POPULATION STRUCTURE AND MIGRATION LINKS OF SOUTHERN AFRICAN EAST COAST HUMPBACK WHALES (*MEGAPTERA NOVAEANGLIAE*) USING PHOTOGRAPHIC-IDENTIFICATION TECHNIQUES

by

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DECLARATION

I, Bianca Tree, declare that the content of this thesis represents my own unaided work, and that the thesis has not previously been submitted for academic examination towards any qualification. Furthermore, it represents my own opinion and not necessarily those of the Cape Peninsula University of Technology.

Signed: **Date:** 16 August 2022

ABSTRACT

The conservation of humpback whales is of global concern, particularly due to their extensive exploitation during the 19th and 20th centuries. For such conservation to be effective, continuous assessments of the post-whaling status of the populations are essential, which requires detailed information on population structure and migration patterns. Seven Southern Hemisphere humpback whale Breeding Stocks have been identified (named Breeding Stocks A to G). Some of these are further divided into sub-stock, with limited information available on their structure and inter-relationship, as in the case of the Western Indian Ocean (WIO) C Breeding Stock, particularly the C1 sub-stock migrating past the south-eastern coast of Southern Africa. Photo-identification has proven to be a valuable non-invasive method to obtain key information on migration patterns, as well as to provide information on the structure of stocks and levels of connectivity that occur between stocks and sub-stocks. The unique black and white pigmentation patterns on the ventral surface of humpback whales' tail fluke is amongst the most important characteristics used for the photo-identification of these animals. Preceding this study, no single photo-identification catalogue was available for the humpback whales associated with the C1 sub-stock. The development of such a catalogue was one of the key objectives of this Masters' project, where an extensive collection of historic fluke images (collected by several sources since 1988) and new fluke images (collected as part of this Study) were included. The collection of the new fluke images was carried out during dedicated scientific research surveys off Bazaruto, Mozambique, and Durban, South Africa, as well as during opportunistic surveys on commercial BBWW platforms. The development of such an identification catalogue representing 1,746 unique individuals, has the capability to provide novel information on the intra-regional migration patterns and connectivity, migration fidelity and structure of the C1 sub-stock. Photo-identification matching analyses applied to this catalogue's images revealed 11 within-year matches of individuals, and 48 between-year matches representing 45 individuals. The within-year match results confirmed that humpback whales from the C1 sub-stock are broadly seasonally present for extensive periods. Furthermore, the within-year match results confirmed that multiple regions along the south-eastern African coast, including the south coast and north-eastern regions are visited by individuals from this sub-stock. From the between-year matches, long-term fidelity to this coastline was demonstrated. Moreover, five between-year matches obtained between South Africa and Mozambique regions, links the C1 sub-stock migration corridor to the southern and central Mozambique breeding ground. Evaluation of the phenotypic characteristics pertaining to the individual humpback whales identified within the C1 sub-stock provided valuable insight into the geographic structure of the population and suggest strong intra-regional connectivity along the South African coastline, as well as between the migration corridor and breeding region. Overall, the results obtained from this study emphasise the value of using photo-identification as research method and highlights the importance of continuous research to obtain more accurate population parameters of the C1 sub-stock. Furthermore, the findings of this research can play a key part in addressing the challenges of effective marine management (including of the South African east coast whale watching industry).

Key words: humpback whales, photo-identification, fluke images, photo-identification catalogue, migration links, stock structure

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GLOSSARY

Term	Definition/ Explanation
Beaufort scale	Empirical measure that relates wind speed to observed conditions at sea or on land.
Between-year match	An individual that was identified in one or more calendar years in either the same or different origin areas.
Biological Stocks	Population units that are genetically distinct from one another.
Escort	Adult humpback whale male accompanying a mother/calf group.
Historic Dataset	Fluke images collected during past events independently of this study, forming part of the South African humpback whale photo-identification dataset.
Isobath	A contour line on a map or chart joining places of equal depth of water; a depth contour.
Management stocks	Population units that are spatially and geographically separated from one another and be managed independently.
Multiregional	Relating to or involving several regions; Hereafter referring to coastal regions located within the C1 migration corridor and breeding ground along south-eastern Africa.
New Dataset	Humpback whale fluke images collected as part of this study.
Site-fidelity	Probability of an individual to inhabit or remain in a particular area, or the likelihood of the same individual to return to a previously visited area over some time.
Unique fluke image	A fluke image pertaining to an individual humpback whale.
Within-year match	An individual that was identified on one or more occasions within the same calendar year, in either similar or in different origin areas.

ABBREVIATIONS AND ACRONYMS

1AD	Single humpback whale adult
BBWW	Boat-based whale watching
BS	Breeding Stock
C1	Humpback whale C1 breeding sub-stock
C1N	Northern breeding portion of the C1 sub-stock
C1S	Southern breeding portion of the C1 sub-stock
CDS	Centre for Dolphin Studies
CMS	The Convention on Migratory Species
DFFE	Department of Forestry, Fisheries, and the Environment
DYADS	Two humpback whale adults
EIO	Eastern Indian Ocean
EN	North-eastern region of south-eastern Africa
ES	**S**outh-eastern region of south-eastern Africa
GER	Group Encounter Rate; number of groups encountered per survey effort
GPS	Global Positioning System
IUCN	The International Union for the Conservation of Nature
IWC	International Whaling Commission
MC	Central Mozambique region of south-eastern Africa
MMF	Marine Megafauna Foundation
MOC	Humpback whale mother and calf pair
MOCE	Humpback whale mother and calf pair and one escort
MOCE+	Humpback whale mother and calf pair and two or more escorts
MRI	Mammal Research Institute
MS	Southern Mozambique region of south-eastern Africa
NIO	Northern Indian Ocean

NOOA	National Oceanic and Atmospheric Administration
PoP	Platform of opportunity
RER	Re-encounter rate; proportion of between-year re-encountered individuals per total number of individuals encountered within the same year
RIB	Rigid inflatable boat
RS	Research survey
SABBWWA	South African Boat-Based Whale Watching Association
SC	**S**outh coast region of south-eastern Africa
sd	Standard deviation
TRIO	Three humpback whale adults
TRIO+	Four or more humpback whale adults
UF	Unique fluke image collection success rate (%); proportion of unique fluke images collected per total number of individuals encountered
UWC	Union Whaling Company
WIO	Western Indian Ocean

CHAPTER 1 INTRODUCTION AND LITERATURE REVIEW

1.1 Background

The management and protection of whale populations has been an influential topic in conservation sciences, mainly due to the global and extensive exploitation of many large whale species during the 19th and 20th centuries. The large-scale whaling, a lack of knowledge of whale behaviour and ecology, insufficient legislation, and inadequate conservation and management efforts resulted in the collapse and near extinction of many great whale species' populations during this period.

Several great whale species, particularly those belonging to the Balaenopteridae family (the rorqual whales), such as the humpback whale (*Megaptera novaeangliae*), were especially targeted by the whaling industry, resulting in global concerns regarding the future recovery and survival of these species (Tønnessen & Johnsen, 1982; Clapham & Baker, 2002; Jackson *et al.*, 2008). Almost two million whales were estimated to have been killed in the Southern Hemisphere alone between 1904 and 2005 (including those captured by scientific whaling programs) (*e.g.*, Rocha *et al.*, 2014) with deep impacts on their populations and to the marine ecosystem (*e.g.*, Roman *et al.*, 2014). Following the collapses and global near extinction of several great whale species, uncertainty around adequate management and protection measures, and the status of the remaining whale populations, the International Whaling Commission (IWC) was forced to implement an international moratorium on the commercial whaling of all large whale species in 1982 (Donovan, 1989). Along with the moratorium, the IWC noted the urgency to obtain accurate information on the status of all the remaining whale populations if future adequate protection and management are to be obtained. The IWC Scientific Committee was tasked to undertake comprehensive assessments of all remaining whale populations, particularly to determine how each population was affected by the whaling era, their recovery rates, and which future management and protection measures to take (Donovan, 1989; IWC, 2011). During the IWC Scientific Committees' preparation and planning for these assessments, it was emphasised that the accurate determination of the post-whaling status of populations relies on information surrounding their structure (Donovan, 1989).

Literature broadly describes population structure as the composition of a given population in terms of its dynamics, genetics, geographic distribution (spatial and temporal), movement patterns, and the levels of exchange that occur between stocks and sub-stocks (Kellogg, 1929; Townsend, 1935; Matthews, 1937; Chittleborough, 1965; Baker *et al.*, 1993; Bowen, 1997).

Some marine mammals' life histories and migratory nature make it particularly challenging for scientists to evaluate and understand how these populations' structuring occurs. Failure to adequately account for the processes that influence and result to the structuring of stocks will significantly impact any stock assessments and compromise any efforts to conserve them. Historical information, such as the seasonal and geographic distribution of catches recorded in commercial whaling records, and Discovery Investigations' whale-marking return data, provided the first evidence on the structuring of humpback whale populations among different geographical regions (Kellogg, 1928; Mackintosh, 1965; Baker *et al.,* 1986; Palumbi & Baker, 1994; Rosenbaum *et al.,* 1995). The first Discovery Mark was used during the 1932 whaling season in Antarctica, whereby a stainless-steel tag was shot into the whale's body and later recovered when the whale was killed and flensed on a flensing platform (Rayner, 1940; Mackintosh, 1942; Nishiwaki, 1962). Consequently, the IWC divided the Southern Hemisphere Antarctic whaling grounds into six management areas (termed Areas I to VI) according to localities where the highest catch numbers of several baleen whale species were annually observed (Mackintosh, 1942; Gambell, 1976; IWC, 1990; Donovan, 1991).

From comprehensive assessments carried out on humpback whale populations globally, the IWC Scientific Committee defined seven distinct migratory breeding stocks (BS) inhabiting the Southern Hemisphere (termed A to G), each stock linked to distinct feeding grounds corresponding to the IWC's historically assigned Antarctic management Areas I-VI (*e.g.,* IWC, 1990, 1997, 1998). In terms of the BSC, four distinct sub-stocks (termed C1 to C4) are present, each defined to a distinct migratory pathway and breeding ground located within the Southern Western Indian Ocean (SWIO) (IWC, 2006; Barendse *et al.,* 2010). Some literature suggest that the C1 sub-stock consist of two distinct breeding groups of whales, referred to as the C1 North (C1N) and a C1 South (C1S) components, where C1S's breeding range extends from 24°S to 15°S, and C1N's breeding range extends northwards from Mozambique Islands (15°S) to the northern breeding range limit around southern Kenya (4ºS) (Berggren *et al.,* 2001; IWC, 2006; Jackson *et al.,* 2014). Although it is suggested that the two breeding components should be treated as distinct sub-stocks, the IWC Scientific Committee refers to them as one breeding sub-stock for practical management purposes (IWC 2011).

Information on the seasonal and temporal distribution patterns on migration routes within feeding and breeding grounds and site-fidelity trends of populations can provide important information on populations' geographic structure (Corkeron & Brown, 1995). As mentioned, the distribution of baleen whales and their migration routes were historically identified through whale-marking data from the Discovery investigations and whaling records from the modern whaling era (Mackintosh, 1942; Donovan, 1989). However, in recent years, a significant shift has occurred in the methods used to collect data from migrating marine mammal populations, centred on non-lethal research techniques such as:

a) photo-identification,

b) genetic population information,

c) genetic marks of individuals, and

d) satellite tracking.

With these techniques, scientists can identify any physical and genetic interchange that occurs between stocks and sub-stocks, and at which rate this occurs, providing valuable information on the inter- and intra-regional structure of stocks (*e.g.,* Calambokidis *et al.,* 1997; Craig & Herman, 2000; Stevick *et al.,* 2004; Pomilla, 2005; Stevick *et al.,* 2010; Garrigue *et al.,* 2011). These techniques can also be used to estimate levels of philopatry/site fidelity and intra-regional migration patterns (Weinrich *et al.,* 1993; Cerchio *et al.,* 2008b; Barlow *et al.,* 2011; Barendse *et al.,* 2011).

Although the present conservation status of the humpback whale C1 sub-stock is of "Least Concern", having been downgraded from the previous "Endangered" status, information surrounding the present status of the sub-stock is limited. The intra-regional temporal and spatial migration behaviour, migration site-fidelity trends, inter-regional connectivity, and seasonal migration patterns of the C1 sub-stock have previously been investigated, however; the information is limited to a few outdated studies (Best *et al.,* 1998; Findlay *et al.,* 1994; Cerchio *et al.,* 2008b; Findlay *et al.,* 2011). The intra- and inter-regional stock structure and the C1 sub-stocks' role on the overall functioning of the C Breeding stock is also poorly understood and in serious need of investigation. The last informative population survey was conducted in 2003 (Findlay *et al.,* 2011), a considerable time ago, which suggests a need to re-survey this sub-population. Consequently, the study aims to obtain novel updated information on the temporal and spatial intra-regional distribution, migration fidelity, and stock structure of the humpback whale C1 sub-stock using photo-identification methods. To date, no single photo-identification catalogue has been developed for southern Africa and its associated humpback whale C1 sub-stock, however; there are several historic photo-identification image collections available that require consolidation into a multiregional catalogue system. Such catalogue, to be developed as part of this study, and information obtained therefrom through photo-identification analyses, will be valuable for addressing the aims of this study, as well as future studies to determine the current abundance of the sub-stock and the level of connectivity between other humpback whale stocks within the WIO, and between the south-eastern Atlantic stock (Breeding Stock B). Moreover, this research will also help address the challenges of effective marine management of a recovering whale population (including the east coast whale watching industry).

1.2 Literature Review

1.2.1 Humpback Whales

Humpback whales (*Megaptera novaeanliae)* are known to have an extensive geographic range and can be found across the world's oceans (Clapham & Mead, 1999; Rizzo & Shulte, 2009; Jackson *et al.*, 2014). In the Northern Hemisphere, the species distribution ranges between the tropics (0°) and temperate waters (60°N), whereas in the Southern Hemisphere they range from the tropics to the Antarctic ice edge (up to 68°S) (Clapham & Mead, 1999; Rizzo & Shulte, 2009; Jackson *et al.*, 2014). The location and timing of reproduction of humpback whales differ between the two hemispheres in that they are typically six months apart, reflecting the seasonal difference between the two hemispheres (Rosenbaum *et al.*, 1995; Clapham, 1996). Ovulation timing is seasonally linked, resulting in limited reproductive intermixing between humpback whales across hemispheres (Chittleborough, 1955, 1958; Rosenbaum *et al.*, 1995; Clapham, 1996). Baker & Palumbi (1997) suggested genetic exchange between the two Hemispheres to be limited to only an approximated average of two humpback whale females per generation. Based on genetic evidence, humpbacks whales in the North Pacific, North Atlantic and Southern Hemisphere are believed to have evolved on independent evolutionary trajectories, supporting taxonomic revision of *Megaptera novaeangliae* to three subspecies (Jackson *et al.*, 2014). Humpback whale gestation typically ranges between 11 to 12 months, with an estimated mean calving rate of 0.38 to 0.50 calves per mature female per year (Matthews, 1937; Clapham & Mayo, 1990; Wiley & Clapham, 1993; Straley *et al.*, 1994; Barlow & Clapham, 1997).

Humpback whales' movement and seasonal appearance along coastlines have been noted and documented for decades, initially through the distribution and seasonal abundance of whale catches by latitude (Risting, 1912; Kellogg, 1929; Harmer, 1931; Mackintosh, 1965; Dawbin, 1966). The introduction of lethal mark-recapture techniques during the 1930 Discovery marking program provided fundamental evidence on the movement of humpback whales between polar and tropical regions (Rayner, 1940). The first Discovery Mark was used during the 1932 whaling season in Antarctica, where a stainless-steel tag was shot into a whale's body and later recovered when the whale was killed and processed during commercial whaling activities (Townsend, 1935; Rayner, 1940; Nishiwaki, 1962; Dawbin, 1964; Mackintosh, 1965).The information obtained from these activities indicated that the feeding grounds of the species are typically located in high latitude polar regions over continental shelves with cooler water temperatures, where topographic and oceanographic features allow the highest prey concentration (Kellogg, 1929; Dawbin, 1956; Stevick *et al.*, 1999). Although polar feeding is the norm, observations demonstrated that feeding occasionally occurs in regions outside these polar feeding grounds (*e.g.*, Baraff *et al.*, 1991; Swingle *et al.*, 1993; Gibbons *et al.*, 1998, 2000, 2003; Acevedo *et al.*, 2004; Stockin & Burgess, 2005; Pinto de sa Alves *et al.*, 2009; Danilewicz *et al.*, 2009; Findlay *et al.*, 2017). In the Southern Hemisphere, the species typically feed in the circumpolar Southern Ocean waters south of 55°S around Antarctica (Matthews, 1937; Mackintosh, 1942; Amaral *et al.*, 2016). During spring, winter, and autumn months, most whales disappear from these regions, and winter seasonal abundances increase on the western and eastern coastlines of low latitude continents (Risting, 1912; Matthews, 1937; Dawbin, 1956). The increase of humpback whales within these tropical low-latitude warm waters (± 21.1° to 28.3° C) is coupled with mating, calving, and nursing behaviour throughout the winter and spring season (Clapham & Mead, 1999; Rasmussen *et al.*, 2007; Clapham *et al.*, 2009). There is currently no available evidence suggesting that nursing and calving occur outside of low latitude breeding regions; however, some mating displays and song have been recorded in high latitude regions during late spring (Clark & Clapham, 2004). Humpback whale females with calves are commonly found in extensive shallow areas (<20 m deep), whereas in contrast, competitive mating groups favour deeper areas (Craig & Herman, 2000; Erst & Rosenbaum, 2003).

