wilcoxon rank test indicates that the two years are also statistically significantly different *T* = 73657, *z* = -7.124 *p < 0.05*. Therefore, whales in 2018 were travelling a faster speed to those in 2019 confirmed by both towers' observations.

The means of the ten-day periods were plotted with linear regression to illustrate the trend of the speed at which the humpback whales were migrating throughout the survey periods (refer to Figures 3.26 and 3.27). In 2019 during the third and fourth ten-day periods there was a decrease in the distance offshore the whales were recorded from both in the north and the south tower.

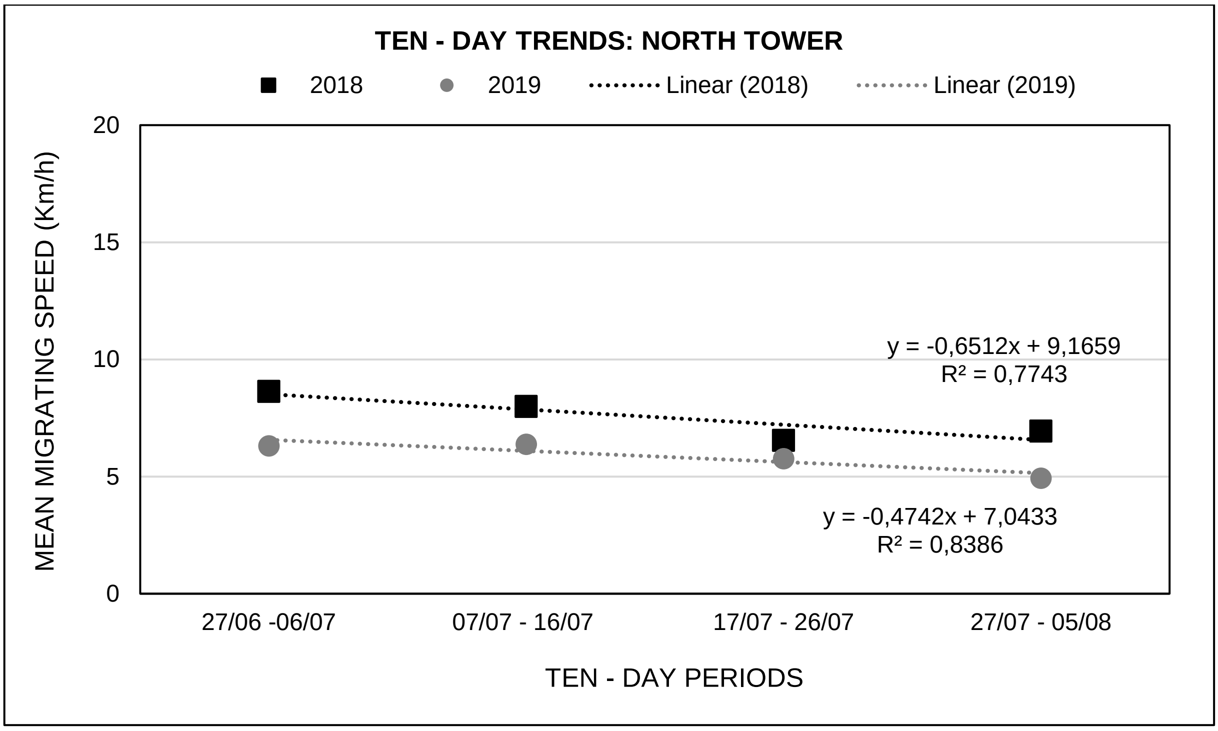


Figure 3.26: Trend in the humpback whale groups mean speed when migrating past Cape Vidal per ten -day periods in the 2018 and 2019 field seasons, as observed from the north tower

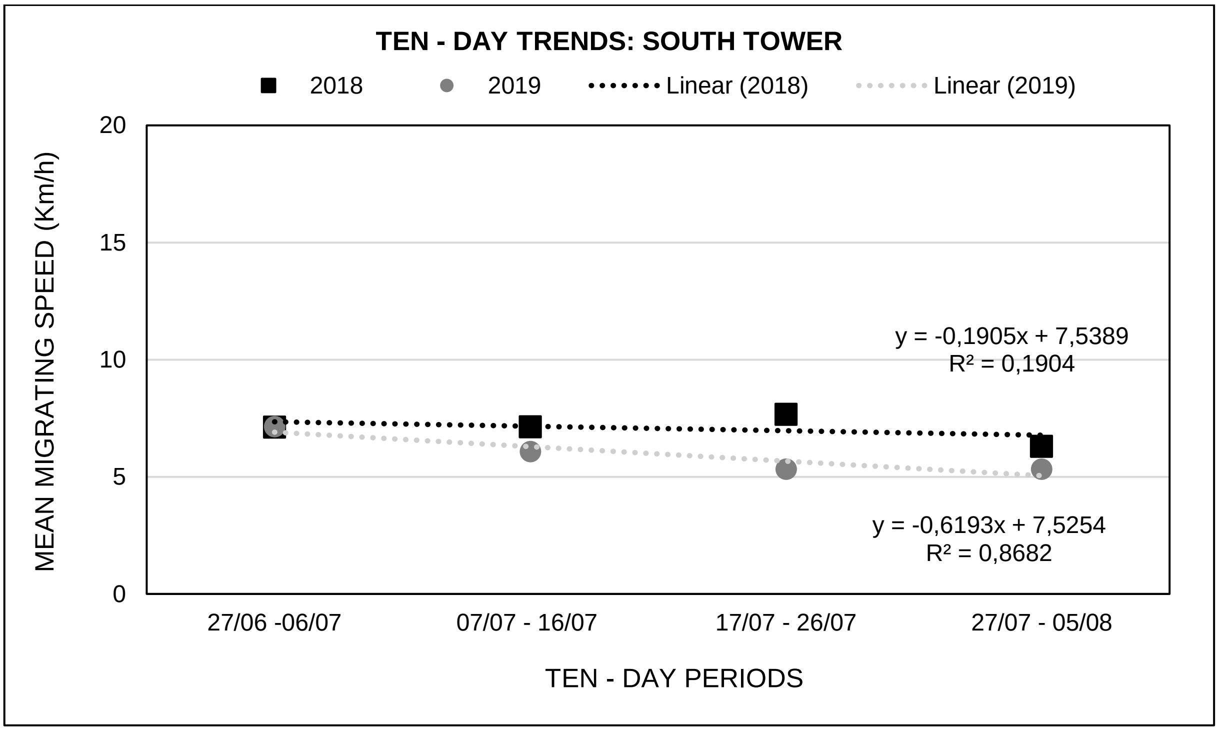


Figure 3.27: Trend in humpback whale groups mean speed when migrating past Cape Vidal per ten -day periods in the 2018 and 2019 field seasons, as observed from the south tower

3.3.4.4 Migration heading

The mean bearing observed from the north tower was 9.07° (± 1.83°) in 2018 and 6.60° (± 2.19°) for 2019 (Figure 3.19 and 3.30). The mean bearing of the groups observed from the south tower was between 5.41° (± 2.24°) for 2018 and 4.22° (± 2.59°) for 2019 (Figure 3.28, 3.29, 3.30 and Table 3.7).

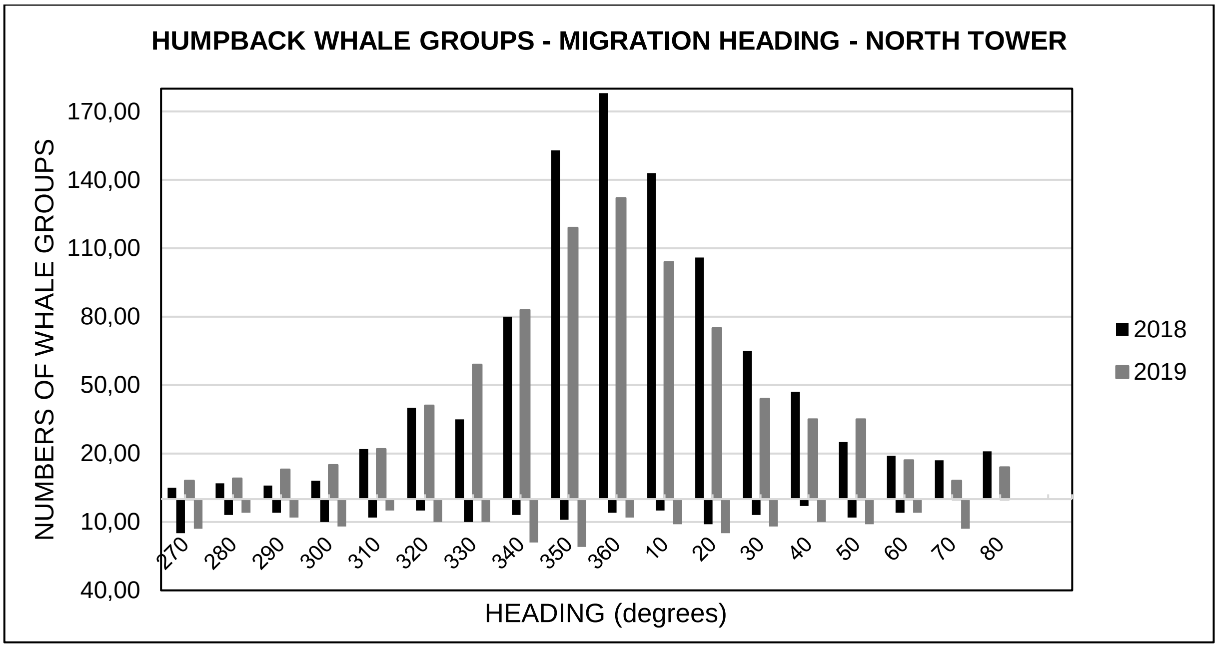


Figure 3.28: Distribution of migration headings of humpback whales sighted from the north tower in 2018 and 2019 in Cape Vidal, South Africa

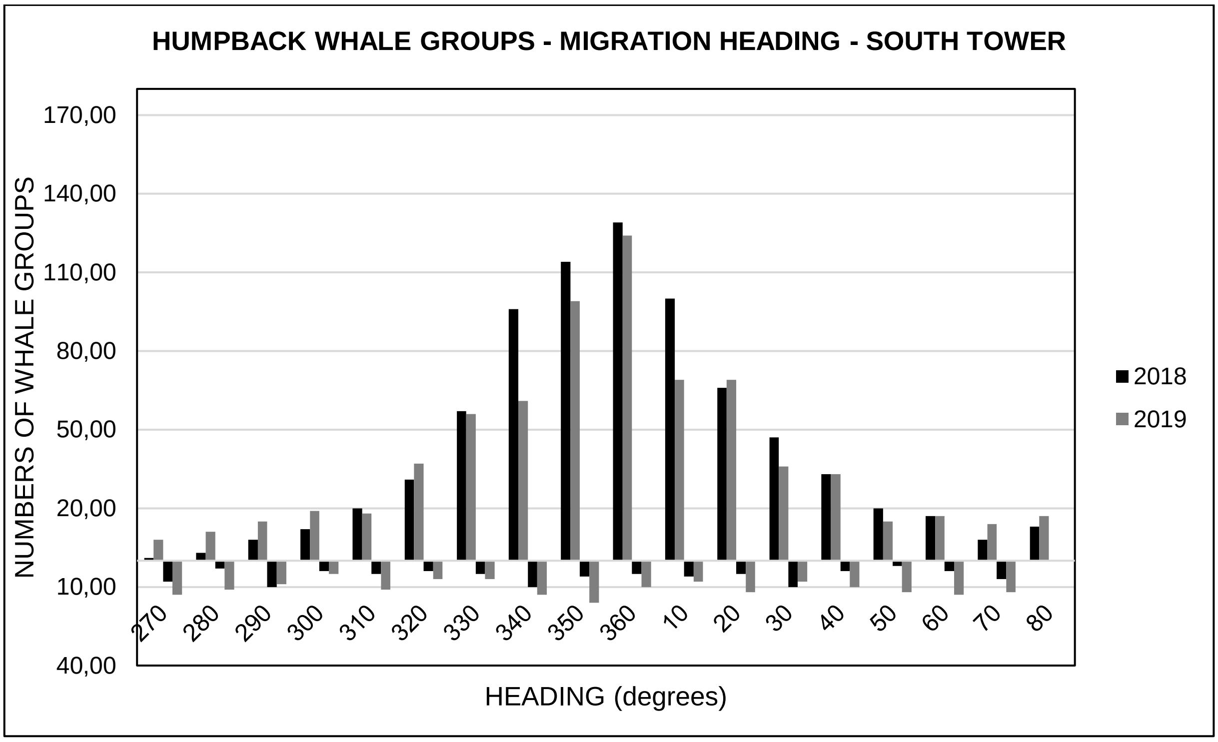


Figure 3.29: Distribution of migration headings of humpback whales sighted from the south tower in 2018 and 2019 in Cape Vidal, South Africa

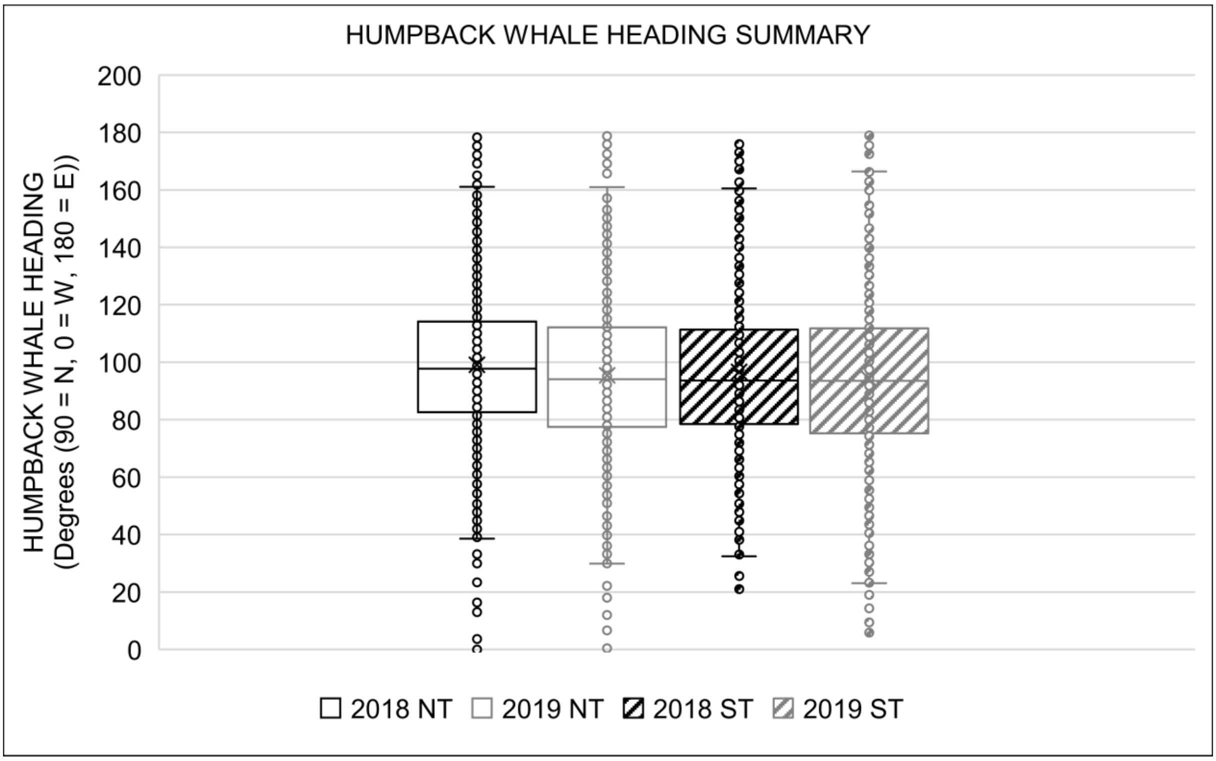


Figure 3.30: A box whisker plot summarising the mean, median, upper, and lower quartile as well as the extreme maximums of the humpback whales' group headings measured from both towers during the 2018 and 2019 surveys at Cape Vidal, South Africa

A Shapiro Wilks test for normality found the data to skewed for both towers in 2018 (p < 005) and 2019 ($p < 0.05$) and are therefore suitable for non-parametric testing. The north tower recorded a median migrating heading of 357. 975° (*SD* = 35.376) for the humpback whales in 2018, while in 2019 had a median migrating heading of 359.045° (*SD* = 32.262). Although both years reflects the whales are heading due north, a Wilcoxon signed rank test indicates that the difference in the north tower is statically significant between the years, $T = 19851$, $z = -18.617$ $p < 0.05$. Similarly, when analysing the data from the south tower, in 2018 the median migration heading was 6.715° (*SD* = 29.88) and 3.465° (*SD* = 31.445) in 2019.The Wilcoxon rank test indicates that the two years are also statistically significantly different $T = 12182$, $z = -17.588$ $p < 0.05$. Therefore, the observations in the towers confirmed the whales in were 8° (2018) and 4° (2019) closer to due north.