Historically, humpback whale migration was suggested to exclusively occur within nearshore coastal waters, predominantly in a north-south direction (Dawbin, 1966). However, novel evidence indicates that pelagic migrations do exist, and not all migration routes are located within nearshore coastal waters (Corkeron & Connor, 1999; Norris *et al.*, 1999; Stevick *et al.*, 1999; Charif *et al.*, 2001; Reeves *et al.*, 2004; Fleming & Jackson; 2011). More recently, non-lethal techniques, such as acoustic monitoring, photo-identification, satellite telemetry, and microsatellite-based genetic sampling, provide more recent evidence for humpback whale migrations (Katona & Whitehead, 1981; Clapham & Mattila, 1990; Zerbini *et al.*, 2006). Extensive humpback whale migration can be considered a trade-off between the feeding and breeding requirements of the species (Corkeron & Connor, 1999). The temporal and spatial distribution and migration timing of humpback whales are seasonally influenced by various factors, such as age (juvenile vs mature) and sex (male vs female) classes (Chittleborough, 1965; Dawbin, 1966), the reproductive cycle and status of mature females (Dawbin, 1966; Craig *et al.,* 2003), ocean-climate driven factors such as current regimes (Dawbin; 1966; Findlay & Best, 1996), sea-ice extent and food availability in foraging grounds (Chaloupka *et al.,* 1999; Friedlaender *et al.,* 2006). Some evidence suggests that different reproductive classes of humpback whales migrate to and from their breeding grounds in the tropics at slightly different times (Chittleborough, 1965; Dawbin, 1966; Craig *et al.,* 2003; Barendse *et al.,* 2010). Lactating females appear to migrate to breeding grounds first, followed by immature whales, mature males, and resting non-pregnant and non-lactating females, respectively. Pregnant females migrate last towards their associated breeding ground (Chittleborough, 1965; Dawbin, 1966). It has also been discovered that an animal's reproductive status may be an essential factor in determining the migration behaviour and overall habitat preferences of humpback whales (Martin *et al.*, 1984; Baker *et al.*, 1990; Craig & Herman, 2000).

1.2.2 History of Whaling and the International Whaling Commission (IWC)

Globally, humpback whale populations were severely targeted by modern commercial whaling fleets in the 20th century and were among the first great whale species to be exploited (Tønnessen & Johnsen, 1982). Their vulnerability to exploitation could primarily be due to the regularity of their coastal migrations, coastal habitat preference, and general slow movement, which made it less challenging to exploit them (Kellogg, 1929; Tønnessen & Johnsen, 1982). Relatively low numbers of humpback whales were caught during the pre-modern whaling period, as they were difficult prey to catch using mainly hand-thrown harpoons from rowed catcher boats. The invention of explosive harpoon guns mounted on fast steam catcher boats and the overall advancement in catch techniques gave rise to the modern whaling era at the end of the 19th century (Tønnessen & Johnsen, 1982; Paterson, 2001).

With the onset of the modern-whaling era, the IWC was implemented under the International Convention for the Regulation of Whaling in December 1946, to supervise and regulate the commercial whaling industry effectively, and to provide efficient management and conservation efforts for all known whale species (Donovan, 1989). Consequently, the Convention developed a "schedule" that stipulated detailed measurements that the IWC considered essential for the effective regulation of the whaling industries, and for the successful conservation of all known whale stocks (Donovan, 1989). Irrespective of their efforts, a combination of coastal catches from land-based whaling stations in winter breeding grounds, catches from land-based whaling stations in high and low-latitude regions, and pelagic fleet catches within Antarctic feeding grounds and some low latitude breeding grounds caused several large whale populations within the Southern Hemisphere to become rapidly heavily depleted last century (Zemsky *et al.*, 1996; Findlay, 2001; Clapham *et al.*, 2005; Clapham *et al.*, 2009).

In the Southern Hemisphere, the first exploitation of whales by modern whaling occurred in 1904 following the depletion of whale stocks in the Northern Hemisphere (Tønnessen & Johnsen, 1982). Around the Falkland Island Dependencies region in the South Atlantic Ocean (IWC Management Area II), large scale whaling commenced in 1904 from land stations and floating factories, and approximately 34,683 humpback whales were killed from these localities up to 1963 (Tønnessen & Johnson, 1982; Findlay, 2001; Clapham *et al.*, 2005; Clapham *et al.*, 2009) (Table 1.1). Between 1908 and 1963, whaling within low latitude waters surrounding Africa took place from floating factories and land-based stations on both the western and eastern coast of the continent between Gabon and Mozambique, leading to the demise of approximately 47,134 humpback whales during this time (Findlay, 2001) (Table 1.1).

Additionally, the Soviet Union conducted large-scale illegal whaling from four floating factory fleets throughout much of the North Pacific, Indian, and Southern Oceans for nearly three decades between 1947 and 1973. Recent evidence suggests that an estimated total number of 48,724 humpback whales were captured during this time; however, only 2,710 of these catches were formerly reported to the IWC (Yablokov, 1994; Yablokov *et al.*, 1995; Yablokov *et al.*, 1998; Findlay, 2001; Clapham *et al.*, 2005; Clapham & Ivashchenko, 2009). Illegal whaling by the Soviet Union captured approximately 1,412 (Area II) and 921 (Area III) humpback whales between 1947 and 1973 (Yablokov, 1994; Yablokov *et al.*, 1998; Clapham *et al.*, 2005). Altogether, over 215,000 humpback whales were hunted in the Southern Hemisphere during the historic modern whaling era (Zemsky *et al.*, 1996; Findlay, 2001).

Table 1.1 Catches of humpback whales by modern whaling in the Southern Hemisphere between 1904 and 1974 (A = Low Latitudes, North of 40°S; B = High Latitudes, South of 40°S) (modified from Findlay, 2001) (Areas I to VI refer to the International Whaling Commission Management Areas).

A) LOW LATTITUDE	
LOCATION	CATCH
Southern Africa (Total)	**47,134**
Cape (West Coast)	1,571
Namibia (West Coast)	1,284
Angola (West Coast	10,027
Gabon (West Coast)	15,158
Natal (East Coast)	9,785
Mozambique (East Coast)	3,128
Madagascar (East Coast)	6,181
South America (Total)	**3,542**
West Coast	1,985
East Coast	1,557
Australia (Total)	**27,864**
West Coast	19,557
East Coast	8,307
New Zealand (Total)	**5,224**
Pelagic Whaling (Total)	**9,622**
West Australia	7,243
Western Southern Africa (Gabon)	2,309
South America (Peru and Chile)	70
***Olympic Challenger* Fleet (Total)**	**105**

B) HIGH LATITUDE	
LOCATION	CATCH
Land Station & Floating Factories (Total)	**34,683**
South Georgia	24,770
South Shetland Is	8,879
South Orkney Is	405
Falkland Is	200
Kerguelen Island	429
Antarctic Pelagic Whaling (Total)	**25,393**
AREA I	1,295
AREA II	1,537
AREA III	7,074
AREA IV	11,988
AREA V	2,405
AREA VI	1,094
***Olympic Challenger* Fleet (Total)**	**4,554**
Soviet Antarctic Whaling Fleet (Total)	**48,724**
AREA I	414
AREA II	1,364
AREA III	1,280
AREA IV	2,638
AREA V	4,861
AREA VI	3,332
Unknown	34,835

Due to escalating collapses and global near extinction of several large whale species in both hemispheres, the lack of information on the status of the remaining whale populations, and uncertainty around sufficient management and protection measures, the Convention and IWC was forced to propose an international moratorium on the commercial whaling of all large whale species in 1982 (Donovan, 1989). This proposal initially stated that: "*Catch limits for the killing of all whales for commercial purposes shall be zero*". However, the rewording of this phrase at the insistence of whaling nations meant it was rewritten, stating that "*Catch limits for the killing of all whales for commercial purposes shall be zero. This provision will be kept under review, based upon the best scientific advice, and by 1990 at the latest, the Commission will undertake a Comprehensive Assessment of the effects of this decision on whale stocks and consider modification of this provision and the establishment of other catch limits*" (Donovan, 1989). The moratorium was effective from 1985 for all pelagic whaling and 1986 for coastal whaling (Donovan, 1989; Gambell, 1999). Consequently, humpback whales were listed as "Endangered" in 1986 under the Endangered Species Conservation Act of 1969 in December 1970 and under the IUCN Red Listing (Tønnessen & Johnsen, 1982; Price, 1985; Duffey, 1987; Clapham *et al.,* 1997; Smith & Reeves, 2003; Fleming & Jackson, 2011).

Following the establishing the commercial whaling moratorium, the IWC' scientific committee was tasked to conduct comprehensive assessments of the remaining whale population. Such assessments had to include extensive evaluations of all whale populations status and trends, including analyses of their current sizes, productivity, population trends, and carrying capacity (Donovan, 1989; Gambell, 1999). For these comprehensive assessments to be successful, three critical areas of work had to be carried out. Firstly, the Scientific Committee had to review and revise all the available data and data collection procedures, and all the available information and knowledge regarding the classification of whale populations in terms of "stocks". Secondly, new data collecting methods had to be developed strategically, followed by extensive data collecting efforts for all great whale species. Lastly, based on all newly gathered and processed evidence, the Scientific Committee had to examine and suggest alternative management protocols for the future successful recovery and effective conservation of the depleted whale stocks (Donovan, 1989). One of the most significant concerns the IWC's Scientific Committee raised during the historic data and information review stage of the comprehensive assessment procedure was that no clear description and procedure existed to identify whales in terms of "stocks" (Donovan, 1989).

1.2.3 Humpback Whale Stocks

Literature describes two classes of stocks: biological stocks, which are genetically distinct population units, and management stocks, which are spatially and geographically distinct population units that can be managed independently (Donovan, 1991; Bossart & Prowell, 1998). Olavarria *et al.* (2007) reported that the extensive exploitation of humpback whales in the Southern Hemisphere provided the initial baseline information on structures of different populations of the species, which was mainly determined through the seasonal and geographic distribution of catches by whaling fleets. Historically, humpback whale populations in the Southern Hemisphere were grouped according to feeding ground aggregations associated with the Antarctic Management Areas (termed I to VI), each linked to a specific proposed breeding region (Mackintosh, 1942; IWC, 1976). However, little was known about the biological distinctiveness of these aggregations. It was also noted that the initial catch quotas set by the IWC were primarily established for spatial groupings of whales (management units) instead of distinct genetic sub-populations (Donovan, 1991).

Numerous studies have attempted to evaluate and confirm the migratory linkages between the feeding and breeding ground aggregations proposed by Mackintosh (1942), which was based on a combination of phenotypic marker data (*e.g.*, Lillie, 1915), catch distribution data (*e.g.*, Hjort *et al.*, 1933; Hansen, 1936), discovery marking data, and encounter records (*e.g.*, Rayner, 1940; Dawbin, 1956; Brown, 1957; Chittleborough, 1959; Dawbin, 1959; Nishiwaki, 1962). Furthermore, scientists have also attempted to evaluate the levels of intermixing that occurs between these feeding and breeding aggregations to gain an understanding of how these groups were genetically structured, allowing scientists to classify them more accurately as biological stocks (Brown, 1956; Brown, 1962; Chittleborough, 1958; Chittleborough, 1963; Clapham & Mayo, 1987; Dawbin, 1956, 1959, 1964; Katona & Beard, 1990; Baker *et al.,* 1993; Clapham *et al.,* 1993; Baker *et al.,* 1994; Palsbøll *et al.,* 1995; Larsen, 1996; Baker & Palumbi, 1997; Baker *et al.,* 1998; Berube *et al.,* 1998; Kershaw, 2015; Rosenbaum *et al.,* 2009). Since then, the stock identity model has been reviewed and modified, suggesting that stocks should be identified based on their separate breeding ground locations, considering demographic and genetic exchanges (IWC, 1998).

Continuous assessments of the post-whaling status of stocks are imperative for efficient and effective conservation and management, and accurate evaluation of the degrees to which a whale population is at risk of extinction. Clapham *et al.* (2008a, b) advised combining genetic data with several other information sources, such as tag return, animal marking, and behavioural data, to distinguish population units more accurately from one another. Furthermore, it is fundamental to accurately establish migrating populations' geographic temporal and spatial boundaries before evaluating their structure, dynamics, and status (Donovan, 1991). To do so, gender-specific migration and site fidelity trends need to be understood and accounted for as these factors may ultimately determine migrating populations' geographic extent (Prugnolle & de Meeus, 2002). The occurrence of sex-biased migration often occurs in marine mammal species such as humpbacks, where female philopatry (the tendency of females to stay or routinely return to a particular area) and male dispersal (movement of males from birth to breeding site, or movement between different breeding sites) frequently occurs (Brown *et al.,* 1995; Baker *et al.,* 1998; Prugnolle & de Meeus, 2002; Pomilla *et al.,* 2006). Determining migrating mammal populations' geographic temporal and spatial boundaries may further be challenged by the fact that any expected geographical extent of populations may be confounded by the tendency of individual to migrate extensive distances between their breeding and feeding grounds, and the possibility of some migrating to other breeding and feeding grounds. Furthermore, some habitats utilised by these animals during migration are often challenging to access, with a limited understanding surrounding the boundaries of these regions, and no obvious geographic barriers present between migratory corridors (Kellogg, 1929; Rayner, 1940; Mackintosh, 1942; Dawbin, 1966; Bowen, 1997). Moreover, our knowledge of these animals' site-fidelity behaviour is limited, and they can display complex gender-driven and social behaviour, often leading to a subdivision in the population (Chittleborough, 1965; Dawbin, 1966; Bowen, 1997; Rosenbaum *et al.,* 2009; Amaral *et al.,* 2016).

Although humpback whales are known to generally display strong fidelity to feeding and breeding grounds (Bowen, 1997; Rosenbaum *et al.,* 2009), several studies have displayed that mixing between different stocks on feeding and breeding grounds occasionally occurs (Chittleborough, 1965; Dawbin, 1966; Darling *et al.,* 2019; Schall *et al.,* 2022). Humpback whales found in the Northern Hemisphere, especially within the North Pacific and North Atlantic, have previously been observed to disperse to multiple feeding grounds (Calambokidis *et al.,* 2008). Similarly, the mixing of Southern Hemisphere stocks, such as those belonging to Africa's west and east coast, has also been observed in the Antarctic feeding grounds (IWC, 2011; Kershaw, 2015). It is believed that individual humpback whale exchange between different feeding grounds is negatively correlated with distance, where the frequency of exchange decreases with increasing distance (Katona & Beard, 1990, Stevick *et al.,* 2010). Furthermore, although some mixing occasionally occurs, it is believed that the rate at which genetic exchange occurs between these distinct populations is significantly low (Katona & Beard, 1990; Clapham *et al.,* 1993; Darling & Cerchio, 1993). Factors that may influence or limit gene flow between individuals, such as behavioural barriers, also need to be considered when evaluating migratory mammals' stock structure (Bowen, 1997). The behaviour of individual animals collectively determines the population's migration outcomes, which subsequently affects the populations' reproductive success (Clapham, 2001; Dingle & Drake, 2007). Failure to account for all these confounding factors will significantly impact any stock structure assessments' accuracy and implicate any efforts to conserve these stocks.

A collection of assessments indicates that strong structuring often occurs in cetacean populations in terms of genetics, age, gender, and distribution (Baker *et al.,* 1993; Calambokidis *et al.,* 1997; Whitehead *et al.,* 1998; Calambokidis *et al.,* 2001; Calambokidis *et al.,* 2008; Rosenbaum *et al.,* 2009). This is especially true for humpback whale populations, for which strong structuring is observed during migration and on breeding grounds (Chittleborough, 1960; Chittleborough, 1965; Dawbin, 1966; Clapham & Mayo, 1987; Katona & Beard, 1990; Baker *et al.,* 1993; Clapham *et al.,* 1993; Baker *et al.,* 1994; Palsbøll *et al.,* 1995; Larsen, 1996; Baker & Palumbi, 1997; Baker *et al.,* 1998). Nowacek *et al.* (2011) suggest that prey availability and dynamics and cultural and/or maternal transmission may act as key drivers in determining humpback whale populations' subdivisions on feeding grounds. The complex population structuring occurring within these humpback whale stocks may play a vital role in these stocks' dynamics and gene flow (Baker *et al.,* 1990).

Between 2001 and 2011, the IWC Scientific Committee carried out a comprehensive assessment of humpback whales across the Southern Hemisphere (IWC, 2012, 2013). These assessments provided information on the post-whaling abundance, distribution, migration, and biological structure of populations (IWC, 2013). Consequently, the IWC currently recognises seven populations/Breeding Stocks (BS) of humpback whales across the Southern Hemisphere (IWC, 1998; IWC, 2012, 2013). It is believed that each of these stocks are geographically isolated and distribute to specific winter breeding grounds on the east or west coasts of Southern Hemisphere continents and in the central Pacific Ocean islands (IWC, 1998). These stocks are referred to as Breeding Stocks A-G, where A is defined to breeding grounds in the Southwest Atlantic; B to Southeast Atlantic; C to Southwest Indian Ocean; D to Southeast Indian Ocean; E to Southwest Pacific; E and F to Oceania; and G to Southeast Pacific, respectively (IWC, 1998) (Figure 1.1). These seven stocks each are linked to Antarctic Management Areas I-VI (Mackintosh, 1942; IWC, 1997, 1998). Additional to these seven stocks, an eighth stock breeding in the Northern Indian Ocean, referred to as Breeding Stock X, or the "Arabian Sea Population", was identified (IWC, 2011). BSX is believed to be a non-migratory population, and no apparent gene flow to any Antarctic feeding areas is present. Furthermore, some of these Breeding Stocks have been divided into sub-stocks based on genetic differentiation and distinct migration routes within these stocks, including the C stock of which the division is discussed herafter (Best *et al.*, 1998; IWC, 2006; Erst *et al.*, 2011).

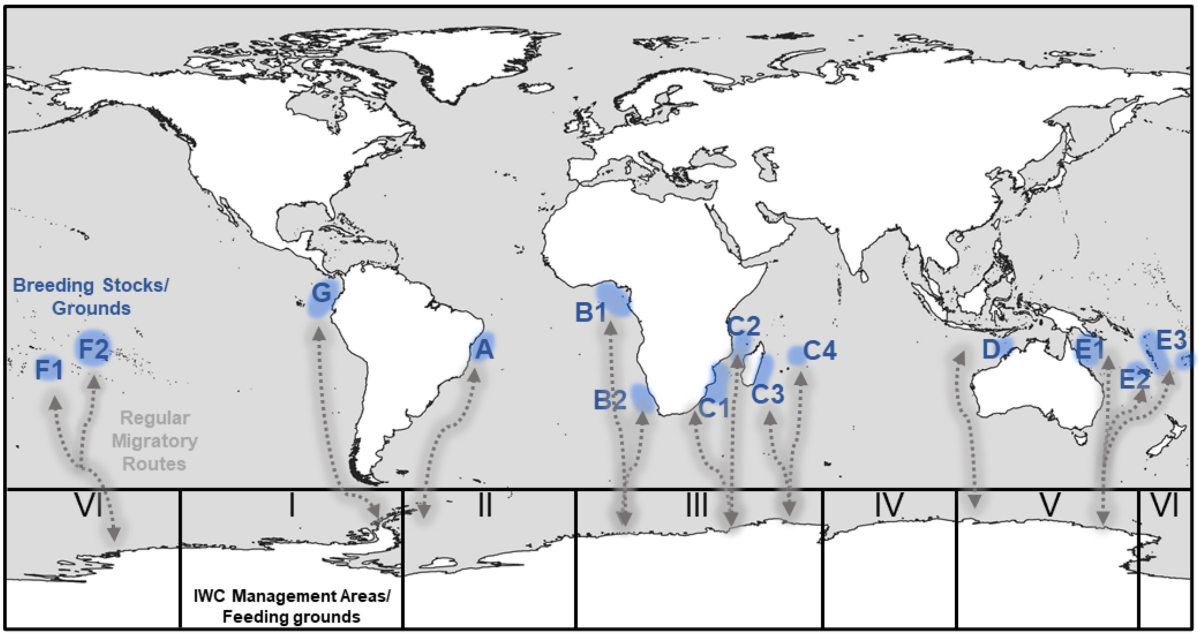


Figure 1.1 Representation of the IWC's Management Areas/feeding grounds, breeding grounds, and known migratory routes utilised by the Southern Hemisphere humpback whale Breeding Stocks and sub-stocks.

Humpback whales belonging to the IWC recognised BSC (Breeding Stock C) utilise the southern WIO coastal waters as migration corridors and breeding grounds (Wray & Martin, 1983; Best *et al.*, 1998; IWC, 1998; Erst *et al.*, 2011; Fossette *et al.*, 2014; Cerchio *et al.*, 2016). Evidence proposes three sub-stocks within BSC, termed C1 to C3, which utilises a separate breeding ground within the WIO (Best *et al.*, 1998; Erst *et al.*, 2011). Furthermore, evidence-based on a combination of whaling, sighting, survey, and acoustic data suggest that three or more humpback whale migratory pathways are evident in this region (Best *et al.*, 1998; Erst *et al.*, 2011).

Humpback whales from the C1 sub-stock utilise the first proposed pathway where they arrive on the south-eastern coast of South Africa at Knysna (33°S; 23°E) from April onwards, migrating northwards within the coastal waters of the east coast (Eastern Cape & KwaZulu-Natal Province) to breed between Mozambique (24°S) and southern Kenya (4ºS) (Findlay *et al.*, 1994; Wamukoya *et al.*, 1996; Berggren *et al.*, 2001; O'Connor *et al.*, 2009; Erst *et al.*, 2011). Best *et al.* (1998) suggest that the proportion of humpback whales that utilise this migration stream during the northbound and southbound migration is comparable; however, the northern migration is generally faster than the southern migration. The coastal corridor and areas utilised by the C1 humpback whale sub-stock during their annual migration along the southern African east coast are depicted in Cerchio *et al.* (2008a). Six coastal areas, including the south coast (SC), south-eastern coast (ES) and north-eastern coast (EN) of South Africa, and the South Mozambique (MS), central Mozambique (MC), and North Mozambique (MN) coasts, were outlined to assist in assigning valuable data collected on the C1 sub-stock to specific areas (Cerchio *et al.,* 2008a). Although several studies suggest that the C1 sub-stock should be further sub-divided into a C1 North (C1N) and a C1 South (C1S) components of the sub-stock, the IWC Scientific Committee refers to them as one breeding sub-stock for practical management purposes (IWC, 2011). The C1N extends northwards from the Mozambique Islands (15°S) to the northern breeding range limit around southern Kenya (4ºS), where the C1S extends from 24°S to 15°S (Berggren *et al.,* 2001; IWC, 2006; Jackson *et al.,* 2014).

The C2 sub-stock migrates through the second proposed pathway within the coastal waters of the central Mozambique Channel and breed around the Mozambique Channel Islands, including the Comoros Archipelago, Aldabra, and Mayotte; and southern Seychelles (Reeves *et al.,* 1991; Ersts *et al.,* 2006; Kiszka *et al.,* 2007; Hermans & Pistorius, 2008). The third proposed pathway is suggested to be offshore along the Madagascar Ridge (between Madagascar and ~40°S) and is utilised by the C3 sub-stock travelling towards breeding grounds along the east and south coast of Madagascar (15° to 25°S), where most literature describes the Antongil Bay breeding ground (Rosenbaum *et al.,* 1997; Best *et al.,* 1998). Additionally, the IWC now recognises a fourth sub-stock breeding within the southern WIO, the C4 sub-stock, which migrates to the Mascarene Islands' waters, including Mauritius and Reunion (55°E) (Dulau-Drouot *et al.,* 2008; Fleming & Jackson, 2011).

The breeding and feeding ground migratory connections of humpback whales wintering within the WIO is described by numerous studies, suggesting that humpback whales belonging to the BSC typically feed during summer within Antarctic Areas III and IV (extending eastwards from Queen Maud Land) between 0° and 130°E (Rayner, 1940; Mackintosh, 1942; IWC, 1998, 2011). A clear understanding of the relationship between stocks, sub-stocks, and the population structure on both feeding and breeding grounds is required to accurately determine the post-whaling status of humpback whales wintering within the WIO. Updated evidence on the connectivity, stock structure, and status of Southern Hemisphere humpback whale populations is mostly only available for the A, D, and G Breeding Stocks (IWC, 2011), with limited information on the B, C, E & F stocks. Furthermore, information on the population structures within the C sub-stocks is outdated, and little is known about the overlap and connectivity between these aggregation (Ersts *et al.,* 2006; Pomilla *et al.,* 2006; Cerchio *et al.,* 2008a, b; Rosenbaum *et al.,* 2009).

The genetic structure and connectivity of each Southern Hemisphere BS (A-G) on their proposed Antarctic feeding grounds (IWC Management Areas I-IV) was investigated by Amaral *et al.* (2016). This investigation was one of the first studies to collect and analyse genetic samples representing humpback whales from all six Antarctic management areas. This study also provided the most complete and extensive circumpolar genetic dataset to determine the Southern Hemisphere stocks' genetic differentiation and population structure on their feeding grounds. The results suggested that humpback whale populations feeding off Antarctica displayed high genetic differentiation between populations from different feeding areas, suggesting restricted gene flow between regions. The results provided valuable evidence on the structuring of the BSC humpback whales within their Antarctic feeding ground, suggesting that little interchange occurred between the individuals from the adjacent areas, resulting in strong structuring of the populations (Amaral *et al.,* 2016). Such results closely correspond to other studies focusing on humpback whales' stock structure within feeding grounds, where insignificant levels of genetic exchange between different feeding grounds have also been observed (Katona & Beard; 1990; Palsbøll *et al.,* 1995; Stevick *et al.,* 2003).

Pomilla *et al.* (2006) and Rosenbaum *et al.* (2009) assessed the population structure of Breeding Stocks A, B, C, and X, using mitochondrial DNA, and compared the results of each stock to determine the level of connectivity between each. Mitochondrial and nuclear genetic comparisons were also conducted between the humpback whale C sub-stocks (C1 - East African Mainland; C2 - Comoros Archipelago, and C3 – Madagascar - Antongil Bay). Humpback whales from the C1 and C2 and the C1 and C3 sub-stocks indicated that significant genetic differentiation occurred, suggesting restricted interchange and connectivity between these two breeding regions (Pomilla *et al.,* 2006; Rosenbaum *et al.,* 2009). Furthermore, no significant genetic differentiation occurred between C2 and C3, suggesting that individual humpback whales travel between the two areas (Pomilla *et al.,* 2006). The results were further supported by nine recaptures obtained by photographic comparisons (four fluke and two dorsal fins) and genetic (3 genotypes) evidence between the C2 and C3 breeding areas (Ersts *et al.,* 2011). Overall, when considering and comparing the C-stock as a grouped population, genetic evidence suggested that all sub-stocks assessed displayed significant degrees of structuring (Pomilla *et al.,* 2006; Rosenbaum *et al.,* 2009).

Cerchio *et al.* (2008a) examined the connectivity between sub-stocks C1 and C3 based on photographic tail fluke images. Fluke images representing the C1 sub-stock were collected between 2002 and 2005 by commercial boat-based whale watching (BBWW) operators within the coastal waters off the South African east coast (stretching from the Eastern Cape to northern KwaZulu-Natal). Additionally, fluke images were collected during three research cruises carried out within the coastal waters of southern Mozambique. Fluke and dorsal fin photographs and genetic samples were collected for the C3 sub-stock on the breeding area of Antongil Bay, Madagascar, between 2000 and 2006. Fluke images collected from the eastern South African coastline contributed to the most significant portion of the image collection (93%), where a total of 458 individuals were identified for the C1 sub-stock. Two individual humpback whales belonging to the C1 sub-stock were photographed (captured) in 2003 and re-photographed (recaptured) within the C3 sub-stock in 2006, resulting in only two recaptures between the C1 and C3 sub-stocks. However, one of the photographs was too poor in quality to constitute an adequate match. The low number of recaptures provided additional evidence indicating restricted interchange and connectivity between these two sub-stocks.

The connectivity and exchange between the C3 and C4 sub-stocks were investigated through photo-identification techniques (Dulau-Drouot *et al.,* 2011). A photo-identification catalogue representing individuals from the C3 sub-stock, which contained fluke images captured between 2000-2006, was compared to the C4 sub-stocks catalogue, which contained fluke images captured between 2001-2010. Three individual humpback whales were recaptured between these two sub-stocks, where they were first captured within the C3 sub-stock region (Madagascar) between 2001-2002 and recaptured within the C4 sub-stock region (Reunion) between 2008-2010. Furthermore, Pomilla & Rosenbaum (2005) reported a single individual travelling between the B1 sub-stock (off Gabon on the African west coast) and the C3 sub-stock. Although these studies indicate some levels of connectivity between the C stock and other humpback whale stocks within the south-eastern Atlantic and WIO, the evidence is limited. Subsequently, further analyses are needed to determine the migration links and level of genetic distinctiveness, and therefore, the stock structure of these sub-stocks.

Furthermore, several studies have investigated the connectivity between the southern WIO sub-stocks and the Eastern Indian Ocean (EIO) population (Australia; BSD) (*e.g.,* Murray *et al.,* 2012), the Northern Indian Ocean population breeding in Oman (BSX) (*e.g.,* Pomilla *et al.,* 2006; Minton *et al.,* 2011), and the south-eastern Atlantic (BSB) (*e.g.,* Pomilla *et al.,* 2006; Razafindrakoto *et al.,* 2009; Rosenbaum *et al.,* 2009; Banks *et al.,* 2010). By comparing humpback whale songs from BSC (sub-stock C3) and BSD, Murray *et al.* (2012) suggested limited exchange between these populations. Results indicated that only one song theme was shared between the two regions, where the C3 sub-stock had four unique song themes, and the

BSD population had six (Murray *et al.*, 2012). Minton *et al.* (2011) compared fluke photo-identification catalogues from the X and C humpback whale sub-stocks (C1, C2, and C3), where no matches between the X and any of the C breeding sub-stocks were found. Furthermore, fluke photo-identification catalogues from the south-eastern Atlantic breeding sub-stock (B2) and southern WIO breeding sub-stock C1 were compared (Banks *et al.*, 2010). Subsequently, no matches of individuals were found between the Breeding Stocks, suggesting that exchange between the two populations is limited.

Although literature suggests strong structuring between the WIO humpback whale populations, more information is required to determine whether the C1 sub-stock should be further divided into two components of the sub-stock (C1S and C1N) (IWC, 2011). There is also only limited and outdated information on the intra-regional stock structure and fidelity trends of the C1 sub-stock. Furthermore, assessment of the degrees to which humpback whale Breeding Stocks from the WIO were hunted is challenging for several reasons:

a) The feeding grounds associated with the south-eastern Atlantic (B) and WIO (C) stocks are overlapping, with evidence indicating that some interchange between humpback whales from each of these feeding regions occasionally occur, making it difficult to accurately assign the Southern Ocean catches to each breeding stock (Olsen, 1914; Mackintosh, 1942);

b) No records are available for the number of whales that were struck and lost by whalers as catches were only recorded if successful (Reeves & Smith, 2006); and

c) WIO stocks were rapidly and drastically depleted long before any stock status analysis could be conducted (Best & Ross, 1996).

Between 1955 and 1975, the Union Whaling Company (UWC) conducted daily aerial surveys within the Durban whaling grounds to determine whales' locations during the whaling seasons (Findlay & Best, 2006, 2016). Sighting data obtained between 1972 and 1975 was used to determine the monthly seasonal abundance, displayed as the total number of individuals sighted each month. Only a total of 38 humpback whales were sighted over these four years, reflecting the prior collapse of the C breeding stock. However, migration might have taken place outside the range within which the aerial surveys were performed (Findlay & Best, 2006, 2016).