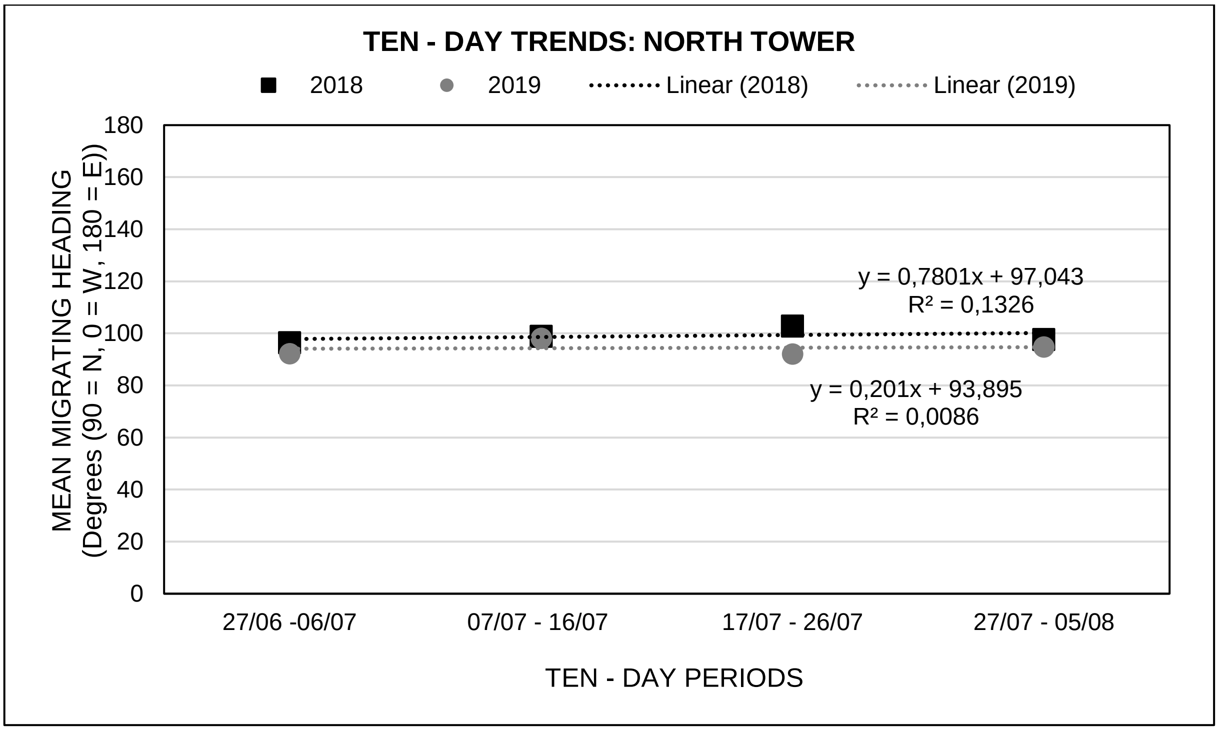


Figure 3.31: Trend in humpback whale groups mean heading when migrating past Cape Vidal per ten -day periods in the 2018 and 2019 field seasons, as observed from the north tower

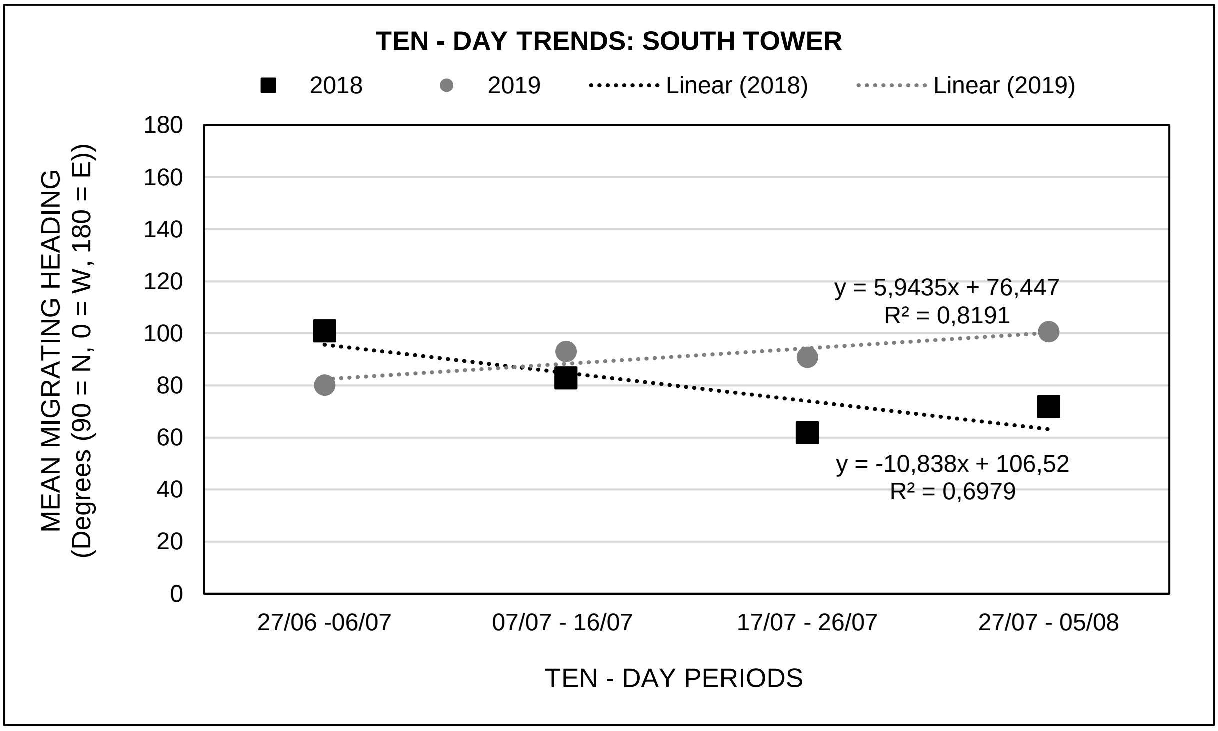


Figure 3.32: Trend in humpback whale groups mean heading when migrating past Cape Vidal per ten -day periods in the 2018 and 2019 field seasons, as observed from the south tower

The means of the ten-day periods were plotted with linear regression to illustrate the trend of the heading at which the humpback whales were migrating throughout the survey periods (refer to Figures 3.31 and 3.32). The north tower reflects a more consistent mean northward heading throughout the survey period. However, the south tower headings are more inconsistent, especially in 2018 around the 3rd and 4th periods. During these periods, the whales seem to be heading slightly more west which relates to heading closer to the shore.

3.3.5 Comparisons between migration parameters

A spearman rank correlation matrix was used to determine if any of the above migration characteristics influenced or related to any other characteristic.

In 2018 (Figure 3.33) it was found that it was a statistically significant difference in the migrating humpback whales group speed when compared to their migrating difference offshore. There were no other characteristics that were significantly influenced by another.

In 2019 (Figure 3.34) found that there was statistically significant difference in the migration heading and the speed of the humpback whale groups. There were no other characteristics that were significantly influenced by another.

Table 3-2: A spearman rank correlation matrix illustrating the correlations between the humpback whales migrating characteristics from 2018, observed from Cape Vidal, South Africa

2018 MIGRATION CHARECTERISTICS CORRELATION MATRIX						
			Group size	**Migration speed**	**Distance offshore**	**Migration heading**
Spearman's rank correlation	**Group size**	Correlation Coefficient	1.000	.019	.066**	-.003
		Sig. (2-tailed)	.	.451	.008	.897
		N	1599	1599	1599	1599
	Migration speed	Correlation Coefficient	.019	1.000	.174**	.024
		Sig. (2-tailed)	.451	.	<,001	.340
		N	1599	1599	1599	1599
	Distance offshore	Correlation Coefficient	.066**	.174**	1.000	.032
		Sig. (2-tailed)	.008	<,001	.	.194
		N	1599	1599	1599	1599
	Migration heading	Correlation Coefficient	-.003	.024	.032	1.000
		Sig. (2-tailed)	.897	.340	.194	.
		N	1599	1599	1599	1599

**. Correlation is significant at the 0.01 level (2-tailed).

Table 3-3: A spearman rank correlation matrix illustrating the correlations between the humpback whales migrating characteristics from 2019, observed from Cape Vidal, South Africa

2019 MIGRATION CHARECTERISTICS CORRELATION MATRIX						
			Group size	**Migration speed**	**Distance offshore**	**Migration heading**
Spearman's rank correlation	**Group size**	Correlation Coefficient	1.000	.004	.043	-.082**
		Sig. (2-tailed)	.	.885	.101	.002
		N	1445	1445	1445	1445
	Migration speed	Correlation Coefficient	.004	1.000	.043	.103**
		Sig. (2-tailed)	.885	.	.104	<,001
		N	1445	1445	1445	1445
	Distance offshore	Correlation Coefficient	.043	.043	1.000	-.076**
		Sig. (2-tailed)	.101	.104	.	.004
		N	1445	1445	1445	1445
	Migration heading	Correlation Coefficient	-.082**	.103**	-.076**	1.000
		Sig. (2-tailed)	.002	<,001	.004	.
		N	1445	1445	1445	1445
**. Correlation is significant at the 0.01 level (2-tailed).						

3.4 DISCUSSION

The coastal migratory routes of Southern Hemisphere humpback whales, which once made them highly susceptible to shore-based whaling in mid and low latitude waters, has made them a prime candidate for shore-based monitoring of their migrations in more recent years. The specific survey methodology applied in this study was consistent with previous surveys at Cape Vidal (Findlay and Best, 1996a; b; Findlay et al., 2011) to ensure data comparability and estimate population trends accurately. More specifically, the use of theodolites allowed precise measures of the whales' distance from shore, heading and speed, whereas the application of two observer platforms allowed the estimation of the proportions of whales missed by each tower, which were then accounted for in the final abundance estimates.

3.4.1 Observation effort

Overall, the survey effort was relatively successful, considering the high percentage of observation days with more than eight hours of monitoring effort. This reflects the good weather conditions during the surveys, resulting in mostly adequate sightability for observations to be conducted successfully.

The survey methodology used in this study required volunteers, many of whom participated in both years, ensuring the pairing of experienced with inexperienced observers in the second year. Due to the high density of whales throughout the survey, more handling time for obtaining and recording fixes off the theodolite was required; therefore, less effort was available to search new groups, especially at the limits of sightability. Interestingly, Buckland et al. (1993) noted that when doing two-platform shore-based surveys, the detection rates of whales were higher when observers were motivated by viewing many whales. Therefore, this study made every attempt to encourage observers to continuously search and detect whales and keep enthusiasm high, especially on low-density days.

3.4.2 Sightability conditions

Although no differences were found in sightability conditions between years, early in the 2019 survey, observers had to contend with low grey haze due to inland sugar cane burning in the area. Such burning was experienced by Findlay (1994) in previous surveys. Due to the lower magnification of the theodolite (than the binoculars), it was sometimes impossible to track whales in the haze. These conditions improved when the breeze increased throughout the day and was no longer a factor by the first week of July, and optimal tracking of whale groups continued for the rest of the survey. Whales could only be detected when breaching in the haze by the white water left after the splash. Although this may have impacted some of the migration characteristics (see further in 4.5), such a limitation is still accounted for in estimating the daily whale densities (through proportions missed) and the mean distance offshore of the whale groups.

The lack of a significant difference in the sightability conditions between years might be related to the surveys being undertaken over the same time each year, and therefore, seasonal weather patterns related to similar sightability conditions over all surveys. The sun's glare off the sea affected only the northernmost limits of each tower's visibility, and observers were encouraged to record groups before they reached this glare. Specially between 07h00 and 08h00 on cloudless days, sun glare affected the detection of whales. After 08h00, the suns position was high enough for the glare to not affect sightability. However, the two-platform methodology allowed estimating the proportions of whales missed due to glare and observations of whales in the early morning is often easier, as facing east allows whale blows to be backlit by the sun. Paterson and Paterson (1989) found that glare of the sun experienced by observers before 06h00 was a significant factor influencing the sighting humpback whales off east Australia, indicating that observations had a high sighting rate between 06h00 and 08h00 as observers caught up whales that moved out of the glare and within the visible limits.

3.4.3 Densities

The surveys at Cape Vidal in 2018 and 2019 showed an increase in northward migrating humpback whales throughout the survey period, peaking in late July/early August, which corresponded with the peak period found in the same area by Findlay and Best (1996b). The results also indicated that there were not statistically significant differences between the numbers of whale migrating past in both years (from both towers). However, Findlay and Best 9 (op. cit.) described the local density peaks to appear as waves throughout July, illustrating a link between migrations and the reproductive cycles of humpback whales. These waves in whale numbers may be due to individuals of different age, sex and reproductive class migrating past, in the order they would arrive at the breeding grounds. Lactating females with young calves would arrive first, followed by sexually immature individuals, mature males, resting females, and finally pregnant females (Dawbin, 1956; Chittleborough, 1965). The peaks found by Findlay (1994) were not as pronounced in this study; a hypothesis for this difference is that the successive waves may have become less defined due to the increased number of whales in the migration stream. Noad et al. (2008), observed such change and noted a delayed first peak in the number of northward migrating humpback whales off the east coast of Australia and suggested that this resulted in the first two peaks being converged, leading to a sustained longer and higher single peak. Further and more detailed studies (including potential genetic studies) are needed to confirm this in the C1 sub-stock. In contrast to this general behaviour of the species, Stevick et al. (2003) reported that within the North Atlantic humpback whale population migrating to the breeding grounds in the West Indies, the males were the earliest arrivals and suggested that different selection pressures between different populations may be responsible for differences in migratory schedules. Unfortunately, it was impossible to assign gender or age class to the different individuals passing by the towers in the present study, to assess possible temporal segregation in migrating humpback whales' age and reproductive classes. However, the presence of newborn calves in the migrating stream was unusual, and comparisons of this study with those of Findlay and Best (1996a) and Findlay et al. (2011) indicate numbers of calf births on the migration are increasing over time. In addition, fishermen off Maphelane (about 100 km south of the observation site) reported the birth of a humpback whale in July 2019 (Bearno Phillipson, pers. comm.), unusual for the area as it is located several hundreds of kilometres south of the calving ground. This increased presence of new-born calves in the migration stream may indicate whales are leaving their Southern Ocean feeding grounds later than usual pointing towards increased time needed for pregnant females to acquire sufficient body conditions for the migration, calving, and nursing of young, in turn possibly linked to reduced prey availability in the feeding grounds. Christiansen et al. (2018) have shown that reproductive performance in baleen whales is linked to body condition given the influence of food availability on individuals (Seyboth et al., 2021). Studies assessing the body condition and age of the migrating humpback whales in conjunction with hormone analyses could assess possible segregation by the age and reproductive classes in the timing of migration and the general nutritional condition of these whales. Genetic studies, isotope analysis and photo-identification matching of humpback whales migrating along the South African east coast are being investigated. Such data will assist a better understanding of the timing, segregation and trophic ecology of migrating humpback whales observed from Cape Vidal.

3.4.3.1 Migration characteristics

Before discussing the findings regarding these characteristics, it is essential to note that Findlay et al. (2011), a key reference used here for comparison, included only those sightings with two or more fixes to assess swim speed and heading, and only those sightings with three or more fixes to assess group size. The present study amended this data selection procedure slightly to include only those sightings with three or more fixes to assess all these parameters. This change was made based on the larger number of sightings with three or more fixes available, compared to Findlay et al. (2011).

3.4.3.2 Group size

The mean and median group sizes observed in this study were similar to those from previous studies conducted on the species' breeding grounds, including South Africa and east Australia, albeit they are drawn from a significantly larger sample size. During the past studies in Cape Vidal, the mean group size of northward migrating humpback whales ranged between 2.10 (± 0.07) in 2002 and 2.73 (± 0.18) in 1988 (Findlay et al., 2011), very similar to the findings of this study (2.25 (± 0.07) in 2018 and 2.05 (± 0.08) in 2019). Another land- and boat-based study in South Africa (on the west coast) indicated group sizes ranged from one to seven with a mean group size of 2.09 (± 0.12) (Barendse et al., 2010).

In east Australia, Bryden (1985) reported group sizes ranged between one and five individuals, with a mode of two. The same author suggested that up to 30 minutes per observation is needed to accurately determine the group size of whales observed from shore. However, during the present study, whale densities were high, and the number of fixes needed to be limited to a maximum of four, which were taken in a period much shorter than 30 minutes. To ensure the quality of group size estimates, the high-powered binoculars used to scan the area were used additionally to the theodolite to verify the numbers of individuals in any group.

The results indicated that the north tower was statistically significant, however this can be attributed to the larger sample size in 2018. Of more interest is that both towers recorded larger group sizes over the third ten-day period, which corroborates the Dawbin (1956) and Chittleborough, (1965) theory of different classes of humpback whales leaving the feeding grounds at different time. This increase in group size might indicate the presence of larger groups of males competing over receptive females.

3.4.3.3 Distance offshore

The results from the present study indicate that humpback whales migrate northwards close to shore (between 3.2km and 4.1km from shore) strengthen the hypothesis made by Findlay et al. (2011), who suggested that northward migrating whales remain relatively close to shore to avoid the southward moving Agulhas Current. Findlay et al. (2011) also reported that southward migrating humpback whales are located further offshore, likely using this strong southerly current to facilitate migration. However, in 2019 both towers recorded that it was statistically significant that whales were travelling further offshore in that year. This may be a result of an altered southward flow intensity of the Agulhas current in 2019 compared to 2018. Therefore, whales in 2018 whales migrated further in shore to avoid the strong southward current. Unfortunately, this remains a theory as there is no dedicated current meter in place.

The distance from the shore from which individuals are found might also be related to age, or reproductive class, aligned to the timing of the migration, as discussed before. Gonçalves et al. (2018) documented that humpback whale groups that include a calf migrate closer to shore when the calves are younger, presenting a gradual movement to deeper water with the maturation of the calves. Again, as such information was impossible to determine as part of this study, further (on-water), investigations are needed to evaluate if this is also true for whales migrating past Cape Vidal. However, in both years the third and fourth ten-day period recorded whales migrating closer to shore than earlier in the season. This may indicate the presence of mother and calf pairs migrating closer to shore for protection.

Without such on-water research, it remains impossible to fully determine how the decreased detectability of whales biases the observed distances from shore at greater distances from shore. To overcome this limitation, a line transect could be conducted by on or over water (aerial) survey simultaneously with the shore-based observations, allowing verification of the distances from shore and group sizes estimated from shore-based observations as done by Barendse et al. (2010). Similarly, Findlay et al. (2011) conducted one 55 km long transect (before other transects were compromised by vessel breakdown) perpendicular to the coast, which resulted in 17 sightings of 26 humpback whale groups up to 39 km of the shore. However, 96% of the observed groups were within 10 km from the shore (Findlay et al., 2011), well within the visual range of shore-based observers. Similarly, in eastern Australia, Bryden (1985) and Noad et al. (2008) found that 96% of humpback whale groups observed from aerial surveys were within 10 km of the land observation positions.

3.4.3.4 Group speed

The swim speeds reported in this study relate to the instantaneous speeds recorded at a given point in time, and they are assumed to represent the swim speed of the whales during their entire northward migration. Results from this study indicate a faster swim speed than those reported by Findlay et al. (2011), who reported means of between 3.63 (± 0.21) km/h and 5.41 (± 0.59) km/h. This apparent difference may be due to the increased sample size and more accurate measurements due to the increased number of fixes per observation in this study. However, the present data also had a considerable variation interannually, with whales swimming at higher speeds in 2018 compared to 2019. As with the distance offshore this could be related to the influence of the Agulhas Current (Lutjeharms and Ansorge, 2001) and remains to be determined. Barendse et al. (2010) noted that humpback whales off the west coast of South Africa had also had a considerable variation in their swim speed, ranging from 0.5 km/h to 11 km/h. Furthermore, they reported a reduced swim speed during spring, related to increased feeding behavior at that time. Such associations are not expected in the monitored population as feeding behavior is not known to be performed by the individuals on the east coast of South Africa. Also, a telemetry study by Cerchio et al. (2013) revealed significant variations in swim speed among individual humpback whales, with one of the tagged whales swimming 1,100 km over 13 days (mean speed = 3.52 km/h), while another covered 2,300 km in 23 days (mean speed = 4.16 km/h). Although such longer-term data derived from telemetry studies are not directly comparable to the instantaneous speed recordings from shore-based surveys, Cerchio et al. (2013) did indicate that the swim speed during migration may not be uniform and may include periods of resting or other activities.

3.4.3.5 Migration heading

Results from this study confirmed that most humpback whales are migrating northwards between June and August. Also, the migrating whales' track heading lies parallel to the coastline, suggesting no convergence on or divergence away from the coast. These are similar to the finding of Findlay and Best (1996b), which implied whales migrated from headland to headland and did not move inshore to explore any bays. Such results suggest that the orientation of the coastline is the main factor in determining the migration heading of individuals in the C1 sub-stock of the species. A study of humpback whales migrating off New Zealand support this assumption, as whales showed no relationship to either depth or proximity from the coastline but relied on the orientation of the coastline for direction (Dawbin, 1956).

3.4.4 Comparisons between migration parameters

In 2018 the only correlation found between all the parameters indicated that whales were travelling at a faster speed the further offshore they were observed. This reinforces what has been reported on under both group speed and distance offshore and the influence of the Agulhas current on the migration stream that year. In addition, mother pairs would travel closer to the shore at a slower speed to protect and nurse the calf.

In 2019 a correlation between migration heading and speed was observed. This also has connotations to the Agulhas current speed, direction and distance offshore influences the migration path of the humpback whales. Whales migrating closer to north were travelling where travelling faster, these whales also reinforce the fact that whales travel parellel to the coastline from headline to headland, and do not explore the bay at Cape Vidal.

CHAPTER 4: RELATIVE ABUNDANCE AND TRENDS OF HUMPBACK WHALES MIGRATING UP THE EAST COAST OF SOUTH AFRICA WITH A COMPARISON BETWEEN 1988 AND 2019.

4.1 BACKGROUND

The rate at which populations change is a fundamental demographic parameter used to assess wildlife populations (Skalski et al., 2005) and has important implications for conservation and management. Additionally, the rate of increase (ROI) of a population is often an essential parameter for population assessments and viability studies in ecosystem modelling (Mori and Butterworth, 2006, Zerbini et al., 2010b). Since their international protection from whaling in 1963 (Gambell, 1993), humpback whale populations started to recover steadily from previous exploitation by the whaling industry (Zerbini et al., 2010a). There are estimates of population ROI for all the humpback whale populations (Jackson et al., 2015), including the C1 sub-stock (Findlay et al., 2011). However, these C1 sub stock estimates are based on data collected between 1988 and 2002. Considering the population's expected continued ROI, an update of these data is warranted to provide current information for conservation management. Furthermore, given that the IWC Comprehensive Assessment of humpback whales suggested that the C1 sub-stock in 2010 was approaching 65% - 98% of its population size, a deceleration of the ROI can be expected (IWC 2011; Jackson et al., 2015) (see Figure 1.2).

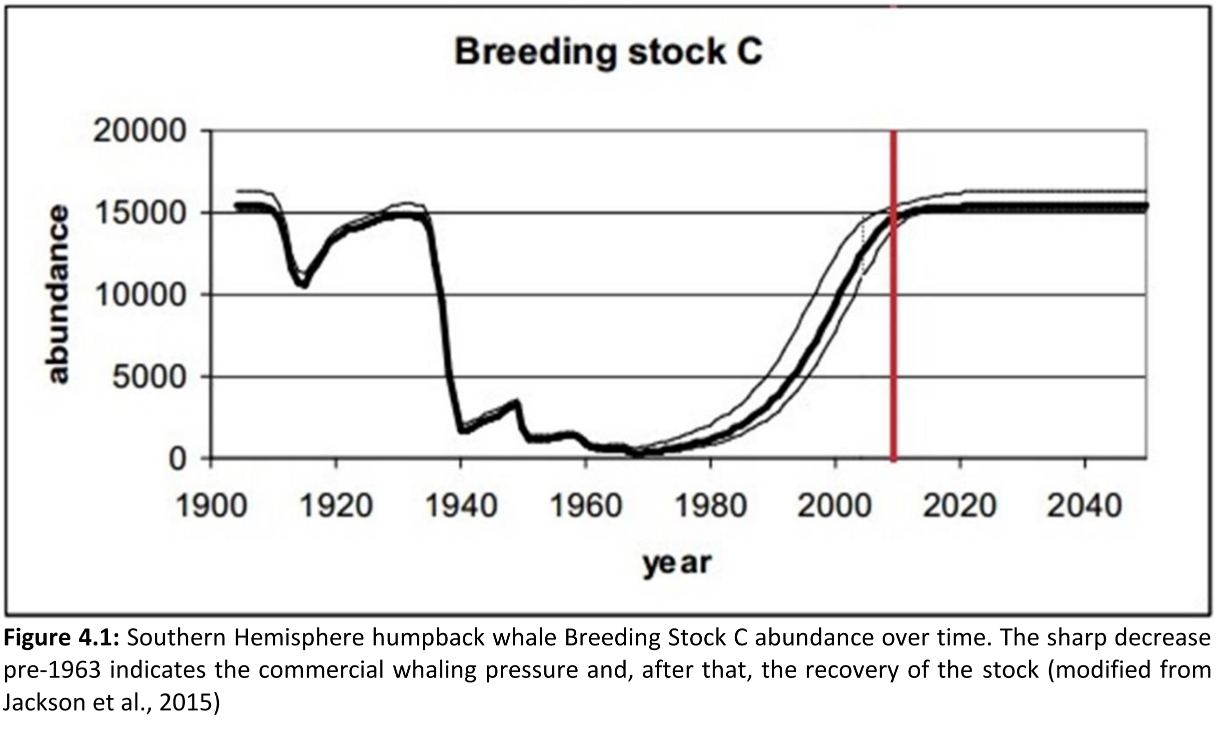


Figure 4.1: Southern Hemisphere humpback whale Breeding Stock C abundance over time. The sharp decrease pre-1963 indicates the commercial whaling pressure and, after that, the recovery of the stock (modified from Jackson et al., 2015)

Additionally, as anthropogenic factors affect the environmental conditions in breeding and feeding grounds (Trathan et al., 2007) up-to-date information on population trends is critical to monitor population responses to environmental change.

Findlay and Best (1996a; b) conducted dedicated daily observations from platforms specifically built for shore-based whale monitoring at Cape Vidal, South Africa during June, July, and August from 1988 to 1989 (south tower). The authors introduced a second tower during the 1990 and 1991 surveys (north tower), and simultaneous observations were introduced to determine observer efficiency through independent mark-recapture an using the same tower platforms, equipment and sampling protocol.

Findlay and Best (1996a; b) and Findlay et al. (2011) adjusted tallies of migrating whales in each of three distance bins (Near, Mid, Distant) and sightability conditions (Good, Fair, Poor) to account for proportions of whales missed through independent mark-recapture analyses. It is important to account for these proportions missed by observers into relative abundance estimations for the estimation of population trend. These studies proved that this methodology could successfully monitor the migration characteristics and the relative abundance of the C1 sub-stock of humpback whales. The results from the study (including the stock ROI) have been included in a stock assessment model, which has indicated that the population is approaching pre-exploitation numbers (see Figure 4.1; IWC, 2011).

Although such results contributed to the knowledge of the species and helped understand the status of the C1 sub-stock, given its recovery from whaling and current threats the continuation of data collection for the monitoring and updating of the numbers is essential to track how it is recovering from lack of whaling pressure, and to be able to propose effective management strategies for the future.

4.2 METHODS

4.2.1 Field methods

All data was collected by observing whales from two observation towers as per field methods 3.2.1.

4.2.2 Data analyses

Data were captured then digitised and analysed through custom Python coded applications, using the Anaconda Spyder console version 3.8 (Spyder-IDE.org). Initial analyses converted the horizontal and vertical theodolite angles into distances and bearing from the platform, taking both a refraction correction factor and the curvature of the Earth into consideration. These were subsequently converted into GPS coordinates on a cartesian plane (as positional fixes).

As observations could only occur during daylight hours, and whales were assumed to continue migration at night, the daily densities of migrating whales (over 24 hours) needed to be extrapolated by the number of groups sighted during the watch periods each day. Such extrapolation requires an assumption that whales' migration speeds are constant across the 24 hours (Findlay and Best, 1996b). This assumption of constant diel migration has been confirmed by Zerbini et al. (2006), Cerchio et al. (2013) and Riekkola et al. (2019) through satellite tagging and telemetry tracking of migrating humpback whales.

For a group to be included in the daily density estimations, the group must have crossed the midline of the observation area within the observation period, as daily densities would be inflated. Groups not seen crossing the midline of the observation area were projected forwards or backwards using their measured speed and bearing to calculate their projected time of midline crossing. Further coding was developed to accomplish this. Such groups were included in the analyses only if the projected time of their projected intersection fell within the observation period.

It is important to note that observers may miss detections of whale groups due to both availability and perception biases (Marsh and Sinclair, 1989). Several assumptions indicated by Seber (1982) and Findlay and Best (1996b) for the accurate estimation of the number of groups through mark-recapture analyses in the area were adopted in the present study, and are detailed below:

(i) The population is closed.

As the towers are 22 m apart, samples were taken instantaneously, and emigration from (or mortality) or immigration (or birth) to the sampled population is zero. Splitting or merging groups within the observation area would be paramount to births and deaths, respectively, as the group is sampled. Groups that split or joined during the observation period were recorded as single or multiple groups depending on when the split or merge occurred in the observation area.

However, due to the large number of whales passing the observation area in both 2018 and 2019, the observation groups were limited to a maximum of six fixes (most groups had four fixes). Although group numbers were counted on each sighting fix, observation time was often too short to record any splitting or merging of groups. It is assumed that for each group, the population remained closed.

(ii) The detection or probability of being captured within the first samples (marked) or second samples (recaptured) is the same.

The heterogeneity results from the north and south towers are conditionally independent rather than unconditionally independent (Schweder, 1990; Findlay and Best, 1996a). For example, some whales, such as those that breach or fin slap, are detected by observers in both towers. In contrast, whales simply traversing through the observation area are less noticeable (and therefore have higher chances of being missed) by both towers.

This problem is partly circumvented through temporal and spatial stratification of sighting conditions and the distances of sightings, respectively. Analyses were conducted on both stratified and unstratified data. Therefore, this assumption is considered to be met.

(iii) Marking does not affect recapturing.

As there is no physical marking of the animals, this assumption is met. However, the cueing of one tower by the other tower of whale groups could violate this assumption. This potential violation was overcome by ensuring that the towers worked independently, observers being visually and acoustically isolated from each other. Supervision at the towers, training and regular debriefings were held to prevent the violation of this assumption.

(iv) Marks are not lost between the two samples, and all marks are recorded on recapture in the second sample.

This assumption is also considered met, as only sightings seen by both towers were recognised. Due to the large numbers of whales recorded daily, various times and distances crossing the midline were tested for optimum matches.

The Petersen estimate estimates the population of marked individuals in the second sample and reflects the proportion of marked individuals in the population (Findlay, 1994). The total number of groups (N) recorded from the north tower (nn) and the south tower (ns), as well as the number of duplicates (matched) sightings between towers (m), were tallied in each of three distance bins and under three sightability conditions for each day's observations for the estimate of the total number of groups in the area.

$$N = (nn.ns)/m \quad (1)$$

The proportion of groups (p) seen by the north tower (pn) and by the south tower (ps) of the total number of matches seen are given by:

$$pn = \frac{m}{ns} \quad (2)$$

and

$$ps = \frac{m}{nn} \quad (3)$$

Chapman (1951) noted that the Petersen estimate of N is biased for small samples and thus modified the estimate to:

$$N = \left(\frac{(ns+1)(nn+1)}{(m+1)}\right) - 1 \quad (4)$$

The use of this method is comparable to Gentleman and Zeh's (1987) method, which compares samples of tracks rather than groups. Consequently, it includes additional variances arising from the uncertainty of linking sightings into tracks. All final number calculations will use Chapman's estimate.

The proportion of tracks seen by the south tower (ps) and north tower (pn) of the total present are given by:

$$ps = m(nn + 1) \quad (5)$$

and

$$pn = m(ns + 1) \quad (6)$$

The estimated sampling variances are given by:

$$\frac{(nn+1)(ns+1)(nn-m)(ns-m)}{(m+1)^2\ (m+2)} \text{ for N} \quad (7)$$

$$\frac{\left(1-\frac{\mathrm{m}}{\mathrm{ns}}\right)\left(\frac{\mathrm{m}}{\mathrm{nn}}\right)\left(1-\frac{\mathrm{m}}{\mathrm{nn}}\right)}{\mathrm{nn}-1} \text{ for ps} \quad (8)$$

and

$$\frac{\left(1-\frac{\mathrm{m}}{\mathrm{nn}}\right)\left(\frac{\mathrm{m}}{\mathrm{ns}}\right)\left(1-\frac{\mathrm{m}}{\mathrm{ns}}\right)}{\mathrm{ns}-1} \text{ for pn} \quad (9)$$

The *total number of groups* (N) crossing the midline on each day in three perpendicular distance interval bins from the coast (*i*) were tallied, as follows:

i = 1, between 0 and 3 km offshore

i = 2, between 3.0 and 6 km offshore

i = 3, greater than 6 km offshore

The proportion of missed groups by the towers in each of the distance intervals (i) was estimated by mark-recapture as per Findlay and Best (1996a) under different sightability conditions (w). Sightability estimates were collected hourly during weather observations. Sightability was estimated subjectively by the observers on their ability to detect and track whales. A decrease in sightability could be attributed to several factors.

(i) An increase in wind speed generates an increase in spray on the sea, thus decreasing the probability of detecting whales.
(ii) An increase in smoke or haze over the sea occurs in the winter when sugar cane farmers burn foliage before the sugar harvest. This smoke drifts down on the predominant north-westerly wind and reduces the visibility from the towers.
(iii) The occurrence of rain across the survey area or on the horizon decreases the sightability of whales.

w = 1, poor sightability, ratings 0 - 2

w = 2, fair sightability, ratings 2.01 - 4

w = 3, good sightability, rating 4.01 - 5

Matching groups for the mark-recapture analyses were conducted through Python coding to compare the spatial and temporal components of when and where groups crossed the midline of the observation area. The midline crossing time and position of each sighting made on any day from the south tower were compared with the equivalent time and position parameters from the north tower. The groups regarded as matches or duplicates, the crossing time and distance offshore had to fall within a spatial and temporal threshold. Spatial and temporal thresholds included 10 min and 500 m, 15 min and 1,000 m, and 20 min and 2,000 m threshold combinations. Based on comparisons of the results, the 20 min and 2,000 m threshold combinations were adopted for this study.

Daily tallies of the whale groups recorded in each distance bin were adjusted for proportions missed in the distance bin under the day's weather conditions. Adjusted tallies in each distance bin (*ad, i*) were produced:

$$a_{d,i} = n_{d,i}(1 + P_{w(d),i}) \qquad (10)$$

Adjusted counts within the three distance bins were summed and divided by the total observation effort for that day to give an estimate of sighting densities (*Jd*) of groups sighted per hour:

$$J_d = (\sum_{i=1}^{3}(a_{i,d}))/e_d \qquad (11)$$

Hourly estimates were multiplied by 24 to produce a daily tally (Dd). Migration rate was assumed to be consistent throughout the day and night so that hourly tallies could be extrapolated:

$$D_d = J_d \times 24 \qquad (12)$$

Tallies of individuals per day (Id) were determined as the product of daily group sighting densities, and the mean group size recorded in that year (S):

$$I_d = D_d S \qquad (13)$$

The total numbers of whales migrating past Cape Vidal (N) each year were estimated by adding the daily tallies recorded for each day, where *h* is the length of the survey in days:

$$N = \sum_{d=1}^{h}(i_d) \qquad (14)$$

4.2.3 Statistical analysis

As the sample sizes is between 0 and 2000 a Shapiro Wilk normality test would be run to indicate if the data were distributed normally, and if a parametric test could be used. If the data is found to be skewed and non-parametric tests would be used. Testing will be done using the same methodology, between the years to measure any differences in the population migration characteristics, and we will be comparing one variable at a time. In that regard the parametric test to be used be a T – Test, and the non-parametric test will be a Wilcoxon signed rank test.

4.3 RESULTS

4.3.1 Resolution testing

The 2018 and 2019 surveys observed and tracked more humpback whale groups than any other of the previous surveys. This necessitated the need to accurately match whale groups between the north and south tower to execute the Chapmans estimate (see equation 4) to allow the estimation of whale groups being missed by each tower to be explored. A midline between the two towers was established (in the midline of the observation area), and the time difference of groups crossing the midline and the proximity (distance from shore) of each group were used to determine if the groups were a match This required both time and distance bounds to be investigated to optimize the matching process.

Three time and distance bounds were tested (10min and 500m, 15min and 1000m, 20min and 2000m). The 20min and 2000m bounds were chosen for this study as these minimised the proportion of groups missed, and therefore provided lowest relative abundance estimate.

Matches were also stratified into distance bins offshore, near middle and distant. The daily sightability score were used to stratify the matched in to three weather bins, good, fair, and poor. These two groups of bins were also combined to illustrate the number of matches per combination of distance and weather bins.

Appendix C (2018), D (2019) and Table 4.1 (combined 2018 and 2019) illustrates the testing of the resolutions and that the 20min and 2000m was the best fit.

Table 4-1: Matching resolutions between north and south tower for both 2018 and 2019 combined, considering data unstratified, stratified into distance bins and weather bins and stratified by both. Nn = number of humpback whale sightings from the north tower, Ns = number of humpback whale sightings from the south tower, M = number of matches, N = total number of whales calculated by Chapman's estimation, SD= standard deviation

				10 min & 500m			**15min & 1000m**			**20min & 2000m**		
Year	**Stratification**	**Nn**	**Ns**	**Matches**	**N**	***SD***	**Matches**	**N**	***SD***	**Matches**	**N**	***SD***
2018/2019	Unstratified	**2552**	**2406**	**737**	8325.7	*215.06*	**1073**	5720.7	*98.84*	**1417**	4332.6	*49.17*
	Distance bins											
2018/2019	Near	1241	1026	**519**	2452	*57.57*	**659**	1931.6	*30.76*	**777**	1638.5	*17.68*
	Middle	844	849	**195**	3663.5	*200.71*	**356**	2010.9	*61.54*	**525**	1364.5	*22.56*
	Distant	394	433	**23**	7141.9	*1345.68*	**58**	2904.6	*321.59*	**112**	1516.1	*103.25*
	Disregard	73	98									
	Total	**2552**	**2406**									
	Weather bins											
2018/2019	Good	1577	1550	**424**	5757.8	*203.21*	**657**	3718.6	*83.95*	**880**	2777.1	*40.86*
	Fair	866	767	**269**	2465.1	*100.1*	**358**	1853.8	*54.61*	**476**	1394.9	*26.36*
	Poor	109	89	**44**	219	*17.63*	**58**	166.8	*8.66*	**61**	158.68	*7.41*
	Total	**2552**	**2406**									
	Combined bins											
2018/2019	Poor / Near	56	49	**36**	76.03	*3.77*	**45**	60.96	*1.12*	**43**	63.77	*1.6*
	Poor / Middle	30	29	**6**	131.86	*36.19*	**10**	83.55	*15.6*	**14**	61	*7.87*
	Poor / Distant	20	9	**2**	69	*27.11*	**3**	51.5	*16.36*	**4**	41	*10.58*
	Fine / Near	502	404	**203**	997.6	*37.88*	**245**	827.11	*23.6*	**307**	660.41	*11.47*
	Fine / Middle	268	252	**63**	1062.4	*99.52*	**103**	653.39	*38.38*	**154**	438.08	*14.24*
	Fine / Distant	79	85	**3**	1719	*732.09*	**10**	624.45	*156.59*	**14**	457.67	*93.91*
	Good / Near	683	573	**280**	1396.2	*45.63*	**369**	1060.1	*22.25*	**427**	916.33	*13.66*
	Good /Middle	546	568	**126**	2449.7	*167.29*	**243**	1274.6	*45.84*	**357**	868.39	*16.42*
	Good / Distant	295	339	**18**	5295.8	*1113.29*	**45**	2186.8	*272.72*	**94**	1058.4	*75.63*
	Disregard	73	98									
	Total	**2552**	**2406**									

4.3.2 Proportions of whale groups missed

It was expected that observers would miss whale groups, a result of the large numbers of whales migrating through the observation area. It is essential however to estimate this proportion if groups missed to factor them into the total estimate (see equations 5 and 6). When considering unstratified data from both years (see table 3.36), it was estimated that observers from the north tower missed 41% of groups and those in the south tower missed 44% of groups.