The nearshore migrations of humpback whales along the eastern coast of southern Africa makes it possible to monitor and evaluate the spatial and temporal distribution patterns of the C1 stock using various methods allowing essential population parameters such as abundance, stock structure and connectivity to be investigated (Findlay & Best, 1996). During August and September 1991, Findlay *et al.* (1994) conducted a line transect survey of abundance on humpback whales wintering within the coastal waters of Mozambique (C1 sub-stock), where the survey ranged from coastal waters to the 200 m isobath (Findlay *et al.*, 1994). Results indicated that the sub-stocks' relative abundance was estimated to be 1,954 animals (CV = 0.38). However, this was considered an underestimate as no correction factor was used for individual whales missed on the track-line (Findlay *et al.*, 1994). A second line-transect survey (corresponding to the 1991 survey) was carried out between August and September 2003, where a larger region of the Mozambique coastal waters was surveyed between Cabo Inhaca (26°00'S, 33°05'E) and north of Mozambique Island (14°26'S, 40°53'E), and between the 20 and 200m Isobaths (Findlay *et al.*, 2011). The only large whale species identified throughout the survey were humpback whales, where an estimated 1,130 individuals (691 sightings) were observed. Further analysis suggested that the abundance for the C1 sub-stock was estimated to be 5,965 whales (CV = 0.17) (Findlay *et al.*, 2011). However, these estimates were regarded as negatively biased as there was no correction factor for whales observed outside of the survey area boundaries, individual whales missed on the track-line during the survey, or whales migrating before or after the duration of the survey (Findlay *et al.*, 1994; Findlay *et al.*, 2011).

Shore-based monitoring surveys of the C1 sub-stock humpback whales were conducted from Cape Vidal, South Africa between 1988 and 1991 *en route* their northward migration, and in 1990 during southward migration (Findlay & Best, 1996). Results obtained during the 1990 northward migration produced the best population size estimate (1,711 animals), however; these results were likely biased downwards as it was believed that a proportion of the population migrated outside of observers' offshore view. Irrespective of the bias, the number of humpback whales sighted during these surveys demonstrate the population to have undergone considerable recovery since protection in October 1963. A replication of the aforementioned surveys was conducted in 2002 during the northward migration of humpback whales past Cape Vidal. Abundance estimates from this study indicated that the C1 sub-stock had further increase to 2,406 in 2002 (Findlay & Best, 2006). Considering results from all these surveys, the numbers passing Cape Vidal during co-incident periods of 17 days over the 1988 to 2002 surveys (6 July to 22 July) and 25 days over the 1990, 1991 and 2002 surveys (6 July to 30 July) provide preliminary increase rates of 12.3% and 0.90% per annum respectively.

1.2.4 Mark-Recapture and Photo-identification

The success of effectively managing and protecting endangered species is subject to the accuracy and reliability of the methods used to monitor and collect information from them. One of the key challenges faced by conservation managers is the accurate assessment of the state of species, particularly in terms of population abundance and stability. Such information is essential for establishing appropriate management and protection protocols for the species in focus.

The mark-recapture, or capture mark-recapture (CMR) method is a powerful tool for estimating valuable population parameters, such as size or abundance, structure, recruitment, survival, and growth rates, as well as to study movement patterns, evaluate population trends, assess the influence of threats on the survival of populations and gather data for population viability analyses (Buckland, 1982; Hammond *et al.*, 1990; Pradel, 1996; Lettink & Armstrong, 2003; Hammond, 2009).

The conventional CMR method involves physically capturing a random portion of the focus population, marking them with tags or wounds, and then releasing them back into nature. Following some time, a second random proportion of individuals are captured and the ratio of previously marked to unmarked individuals are evaluated. By repeating this process, a set of capture histories for the previously marked individuals is recorded by appointing the value "1" to the recaptured marked individuals, and "0" to individuals that have not previously been marked or captured (Lettink & Armstrong, 2003; Hammond, 2009).

The CMR method's effectiveness in population analyses relies on the dynamics of the target population, which determines the appropriate CMR data analysis model, and influences the meeting of the chosen CMR model's assumptions (Hammond *et al.*, 1990; Lettink & Armstrong, 2003; Hammond, 2009). An important distinction can be made between open and closed populations: closed populations remain constant in size and composition throughout the study period, whereas open populations' size and composition fluctuate due to births, deaths, emigration, and immigration. Closed population CMR methods are generally considered where an estimate of the total number of animals in a population is required, *i.e.*, to provide an estimate of absolute abundance, where as few as two capture sessions may be sufficient (Hammond *et al.*, 1990; Lettink & Armstrong, 2003; Hammond, 2009). When a closed population CMR method is considered, the following conditions are assumed:

1) No births, deaths, emigration, or immigration takes place in the target population over the study period;
2) All individuals in the target population have an equal probability of being captured; and
3) Marks are not lost or overlooked.

Open population CMR model assumes the following conditions:

1) All individuals in the target population have the same survival probability;
2) All individuals in the target population have an equal probability of being captured;
3) Marks are not lost or overlooked; and
4) The duration of each sampling or capture occasion is instantaneous in comparison to the intervals between sampling sessions and the total study period.

The process of applying CMR models to capture history data is relatively simple. However, it is important to carefully consider the consequences of violating the chosen model's assumptions, as this may have serious implications on population estimates, especially abundance. Furthermore, the process of analysing data from open population CMR studies is often more complex compared to closed population CMR studies, as it may be considerably challenging to identify births, deaths, immigration, or emigration of individuals in a population (Hammond, 2009).

Although the traditional CMR method requires the physical marking of animals, this process may be challenging for species that are difficult to capture or relocate, detrimental to species that are vulnerable to handle, and low mark or tag retention rates may compromise long-term studies (Hammond *et al.*, 1990; Lettink & Armstrong, 2003; Hammond, 2009). Furthermore, physical trap setups or capture events may induce an alteration in the behavioural response of some individuals to the traps or capture method, for instance, an animal might become either trap happy or trap shy (Pollock, 1982). For such species, alternative methods of identifying individuals are necessary.

Many terrestrial and aquatic mammals possess distinctive natural markings on one or more body parts. These natural markings have allowed scientists to identify individuals in the field non-invasively, on a recurring basis, using photographic methods (Hammond *et al.*, 1990; Parsons *et al.*, 2013). The photo-identification of individual animals using natural markings has played a significant role in research since the 1970s (Würsig & Würsig, 1977; Hammond *et al.*, 1990). Photo-identification of mammals has grown extensively over the last century, and has already been applied to terrestrial mammals such as zebra (*e.g.* Petersen, 1972), leopards (*e.g.,* Miththapala *et al.,* 1989) and cheetahs (*e.g.,* Kelly, 2001), as well as to marine mammals such as polar bears (*e.g.,* Anderson *et al.,* 2010), grey seals (*e.g.,* Vincent *et al.,* 2001), manatee (*e.g.,* Beck & Reid, 1995; Langtimm *et al.,* 1998), porpoises (*e.g.,* Würsig & Würsig, 1977), bottlenose dolphins (*e.g.,* Defran *et al.,* 1990; Wells & Scott, 1990), grey whales (*e.g.,* Kehtarnavaz *et al.*, 2003), sperm whales (*e.g.,* Whitehead, 1990, 2001; Huele & de Haes, 1998; Huele *et al.,* 2000), killer whales (*e.g.,* Reisinger *et al.,* 2011), southern right whales (*e.g.,* Best, 1990; Burnell & Shanahan, 2001; Hiby & Lovell, 2001), and humpback whales (*e.g.,* Perry *et al.,* 1988; Katona & Beard, 1990; Mizroch *et al.,* 1990; Stone *et al.,* 1990; Blackmer *et al.,* 2000; Stevick *et al.,* 2001) amongst other.

Unlike traditional CMR methods, which are costly and requires highly invasive marking or tagging which may be damaged or lost over time, photo-identification is non-invasive, cost-effective, and markings are usually more permanent (Würsig & Würsig, 1977; Hammond, 1986; Hammond, 1990). Furthermore, photo-identification as a research method is highly beneficial as it allows for the monitoring of species over extensive temporal and spatial scales (Acevedo *et al.,* 2007; Guidino *et al.,* 2014), provide the opportunity to identify multiple individuals within a single sighting, and permits the participation of non-specialists in the data collection process, such as public participants contributing to science as citizen scientists.

Although the advantages of photo-identification as CMR method are extensive, there are some drawbacks to consider. Since the early development of the technique, the practice of using natural markings for individual recognition has been known to result in identification errors (Bateson 1977; Hammond, 1986; Gunnlaugsson & Sigurjonsson, 1990; Yoshizaki *et al.,* 2009; Morrison *et al.,* 2011). Identification errors or misidentification occurs when two different individuals are identified as the same individual (false positive error), or when a previously identified individual is re-identified as a different individual (false negatives) (Hammond, 1986; Gunnlaugsson & Sigurjonsson, 1990; Yoshizaki *et al.,* 2009; Morrison *et al.,* 2011). Several factors are considered to influence misidentification, including photographic quality, the uniqueness or distinctiveness of the natural markings, and stability of the markings over time (Hammond, 1986; Friday *et al.,* 2000, 2008; Stevick *et al.* 2001).

Photographic quality may influence how much of the information contained in the natural markings is reflected (Hammond, 1986; Hammond *et al.,* 1990; Friday *et al.,* 2000, 2008;

Stevick *et al.* 2001). Stevick *et al.* (2001) concluded a strong negative correlation between photographic quality and identification errors, in such that the rate of error increases with decreasing photographic quality. In addition, the distinctiveness of an individual's natural markings further affects the likelihood of successful future re-identification (Friday *et al.,* 2000, 2008; Stevick *et al.* 2001). These two factors have been shown to mutually influence misidentification, as individuals with very distinctive features have a higher chance of identification in poor-quality photographs (Hammond *et al.,* 1990; Friday *et al.,* 2000, 2008; Stevick *et al.* 2001). Furthermore, variability in photographic quality and the distinctiveness of features means that the use of natural markings for individual identification does not guarantee an equal probability of recognition among individuals, consequently violating a CMR model assumption (Hammond 1986; Hammond *et al.,* 1990). Depending on the objectives of the study, such a violation could have a significant impact on the study outcome, particularly in cases where abundance estimates using CMR methods are required (Hammond 1986; Hammond *et al.,* 1990).

Variations in the stability of individuals' natural markings have also been demonstrated to cause misidentification (Carlson *et al.,* 1990; Dufault & Whitehead, 1995; Stevick *et al.,* 2001; Vincent *et al.,* 2001). Considering that CMR methods assume that marks are not lost or changed over time, it is recommended that the most unchanging natural marks should be used for identification (Carlson *et al.,* 1990; Blackmer *et al.,* 2000). Multiple studies have investigated this assumption, where changeable physical features were identified as age-dependent, stable, or transitory (Hammond, 1986, 1990; Carlson *et al.,* 1990; IWC, 1990; Blackmer *et al.,* 2000; Gowans & Whitehead, 2001; Stevick *et al.,* 2001). Age-dependent physical features are classified as the features that change as an animal age. For humpback whale flukes, the variability in change can either increase (such as fluke peaks and notches) or decrease (such as ventral fluke marks/scarification and pigmentation patterns) over the animals' lifespan (Blackmer *et al.,* 2000). Evidence suggests that drastic changes in humpback whales' fluke pigmentation only occur in the transitions between the juvenile life stage and adulthood, and most significantly in calves with darker fluke colouration (Carlson *et al.,* 1990; Stevick *et al.,* 2001). Features that do not show significant change over time are classified as stable, including the throughs of humpbacks' flukes. Transitory features are the physical features that continuously change over time and are neither age-dependent nor ever stable; however, no transitory features have yet been identified on humpback whale flukes (Carlson *et al.,* 1990; Dufault & Whitehead, 1995; Stevick *et al.,* 2001; Vincent *et al.,* 2001).

The varying capabilities of scientists to accurately match natural markings from photographs can further limit the value of the photo-identification method (Katona & Whitehead, 1981). Moreover, photo-identification remains one of the most labour-intensive research methods, as the photographic material gathered during field surveys requires innumerable hours of meticulous processing. The process of matching new photographs to already catalogued photographs become considerably cumbersome as the number of identified individuals increase, enhancing the chance of misidentification (Hillman *et al.,* 2003). The use of computers to match photographs for identification purposes has demonstrated to considerably reduces the time required to perform matching, and ultimately improves the accuracy in comparing images (Mizroch *et al.,* 1990; Adams *et al.* 2006).

Succeeding the origination of digital cameras, recent advances in digital photography, and the general reduction in costs related to digital photographic equipment, the use of photo-identification methods have increased and improved considerably over the last two decades (Markowitz *et al.,* 2003; Adams *et al.,* 2006). Compared to traditional film photography, digital photography has significantly enhanced the efficiency of data collection, allowing the rapid accumulation of large quantities of high-quality images within short periods and at low costs (Markowitz *et al.,* 2003; Adams *et al.,* 2006). However, without the proper data processing and managing tools, such advances could pose challenges. Advanced digital software that automatically applies pattern-recognition algorithms to digital photographic databases offers a promising opportunity to identify and match individuals over multiple years and multiple sites (Gamble *et al.,* 2008; Holmberg *et al.,* 2008; Cheeseman *et al.,* 2022).

1.2.5 Photo-identification of Humpback Whales

It is well known that humpback whales have several varying and unique natural markings making it possible to identify individuals for study purposes (Lillie, 1915; Matthews, 1937; Pike, 1953; Schevill & Backus, 1960; Katona *et al.*, 1979; Katona & Whitehead, 1981; Hammond *et al.,* 1990; Stevick *et al.,* 2001; Urian *et al.,* 2015). These markings include the variation in black and white pigmentation patterns on the ventral side of their tails (flukes), as well as irregularity and scarification of trailing edges of the fluke and the shape of the dorsal fins (Schevill & Backus, 1960; Katona *et al.,* 1979; Carlson *et al.,* 1990; Katona & Beard, 1990). The unique colouration and pattern of the natural markings on the ventral side of a humpback whales' fluke provides the most positive discrimination between individuals (Katona *et al.,* 1979; Katona & Beard, 1990) and gives the most reliable data for distinguishing individual animals on a large scale (Stevick *et al.,* 2001). In the 1990s, fluke variation was already determined to help identify individuals through photographic methods, thus making tracking over some time possible (Mizroch *et al.,* 1990). Thousands of individual humpback whales have been identified over the last 40 years through their unique patterns on the ventral surface of the tail fluke (Clapham, 2018), and catalogues of individual humpbacks' have been compiled for several oceans, including the North Pacific, North Atlantic, and Southern Hemisphere oceans (*e.g.,* Perry *et al.,* 1990; Katona & Beard, 1990; Mizroch *et al.,* 1990; Stone *et al.,* 1990; Darling *et al.,* 1996; Chaloupka *et al.,* 1999; Salden *et al.,* 1999; Smith *et al.,* 1999; Blackmer *et al.,* 2000; Baracho-Neto *et al.,* 2012).

The use of photo-identification as a research method to study humpback whale populations is particularly advantageous as it can be used in a wide range of analyses and has already extensively been used to monitor and document humpback whale populations globally (Katona *et al.,* 1979; Carlson *et al.,* 1990; Hammond *et al.,* 1990; Würsig & Jefferson, 1990; Hillman *et al.,* 2003; Parsons *et al.,* 2013). Photo-identification techniques carried out on humpback whales has allowed scientist to collect extensive amounts of information on the species biology (*e.g.,* Steiger & Calambokidis, 2000; Chero *et al.,* 2020), geographic distribution and habitat range (*e.g.,* Dulau-Drouot *et al.,* 2011; Rasmussen *et al.,* 2012), spatial and temporal movement and migration patterns (*e.g.,* Corkeron & Brown, 1995; Jenner *et al.,* 2001; Rock *et al.,* 2006; Witteveen & Wynne, 2017), site-fidelity trends (*e.g.,* Wedekin *et al.,* 2010; Baracho-Neto *et al.,* 2012; Horton *et al.,* 2017; Witteveen & Wynne, 2017), social organization structure (*e.g.,* Garrigue *et al.,* 2011; Clapham & Zerbini, 2015), abundance (*e.g.,* Calambokidis *et al.,* 2001; Barlow *et al.,* 2011; Constantine *et al.,* 2012; Felix *et al.,* 2020), population/stock structure (*e.g.,* Baker *et al.,* 1986; Calambokidis *et al.,* 2001; Garland *et al.,* 2015), and levels of connectivity between stocks and sub-stocks from different feeding and breeding grounds (*e.g.,* Calambokidis *et al.,* 1997; Craig & Herman, 2000; Stevick *et al.,* 2004; Pomilla, 2005; Stevick *et al.,* 2010; Garrigue *et al.,* 2011).

It is widely assumed that humpback whales' journey directly through their migration corridor *en route* to their breeding and feeding grounds, with little deviation from the path (Horton *et al.,* 2011; Burns *et al.,* 2014). However, humpback whales display subtle and intricate social behaviour, which may ultimately influence and determine the migration outcomes (Corkeron & Brown, 1995; Burns *et al.,* 2014). By using photo-identification techniques, scientists can determine the likelihood of an animal to inhabit or utilise a particular area, or the probability of the same animal to return to a previously visited area over some time, a phenomenon termed "site fidelity" (White & Garrot, 1990). Additionally, photo-identification techniques can be instrumental in tracking the movement of individuals over temporal and spatial scales, confirming the presence and utilisation of distinct migration corridors. By forming connections between photographs of individual animals taken within different regions, scientists can form linkages between the different regions used by the animal, subsequently predicting migration pathways and corridors.

It is essential to evaluate and understand the degrees of site fidelity displayed by a particular animal or species, as it is one of the key factors to consider when planning a species conservation and management. Information on site fidelity may also provide essential information to consider during marine spatial planning and the development of marine protected areas (Bräger *et al.,* 2002; Wedekin *et al.,* 2010). The degrees to which baleen whales display site fidelity have been examined extensively and could be one of the main factors contributing to the excessive exploitation of the species during the whaling era. The examination of site-fidelity trends displayed by humpback whales has also been used extensively to describe the geographical structures of different stocks (Rambeau, 2008; Wedekin *et al.,* 2010).

Photo-identification methods have aided as a valuable tool for examining humpback whales' migration and site-fidelity trends. Through the comparison of photographic evidence and matching of individuals over a spatial and temporal frame, scientists can determine essential parameters such as the seasonal appearance and migration timing, movement patterns, levels of regional residency, and the return rate of individuals to a specific area over a given period (*e.g.,* Baker *et al.,* 1986; Mattila *et al.,* 1994; Craig & Herman 1997; Clapham, 2000; Wedekin *et al.,* 2010). Furthermore, information on site-fidelity trends and migration links extracted from photo-identification analyses can provide valuable insight into humpback whale populations' intra-and inter-regional stock structure (Minton *et al.,* 2011; Wedekin *et al.,* 2010; Burns *et al.,* 2014; Lavin, 2017). The site fidelity trends of humpback whales on both feeding and breeding grounds has widely been documented, where different levels of fidelity have been suggested for each area (*e.g.,* Dorsey *et al.,* 1990; Craig & Herman 1997; Best, 2000; Calambokidis *et al.,* 2001; Acevedo *et al.,* 2006; Clapham *et al.,* 2008; Wedekin *et al.,* 2010). In general, it is well known that humpback whales display strong site fidelity, and in most cases, utilise only one specific feeding and breeding ground (Chittleborough, 1965; Darling & McSweeney, 1985; Darling *et al.,* 1996). Some evidence indicates site fidelity to feeding grounds to be maternally directed, displaying annual rates of return of up to 90% (Clapham & Mayo, 1987; Clapham *et al.,* 1993; Acevedo *et al.,* 2006; Wedekin *et al.,* 2010). Although fidelity is still considered high in breeding grounds, annual return rates are somewhat lower than feeding grounds (Mattila *et al.*,1994; Calambokidis *et al.*, 2001). Furthermore, there are only a few cases where humpback whales would utilise more than one feeding or breeding ground, but is usually only limited to a few individuals, making genetic exchange between different populations insignificant (Chittleborough, 1959; Baker *et al.*, 1986; Darling & Cerchio, 1993; Darling *et al.*, 1996; Hoelzel, 1998).

Several software and online platforms have been developed for the use of humpback whale fluke identification and matching, including Fluke Matcher, Match My Whale (matchmywhale.org), Happywhale (happywhale.com), Wildbook (https://www.wildme.org), Flukebook (flukebook.org), and others.

Wildbook is an effective computer-based system that can be used for the photo-identification of both terrestrial and marine animals. This software allows its users to add biological data such as the status (alive or deceased), gender, behaviour, group role and life stage of each encounter, geographic information such as its location, tracking data and habitat conditions, and descriptions on physical markings and scarring on individuals. Once an encounter has been submitted, Wildbook can automatically search for matches within its photo database or determine if an individual is new (Berger-Wolf *et al.*, 2017). Once an individual has been identified within the system, Wildbook can re-identify that same individual in any further submitted photographs. Subsequently, Wildbook provides researchers and scientists with an opportunity to determine population trends, stock size estimates, species geographic range, temporal and spatial migration patterns, stock structure and levels of connectivity between stocks and sub-stocks from different breeding and foraging grounds, as well as intra-regional stock structure (Berger-Wolf *et al.*, 2017).

Flukebook (http://flukebook.org) is an online-based project developed under the Wildbook Software environment, as a secure non-profit platform where researchers and scientists can organise, store, analyse, match catalogues of whale sightings (Blount *et al.*, 2018). Flukebook can automatically identify individual animals with artificial intelligence and computer vision through visible features on fluke photographs. Flukebook compares all new images, based on specific fluke features, including trailing edge, scarification patterns and colouration, to previously uploaded and identified individuals in the Flukebook catalogue. Flukebook also allows users to add specific features according to their research needs, which becomes available to all users. Information and data uploaded to the Flukebook platform remain the property of the uploader and can only be viewed and controlled by this user unless the user permits a two-party partnership agreement with another Flukebook user (Blount *et al.*, 2018). Some of the features already available in Flukebook include geographical tracking of individuals, visualising the simultaneous occurrence of individuals within a population, and exporting information in a standard format for use in analysis and mapping software (Blount *et al.*, 2018).

1.3 Research Rationale, Aims and Objectives

Since information surrounding the migration behaviour of humpback whales associated with the C1 sub-stock is outdated, and little is known about the current structure of this breeding sub-stock, the key aims of the study was to utilize photo-identification methods to

1) obtain updated information on the intra-region temporal and spatial migration patterns and migration fidelity trends of the humpback whales utilising the migration corridor on the east coast of South Africa; and

2) investigate the intra-regional structure of the humpback whale C1 sub-stock.

Consequently, the research objectives of this study were to:

1) gather historic humpback whale fluke image collections available for the C1 sub-stock;

2) contribute new fluke images taken during this study during opportunistic surveys with permitted commercial boat-based whale watching (BBWW) operators based in KwaZulu-Natal, designated scientific research field studies off Bazaruto, Mozambique, and Durban, South Africa, and other photo-identification data collection opportunities;

3) develop a multiregional photo-identification catalogue representing humpback whales associated with the C1 sub-stock, by combining the historic (1988 – 2018) and new (2018 – 2019) collection of photo-identification tail fluke images congregated during this Masters' study period;

4) conduct photo-identification analyses with the newly developed C1 sub-stock photo-identification catalogue, to reveal novel information pertaining to the sub-stock.

During this study, all available historic photo-identification fluke image data collections were obtained from DFFE, CDS, MRI and several commercial BBWW operators situated along the proposed migratory corridor for the C1 sub-stock. New humpback whale fluke photographs representing the C1 sub-stock were collected in collaboration with permitted commercial BBWW operators associated with the South African Boat Based Whale-Watch Association (SABBWWA) and designated humpback whale research surveys along the east coast of South Africa and in Mozambique. All available photo-identification data was consolidated into a multiregional photo-identification catalogue representing the humpback whale C1 sub-stock. This extensive dataset represents 32 years of data (1988 to 2019) and covers locations within the entire known migration corridor and a portion of the sub-stocks' breeding ground.

1.4 Thesis Overview

This thesis is divided into four main chapters.

In Chapter 1, an introduction to the research theme, and the aims and objectives of the Study are provided, along with a comprehensive literature review outlining the research problem.

Chapter 2 focuses on the research protocol followed to obtain data for this study. It describes the study sites and the methodology used to gather, process, and analyse all the data contributing to this research.

Chapter 3 encompasses the results obtained for this study through photo-identification methods and others.

Chapter 4 discusses the study's results in detail.

In Chapter 5, the overall outcome of the study is concluded, and recommendations for future investigations are provided.

CHAPTER 2 METHODS AND MATERIALS

2.1 Study Area

The study area comprises the known migration corridor (34°S to 18°S) and breeding grounds (24°S to 15°S) proposed for the humpback whale C1S sub-stock (Best *et al.,* 1998; Findlay *et al.,* 1994). Following Cerchio *et al.* (2008a), the study area has been divided into several coastal regions based on photographic data collection, to represent and describe sub-regional structure (Figure 2.1a and b). These regions are, the south coast (SC), south-eastern coast (ES), north-eastern coast (EN), southern Mozambique coast (MS), and central Mozambique coast (MC) (Figure 2.1b).

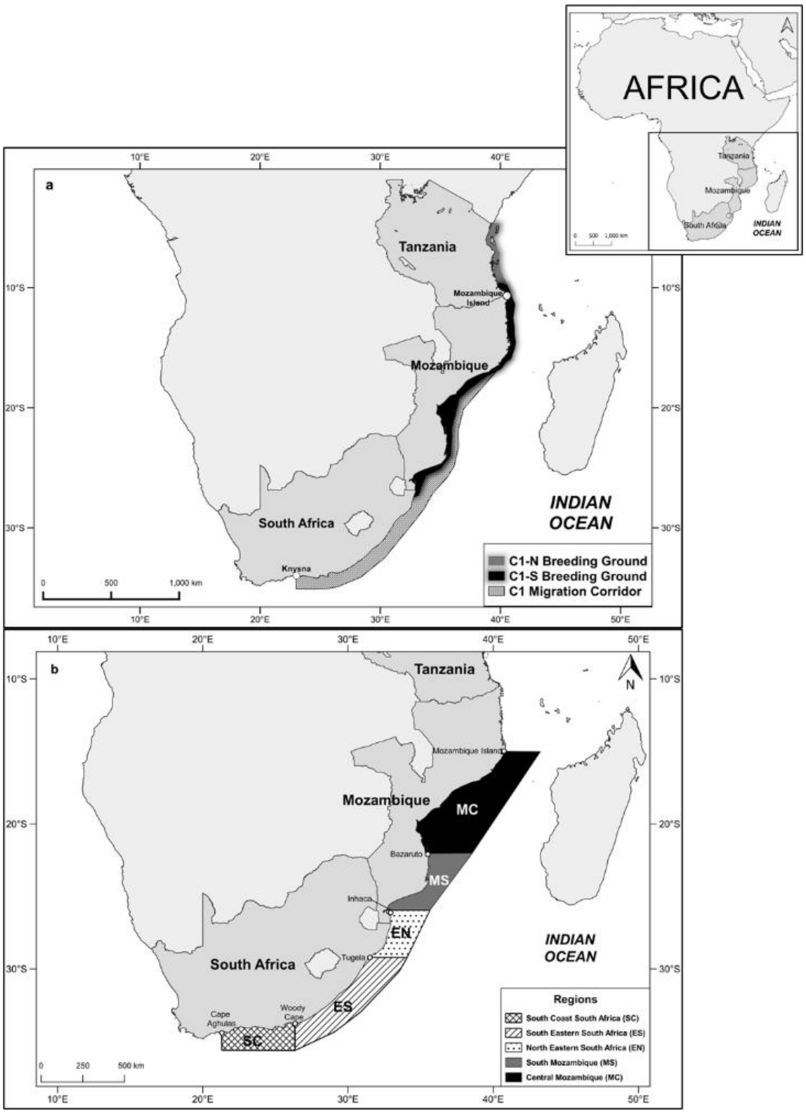


Figure 2.1 a) The known migration corridor and breeding ground used by the C1 South (C1S) and C1 North (C1N) humpback whale sub-stocks, and b) the photographic data collection coastal regions within the C1S migration corridor and breeding grounds (modified from Cerchio *et al.* 2008a).

2.2 Humpback Whale Fluke Image and Data Collection

Two independent humpback whale fluke image datasets were collated and compiled for the development of a multiregional photo-identification catalogue representing the C1 sub-stock of the species. One dataset comprised historic fluke images and associated data from South African data collections, and a second includes new fluke images and associated data collected over the study period. Within both datasets, two types of data collection survey methods were used to obtain the photo-identification data, including dedicated scientific research surveys and data collection efforts from commercial boat-based whale watching (BBWW) platforms of opportunity (PoP).

Literature broadly defines a dedicated scientific research survey as a logically and systematically planned effort to acquire information and gain scientific knowledge to explain specific occurring phenomena (Wilson, 1990; Çaparlar & Dönmez, 2016). In this study, the humpback whale fluke images and their associated data collected during dedicated scientific research surveys are referred to as "research survey (RS)" data. Humpback whale fluke images and associated data collected on commercial boat-based whale-watching vessels, either during opportunistic surveys or as citizen science, are referred to as "BBWW" data. The data collecting methods applicable to each dataset is described in the following sections.

2.2.1 The historic dataset

The historic dataset was composed of a collection of humpback whale fluke images and data representative of the C1 sub-stock collected from several independent dedicated humpback whale research surveys, commercial BBWW operations and other PoP's within South Africa and Mozambique, between 1988 and 2018, independent of this study. These fluke images and data were provided by the Department of Forestry, Fisheries and the Environment (DFFE) [based in Cape Town, South Africa; formerly the Department of Environmental Affairs (DEA), and Department of Environment, Forestry and Fisheries (DEFF)], the Centre for Dolphin Studies (CDS) [based in Plettenberg Bay, South Africa], the Mammal Research Institute (MRI) [based at the University of Pretoria, South Africa], and several commercial BBWW companies operating along the south-eastern coastline of South Africa. A description of the data provided by each of the above-mentioned contributing sources is provided below.

a) Department of Forestry, Fisheries, and the Environment (DFFE)

Tail fluke images and data collected through several independent dedicated humpback whale research surveys (RS) and commercial BBWW operations between 2000 and 2018 are held by DFFE as a historic photo-identification national database. The RS data component included fluke images and data collected during research work directed at humpback whales or during multidisciplinary scientific surveys carried out by the Department. The BBWW data component included fluke images and data collected by commercial BBWW company members of the South African Boat-Based Whale Watching Association (SABBWWA), which was provided to the Department as part of commercial BBWW licence agreements. All the available fluke images and data pertaining to the C1 sub-stock that was stored in the Departments' archives were retrieved and investigated, whereafter digital duplicates were created and saved. These image and data collections were provided as raw/unprocessed data. Altogether, 4,007 fluke images were duplicated.

b) Centre for Dolphin Studies (CDS)

The Centre provided digital copies of archived humpback whale fluke images and associated data which was collected as RS data between 2000 and 2009. This dataset was provided as a pre-developed fluke image catalogue comprising 307 fluke images.

c) Mammal Research Institute (MRI) - Whale Unit

The Institute provided digital copies of their archived humpback whale fluke images and data collected during dedicated research surveys between 1988 and 1992. These image and data collections were provided as raw/unprocessed data, totalling to 85 fluke images.

d) Additional - Commercial BBWW operators

Licenced commercial BBWW companies operating within the south-eastern coastal waters of South Africa between Knysna (34°S), and Kosi Bay (26°S) were sourced through the internet. The companies were contacted telephonically or via email and queried whether they would be willing to contribute any archived collections of humpback whale fluke images. Willing companies included Ocean Odyssey Whale Watching (Knysna) and Ocean Safaris Whale and Dolphin Watching (Plettenberg Bay). Based on the companies' licenced operation region, the fluke images and data were assumed to represent the within-subregion distribution of C1 sub-stock humpback whales. The fluke images and data collections provided by these sources were received via email, and represented data collected between 2007 and 2018. Altogether, 58 fluke images were received from these sources.

Table 2.1 provides a detailed inventory of all the duplicated historic fluke images and data, including information on the original data contributors (within each data source), the survey/data collection year/s and the number of fluke images duplicated. A total of 4,457 fluke images were collected as the historic dataset.

Table 2.1 The number of historic fluke images received/duplicated from each data source, subdivided by data collection method, year, and the original data contributor/project (DFFE = Department of Forestry, Fisheries, and the Environment; CDS = Centre for Dolphin Studies; MRI = Mammal Research Institute; RS = research survey; BBWW = boat-based whale watching).