Table 4-2: Independent sightings, matches and proportions missed from the north and south towers during the survey period at Cape Vidal, South Africa, in 2018 and 2019. Results are presented as both unstratified and stratified into different distance and weather bins and a combination of both. Nn = number of humpback whale sightings from the north tower, Ns = number of humpback whale sightings from the south tower, M = number of matches, N = total number of whales calculated by the Chapman's estimation, SD= standard deviation, Pn = proportion of humpback whale missed by north tower, Ps = proportion of humpback whale missed by the south tower

Year	Stratification	Nn	Ns	M	N	SD	Pn	PS
2018/2019	Unstratified	**2,552**	**2,406**	1,417	4,332.62	*49.17*	**0.41**	**0.44**
2018/2019	**Distance bins**							
	Near	1,241	1,026	777	1,638.50	*17.68*	**0.24**	**0.37**
	Middle	844	849	525	1,364.49	*22.56*	**0.38**	**0.38**
	Distant	394	433	112	1,516.08	*103.25*	**0.74**	**0.72**
	Disregard	73	98					
	Total	**2,552**	**2,406**					
2018/2019	**Weather bins**							
	Good	1,577	1,550	880	2,777.07	*40.86*	**0.43**	**0.44**
	Fair	866	767	476	1,394.92	*26.36*	**0.38**	**0.45**
	Poor	109	89	61	158.68	*7.41*	**0.32**	**0.45**
	Total	**2,552**	**2,406**					
2018/2019	**Combined bins**							
	Poor / Near	56	49	43	63.77	*1.60*	**0.14**	**0.25**
	Poor / Middle	30	29	14	61.00	*7.87*	**0.53**	**0.55**
	Poor / Distant	20	9	4	41.00	*10.58*	**0.60**	**0.81**
	Fine / Near	502	404	307	660.41	*11.47*	**0.24**	**0.39**
	Fine / Middle	268	252	154	438.08	*14.24*	**0.39**	**0.43**
	Fine / Distant	79	85	14	457.67	*93.91*	**0.84**	**0.83**
	Good / Near	683	573	427	916.33	*13.66*	**0.26**	**0.38**
	Good /Middle	546	568	357	868.39	*16.42*	**0.37**	**0.35**
	Good / Distant	295	339	94	1,058.37	*75.63*	**0.72**	**0.68**
	Disregard	73	98					
	Total	**2,552**	**2,406**					

4.3.3 Sighting matches

The stratification into distance and weather bins allows for determining the areas and conditions where matches of whale groups (and sighting probabilities of whale groups) are optimal. During the combined 2018 and 2019 field seasons, a total of 4332.62 groups of humpback whales were observed to cross (or were projected to cross) the midline during the combined survey periods by the north and south tower, respectively. Using the 20 min time interval and 2,000 m crossing resolution, a total of 1,417 whale groups were matched between towers. Results indicate that 59% of the whale groups were observed by the north tower and 56% by the south tower. The sighting probability of whale groups is proportionate to the number of matches between both towers. The distance bin with the highest sighting probability was the near bin, with 777 matches, the north tower seeing 76% of whale groups and the south tower seeing 63% of whale groups within this bin (Figure 3.38). Concerning the weather bins, the "good" weather bin recorded the highest matches at 880 (Figure 3.39). In the combined bins (distance and weather) the "poor / near" bin, had 43 matches, whereby the north tower saw 86% of those whale groups and the south tower 75%. This made it the bin (area and conditions) where most matches would occur (Figure 3.40).

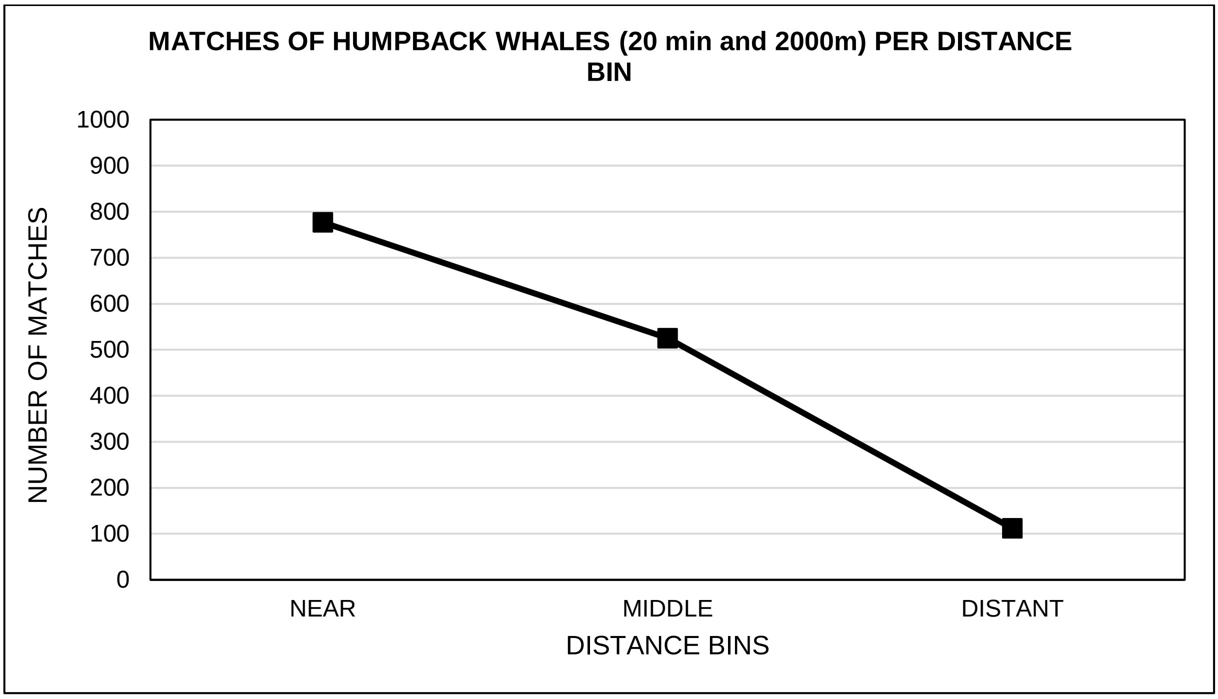


Figure 4.2: The number of humpback whale groups matches (using a match from within 20min and crossing the midline with in 2000m of each other). between towers per distance bin over the combined 2018 and 2019 surveys from Cape Vidal, South Africa

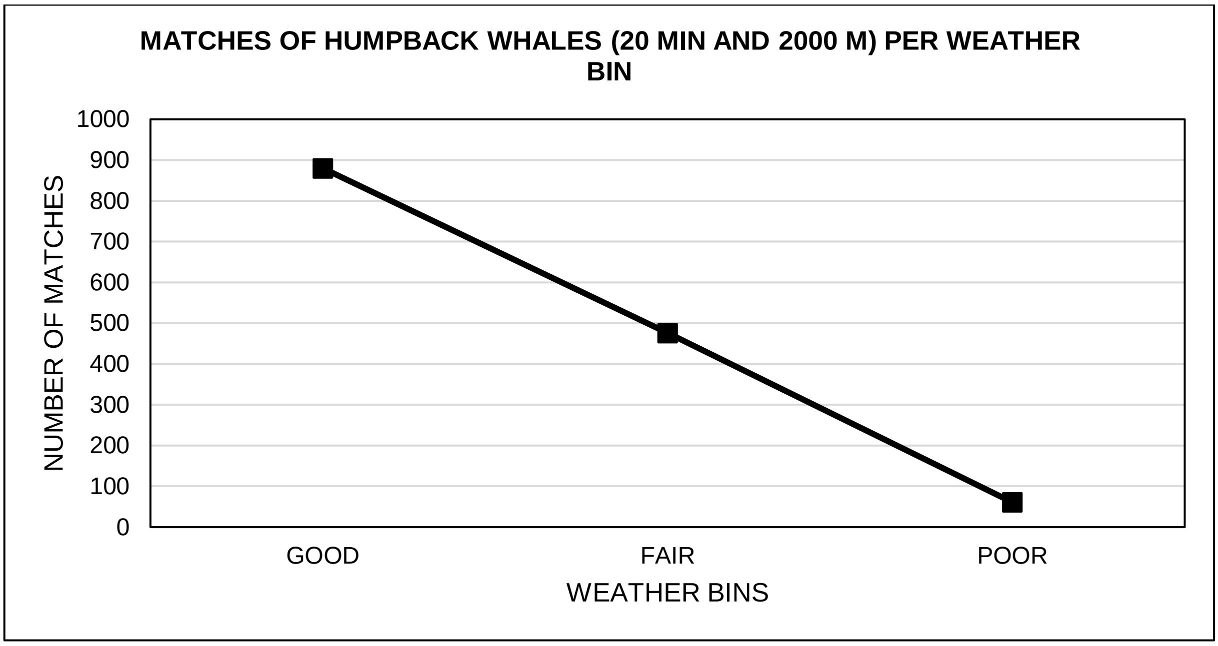


Figure 4.3: The number of humpback whale groups matches (using a match from within 20min and crossing the midline with in 2000m of each other). between towers per weather bin over the combined 2018 and 2019 surveys from Cape Vidal, South Africa

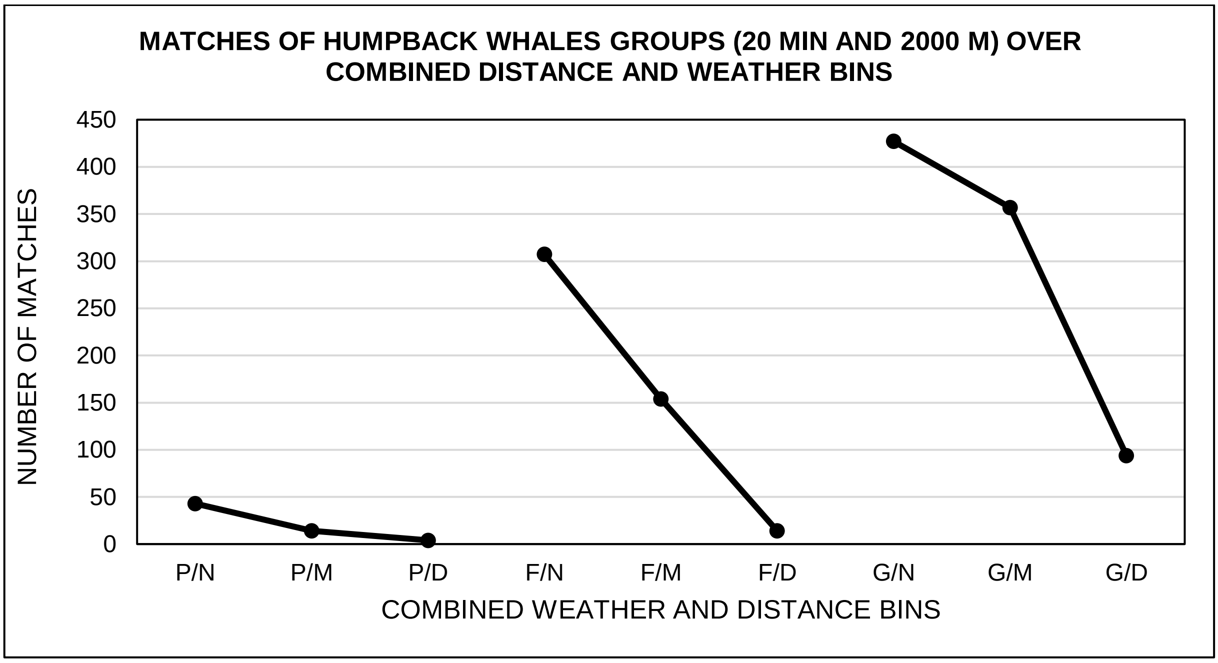


Figure 4.4: The number of humpback whale groups matches (using a match from within 20min and crossing the midline with in 2000m of each other). between towers per combine distance and weather bin over the combined 2018 and 2019 surveys from Cape Vidal, South Africa. P/N = poor / near, P/M = poor /middle, P/D = poor / distant, F/N = fair /near, F/M = fair /middle, F/D = fair /distant, G/N = good / near, G/M =good /middle and G/D = good / distant

4.3.4 Sighting probabilities

Combined 2018 and 2019 data were stratified by distance from shore and sighting conditions to determine the influence of such variables on sighting probabilities. Such probabilities were highest in the near distance bin (north tower = 0.76, south tower = 0.63) followed by the middle-distance bin (north tower = 0.62, south tower = 0.62), with lower probabilities recorded the greater the distance offshore (north tower = 0.26, south tower = 0.28) (Figure 3.35). The main difference between towers was that the observers working from the north tower were 13% better at detecting whales closer to shore. However, the lower offshore sighting probabilities resulted from farther offshore groups being less conspicuous than closer groups.

Regarding the sighting probabilities over the various weather conditions, these either stayed consistent over the good (north tower = 0.57, south tower = 0.56) and fair (north tower = 0.62, south tower 0.55) weather bins, and increased in the north tower as the weather conditions deteriorated (north tower = 0.68, south tower = 0.55) (Figure 3.36).

The combined sighting probabilities of the distance and weather bins is illustrated in figure 3.37, interestingly the highest probabilities to sight whales were from the north tower during poor weather conditions and when they were close to shore (86%). As expected, the furthest whales were hardest to sight during poor weather conditions.

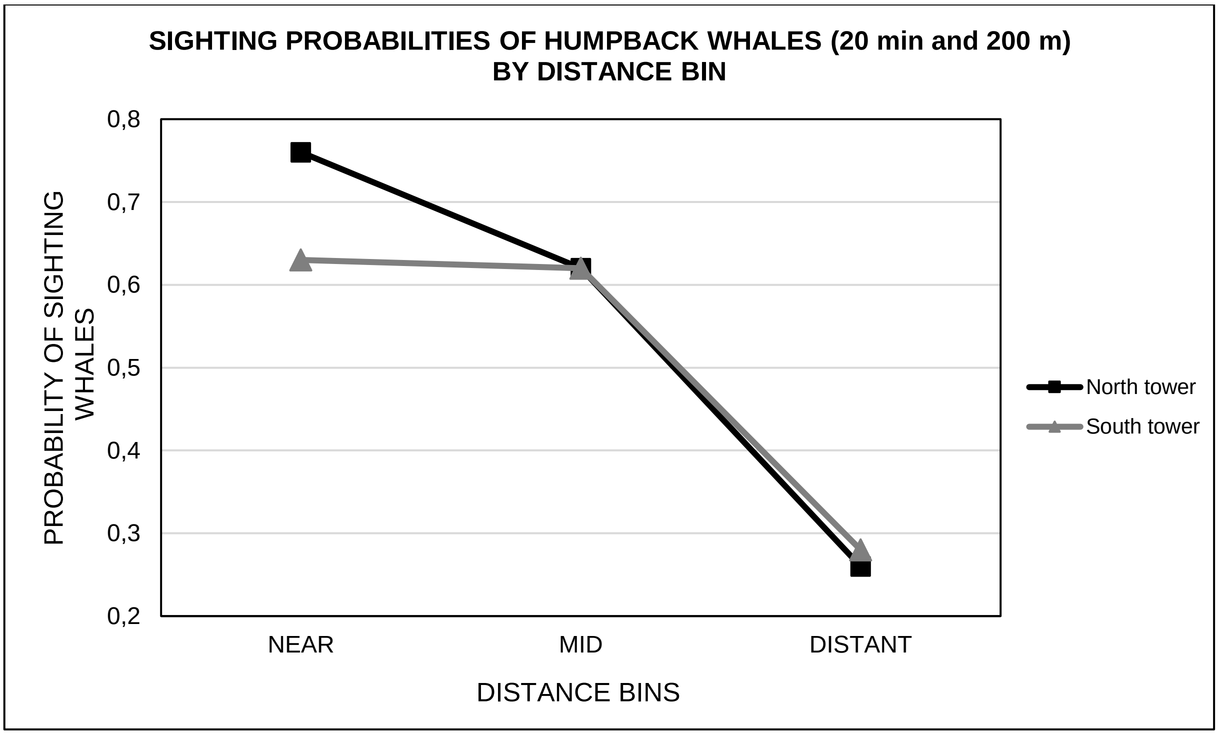


Figure 4.5: Sighting probabilities of humpback whale groups (using a match from within 20min and crossing the midline with in 2000m of each other), stratified over distance bins from combined 2018 and 2019 survey from north and south tower, off Cape Vidal, South Africa

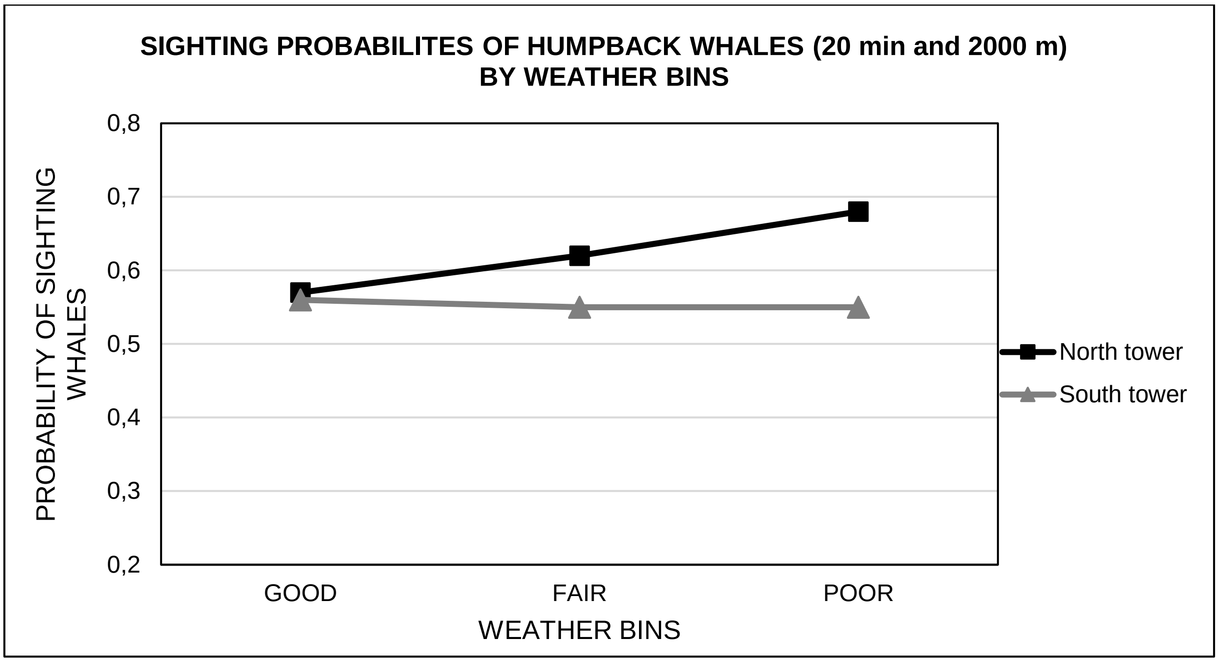


Figure 4.6: Sighting probabilities of humpback whale groups (using a match from within 20min and crossing the midline with in 2000m of each other), stratified over weather bins from combined 2018 and 2019 survey from north and south tower, off Cape Vidal South Africa

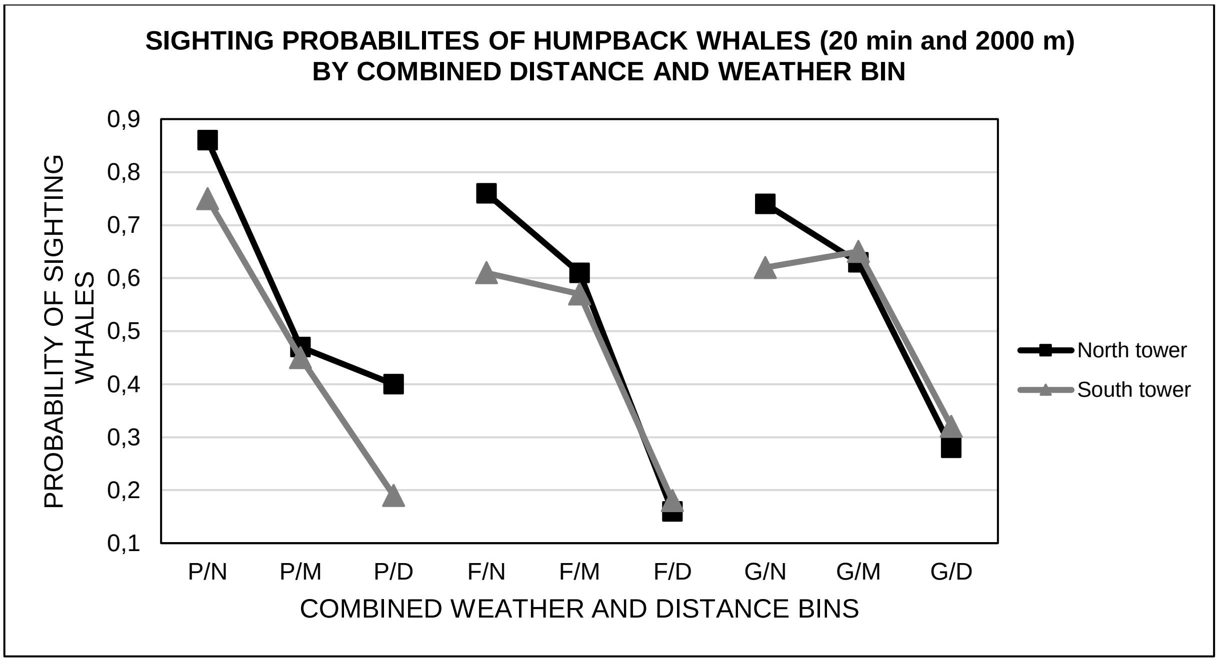


Figure 4.7: Sighting probability of whale groups stratified over distance and weather bins (using a match from within 20min and crossing the midline with in 2000m of each other). Codes on the x-axis represent the combined sightability conditions and distance bins.; P/N = poor / near, P/M = poor /middle, P/D = poor / distant, F/N = fair /near, F/M = fair /middle, F/D = fair /distant, G/N = good / near, G/M =good /middle and G/D = good / distant

4.3.5 Relative abundance estimates

4.3.5.1 Relative abundance estimates 2018

The daily observed whale groups matched where stratified into distance bins between towers. The proportions of whale numbers estimated to have been missed within each distance bin were adjusted (equation 10) under the average weather conditions for the day (Figure 3.41). Where days of zero observations were conducted, the average number of whale groups before and after was calculated and used.