DATA SOURCE	DATA COLLECTION METHOD	CONTRIBUTOR/PROJECT	DATA COLLECTION YEARS	NUMBER OF FLUKE IMAGES DUPLICATED
DFFE	RS	Dave Rissik_Plettenberg Bay	2001	1
		Algoa_East Coast Humpback Whale Cruise	2002	111
		Algoa_Mozambique Humpback Whale Cruise	2003	128
		Sardine Run_Port St Johns Humpback Whale Survey	2005	52
		East Coast Whale Cruise_RV Ellen Khuzwayo_East London & Port Elizabeth	2015	138
		East Coast Whale Cruise_Land Based_East London & Richards Bay	2016	232
		East Coast Whale Cruise_Land based_Bluff_Small Boat work	2017	111
	BBWW	Advantage Tours_St Lucia	2000-2011; 2018	3,231
		Advantage Tours_Richards Bay	2014	3
TOTAL				4,007
CDS	RS	CDS Research	2000-2005	14
		CDS_Aaron Banks Research_Plettenberg Bay & Knysna	2006	50
		CDS_Aaron Banks Research_Bazaruto, Mozambique	2007	129
		CDS_Aaron Banks Research_Plettenberg Bay & Knysna	2008	74
		CDS_Aaron Banks Research_Ponta Mamoli, Mozambique	2009	40
TOTAL				307
MRI	RS	MRI Whale Unit Research_Cape Vidal	1988-1990; 1992	34
		MRI Whale Unit Research_Mozambique	1991	51
TOTAL				85
COMMERCIAL BBWW	BBWW	Ocean Odyssey Whale Watching (Knysna)	2007; 2013; 2014; 2017; 2018	56
		Ocean Safaris Whale and Dolphin Watching (Plettenberg Bay)	2018	2
TOTAL				58
TOTAL (ENTIRE DATASET)				4,457

2.2.2 The new dataset

New humpback whale fluke images and data were collected in 2018 and 2019 during the C1 sub-stock's winter migration months, under activities of the current project. These photo-identification data were collected during opportunistic surveys conducted on commercial BBWW platforms within South Africa, and dedicated humpback whale research surveys conducted along South Africa and Mozambique.

Unless stated otherwise, a standard protocol of locating, photographing, and data capturing was followed throughout these data collection opportunities. Once humpback whales were discovered through their above surface behaviour such as blows, flipper slapping, tail lobbing, and breaching, the individual/groups were cautiously approached. The date (year/month/day), encounter start and end time, group size and composition, and encounter GPS location (latitude and longitude) were recorded for each group encountered. Photographic data collected under this project were captured by a single photographer using a handheld digital Nikon D3400 camera with a 70-300 mm auto-focus zoom lens.

A group was defined as one or more individuals who exhibited noticeable synchronised behaviour or movement and were not further than approximately 100 m from one another, as described by Whitehead (1983) and Corkeron *et al.* (1994). A humpback whale calf was defined as an individual near another whale, visually estimated to be less than half of the accompanying whale's length. A lactating female was considered an adult accompanied by a calf (Chittleborough, 1958; Chittleborough, 1965). Whales that were not defined as calves were assumed to be adults, as it was impossible to distinguish juveniles and sub-adults from mature individuals visually. The time of encounter with cow/calf pairs was kept to a minimum to avoid disturbances.

Upon encountering a humpback whale group, an attempt was made to capture fluke images of all adults within the group, whereafter the end encounter location and time were recorded. Each photographed whale was assigned an alphanumeric code (the letter attributed to the group and the number to the individual). After each data collection opportunity, all images were downloaded, stored on external hard drives, and sorted according to survey/project, survey vessel, date (year/month/day), encounter group number (alphabetic), and individual number (numeric).

2.2.2.1 Opportunistic surveys on commercial BBWW platforms

Commercial BBWW platforms of opportunity were accompanied to collect humpback whale photo-identification data at two localities within the KwaZulu-Natal province of South Africa, including Durban (29°52'S; 31°01'E) and St Lucia (28°23'S; 32°25'E). The BBWW companies operated in sea conditions of Beaufort scale of 5 or less. Photography was dependent on sea and weather conditions, and the distance of the whales from the vessel. All the opportunistic BBWW operations occurred between the 20m and 120m isobaths.

a) Durban, South Africa

Two commercial BBWW companies (Umhlanga Ocean Charters and Isle of Capri) provided opportunities to collect humpback whale photo-identification data off Durban (29°52'S; 31°01'E) between June and December 2018 and 2019. Attendance on these platforms depended on space availability, as paying customers received first preference. Launching and beaching of the survey vessels occurred in Durban Harbour. Executions lasted approximately two hours, where some 30 minutes was spent travelling within the harbour (approximately 15 minutes travel towards the Durban Harbour Entrance from the launching site, and approximately 15 minutes travelling from the Durban Harbour Entrance to the beaching site). Survey duration was calculated as the time the survey vessel spent on the open ocean while actively searching for humpback whales (duration between the exiting/entering of the survey vessel at the Durban Harbour Entrance). The Bluff (29°55'S; 31°01'E) and Durban North (29°47'S; 31°03'E) regions marked the southern and northern limits of these BBWW operations.

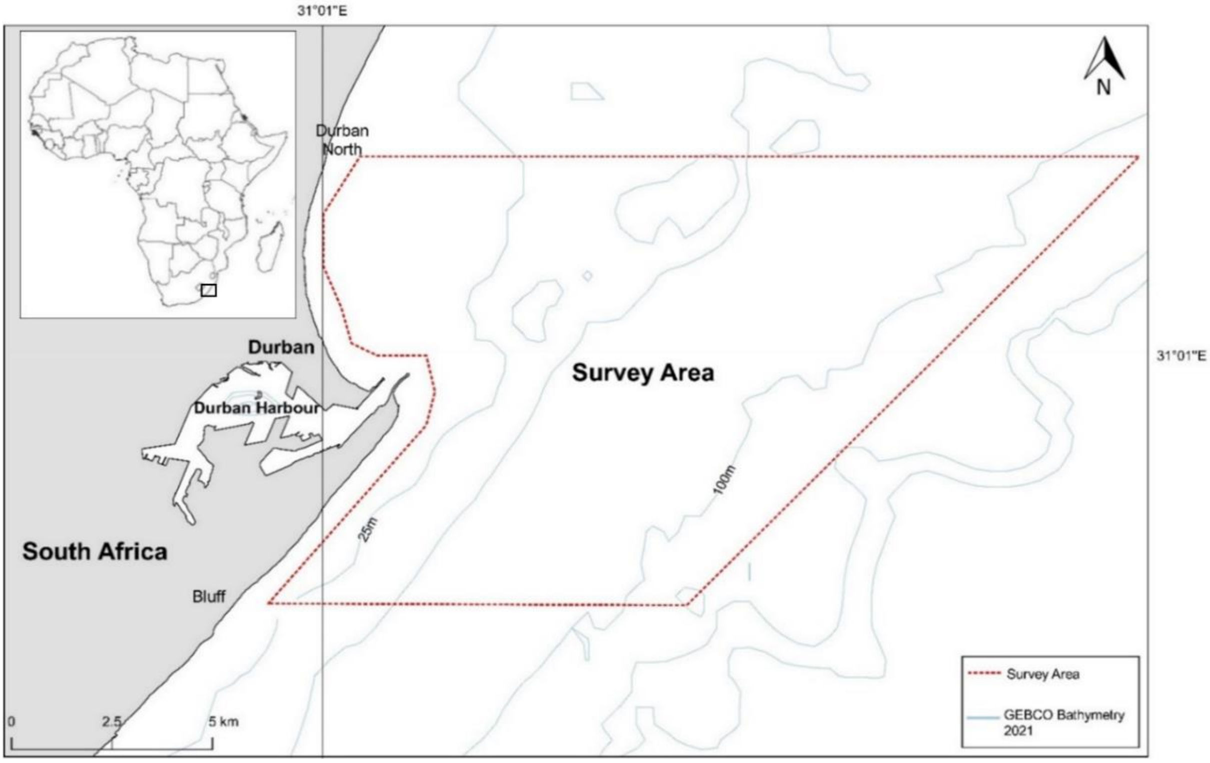


Figure 2.2 A representation of the geographic range explored during the 2018 and 2019 commercial BBWW opportunistic surveys off Durban, South Africa.

b) St Lucia, South Africa

During October 2019, opportunistic BBWW trips were provided by Advantage Tours based in St Lucia (28°23'S; 32°25'E) to collect photo-identification data. An opportunity was secured for each excursion conducted during the survey period. These excursions/trips lasted approximately two hours. Excursions departed from/returned to the beach just south of the St Lucia Estuary (around 28°S). Since no physical obstructions prevented the clear observation of humpback whales from the beach or the survey vessel while launching/beaching took place, the survey duration was calculated as the time between the launching and beaching of the vessel. The Cape St Lucia lighthouse (28°30'S; 32°24'E) and Cape Vidal beach (28°07'S; 32°33'E) regions marked the southern and northern limits of these BBWW operations (Figure 2.3).

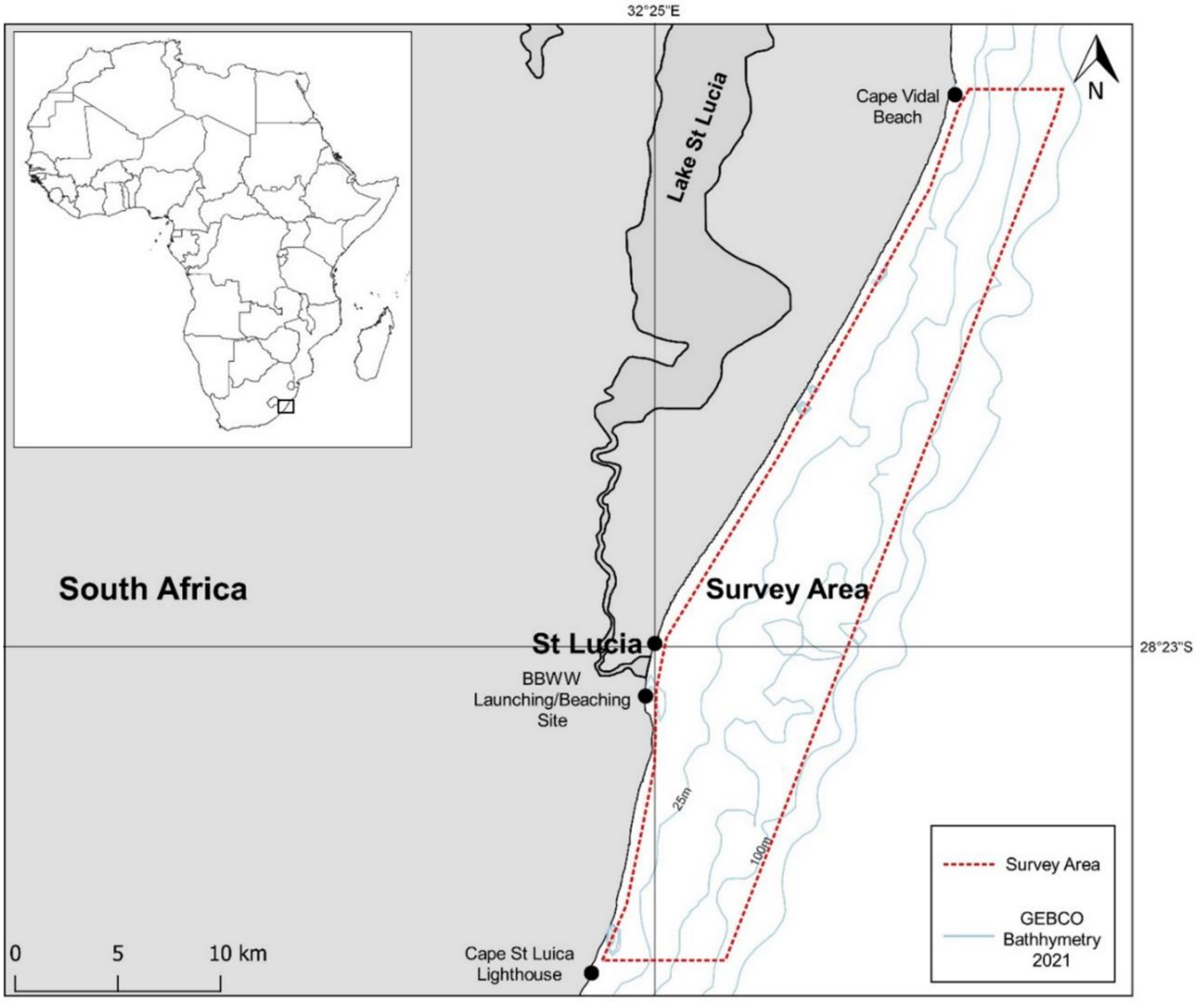


Figure 2.3 A representation of the geographic range explored during the 2019 commercial BBWW opportunistic surveys off St Lucia, South Africa.

2.2.2.2 Dedicated research surveys

Dedicated research efforts were undertaken as part of this project off the Mozambique and South African coasts.

a) Bazaruto, Mozambique

In September 2018, a humpback whale photo-identification research survey was conducted east of the Bazaruto Archipelago, Mozambique (between 21° to 22°S). Surveys were conducted where the highest concentration of humpback whales was expected based on previous years' occurrence data (following Findlay *et al.,* 1994). Six days were dedicated to the research activities in the area. The most suitable weather conditions recommended for photo-identification research on humpback whales consist of low sea states (Beaufort scale three or less with windspeeds of <1 to 18 km/h) with good to excellent visibility of the horizon (Hammond *et al.,* 1990). Over the survey period, three vessels were used, including a 6 m rigid inflatable boat (*RIB*) chartered from Marine Megafauna Foundation (*MMF*) (hereafter referred to as *MMF-RIB*), the 72 ft (22 m) research vessel *Angra Pequena* (hereafter referred to as *R/V Angra Pequena*), and the *R/V Angra Pequenas'* 4 m tender (hereafter referred to as *R/V Angra Pequena tender*). The use of these platforms was dependant on their availability and/or sea and weather conditions. All excursions were launched at approximately 07h00 am, whereafter transits were made to offshore locations east of the Bazaruto Archipelago. Searches of humpback whale groups were planned to occur along random tracks between the 20 m and 120 m isobaths (Figure 2.4).

When the *MMF-RIB* was used, beach launches were conducted from the mainland at Vilanculos (21°58'S, 35°18'E), whereafter transits were made to the open ocean east of the Archipelago. The vessel travelled for approximately 30 minutes between the narrow channels and shallow reefs of the Archipelago, whereafter it entered the open ocean between Benguerra and Margaruque Island. Survey duration was measured as the time between the entering/exiting of the survey vessel towards/from the open ocean region between Benguerra and Margaruque Island. The *R/V Angra Pequena* was anchored in the deeper waters of the Archipelago between the east of Santa Carolina Island and the north-west of Bazaruto Island. On each opportunity when this vessel was used, it would travel north-east around the northern edge of Bazaruto Island towards the open ocean on the north-eastern side of the island. Survey duration was measured as the time between the initiation of actively searching for humpback whale groups and the end encounter time of the last group that was photographed. When the *R/V Angra*

Pequena tender was used, launches were made from the *R/V Angra Pequena* while anchored on the eastern side of Bazaruto Island. Survey duration was measured as the time between the launch/return of the vessel from/to the mother vessel.

Similar survey protocols as described in Section 2.2.2 were undertaken with the exception that two photographers were present throughout this survey to collect photo-identification data. One photographer was equipped with a Nikon D3400 camera with a 70-300 mm lens and another with a Canon model 7D with a 100-400 mm lens. As soon as a group of whales were detected, it was approached cautiously, whereafter an assessment of groups' size and composition was performed before any photographing commenced. In cases where a cow/calf pair was encountered, the sighting was recorded, and no attempts were made to photograph the adult to prevent any disturbances to the calf. Both photographers attempted to capture the same individuals for each other group of whales encountered. Unless stated otherwise, surveys continued to approximately 16h00 each day as light conditions or return transit times precluded adequate photography.