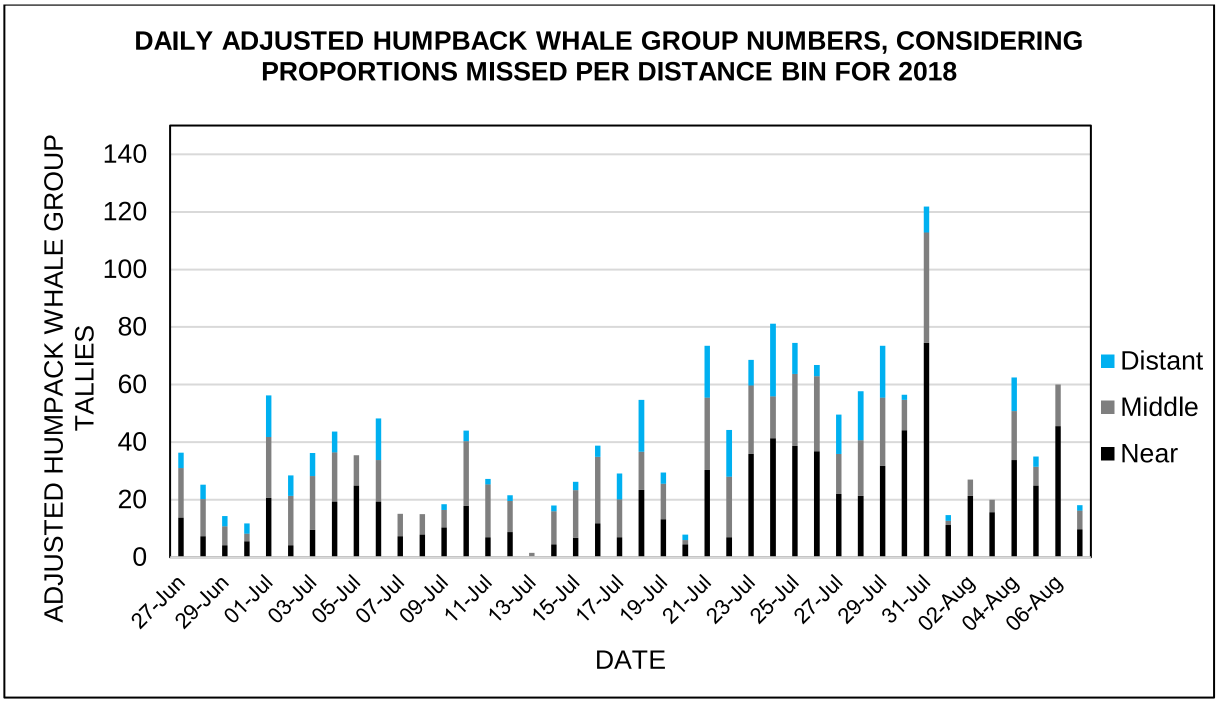


Figure 4.8: Number of humpback whale groups sighted per day, accounting for proportions missed per distance bin for 2018, off Cape Vidal, South Africa

Daily estimated humpback whale group numbers were divided by the observation effort (hours) to give whale groups passing per hour (equation 11), and then extrapolated by 24 hours to give the daily estimate of humpback whale groups passing Cape Vidal (equation 12). For example, on the 31st of July 2018, 90 whale groups were tracked for the day; this was adjusted by accounting for the proportions of whale groups missed; it equated to 121.8 groups during the observation effort. Further, when extrapolated to over 24 hours, it was estimated that 292 groups of humpback whales passed Cape Vidal that day (Figure 3.42).

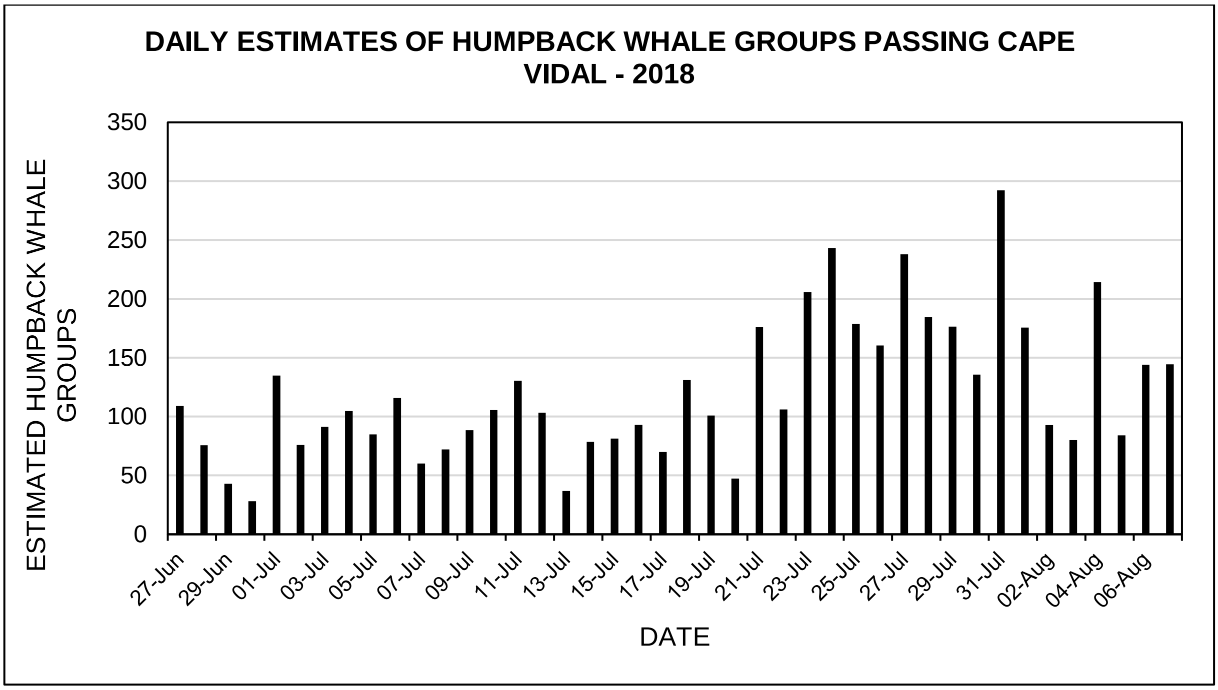


Figure 4.9: Daily estimates of humpback whale groups passing Cape Vidal, South Africa, over the 2018 survey period

The daily estimated for the survey period were added for the 42-day survey period and an estimated 5,096.42 humpback whale groups migrated past Cape Vidal during the 2018 survey (Equation 13). Considering the mean whale group size for 2018 was 2.06 whales per group, a resulting estimate of 10,498.61 humpback whales migrated past Cape Vidal during the survey period (Equation 14).

4.3.5.2 Relative abundance estimates 2019

The 2019 estimate followed the precise methodology of the 2018 estimate. Whale groups matches were adjusted by the proportion missed in each distance bin (Equation 10) for final daily groups per distance bin. Where days of zero observations were conducted, the average number of whale groups before and after was included (Figure 3.43).

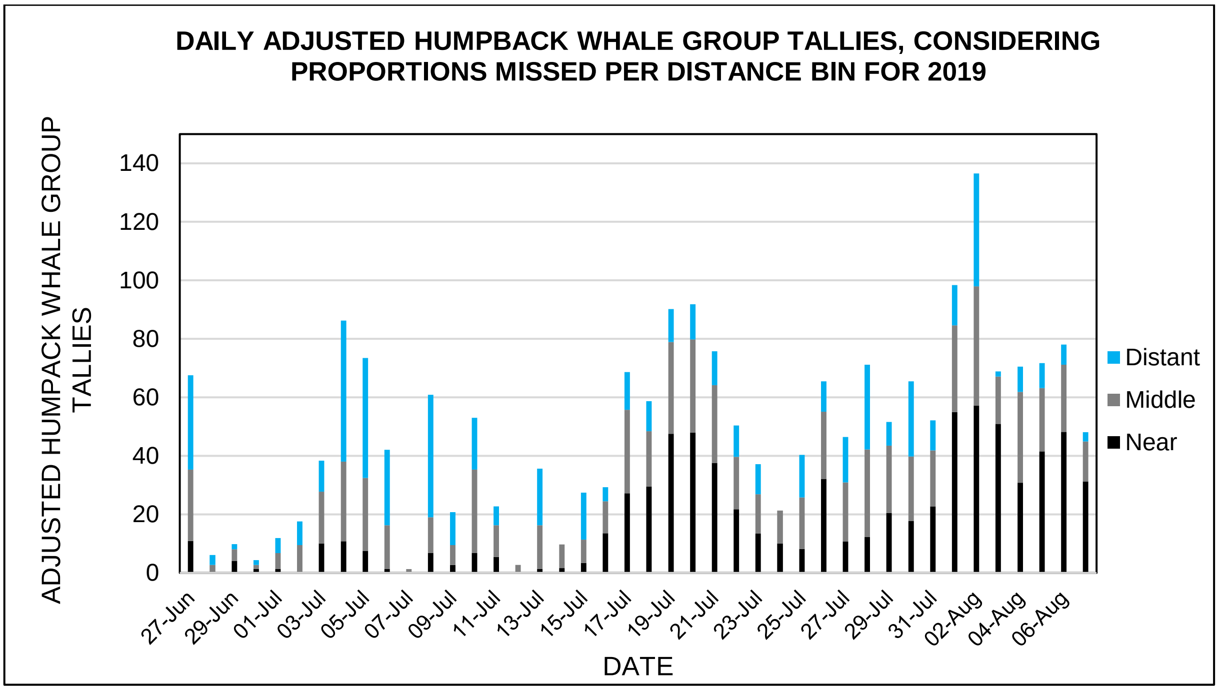


Figure 4.10: Daily adjusted humpback whale groups accounting for proportions missed per distance bin for 2019, off Cape Vidal, South Africa

Daily estimated humpback whale group numbers were dived by the observation effort (whales per hour, Equation 11) and extrapolated by 24 hours to give the number of humpback whale groups passing Cape Vidal during the 2019 survey period (Equation 12) (Figure 3.44).

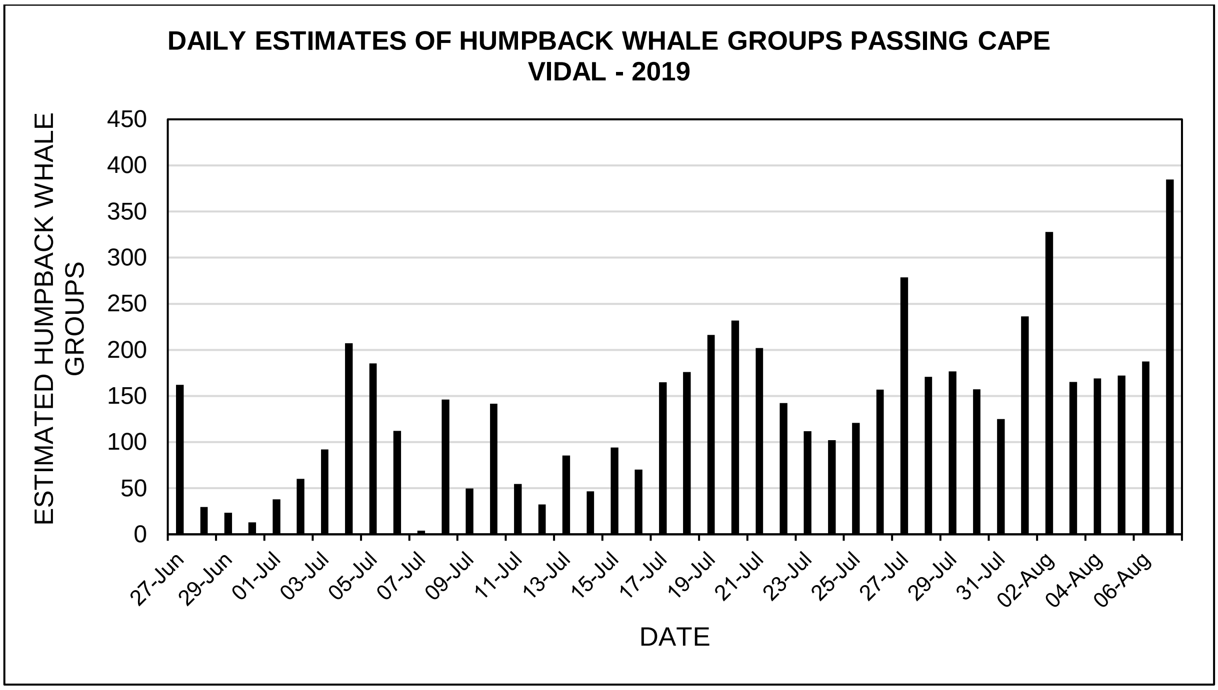


Figure 4.11: Daily estimates of humpback whale groups passing Cape Vidal (east coast of South Africa) over the 2019 survey period

On 7th August, although only three hours of observations were conducted (due to logistic constraints of the observers being collected early), the number of sightings was higher than on other days, with 36 groups observed. Therefore, a projected daily estimate of 384.8 groups would have passed Cape Vidal on that day.

Approximately 5,825.04 humpback whale groups migrated past Cape Vidal during the 2019 survey period (42 days) (Equation 13). Considering the mean whale group size for 2019 was 1.89 whales per group, this estimates 11,009.32 humpback whales migrating past Cape Vidal during the 2019 survey period (Equation 14).

4.3.6 Temporal changes in relative abundance estimates

The 2018 and 2019 numbers of individual humpback whales migrating past Cape Vidal have been compared to other historical surveys from all available corresponding dates (Table 3.39) All available values from the dates 6th to 22nd July1st to 22nd July 27th June to 22nd July and 6th to the 30th of July across all available survey years were used to plot the new ROI range of the humpback whale population migrating past Cape Vidal. Results showed that the current population growth rate is between 7.4% and 8.8%. These updated values indicate a decrease in the population growth rate from previous surveys (1988 to 2002). The previous ROI was estimated between 9% and 11.5% (the maximum biologically possible rate (Zerbini et al., 2010) and is now declined.

Table 4-3: Relative abundance data from Findlay et al. (2011) updated to include the respective tallies of 2018 and 2019, this comparing the total number of humpback whales sighted among all years

Year	Period					
	6-22 July	**1-22 July**	**27 June - 22 July**	**6-30 July**	**17 June - 6 August**	**27 June – 6 August**
1988	358					
1989	249	296	302			
1990	359	420	420	695	1,000	
1991	587	734	831	1,093	1,777	
2002	1,673			2,406		
2018	3,893	4,550	5,105	6,801		10,498.61
2019	4,532	5,928	6,457	7,378		11,009.32

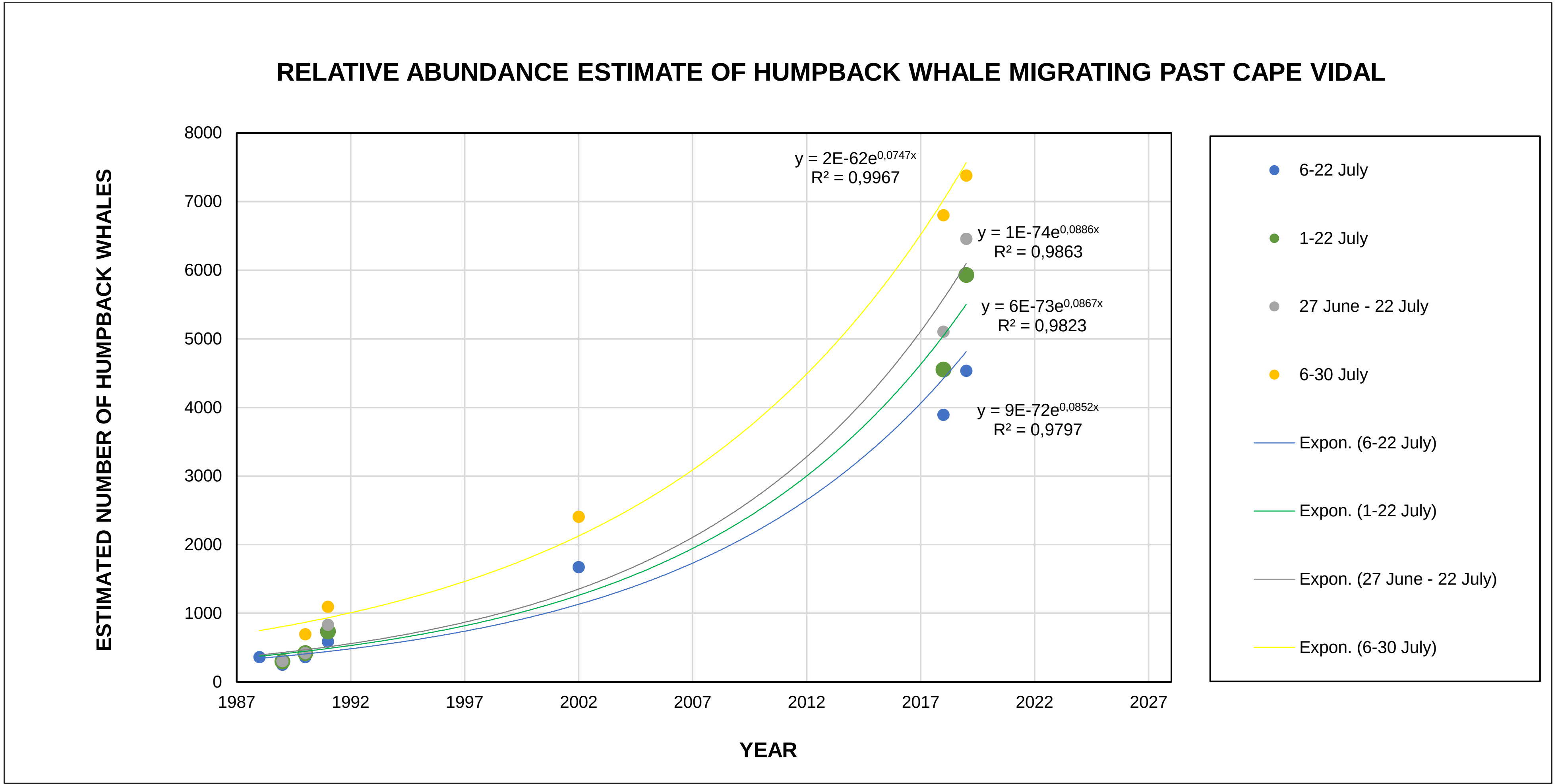


Figure 4.12: Increase in the numbers of humpback whales migrating northwards past Cape Vidal during the dates 6th to 22nd July 1st to 22nd July 27th June to 22nd July and the 6th of July to 30th July, from all available survey years

4.4 DISCUSSION

4.4.1 Sighting probabilities

As expected, the probability of detecting and tracking humpback whales decreased with distance from the shore. However, this was contrary to the findings of a past study at Cape Vidal, which indicated sighting probabilities were highest in the middle distance bin (3 - 6 km offshore) (Findlay and Best, 1996a). Rugh (1989) found a similar result to that of Findlay and Best (1996a): gray whales' sighting probabilities were lower near shore and in the offshore bins. However, the present study results could be confounded by a decreased sightability due to glare or haze (especially in 2019).

Another unexpected result of this study relates to the increased sighting probabilities with deteriorating weather conditions. The increased surface activity (including fin slapping, tail slapping and breaching) of humpback whales related to strong winds (Findlay and Best, 1996a) may have influenced this result. Whales are often increasingly difficult to spot in calm conditions when the behaviour is far more relaxed.

4.4.2 Relative abundance estimates and population trends

Constant or accounted-for detection probabilities are required between years to estimate a population trend through relative abundance. Different levels of effort need to be considered as whale densities (e.g., sightings per hour). Therefore, when comparing all previous humpback whale surveys at Cape Vidal, Findlay et al. (2011) made the following assumptions:

(i) The proportion of the population passing beyond the spatial and temporal limits of the observations is consistent across years. There are believed to be at least three migration streams of humpback whales in the south-western Indian Ocean, including the route along the African mainland to and from Mozambique (the C1 sub-stock), the route along the Madagascar Ridge (C3 sub-stock), and the route in the central Mozambique Channel (C2 sub - stock) (Best et al., 1998). The estimated increase rates through relative abundances assume that whales stick to a specific route and do not shift routes between years. It is believed this assumption can be made based on the markedly different catch histories (in terms of timing) between the different breeding grounds of the C1, C2 and C3 sub-stocks and more recent observations of migrations on the Madagascar ridge and in southern Madagascar (see Findlay et al., 2011). The relationship between this migration stream and others in the Western Indian Ocean is unknown, but the limited interchange identified through photo-identification suggests it is minimal.

(ii) Depending on distance and weather conditions, detection probabilities should remain constant throughout the time series or be accounted for. Weather and sightability data were collected and recorded hourly, and sighting probabilities were considered to account for whale groups missed within each weather and distance offshore bin. However, as Findlay and Best (1996a) indicate, sighting probabilities will not be homogeneous for groups due to distance from the observer, as a group of whales passing at a far distance will be available to the observer for a shorter period than a near group (due to the passing of whales through circular fields of view), regardless the weather conditions. However, this study accounted for probabilities with distance, and sighting conditions set such limits of visibility, so these were also accounted for. Such limits will be constant between years if similar sighting conditions prevail.

(iii) Observer accuracy and precision must be constant throughout the survey series. Every effort was made to ensure that the survey effort and methods remained constant throughout all the surveys, including using almost obsolete theodolite equipment to align with previous surveys. The timing of the survey has been dictated by the Findlay et al. (2011) surveys, and the equipment and towers are the same used in previous surveys. Furthermore, observers were evaluated on skills and paired with appropriately experienced partners. The training was given on the data collection, and supervision in the towers was provided to ensure this assumption was met.

(iv) The pattern of diel migration must remain constant throughout the survey period. Visual observations can only be conducted during daylight hours and within favourable weather conditions. However, to extrapolate actual observation effort to daily totals over 24 h, a constant diel migration rate must be assumed under different sighting conditions. Furthermore, Findlay et al. (2011) found zero variation in migration speeds by weather conditions across the 1988 to 1991 surveys or migration speeds by day during observations.

Results of this study indicate that the C1 sub-stock of humpback whales is increasing steadily (ROI = between 7.4% and 8.5% for 1988 - 2019), but at a decelerated rate in comparison to the 1988 - 2011 period (ROI = 11.5%) (Findlay et al., 2011). Considering that the current size of the BS C1 sub stock is assumed to be close to pre-exploitation levels (IWC, 2011), the results of this study may indicate that the humpback whale C1 sub-stock migrating past Cape Vidal is reaching carrying capacity leading to a slowing down of the population recovery rate.

Contrary to these findings, a comparable study from eastern Australia has shown consistent ROI of the E1 sub-stock of about 11% for over 24 years, with no evidence of slowing down (Noad et al., 2019). As this stock size is near pre-exploitation levels (Noad et al., 2019), a stable high ROI (close to the maximum biologically possible for the species; Zerbini et al., 2010) was believed to be related to intrinsic growth combined with temporary immigration from other populations on the breeding grounds. This means that individuals from low-density populations may be temporarily drawn to larger aggregations in breeding grounds, before moving south to their native feeding grounds (Zerbini et al., 2010b; Clapham and Zerbini, 2015). Relevant to the present study, this suggests that any immigration into the migration stream of the C1 sub-stock from other, neighbouring sub-stocks is negligible, as already suggested by Rosenbaum et al. (2009) or through the photo-identification results of Cerchio et al. (2006).

CHAPTER 5: GENERAL DISCUSSION

Humpback whales are capital breeders, which heavily rely on their foraging success to support their reproductive output (Jönsson, 1997) so that a continued positive population trend seems indicative of a healthy ecosystem in their feeding grounds that provides sufficient prey for these populations to ensure reproductive success. However, the effects of global climate change on krill (Fraser and Hofmann, 2003; Flores et al., 2012) imply that impacts on various marine mammals and birds can be expected (Forcada and Trathan, 2009; Constable et al., 2014). Krill has a vital role in the Southern Ocean trophic ecology, as it is the primary prey source for many species of penguins, seals, and baleen whales. It is therefore expected that bottom-up variation in krill abundance will significantly impact all Southern Ocean predators and the ecosystem in general (Doney et al., 2012), while changes in top-down pressures (e.g. increasing predation from recovering seal or other whale populations) may also play an important role in reducing carrying capacity. For example, Seyboth et al. (2016) demonstrated strong correlations between southern right whale breeding success and krill abundance in their summer feeding ground in southern Brazil; the influence of krill biomass on the reproduction of humpback whales has been indicated (Seyboth et al., 2021), while Williams et al. (2013) demonstrated a decreased reproductive success in fin whales (*Balaenoptera physalus*) due to limited prey availability. Baleen whales' responses to climate change (and other anthropogenic pressures) are confounded by their concurrent recovery from heavy exploitation from the whaling industry (Nicol et al., 2008), and unravelling these factors is a complex task. It, therefore, remains impossible, at this stage, to conclude if the decelerating growth rate of the C1 sub-stock is related to carrying capacity or a response to a changing climate or other anthropogenic factors, or both. There have been many anthropogenic and biological factors in the last 30 years that could affect carrying capacity, including ocean pollution, climate change, overexploitation of whales as well as their prey species, and modifications to the ocean environment (e.g., seismic surveys) (Gaines et al., 2019). The overexploitation of baleen whales during the commercial whaling era has had fundamental impacts on all marine food webs and likely caused critical shifts in the structure of those food webs, both pre-and post-whaling (Nicol et al., 2008). One such shift was believed to be related to an increase in Antarctic minke whales due to an increased krill availability when other whale populations were overexploited, leading to increased intraspecific competition when these populations rebounded (Ruegg et al., 2010). However, Friedlaender et al. (2009) indicated that that interspecific competition between the two species is unlikely due to them targeting different kinds of krill aggregations, while populations of minke whales have not shown marked increases since the cessation of whaling.

The question as to whether a reduction in the rate of increase indicates that carrying capacity is being approached, or is a result of anthropogenic impacts, remains vexing. Both Smetacek and Nicol, (2005) and Constable et al. (2014) identify the difficulty of disentangling such drivers. However, the global increase in humpback populations across the Southern Hemisphere and the results of models suggesting that current abundance estimates are approaching pre-exploitation levels (regardless of changes in carrying capacity – see Jackson et al. 2015) indicate that humpback whales have a potential for population recovery once a particular pressure (in this case – whaling) has been reduced. While modelling suggests humpback whale numbers are approaching pre-whaling numbers, there are several increasing anthropogenically driven changes to the ocean environment.

According to the World Health Organization (WHO), ocean noise has been recognised as a global pollutant and hazardous environmental change (Kunc et al., 2016). Anthropogenic noise in the ocean can affect animals in various ways, including:

(i) auditory damage from exposure to loud noise (Kunc et al., 2016),
(ii) shifts in location as animals avoid sound (Kunc et al., 2016),
(iii) masking of sounds hindering other acoustic messages (Kunc et al., 2016), and
(iv) an increased stress level, leading to an imbalance of physiology (Kunc et al., 2016).

Humpback whales have well-developed hearing and rely heavily on underwater noises for communication between groups and reproductive behaviour on the breeding grounds (Best, 2007). The species has shown responses to each of the effects of anthropogenic noises as mentioned above. For example, stranded individuals have been found to have damaged ears and ear canals from underwater explosions (Lien et al., 1993). Some whales actively avoid seismic surveys when migrating to or on the feeding and breeding grounds, some mother and calf groups avoid the source by 10 – 12 km while others are attracted to the source (McCauley et al., 2000). In addition, singing whales on the breeding grounds have their songs distorted or masked by anthropogenic noise, seismic blasts, and ship noise. All these factors are crucial considerations and all increase stress hormone levels, which will directly influence the reproductive rate, thus ultimately influencing the humpback whales' ROI.

The impacts of climate and environmental change on marine ecosystems are complex to unravel (Constable et al., 2014), and identifying animals that are useful for monitoring such impacts and that allow for future predictions of responses of top marine predators, is deemed critical (Fleming et al., 2016). Indicator species are those species that can be easily monitored and whose status reflect the environmental condition of their habitat (Landres et al., 1988; Cairns and Pratt, 1993; Bartell, 2006; Burger, 2006; Siddig et al., 2016). The humpback whale is considered as crucial trans-ocean indicator species. The ease of monitoring humpback whales on their migration and breeding grounds and their dependence on seasonal foraging success for their breeding success makes them an ideal indicator species for the Southern Ocean ecosystem. It is believed that a multidisciplinary approach needs to be taken to understand better the effects of climate change on humpback whales in the Southern

Hemisphere. Meynecke et al. (2020) proposed a systems approach framework to understand humpback whale abundance and distribution, conducting multidisciplinary, collaborative studies across regions. A challenge in this framework is that the critical process operate at different complex spatial and temporal scales (Meynecke et al., 2020). It will be challenging, but the humpback whale and its cosmopolitan (on a global scale) ecology are important indicators to identify changes over the world's oceans.

Estimating the exploitation of whale stocks and gaining a better understanding of their decline is essential (see 1.2) in accurately assessing the actual effects of whaling. Establishing an accurate baseline for the recovery of the whale stocks is important because if the pre-exploitation numbers of whales are incorrectly estimated, the recovery rate and abundance level in relation to pre-whaling abundance will be biased (Baker and Clapham, 2004). Any error in this pre-exploitation estimate has the potential to mask whales' responses to any ecological and environmental changes (in terms of reduced rates of increase because of these or inherent population demography). Continued monitoring of recovering humpback whale populations is critical to ensure an ability to identify possible effects of Southern Ocean ecosystem changes on these whales’ population health.

CHAPTER 6: CONCLUSION AND RECOMMENDATIONS

Overall, this study has shown that shore-based observation off Cape Vidal and monitoring using theodolite tracking remains a cost-effective and accurate method of estimating the relative abundance of humpback whales off the east coast of South Africa. Considering the findings of the current study, it is possible to conclude that, for the period investigated:

(i) The location of Cape Vidal, on the east coast of South Africa, remains an excellent vantage point to monitor the BS C migrating humpback whales, and
(ii) The humpback whale C1 sub-stock abundance is still increasing, although the rate of increase has decreased over the last two decades.

The present study provided an updated relative abundance and population annual growth rate from shore-based monitoring of Southern Hemisphere humpback whales. It is recommended that such new information is taken into consideration by decision-makers, including the Scientific Committee of the International Whaling Commission.

This study clearly showed that humpback whale numbers off the east coast of South Africa are high between June and August due to north and southward migrating individuals, and most of these animals are found within 20 km from shore. Such spatial and temporal information is essential during ocean governance and marine spatial planning. Although their presence is predictable, the migrating behaviour of these humpback whales, which includes high swim speeds and little rest time, makes them optimal for boat-based whale tourism activity, although suboptimal for any potential "swim-with-whale" activities. In addition, shore-based whale-watching could be a viable option in this area, especially in peak season.

Also, it is recommended that future studies on abundance and rate of increase of the humpback whale C1 sub-stock use additional methodologies, so some of the underlying assumptions of the present study can be verified. Specifically, benefits from additional boat-based line-transect surveys or aerial surveys perpendicularly out from the study area in combination with shore-based surveys in the area can be used to assess the following:

(i) What proportion of the stock passes outside (more than 20 km) of the observers' view?
(ii) How do sighting probabilities change with distance from the shore?
(iii) How accurate are shore-based group size estimations?
(iv) What are the links between the other sub-stocks in the BS C (collecting photo-identification and skin samples for genetic analyses)?

(v) Is there temporal segregation in age and reproductive classes of the humpback whales migrating past Cape Vidal, and what is their body condition on the northward migration (through the collection of aerial photogrammetry data)?

(vi) A change in body condition is expected between northward migrating whales early in the season and whales migrating south returning from the breeding grounds. What is the change in body condition of the BS C 1 whales?

Continued monitoring of this humpback whale sub-stock, and humpback whales globally, is critical. They are excellent trans-ocean indicator species to investigate ocean change linked to increased ocean resource uses and the associated pressures of increasing ocean blue economies across the world.

REFERENCES

Baker, C.S. and Clapham, P.J. 2004. Modelling the past and future of whales and whaling. *Trends in Ecology and Evolution*, 19(7): 365–371.

Barendse, J. 2011. *Local movements, migrations and habitat use of humpback whales off the West Coast of South Africa, including observations of southern right whales*. Ph.D Thesis. University of Pretoria: 175pp.

Barendse, J., Best, P.B., Thornton, M., Elwen, S.H., Rosenbaum, H.C., Carvalho, I., Pomilla, C., Collins, T.J.Q., Meÿer, M.A. and Leeney, R.H. 2011. Transit station or destination? Attendance patterns, movements and abundance estimate of humpback whales off west South Africa from photographic and genotypic matching. *African Journal of Marine Science*, 33(3): 353–373.

Barendse, J., Best, P.B., Thornton, M., Pomilla, C., Carvalho, I. and Rosenbaum, H.C. 2010. Migration redefined? seasonality, movements and group composition of humpback whales *Megaptera novaeangliae* off the west coast of South Africa. *African Journal of Marine Science*, 32(1): 1–22.

Bartell, S.M. 2006. Biomarkers, Bioindicators, and Ecological Risk Assessment—A Brief Review and Evaluation. *Environmental Bioindicators*, 1(1): 60–73.

van den Berg, G.L. 2020. *Foraging ecology of South Africa's southern right whales (Eubalaena australis) in relation to calving success and global climate variability*. M.Sc. Thesis. University of Pretoria: 153pp.

Best, P.B., Findlay, K., Sekiguchi, K., Peddemors, V., Rakotonirina, B., Rossouw, A. and Gove, D. 1998. Winter distribution and possible migration routes of humpback whales *Megaptera novaeangliae* in the southwest Indian Ocean. *Marine Ecology Progress Series*, 162: 287–299.

Best, P.B. 2007. *Whales and Dolphins of the Southern African Subregion*. Cambridge University Press: 41–48

Best, P.B. and Ross, G.J.B. 1986. Catches of right whales from shore-based establishments in southern Africa, 1792–1975. *Reports of the International Whaling Commission*, 10: 275–289.

Best, P.B., Sekiguchi, K. and Findlay, K.P. 1995a. A suspended migration of humpback whales *Megaptera novaeangliae* on the west coast of South Africa. *Marine ecology progress series.* 118(1): 1–12.

Bindoff, N.L., Cheung, W.W.L., Kairo, J., Arístegui, J., Guinder, V.A., Hallberg, R., Hilmi, N., Jiao, N., Karim, M., Levin, L., O'Donoghue, S., Purca Cuicapusa, S.R., Rinkevich, B., Suga, T., Tagliabue, A. and Williamson, P. 2019. Changing Ocean, Marine Ecosystems, and Dependent Communities. *IPCC Special Report on the Ocean and Cryosphere in a Changing Climate*: 447–588.

Bracegirdle, T.J., Connolley, W.M. and Turner, J. 2008. Antarctic climate change over the twenty first century. *Journal of Geophysical Research Atmospheres*, 113(3): 1–13.

Branch, T.A., DeJoseph, B.M., Ray, L.J. and Wagner, C.A. 2013. Impacts of ocean acidification on marine seafood. *Trends in Ecology and Evolution*, 28(3): 178–186.

Brown, M.R. 1996. Population biology and migratory characteristics of east Australian humpback whales, *Megaptera novaeangliae*. Ph.D. Thesis. University of Sydeney: 200pp.

Bryden, M.M. 1985. Studies of humpback whales (*Megaptera novaeangliae*), area V. In J.K. Ling and M. M. Bryden, eds. *Studies of sea mammals in south latitudes*. Northfield S.A.: South Australian Museum: 115–123.

Bryden, M.M., Kirkwood, G.P. and Slade, R.W. 1990. Humpback Whales, Area V. An Increase in Numbers Off Australia's East Coast. In K.R. Kerry and G. Hempel, eds. *Antarctic Ecosystems*. Springer Berlin Heidelberg: 271–277.

Buckland, S.T., Breiwick, J.M., Cattanach, K.L. and Laake, J.L. 1993. Estimated population size of the California gray whale. *Marine Mammal Science*, 9(3): 235–249.

Burger, J. 2006. Bioindicators: Types, Development, and Use in Ecological Assessment and Research. *Environmental Bioindicators*, 1(1): 22–39.

Cairns, J. and Pratt, J.R. 1993. *A history of biological monitoring using benthic macroinvertebrates*. *Freshwater Biomontoring and Benthic Mcroinvertebrates.* Chapman and Hall New York: 10–27

Cerchio, S., Trudelle, L., Zerbini, A., Geyer, Y., Mayer, F.X., Charrassin, J., Jung, J., Adam, O. and Rosenbaum, H. 2013. Satellite tagging of humpback whales off Madagascar reveals long range movements of individuals in the Southwest Indian Ocean during the breeding season. *Paper presented to the Scientific Committee of the International Whaling Commission ; SC/65a/SH22: Unpublished data*.

Chapman, D.G. 1974. Status of Antarctic rorqual stocks. In *The whale problem*. Harvard University Press: 218–238.

Cheng, L., Trenberth, K.E., Fasullo, J., Boyer, T., Abraham, J. and Zhu, J. 2017. Improved estimates of ocean heat content from 1960 to 2015. *Science Advances*, 3(3): 1–11.