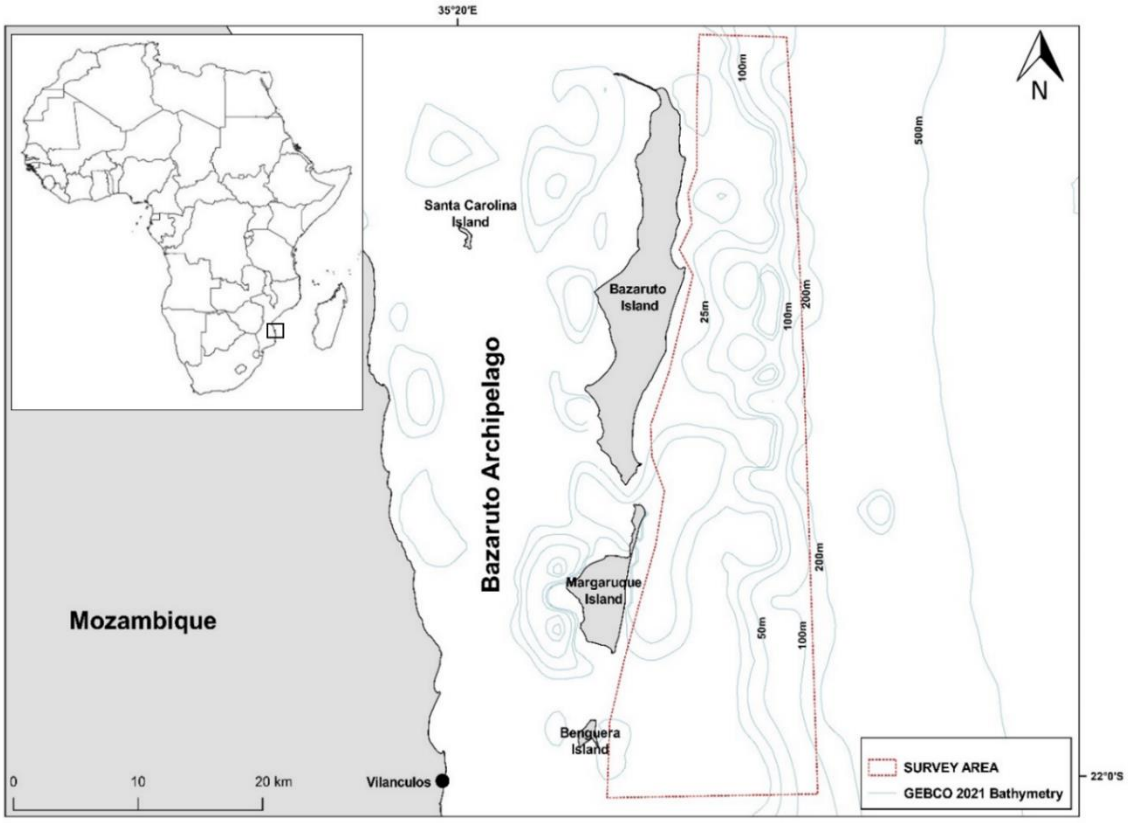


Figure 2.4 A representation of the geographic survey range proposed for the 2018 Bazaruto, Mozambique dedicated humpback whale research survey.

b) Durban, South Africa

In July and August 2019, a dedicated humpback whale photo-identification research survey was conducted off Durban from the research vessel *Phakisa* (hereafter referred to as *R/V Phakisa*). The *R/V Phakisa* is a custom-designed 14.5 meters Legacy-Catamaran. The survey was scheduled over 14 days (the last seven days of July and the first seven days of August).-Each excursion was accompanied by a single photographer equipped with a handheld digital Nikon D3400 camera with a 70-300 mm auto-focus zoom lens and three or more whale observers. Each days' survey started and ended succeeding the entering/exiting of the vessel at the Durban Harbour entrance. A standard survey protocol following a set track was planned to be maintained each day, with the vessel travelling southwards in six offshore-onshore saw tooth legs between seven waypoints (Figure 2.5). Collected data included survey effort, weather, sightings, and all the encounter data associated with the photographed humpback whale groups. As soon as a group of whales were sighted, it was approached cautiously, whereafter an assessment of group size and composition was performed before any photographing commenced. In cases where a cow/calf pair was encountered, the sighting was recorded, and no attempts were made to photograph the adult to prevent any disturbances to the calf. In other encounters, it was aimed to photograph as many individuals in the groups as possible. After working with a group, the vessel returned to the closest waypoint on the track-line, unless another group was spotted in the vicinity, whereafter photographing of the new group commenced. Survey duration was measured for each survey day as the time (decimal hours) between the entering/exiting of the vessel at the Durban Harbour entrance.

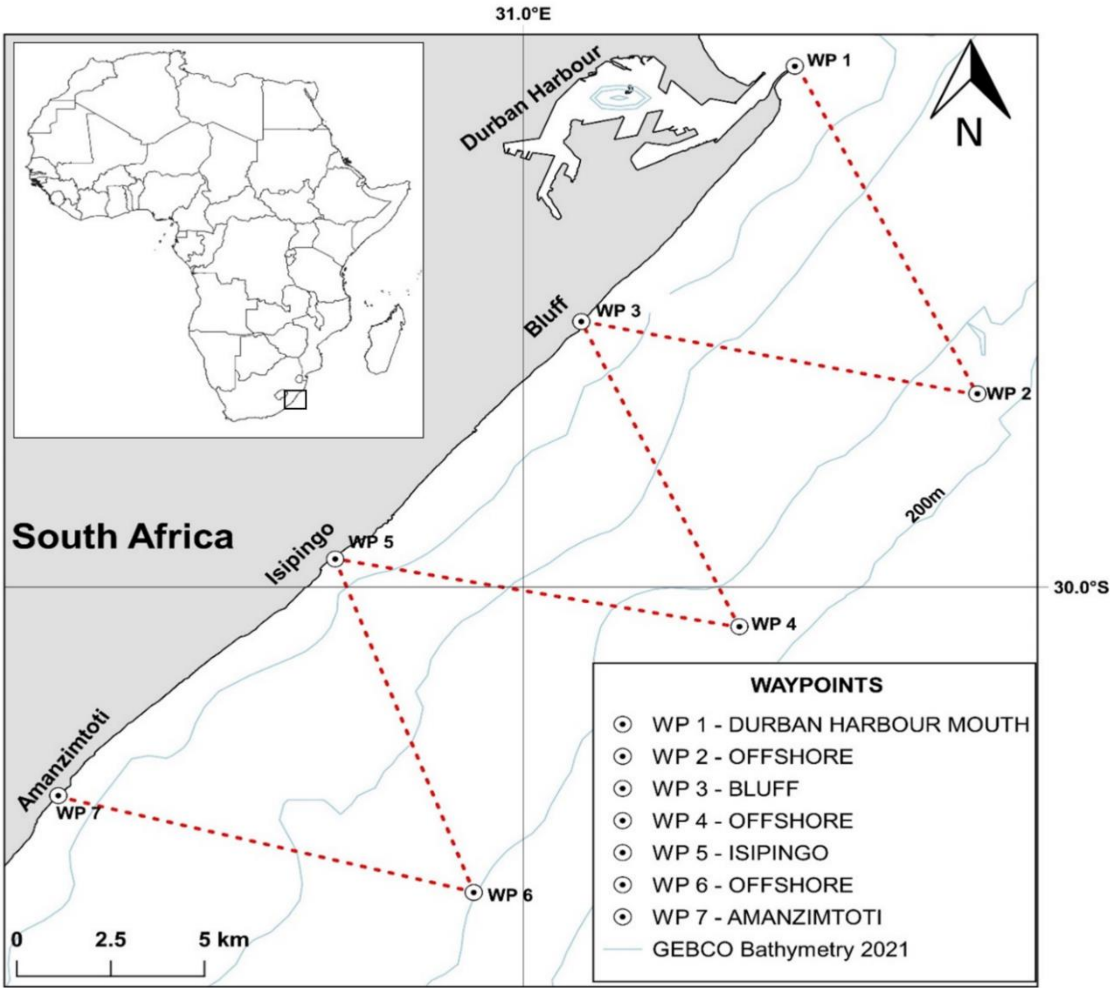


Figure 2.5 A representation of the geographic survey range and track-line/waypoints proposed for the 2019 Durban dedicated research survey.

2.3 Photographic Data Evaluation

As part of the humpback whale C1 sub-stocks photo-identification catalogue development process, several parameters of the historic and new fluke image datasets were evaluated. Unless stated otherwise, the same evaluation procedure was used for both datasets.

For each dataset (historic and new), fluke images were manually organised by data source (for historic fluke images, *e.g.*, DFFE, MRI, CDS), capture year, and survey/project (*e.g.*, Algoa_East Coast HW Cruise; Advantage Tours 2005). For each survey/project, fluke images were further categorised by capture month and day (where possible). In connection to the historic RS fluke images, the capture month/day was extracted from any survey records, notes, or data labels provided, or extracted from the EXIF-data digitally embedded within each image (exclusively when survey records/notes/data labels were unavailable). For each encounter day, fluke images were further sub-categorised into humpback whale groups (alphabetic) and by individual (numerical) (only in cases where survey records provided this information). Where this information was unavailable, fluke images were exclusively categorised by individual. In these cases, individual categorization was achieved through the process of manual visual within-day fluke image matching (all the fluke images collected in a single day was compared to each other).

The success of photo-identification analyses to be conducted as part of this study largely depends on the temporal and spatial metadata associated with the fluke images used. To be able to evaluate the temporal and spatial migration patterns, site fidelity trends and intra-regional migration connections of the C1 sub-stock, the fluke images were required to provide at minimal the capture date (year and month), and location (coastal region and/or encounter GPS coordinates). Subsequently, the availability of temporal and spatial metadata associated with the historic fluke images were evaluated to determine their usability. Considering the historic RS fluke images, spatial metadata was extracted from any additional survey reports or notes provided. For the historic BBWW fluke images, the spatial metadata was inferred from knowledge based on the operators' license region and any additional trip notes supplied by these sources. Regarding the new fluke images, all necessary temporal and spatial metadata was recorded to ensure their usability for further photo-identification analyses.

Photographic quality proved to be an imperative factor influencing the accurate identification of individuals from photographic data (*e.g.,* Friday *et al.,* 2000). Therefore, each historic and new humpback whale fluke image was individually assessed and classified according to photographic quality to determine their usability for further photo-identification analyses. Photographic quality was based on four specific image characteristics relating to the humpback whale flukes (following Friday *et al.,* 2000): (i) clarity (related to the resolution, sharpness and focus of the fluke displayed in the image and how clear the fluke details are presented), (ii) contrast (related to the image colour ratio and brightness level, and how well the different colours on the fluke are distinguishable), (iii) angle/orientation (related to the angle of the fluke displayed in the image in relation to the field plain), and (iv) completeness (related to the proportion of the fluke that is visible in the image). For each fluke image, the four photographic quality characteristics were individually assessed and scored on a scale of 1 to 5 (1 = very poor, 2 = poor, 3 = fair, 4 = good, and 5 = excellent). Examples can be seen in Figure 2.6. Fluke images that scored “1” in any of the photographic quality characteristics were considered "not usable" and discarded. The remaining fluke images (that scored 2 or higher in any of the photographic quality characteristics) were concciderer "useful". For each of the "useful" fluke images, an "overall photographic quality" score was calculated with the following equation:

$$\textbf{overall photographic quality} = \frac{(\textbf{clarity}) + (\textbf{contrast}) + (\textbf{angle}) + (\textbf{completeness})}{\textbf{4}}$$

For each dataset (historic and new), the proportion of fluke images per overall photographic quality score was calculated.

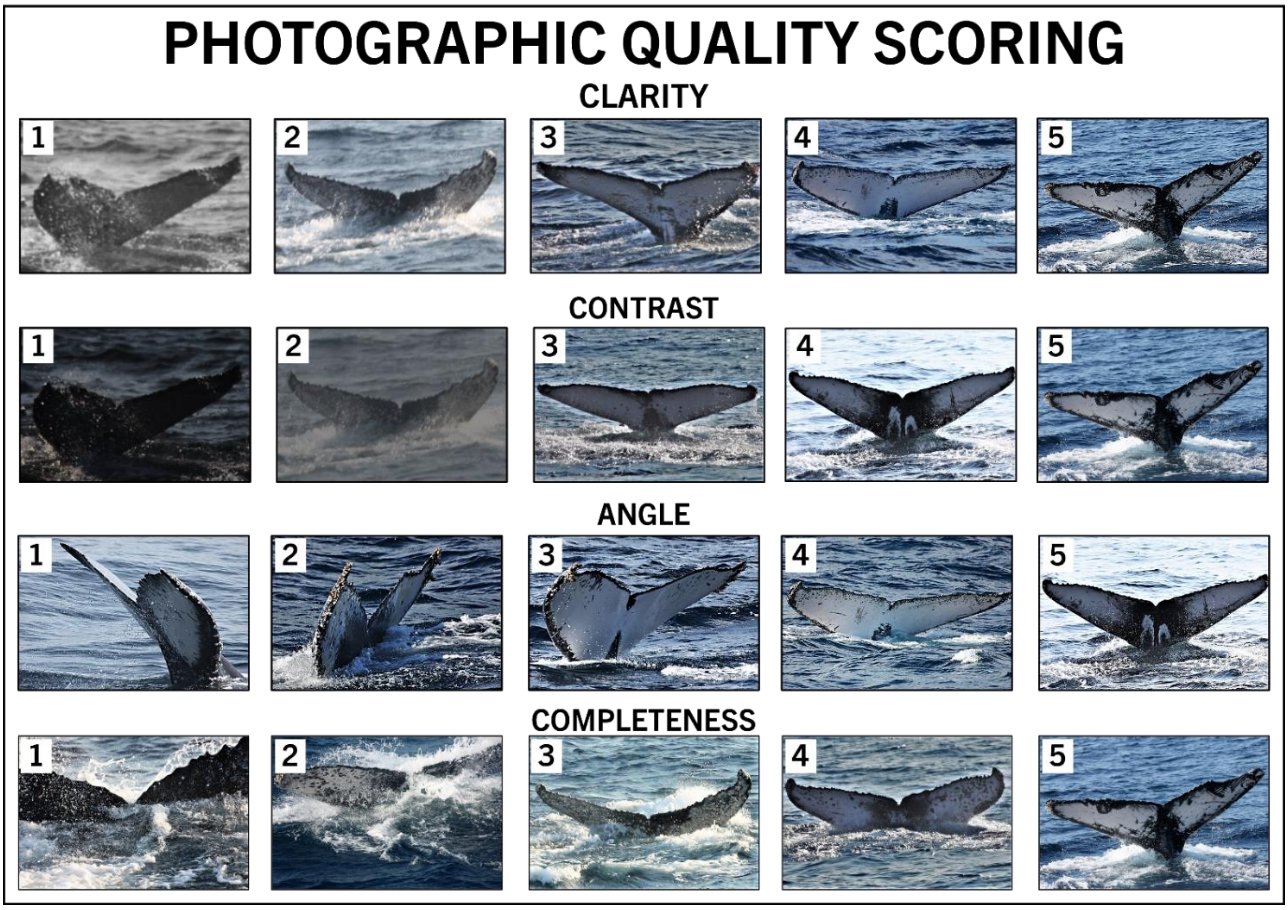


Figure 2.6 Example of humpback whale fluke images scored by photographic quality category on a scale of 1 to 5 (1 = not usable, 2 = poor, 3 = fair, 4 = good, 5 = excellent).

In addition to photographic quality, the accurate identification of individuals from photo-identification data is influenced by the uniqueness (or distinctiveness) of the features or markings used to identify the animals. The term distinctiveness is described as "*the quality of being individual or easy to recognise because of being different from other such things"* (Cambridge University Press, 2021). Several visible fluke features determine the distinctiveness of humpback whale flukes (Mizroch *et al.*, 1990; Friday *et al.*, 2000; Stevick *et al.*, 2001). For each dataset (historic and new), the distinctiveness each individual humpback whale fluke captured was evaluated according to three visual aspects (following Friday *et al.*, 2000): (i) scarification patterns (related to the presence and uniqueness of natural marks or scars caused by predation or injury), (ii) pigmentation patterns (related to the uniqueness of the colouration patterns), and (iii) trailing edge patterns (related to the levels of injury, serration, and smoothness/roughness of the peaks and notches on the edge of the fluke which are especially useful for identifying whales that do not have distinct pigmentation patterns). Each of the three distinctiveness variables evaluated was scored on a scale of 1 to 3 (1 = not unique; 2 = moderately unique; 3 = very unique). Examples of each can be seen in Figure 2.7. The "overall distinctiveness" of each fluke image was calculated as the average score obtained between the three fluke features according to the following equation:

$$\textbf{overall distinctiveness} = \frac{(\textbf{scarification}) + (\textbf{pigmentation}) + (\textbf{trailing edge})}{3}$$

For each dataset (historic and new), the proportion of fluke images per overall fluke distinctiveness score was calculated.