Chittleborough, R. 1965. Dynamics of two populations of the humpback whale, *Megaptera novaeangliae* (Borowski). *Marine and Freshwater Research*, 16(1): 33.

Clapham, P. 2001. Why do baleen whales migrate? A response to Corkeron and Connor. *Marine Mammal Science*, 17(2): 432–436.

Clapham, P.J. and Mead, J.G. 1999. *Megaptera novaeangliae*. *Mammalian Species*, 118(604): 1.

Clapham, P.J. and Zerbini, A.N. 2015. Are social aggregation and temporary immigration driving high rates of increase in some Southern Hemisphere humpback whale populations? *Marine Biology*, 162(3): 625–634.

Colwell, R.K. 1974. Predictability, constancy, and contingency of periodic phenomena. *Ecology*, 55(5): 1148–1153.

Constable, A.J., Melbourne-Thomas, J., Corney, S.P., Arrigo, K.R., Barbraud, C., Barnes, D.K.A., Bindoff, N.L., Boyd, P.W., Brandt, A., Costa, D.P., Davidson, A.T., Ducklow, H.W., Emmerson, L., Fukuchi, M., Gutt, J., Hindell, M.A., Hofmann, E.E., Hosie, G.W., Iida, T., Jacob, S., Johnston, N.M., Kawaguchi, S., Kokubun, N., Koubbi, P., Lea, M.A., Makhado, A., Massom, R.A., Meiners, K., Meredith, M.P., Murphy, E.J., Nicol, S., Reid, K., Richerson, K., Riddle, M.J., Rintoul, S.R., Smith, W.O., Southwell, C., Stark, J.S., Sumner, M., Swadling, K.M., Takahashi, K.T., Trathan, P.N., Welsford, D.C., Weimerskirch, H., Westwood, K.J., Wienecke, B.C., Wolf-Gladrow, D., Wright, S.W., Xavier, J.C. and Ziegler, P. 2014. Climate change and Southern Ocean ecosystems I: How changes in physical habitats directly affect marine biota. *Global Change Biology*, 20(10): 3004–3025.

Corkeron, P.J. and Connor, R.C. 1999. Why do baleen whales migrate? *Marine Mammal Science*, 15(4): 1228–1245.

Cotté, C. and Guinet, C. 2007. Historical whaling records reveal major regional retreat of Antarctic sea ice. *Deep Sea Research Part I: Oceanographic Research Papers*, 54(2): 243–252.

Dawbin, W.H. 1956. The migrations of humpback whales which pass the New Zealand coast. In *Transactions of the Royal Society of New Zealand*. J. Hughes, Printer: 147–196.

Doney, S.C., Ruckelshaus, M., Emmett Duffy, J., Barry, J.P., Chan, F., English, C.A., Galindo, H.M., Grebmeier, J.M., Hollowed, A.B. and Knowlton, N. 2012. Climate change impacts on marine ecosystems. *Annual Review of Marine Science*, 4: 11–37.

Donovan, G.P. 1991. A review of IWC stock boundaries. *A report for the International Whaling Commission, Special Issue* 13: 39–68.

Dudgeon, C.L., Dunlop, R.A. and Noad, M.J. 2018. Modelling heterogeneity in detection probabilities in land and aerial abundance surveys in humpback whales (*Megaptera novaeangliae*). *Population Ecology*, 60(4): 371–387.

Egevang, C., Stenhouse, I.J., Phillips, R.A., Petersen, A., Fox, J.W. and Silk, J.R.D. 2010. Tracking of Arctic terns Sterna paradisaea reveals longest animal migration. *Proceedings of the National Academy of Sciences*, 107(5): 2078–2081.

Eisenmann, P., Fry, B., Holyoake, C., Coughran, D., Nicol, S. and Bengtson Nash, S., 2016. Isotopic evidence of a wide spectrum of feeding strategies in Southern Hemisphere humpback whale baleen records. *PLoS One*, 11(5): e0156698

Evans, P.H. 1987. *The natural history of whales and dolphins*. Facts on File.Inc, New York: 1–43.

Fabry, V., Seibel, B., Feely, R. and Orr, J. 2008. Impacts of ocean acidification on marine fauna and ecosystem processes. *ICES Journal of Marine Science*, 65: 414–432.

Findlay, K. 1994. *The migrations of East Coast Humpback whales (Megaptera novaeangliae)*. Ph.D. Thesis,University of Pretoria: 221pp.

Findlay, K, Best, P. and Meÿer, M. 2011. The migrations of humpback whales past Cape Vidal, South Africa, and a preliminary estimate of the population increase rate. *African Journal of Marine Science*, 33(3): 375–392.

Findlay, K., Meer, M., Elwen, S., Kotze, D., Johnson, R., Truter, P., Uamusse, C., Sitoe, S., Wilke, C., Kerwath, S., Swanson, S., Staverees, L. and Van Der Westhuizen, J. 2011. Distribution and abundance of humpback whales, *Megaptera novaeangliae*, off the coast of Mozambique, 2003. In *Journal of Cetacean Research and Management*. 163–174.

Findlay, K.P. 2001. A review of humpback whale catches by modern whaling operations in the Southern Hemisphere. *Memoirs of the Queensland Museum*, 47(2): 411–420.

Findlay, K.P. 1997. Attitudes and expenditures of whale watchers in Hermanus, South Africa. *South African Journal of Wildlife Research*, 27(2): 57–62.

Findlay, K.P. and Best, P.B. 1996a. Assessment of heterogeneity in sighting probabilities of humpback whales within viewing range of Cape Vidal, South Africa. *Marine Mammal Science*, 12(3): 335–353.

Findlay, K.P. and Best, P.B. 1996b. Estimates of the numbers of humpback whales observed migrating past Cape Vidal, South Africa, 1988–1991. *Marine Mammal Science*, 12(3): 354–370.

Findlay, K. P., Best, P.B. and Meÿer, M.A. 2011. Migrations of humpback whales past Cape Vidal, South Africa, and an estimate of the population increase rate (1988-2002). *African Journal of Marine Science*, 33(3): 375–392.

Findlay, K. P., Meer, M., Elwen, S.H., Kotze, D., Johnson, R., Truter, P., Uamusse, C., Sitoe, S., Wilke, C., Kerwath, S., Swanson, S., Staverees, L., Van Der Westhuizen, J., Meÿer, M.A., Elwen, S.H., Kotze, P.G.H., Johnson, R., Truter, P., Uamusse, C., Sitoe, S., Wilke, C., Kerwath, S., Swanson, S., Staverees, L., Van Der Westhuizen, J. and Der, A.N.V.A.N. 2011. Distribution and abundance of humpback whales, *Megaptera novaeangliae*, off the coast of Mozambique, 2003. *Journal of Cetacean Research and Management*, Special issue 3: 163–174.

Findlay, K.P., Seakamela, S.M., Meÿer, M.A., Kirkman, S.P., Barendse, J., Cade, D.E., Hurwitz, D., Kennedy, A.S., Kotze, P.G.H., McCue, S.A., Thornton, M., Vargas-Fonseca, O.A. and Wilke, C.G. 2017. Humpback whale 'super-groups' - A novel low-latitude feeding behaviour of Southern Hemisphere humpback whales (*Megaptera novaeangliae*) in the Benguela Upwelling System. *PLoS ONE*, 12(3): e0172002.

Flores, H., Atkinson, A., Kawaguchi, S., Krafft, B.A., Milinevsky, G., Nicol, S., Reiss, C., Tarling, G.A., Werner, R., Bravo Rebolledo, E., Cirelli, V., Cuzin-Roudy, J., Fielding, S., Groeneveld, J.J., Haraldsson, M., Lombana, A., Marschoff, E., Meyer, B., Pakhomov, E.A., Rombolá, E., Schmidt, K., Siegel, V., Teschke, M., Tonkes, H., Toullec, J.Y., Trathan, P.N., Tremblay, N., Van De Putte, A.P., Van Franeker, J.A. and Werner, T. 2012. Impact of climate change on Antarctic krill. *Marine Ecology Progress Series*, 458: 1–19.

Forcada, J. and Trathan, P.N. 2009. Penguin responses to climate change in the Southern Ocean. *Global Change Biology*, 15(7): 1618–1630.

Fraser, W. and Hofmann, E. 2003. A predator's perspective on causal links between climate change, physical forcing and ecosystem response. *Marine Ecology Progress Series*, 265: 1–15.

Fraser, W.R. and Hofmann, E.E. 2003. A predator's perspective on causal links between climate change, physical forcing and ecosystem response. *Marine Ecology Progress Series*, 265: 1–15.

Friedlaender, A.S., Lawson, G.L. and Halpin, P.N. 2009. Evidence of resource partitioning between humpback and minke whales around the western Antarctic Peninsula. *Marine Mammal Science*, 25(2): 402–415.

Gaines, S., Cabral, R., Free, C.M., Golbuu, Y., Arnason, R., Battista, W., Bradley, D., Cheung, W., Fabricius, K., Hoegh-Guldberg, O., Juinio-Meñez, M.A., Molinos, J.G., Ojea, E., O'Reilly, E. and Turley, C. 2019. The Expected Impacts of Climate Change on the Ocean Economy. *World Resources Institute* (December): 4–11.

Gambell, R. 1993. International management of whales and whaling: an historical review of the regulation of commercial and aboriginal subsistence whaling. *Arctic*, 46(2): 97–107.

Gambell, R. 1976. World whale stocks. *Mammal Review*, 6(1): 41–53.

George, J.C. 'Craig', Zeh, J., Suydam, R. and Clark, C. 2004. Abundance and population trend (1978 - 2001) of western Arctic bowhead whales surveyed near Barrow, Alaska. *Marine Mammal Science*, 20(4): 755–773.

Gonçalves, M.I.C., Sousa-Lima, R.S. de, Teixeira, N.N., Carvalho, G.H., Danilewicz, D. and Baumgarten, J.E. 2018. Movement patterns of humpback whales (*Megaptera novaeangliae*) reoccupying a Brazilian breeding ground. *Biota Neotropica*, 18(4).

Hammond, P.S., Mizroch, S.A. and Donovan, G.P. 1990. Individual recognition of cetaceans: use of photo-identification and other techniques to estimate population parameters. *Reports for the International Whaling Commission* 12.

Hedley, S.L., Bannister, J.L. and Dunlop, R.A. 2011. Abundance estimates of Southern Hemisphere Breeding Stock 'D' humpback whales from aerial and land-based surveys off Shark Bay, Western Australia, 2008. *Journal of Cetacean Research and Management*, Special issue 3: 209–221.

Herzing, D.L. and Mate, B.R. 1989. Gray whale migrations along the Oregon coast. Jones, L.R, Swartz, S.L, Leatherwood, S (ed), *The gray whale: Eschrichtius robustus*, Academic Press: 289.

Hin. 2015. *A Dictionary of Biology*. Oxford University Press

Hjort, J., Lie, J. and Ruud, J.T. 1932. Norwegian pelagic whaling in the Antarctic. I. Whaling grounds in 1929-1930 and 1930-1931.Hvalradets Skrifter 3: 1932. International Whaling Commission 1998. *Annexure G: Report of the sub-committee on the comprehensive assessment of Southern hemisphere humpback whales.*

Holdo, R.M., Holt, R.D. and Fryxell, J.M., 2009. Opposing rainfall and plant nutritional gradients best explain the wildebeest migration in the Serengeti. *The American Naturalist* 173(4): 431-445.

IWC (International Whaling Commission). 2010. Annex H: Report of the Sub-Committee on Other Southern Hemisphere Whale Stocks. *Journal of Cetacean Research and Management*, 11(2): 218–251.

IWC (International Whaling Commission). 1997. Forty-seventh Report of the International Whaling Commission. *Report of the International Whaling Commssion*: 161 - 191

IWC (International Whaling Commission). 2000. Report of the Sub- Committee on in-depth assessments: *Report of the International Whaling Commission* 52.

IWC (International Whaling Commission). 2011. Report of the Workshop on the Comprehensive Assessment of Southern Hemisphere humpback whales. *Journal of Cetacean Research and Management*, (SPEC. ISS. 3): 1–50.

IWC (International Whaling Commission). 2011. Humpback Whales: Status in the Southern Hemisphere. *Journal of Cetacean Research and Management*, (3): 300.

Jackson, J.A., Ross-Gillespie, A., Butterworth, D., Findlay, K., Holloway, S., Robbins, J., Rosenbaum, H., Weinrich, M., Baker, C.S. and Zerbini, A.N. 2015. Southern Hemisphere Humpback Whale Comprehensive Assessment - A synthesis and summary: 2005-2015. *Report SC/66a/SH/03 to the Scientific Committee of the International Whaling Commission*: 1–38.

James, B.S. 2014. *Natural and human impacts on habitat use of coastal delphinids in the Mossel Bay area, Western Cape, South Africa*. M.Sc. Thesis. University of Pretoria: 170pp

Joly, K., Gurarie, E., Sorum, M.S., Kaczensky, P., Cameron, M.D., Jakes, A.F., Borg, B.L., Nandintsetseg, D., Hopcraft, J.G.C., Buuveibaatar, B., Jones, P.F., Mueller, T., Walzer, C., Olson, K.A., Payne, J.C., Yadamsuren, A. and Hebblewhite, M. 2019. Longest terrestrial migrations and movements around the world. *Scientific Reports*, 9(1): 1–10.

Jönsson, K.I. 1997. Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos*, 78(1): 57.

Katona, S.K. and Whitehead, H.P. 1981. Identifying humpback whales using their natural markings. *Polar Record*, 20(128): 439–444.

Kelbe, P.B. 2021. Isimangaliso webpage. *https://isimangaliso.com/useful-information/climate/*. https://isimangaliso.com/useful-information/climate/.

Kellog, R. 1929. What is known of the migration of some of the whalebone whales. *Annual Reports of the Smithsonian Institute for 1928*: 467–494.

Kovach, R.P., Ellison, S.C., Pyare, S. and Tallmon, D.A. 2015. Temporal patterns in adult salmon migration timing across southeast Alaska. *Global Change Biology*, 21(5): 1821–1833.

Kunc, H.P., McLaughlin, K.E. and Schmidt, R. 2016. Aquatic noise pollution: Implications for individuals, populations, and ecosystems. *Proceedings of the Royal Society B: Biological Sciences*, 283(1836): p.20160839

Landres, P.B., Verner, J. and Thomas, J.W. 1988. Ecological Uses of Vertebrate Indicator Species: A Critique. *Conservation Biology*, 2(4): 316–328.

Levy, D. 2017. T*he environmental factors determining temporal distributions of cetaceans in Mossel Bay, South Africa.* M.Sc. Thesis. University of Cape Town: 1–150

Lien, J., Todd, S., Stevick, P., Marques, F. and Ketten, D. 1993. The reaction of humpback whales to underwater explosions: orientation, movements, and behavior. *The Journal of the Acoustical Society of America*, 94(3): 1849.

Lin, M., Lucas, H.C. and Shmueli, G. 2013. Too big to fail: Large samples and the p-value problem. *Information Systems Research*, 24(4): 906–917.

Lundquist, D., Sironi, M., Würsig, B., Rowntree, V., Martino, J. and Lundquist, L. 2013. Response of southern right whales to simulated swim-with-whale tourism at Península Valdés, Argentina. *Marine Mammal Science,* 29: E24-E45

Lutjeharms, J.R.E. and Ansorge, I.J. 2001. The Agulhas Return Current. *Journal of Marine Systems*, 30(1–2): 115–138.

Lutjeharms, J.R.E. and De Ruijter, W.P.M. 1996. The influence of the Agulhas Current on the adjacent coastal ocean: Possible impacts of climate change. *Journal of Marine Systems*, 7(2–4): 321–336.

Mackintosh, N.A. 1942. The Natural History of Whales. *Polar Record*, 3(24): 553–563.

Mackintosh, N.A. 1965. The stocks of whales. London. *Fishing News (Books) Ltd., 232p*.

Marsh, H. and Sinclair, D.F. 1989. Correcting for Visibility Bias in Strip Transect Aerial Surveys of Aquatic Fauna. *The Journal of Wildlife Management*, 53(4): 1017–1024.

Mate, B.R., Ilyashenko, V.Y.U., Bradford, A.L., Vertyankin, V. V., Tsidulko, G.A., Rozhnov, V. V. and Irvine, L.M. 2015. Critically endangered western gray whales migrate to the eastern North Pacific. *Biology Letters*, 11(4).

McCauley, D.J., Pinsky, M.L., Palumbi, S.R., Estes, J.A., Joyce, F.H. and Warner, R.R. 2015. Marine defaunation: Animal loss in the global ocean. *Science*, 347(6219): 12556411–12556417.

McCauley, R.D., Fewtrell, J., Duncan, A.J., Jenner, C., Jenner, M.-N., Penrose, J.D., Prince, R.I.T., Adhitya, A., Murdoch, J. and McCabe, K. 2000. Marine Seismic Surveys: Analysis and Propagation of Air-gun Signals: and effects of air-gun exposure on Humpback Whales, Sea Turtles, Fishes and Squid: 203.

Meynecke, J., Seyboth, E., De Bie, J., Menzel Barraqueta, J., Chama, A., Prakash Dey, S., Lee, S.B., Tulloch, V., Vichi, M. and Findlay, K. 2020. Responses of humpback whales to a changing climate in the Southern Hemisphere: Priorities for research efforts. *Marine Ecology*, 41(6): e12616.

Mörch, J.A. 1911. On the natural history of whalebone whales. In *Proceedings of the Zoological Society of London*. Wiley Online Library: 661–676.

Mori, M. and Butterworth, D.S. 2006. A first step towards modelling the krill-predator dynamics of the antarctic ecosystem. *CCAMLR Science*, 13: 217–277.

Nerini, M.K., Braham, H.W., Marquette, W.M. and Rugh, D.J. 2009. Life history of the bowhead whale, Balaena mysticetus (Mammalia: Cetacea). *Journal of Zoology*, 204(4): 443–468.

Nicol, S., Worby, A. and Leaper, R. 2008. Changes in the Antarctic sea ice ecosystem: potential effects on krill and baleen whales. *Marine and Freshwater Research*, 59(5): 361.

Noad, M.J., Dunlop, R.A., Paton, D. and Cato, D.H. 2008. An update of the east Australian humpback whale population (E1) rate of increase. *Journal of Cetacean Research and Management*, (January): 1–13.

Noad, M.J., Kniest, E. and Dunlop, R.A. 2019. Boom to bust? Implications for the continued rapid growth of the eastern Australian humpback whale population despite recovery. *Population Ecology*, 61(2): 198–209.

Norris, K.S. 1967. Some observations on the migration and orientation of marine mammals. *Animal Orientated*, 101: 125.

Palsbøll, P.J., Allen, J., Berube, M., Clapham, P.J., Feddersen, T.P., Hammond, P.S., Hudson, R.R., Jørgensen, H., Katona, S. and Larsen, A.H. 1997. Genetic tagging of humpback whales. *Nature*, 388(6644): 767–769.

Paterson, R. and Paterson, P. 1989. The Status of the Recovering Stock of Humpback Whales *Megaptera novaeangliae* in East Australian Waters. , 47: 33–48.

Paterson, R., Paterson, P. and Cato, D.H. 1994. The status of humpback whales *Megaptera novaeangliae* in east Australia thirty years after whaling. *Biological Conservation*, 70(2): 135–142.

Paterson, R.A. 1991. The migration of humpback whales *Megaptera novaeangliae* in east Australian waters. *Memoirs - Queensland Museum*, 30(2): 333–341.

Pearsall, J. and Hanks, P. 2001. *The new Oxford dictionary of English*.

Photopoulou, T., Best, P.B., Hammond, P.S. and Findlay, K.P. 2011. Movement patterns of coastal bottlenose dolphins in the presence of a fast-flowing, prevailing current: shore-based observations at Cape Vidal, South Africa. *African Journal of Marine Science*, 33(3): 393–401.

Pitman, R.L., Totterdell, J.A., Fearnbach, H., Ballance, L.T., Durban, J.W. and Kemps, H. 2015. Whale killers: Prevalence and ecological implications of killer whale predation on humpback whale calves off Western Australia. *Marine Mammal Science*, 31(2): 629–657.

Piwetz, S., Gailey, G., Munger, L., Lammers, M.O., Jefferson, T.A. and Würsig, B. 2018. Theodolite tracking in marine mammal research: From Roger Payne to the present. *Aquatic Mammals*, 44(6): 683–693.

Poole, M.M. 1984. Migration corridors of gray whales along the Central California coast, 1980-1982. Jones, L.R, Swartz, S. L, Leatherwood, S (ed), *The gray whale: Eschrichtius robustus*, Academic Press:389–406.

Rasmussen, K., Palacios, D.M., Calambokidis, J., Saborío, M.T., Dalla Rosa, L., Secchi, E.R., Steiger, G.H., Allen, J.M. and Stone, G.S. 2007. Southern Hemisphere humpback whales wintering off Central America: Insights from water temperature into the longest mammalian migration. *Biology Letters*, 3(3): 302–305.

Reilly, S.B., Rice, D.W. and Wolman, A.A. 1983. Population assessment of the gray whale, Eschrichtius robustus, from California shore censuses 1967 - 80. *Fishery Bulletin*, 81(2): 267–281.

Riekkola, L., Andrews-Goff, V., Friedlaender, A., Constantine, R. and Zerbini, A.N. 2019. Environmental drivers of humpback whale foraging behavior in the remote Southern Ocean. *Journal of Experimental Marine Biology and Ecology*, 517(May): 1–12.

Roberts, M.J., Ribbink, A.J., Morris, T., Van Den Berg, M.A., Engelbrecht, D.C. and Harding, R.T. 2006. Oceanographic environment of the Sodwana Bay coelacanths (Latimeria chalumnae), South Africa. *South African Journal of Science*, 102(9–10): 435–443.

Roche, C. 2008. 'The Fertile Brain and Inventive Power of Man': Anthropogenic factors in the cessation of Springbok treks and the disruption of the Karoo ecosystem, 1865–1908. *Africa*, 78(2): 157–188.

Rosenbaum, H.C., Pomilla, C., Mendez, M., Leslie, M.S., Best, P.B., Findlay, K.P., Minton, G., Ersts, P.J., Collins, T., Engel, M.H., Bonatto, S.L., Kotze, D.P.G.H., Meÿer, M., Barendse, J., Thornton, M., Razafindrakoto, Y., Ngouessono, S., Vely, M. and Kiszka, J. 2009. Population structure of humpback whales from their breeding grounds in the South Atlantic and Indian Oceans. *PLoS ONE*, 4(10), p.7318.

Rugh, D.J. 1989. Census of gray whales at Unimak Pass. Jones, L.R, Swartz, S. L, Leatherwood, S (ed)*The gray whale: Eschrichtius robustus*, Academic Press: 225–248.

Schweder, T. 1990. Independent observer experiments to estimate the detection function in line transect surveys of whales. *Reports of the International Whaling Commission Special Issue* 40: 349–355.

Seber, G.A.F. 1982. *The estimation of animal abundance*. Second edition. New York: Macmillian Publishing Co: 654pp.

Seyboth, E., Félix, F., Lea, M., Dalla Rosa, L., Watters, G.M., Reid, K. and Secchi, E.R. 2021. Influence of krill (*Euphausia superba*) availability on humpback whale (*Megaptera novaeangliae*) reproductive rate. *Marine Mammal Science*: 1–9.

Seyboth, E., Groch, K.R., Dalla Rosa, L., Reid, K., Flores, P.A.C. and Secchi, E.R. 2016. Southern Right Whale (*Eubalaena australis*) reproductive success is influenced by krill (*Euphausia superba*) density and climate. *Scientific Reports*, 6: 1–8.

Siddig, A.A.H., Ellison, A.M., Ochs, A., Villar-Leeman, C. and Lau, M.K. 2016. How do ecologists select and use indicator species to monitor ecological change? Insights from 14 years of publication in Ecological Indicators. *Ecological Indicators*, 60: 223–230.

Skalski, J.R., Ryding, K.E. and Millspaugh, J.J. 2005. *Wildlife Demography*. Elsevier: 656pp.

Smetacek, V. and Nicol, S. 2005. Polar ocean ecosystems in a changing world. *Nature*, 437(7057): 362–368.

Stevick, P.T., Allen, J., Clapham, P.J., Friday, N., Katona, S.K., Larsen, F., Lien, J., Mattila, D.K., Palsbøll, P.J., Sigurjónsson, J., Smith, T.D., Øien, N. and Hammond, P.S. 2003. North Atlantic humpback whale abundance and rate of increase four decades after protection from whaling. *Marine Ecology Progress Series*, 258: 263–273.

Stone, G.S., Florez-Gonzalez, L. and Katona, S. 1990. Whale migration record [9]. *Nature*, 346(6286): 705.

Tonnessen, J.N. and Johnsen, A.O. 1982. *History of modern whaling.* University of California Press. Berkley and Los Angeles: 798pp.

Trathan, P., Forcada, J. and Murphy, E.. 2007. Environmental forcing and Southern Ocean marine predator populations: effects of climate change and variability. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362(1488): 2351–2365.

Waters, C.N., Zalasiewicz, J., Summerhayes, C., Barnosky, A.D., Poirier, C., Gałuszka, A., Cearreta, A., Edgeworth, M., Ellis, E.C., Ellis, M., Jeandel, C., Leinfelder, R., McNeill, J.R., Richter, D.D.B., Steffen, W., Syvitski, J., Vidas, D., Wagreich, M., Williams, M., Zhisheng, A., Grinevald, J., Odada, E., Oreskes, N. and Wolfe, A.P. 2016. The Anthropocene is functionally and stratigraphically distinct from the Holocene. *Science*, 351(6269): aad26221–aad262210

Williams, R., Vikingsson, G.A., Gislason, A., Lockyer, C., New, L., Thomas, L. and Hammond, P.S. 2013. Evidence for density-dependent changes in body condition and pregnancy rate of North Atlantic fin whales over four decades of varying environmental conditions. *ICES Journal of Marine Science*, 70(6): 1273–1280.

Yablokov, A. V. 1994. Validity of whaling data. *Nature*, 367(6459): 108.

Zeh, J.E., George, J.C., Raftery, A.E. and Carroll, G.M. 1991. Rate of increase, 1978–1988, of bowhead whales, Balaena mysticetus, estimated from ice-based census data. *Marine Mammal Science*, 7(2): 105–122.

Zemsky, V.A., Mikhaliev, Y.A. and Tormosov, D.D. 1994. Humpback whale catches by area by the Soviet Antarctic whaling fleets. *Report for the International Whaling Comimission* 47 (1): 151pp.

Zerbini, A.N., Adams, G., Best, J., Clapham, P.J., Jackson, J.A. and Punt, A.E., 2019. Assessing the recovery of an Antarctic predator from historical exploitation. *Royal Society open science*, *6*(10), p.190368.

Zerbini, A.N., Andriolo, A., Heide-Jørgensen, M.P., Pizzorno, J.L., Maia, Y.G., VanBlaricom, G.R., DeMaster, D.P., Simões-Lopes, P.C., Moreira, S. and Bethlem, C. 2006. Satellite-monitored movements of humpback whales *Megaptera novaeangliae* in the Southwest Atlantic Ocean. *Marine Ecology Progress Series*, 313: 295–304.

Zerbini, A.N., Clapham, P.J. and Wade, P.R. 2010a. Assessing plausible rates of population growth in humpback whales from life-history data. *Marine Biology*, 157(6): 1225–1236.

Zerbini, A.N., Clapham, P.J. and Wade, P.R. 2010b. Assessing plausible rates of population growth in humpback whales from life-history data. *Marine Biology*, 157(6): 1225–1236.

APPENDICES

Appendix A: Data sheet used for recording hourly weather conditions**.**

Date	
Group 1	
Group 2	

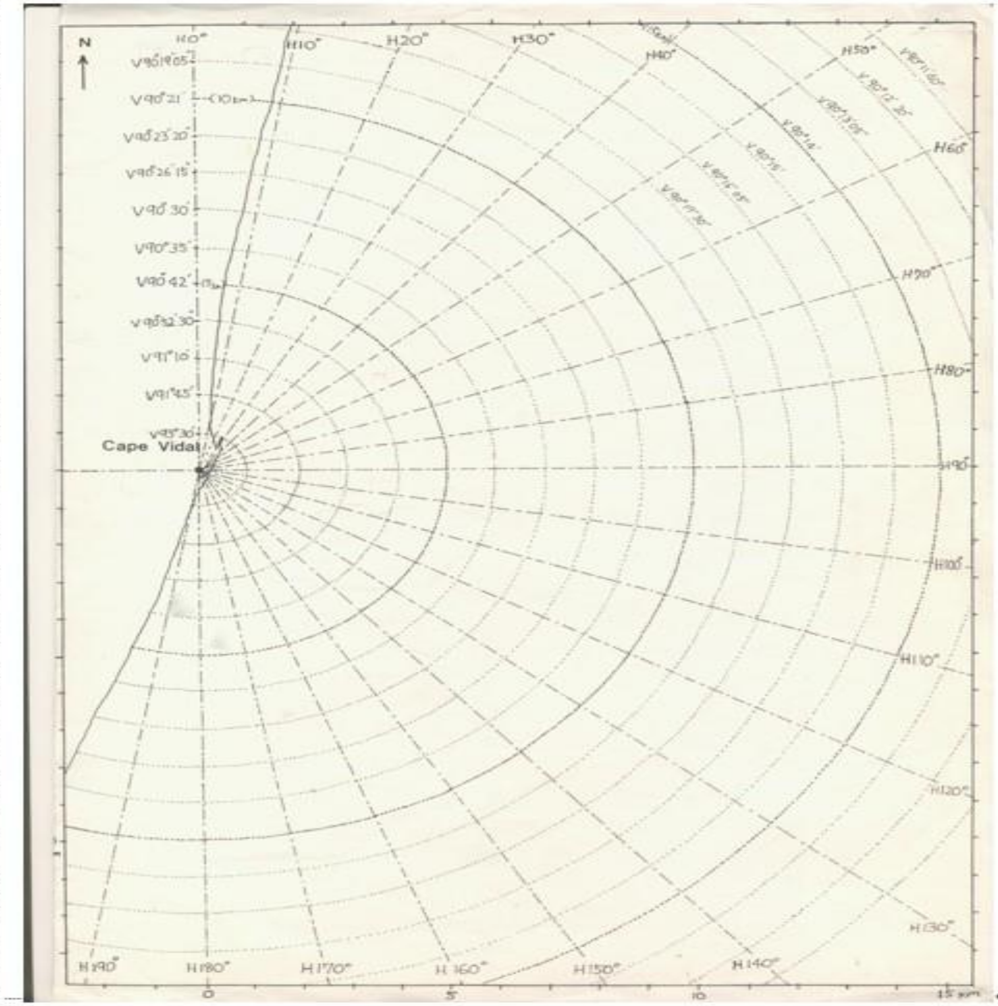
Time (+grp)	Wind speed/ direction)	Cloud Cover	Sea Surface State	Glare	Swell	Vis (V/H)	Sight

Notes :

Cloud Cover : 1/8 -8/8 ths
Sea Surface state: refer to the Beasufort scale
Vis: Visibility limit determined by vertical (v) and horizontal (H) angles
Sight: 1 - very poor; 2 - poor; 3- moderate; 4 - good; 5 - very good

Appendix B: Data sheet used at Cape Vidal for the tracking of humpback whales with a theodolite.

Date:		Team:				
Sighting number						
Species						
Time (1st observed)						
Cue (1st observed)						
Sighted by						
Obs	Time up	Position Horizontal	Position Vertical	Number Lower	Number Upper	Heading
	HH:MM:SS	DD°MM'SS"	DD°MM'SS"	n- Least	n- Most	N/S
1	: :	° ' "	° ' "			
2	: :	° ' "	° ' "			
3	: :	° ' "	° ' "			
4	: :	° ' "	° ' "			
5	: :	° ' "	° ' "			
6	: :	° ' "	° ' "			
Comments /Notes						
Sighting number						
Species						
Time (1st observed)						
Cue (1st observed)						
Sighted by						
Obs	Time up	Position Horizontal	Position Vertical	Number Lower	Number Upper	Heading
	HH:MM:SS	DD°MM'SS"	DD°MM'SS"	n- Least	n- Most	N/S
1	: :	° ' "	° ' "			
2	: :	° ' "	° ' "			
3	: :	° ' "	° ' "			
4	: :	° ' "	° ' "			
5	: :	° ' "	° ' "			
6	: :	° ' "	° ' "			
Comments /Notes						
Sighting number						
Species						
Time (1st observed)						
Cue (1st observed)						
Sighted by						
Obs	Time up	Position Horizontal	Position Vertical	Number Lower	Number Upper	Heading
	HH:MM:SS	DD°MM'SS"	DD°MM'SS"	n- Least	n- Most	N/S
1	: :	° ' "	° ' "			
2	: :	° ' "	° ' "			
3	: :	° ' "	° ' "			
4	: :	° ' "	° ' "			
5	: :	° ' "	° ' "			
6	: :	° ' "	° ' "			
Comments /Notes						
Sighting number						
Species						
Time (1st observed)						
Cue (1st observed)						
Sighted by						
Obs	Time up	Position Horizontal	Position Vertical	Number Lower	Number Upper	Heading
	HH:MM:SS	DD°MM'SS"	DD°MM'SS"	n- Least	n- Most	N/S
1	: :	° ' "	° ' "			
2	: :	° ' "	° ' "			
3	: :	° ' "	° ' "			
4	: :	° ' "	° ' "			
5	: :	° ' "	° ' "			
6	: :	° ' "	° ' "			
Comments /Notes						



Appendix C: Matching resolutions between north and south towers for 2018, considering data unstratified, stratified into distance bins and weather bins and stratified by both. Nn = number of humpback whale sightings from the north tower, Ns = number of humpback whale sightings from the south tower, M = number of matches, N = total number of whales calculated by Chapmans estimation, SD= standard deviation

				10 min & 500m			**15min & 1000m**			**20min & 2000m**		
Year	**Stratification**	**Nn**	**Ns**	**Matches**	**N**	***SD***	**Matches**	**N**	***SD***	**Matches**	N	***SD***
2018	Unstratified	**1281**	**1100**	**367**	3834.6	*137.56*	**519**	2713.4	*66.6*	**703**	2004	*30.45*
	Distance bins											
2018	Near	692	550	**270**	1408	*47.53*	**339**	1122.1	*26.86*	**426**	893.25	*12.7*
	Middle	404	382	**94**	1631.8	*126.43*	**167**	922.3	*40.71*	**253**	609.69	*13.55*
	Distant	150	135	**3**	5133	*2231.82*	**13**	1465.9	*341.68*	**24**	820.44	*132.95*
	Disregard	35	33									
	Total	**1281**	**1100**									
	Weather bins											
2018	Good	912	818	**269**	2768.4	*115.59*	**386**	1931.2	*54.07*	**520**	1434.2	*24.83*
	Fair	316	229	**65**	1103.7	*101.41*	**92**	782.98	*52.46*	**140**	516.09	*20.11*
	Poor	53	53	**33**	84.76	*5.37*	**41**	68.43	*2.35*	**43**	65.27	*1.83*
	Total	**1281**	**1100**									
	Combined bins											
2018	Poor / Near	42	40	**32**	52.42	*1.95*	**37**	45.39	*0.69*	**38**	44.21	*0.48*
	Poor / Middle	8	12	**1**	57.5	*27.4*	**4**	22.4	*5*	**5**	18.5	*3.12*
	Poor / Distant	3	0	**0**	3	*0*	**0**	3	*0*	**0**	3	*0*
	Fine / Near	170	128	**48**	449.18	*42.35*	**63**	343.67	*24.01*	**91**	238.77	*9.05*
	Fine / Middle	101	74	**17**	424	*77.14*	**27**	272.21	*34.21*	**47**	158.38	*9.94*
	Fine / Distant	37	24	**0**	949	*649.46*	**2**	315.67	*142.55*	**2**	315.67	*142.55*
	Good / Near	480	382	**190**	963.52	*38.27*	**239**	766.6	*21.39*	**297**	617.2	*10.39*
	Good /Middle	295	296	**76**	1140.7	*95.7*	**136**	640.69	*29.38*	**201**	434.21	*9.74*
	Good / Distant	110	111	**3**	3107	*1340.08*	**11**	1035	*256.41*	**22**	539.52	*87.57*
	Disregard	35	33									
	Total	**1281**	**1100**									

Appendix D: Matching resolutions between north and south towers for 2019, considering data unstratified, stratified into distance bins and weather bins and stratified by both. Nn = number of humpback whale sightings from the north tower, Ns = number of humpback whale sightings from the south tower, M = number of matches, N = total number of whales calculated by Chapman's estimation, SD= standard deviation

				10 min & 500m			**15min & 1000m**			**20min & 2000m**		
Year	**Stratification**	**Nn**	**Ns**	**Matches**	**N**	***SD***	**Matches**	**N**	***SD***	**Matches**	**N**	***SD***
2019	Unstratified	**1271**	**1306**	**370**	4480.1	*165.48*	**554**	2994.5	*72.35*	**714**	2324.2	*38.7*
	Distance bins											
2019	Near	549	476	**249**	1048.4	*33.75*	**320**	816.29	*16.81*	**351**	744.31	*12.18*
	Middle	440	467	**101**	2022.4	*154.58*	**189**	1085.3	*45.7*	**272**	755	*18.2*
	Distant	244	298	**20**	3487.3	*685.7*	**45**	1591.5	*192.57*	**88**	822.09	*58.02*
	Disregard	38	65									
	Total	**1271**	**1306**									
	Weather bins											
2019	Good	665	732	**155**	3128.4	*193.9*	**271**	1793.8	*66.26*	**360**	1351.3	*34.26*
	Fair	550	538	**204**	1447.7	*62.96*	**266**	1111.3	*34.65*	**336**	880.27	*18.29*
	Poor	56	36	**11**	174.75	*35.6*	**17**		*15.93*	**18**	110	*14.14*
	Total	**1271**	**1306**									
	Combined bins											
2019	Poor / Near	14	9	**4**	29	*7.07*	**8**	15.67	*1.05*	**5**	24	*4.63*
	Poor / Middle	22	17	**5**	68	*18.31*	**6**	58.14	*13.63*	**9**	40.4	*6.26*
	Poor / Distant	17	9	**2**	59	*22.91*	**3**	44	*13.75*	**4**	35	*8.83*
	Fine / Near	332	276	**155**	590.29	*22.74*	**182**	503.05	*14.53*	**216**	424.07	*7.91*
	Fine / Middle	167	178	**46**	638.83	*67.3*	**76**	389.55	*24.57*	**107**	277.44	*10.04*
	Fine / Distant	42	61	**3**	665.5	*274.56*	**8**	295.22	*77.01*	**12**	204.08	*40.7*
	Good / Near	203	191	**90**	429.42	*24.22*	**130**	297.99	*8.77*	**130**	297.99	*8.77*
	Good /Middle	251	272	**50**	1347.9	*150.66*	**107**	636	*35.86*	**156**	437.19	*13.95*
	Good / Distant	185	228	**15**	2661.1	*595.31*	**34**	1216	*168.21*	**72**	582.48	*43.64*
	Disregard	38	65									
	Total	**1271**	**1306**									