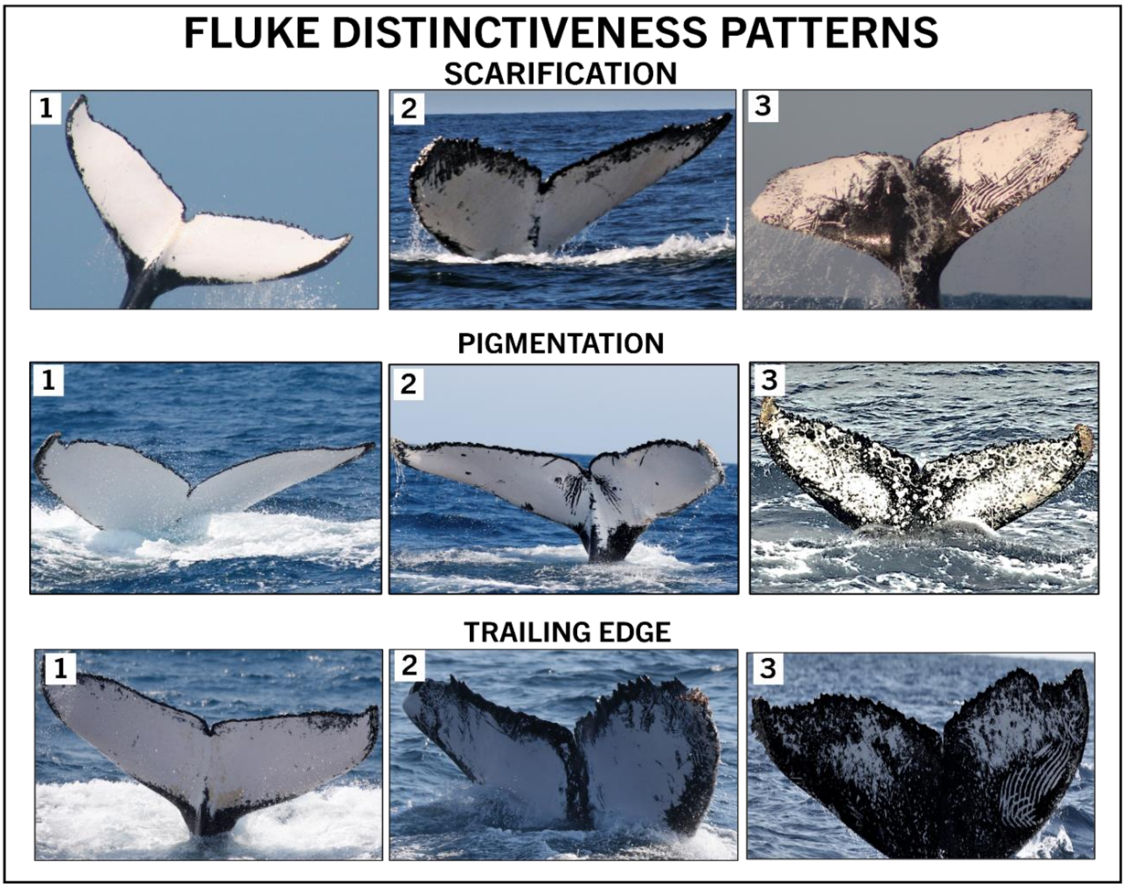


Figure 2.7 Example of humpback whale fluke images scored by fluke distinctiveness category on a scale of 1 to 3 (1 = not distinctive, 2 = moderately distinctive, 3 = very distinctive).

For each dataset (historic and new), the fluke colouration type of each individual humpback whale fluke captured was recorded by scoring the flukes' ventral pigmentation pattern on a scale of 1 to 5, where 1 = 0 - 20% black, 2 = 20 - 40% black, 3 = 40 - 60% black, 4 = 60 - 80% black, and 5 = 80 - 100% black (see Figure 2.8, after Katona *et al.,* 1979 and Carlson *et al.,* 1990).

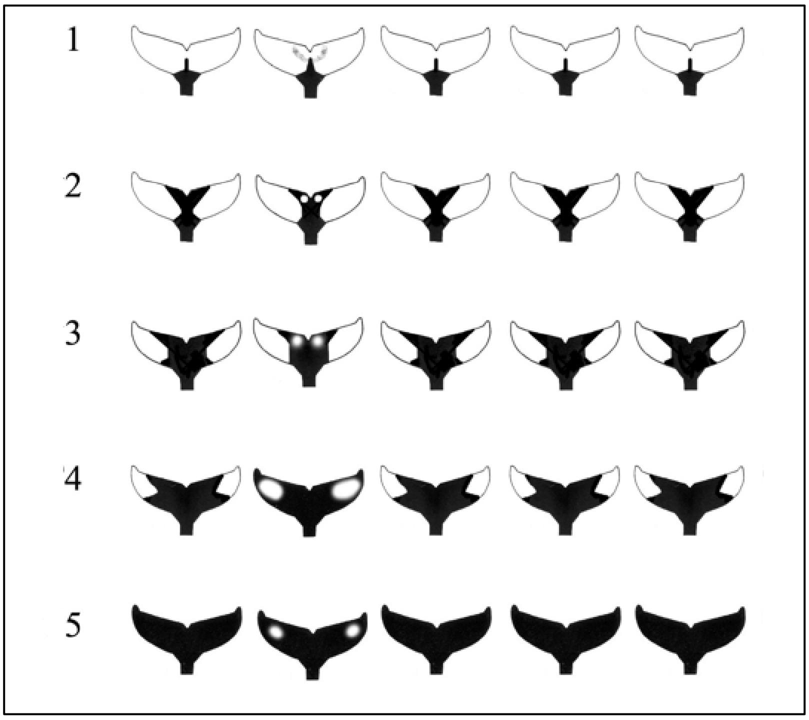


Figure 2.8 Representation of humpback whale fluke colouration types according to the pigmentation pattern on the ventral surface (1 = 0 - 20% black; 2 = 20 - 40% black; 3 = 40 - 60% black; 4 = 0 - 80% black; and 5 = 80 - 100% black) (after Katona *et al.*, 1979 and Carlson *et al.*, 1990).

2.4 Development of the Humpback Whale C1 Sub-Stock Photo-identification Catalogue

All the fluke images (historic and new) that received an overall photographic quality score of 2 (poor) or higher during the photographic data evaluation process were considered "useful" for further analyses. Out of the "useful" collection of fluke images, the absolute best quality image was selected for every single individual humpback whale encounter per day. Each selected fluke image was then duplicated to a folder representing the C1 sub-stock photo-identification catalogue, and received a unique identification code, prescribed by the following information: photographers' identification (initial and surname); survey area; vessel name; survey date (in the format: YYYYMMDD); and individual alphanumeric code, *e.g.,:*

B. TREE_DURBAN_PHAKISA_20190601_A3.

Within this digital catalogue folder, fluke images were grouped by year.

2.5 Photographic Matching

Although it was initially proposed to use the Flukebook application for all matching processes, several limitations prevented the successful use thereof. The online system took a considerable amount of time to analyse only a minor fraction of the images and data. It, therefore, could not limit searchers to specified regions as expected. Furthermore, the system failed to detect any known matches that have previously been confirmed through manual matching procedures. Following the challenges faced using Flukebook, a modified Microsoft *Access* database was developed for this project (by Prof. Ken Findlay, Research Chair: Oceans Economy, Centre for Sustainable Oceans, Cape Peninsula University of Technology). This matching system provided a simple platform for facilitating the viewing and visual matching of humpback whale fluke photo-identification images.

2.5.1 Fluke Image Matching with *Microsoft Access*

The *Microsoft Access* database is initially opened containing no data. To build a digital catalogue within the system, fluke images and data is imported into the system thorough a standardised *Microsoft Office Excel* spreadsheet (The selection of data that is initially imported into the system is dependent on the type of matching that needs to be performed, *e.g.*, *w*ithing-year matching or between-year matching of fluke images; steps for each matching process is described in Sections 2.5.1.1 and 2.5.1.2).

Firstly, the data submitter is required to import an image dataset representing a "Master Catalogue". Subsequently, an additional image dataset is imported as "New" data. For matching to be initiated, the data submitter is required to scroll compare all the images in the New dataset to all the images in the Master Catalogue. Scroll comparison of the fluke images is carried out categorically according to the "fluke type" value (1 to 5; as defined by Katona *et al.,* 1979 and Carlson *et al.,* 1990) assigned to each image in the catalogue , where each fluke image is only compared to other images with the same fluke type value, and a value of 1 lower and 1 higher (*e.g.,* fluke type 1 vs type 1 and 2; fluke type 2 vs type 1, 2 and 3, *etc.*). Such matching subdivision significantly reduces matching time and effort. Matches are identified visually by the data submitter and once identified, written to a "Matched" catalogue within the system. At the end of scrolling through the new dataset, unmatched images can be added to the Master Catalogue, allowing it to be extended as the process progresses. Examples of the system layouts are shown in Figures 2.9 A-D.

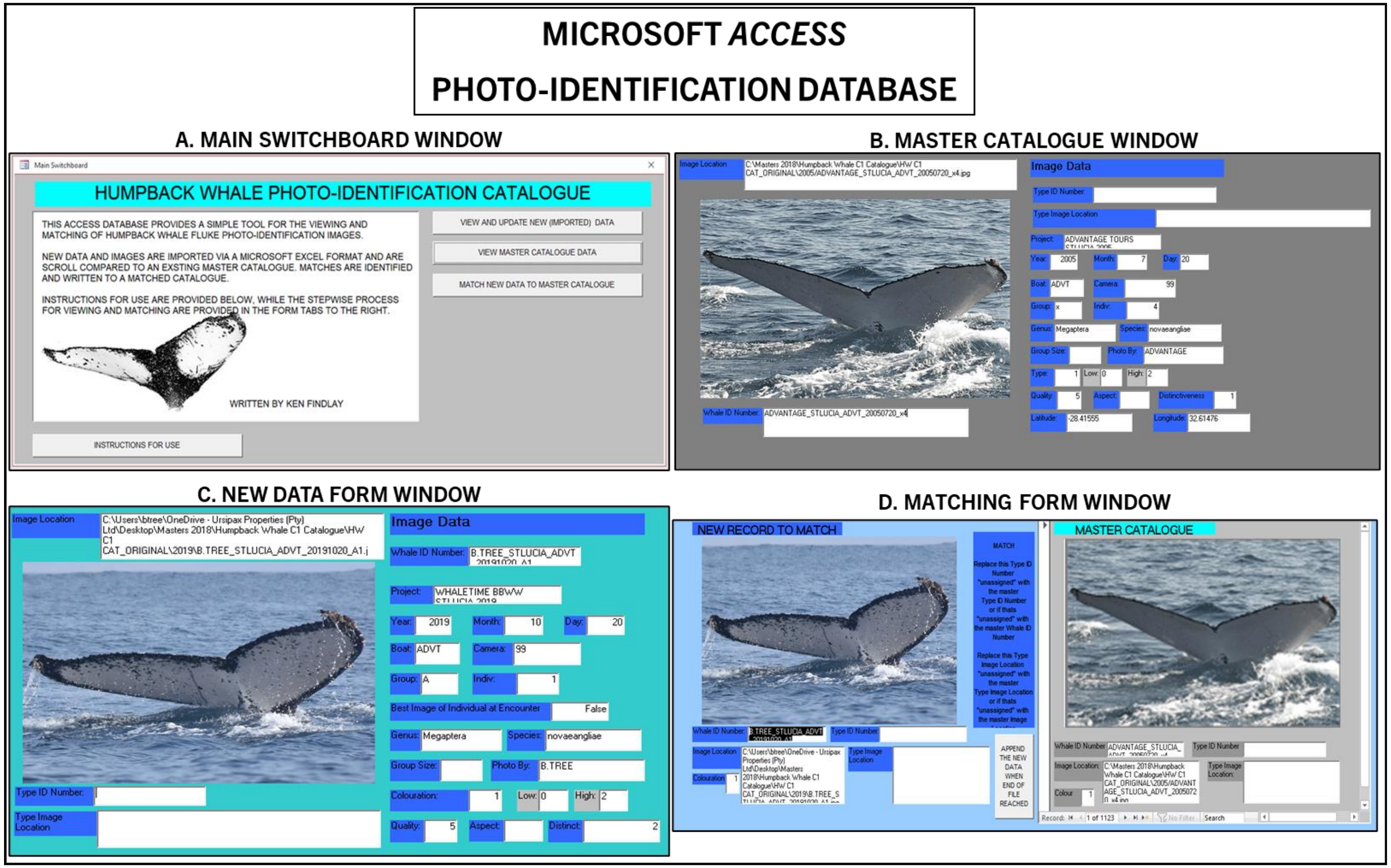


Figure 2.8 A representation of the A) Main switchboard, B) master catalogue, C) new data form, and D) matching form windows displayed in the *Microsoft Access* photo-identification database used for the curation and matching of the humpback whale C1 sub stock photo-identification catalogue.

Within-year and between-year matching of the fluke images were conducted to identify intra- and inter-seasonal migration fidelity, temporal and spatial migration patterns, intra-regional migration connectivity, and overall stock structure of the C1 breeding sub-stock within their migration corridor and breeding grounds.

2.5.1.1 Within-year matching

From the image folder representing the C1 sub-stock photo-identification catalogue, each year's fluke images and associated data (1988-2019) was by turn imported into the *Microsoft Access* database and stored as the Master Catalogue. The same years' data (such as in the Master Catalogue) was then re-imported and subsequently stored as the New data. Within-year matching was performed by comparing the New data fluke images to the Master Catalogue fluke images. A within-year match was obtained when an individual was identified on more than one occasion within the same year (in either the same or in different origin areas). After a single years image matching was completed, the information of the matched images was extracted, and all the imported data was erased from the system. Subsequetly, the next years matching of fluke images continued. After within-year matching was completed for all of the years', all imported data was erased from the system.

The temporal (number of days) and spatial (number of km) distance obtained between subsequent within-year matches was calculated. Such data can be used to calculate valuable parameters such as an individual's approximate travelling speed (kilometres per day). Within-year match results may also reveal important information such as an individuals travelled direction (north or south), intra-seasonal site fidelity trends or regional occupancy, migration routes and migration connectivity.

2.5.1.2 Between-year matching

Within the *Microsoft Access* system (now cotnaining no data), the first available years' data in the catalogue (1988) was imported as the Master Catalogue to initiate the between-year matching process. The following years' data (1989) was then imported into the database as New data, whereafter matching against the Master Catalogue was conducted. After all of the New data fluke images were compared to the Master Catalogue, it was appended to the Master Catalogue. Subsequently, the New data platform was reseset, and the following years' data (*e.g.*, 1990) were then imported into the *Access* database as the next set of New data, whereafter comparisons against the Master Catalogue commenced. This process was repeated until all years of images were imported and matched. A between-year match was obtained when an individual was identified in one or more different calendar years in either the same or different areas.

All the between-year matches were evaluated in terms of the temporal (number of years) and spatial (number of km) distribution between subsequent matches. The temporal and spatial distribution obtained between subsequent between-year matches provides information on the inter-seasonal site fidelity trends, migration routes and migration connectivity of the population.

2.6 Characteristics of individual humpback whales identified within the C1 sub-stock

Following the within-year and between-year matching process, the number of individual humpback whales identified in the C1 sub-stock photo-identification catalogue was calculated using the following equation:

$$\textbf{Total individuals} = \sum \textbf{fluke images in the catalogue} - [\sum \textbf{within-year matches} + \sum \textbf{between-year matches}]$$

Additional knowledge on the structure of the C1 sub-stock was obtained from information on the colouration/pigmentation type and distinctiveness of the flukes pertaining to the individuals identified in the curated photo-identification catalogue. For each photographic data collection region, individual whales identified within each were categorised according to their fluke colouration type and fluke distinctiveness, respectively, to evaluate levels of geographic sub-structure within the C1 sub-stock.

2.7 Data Analyses

For all statistical data analyses, *IBM SPSS Statistics 27* software was used.

2.7.1 The new dataset

2.7.1.1 Opportunistic surveys on commercial BBWW platforms (Durban and St Lucia, South Africa)

For each year, the survey effort was calculated per month as the sum of the survey durations (decimal hours) calculated for the excursions accompanied within that month.

2.7.1.2 Dedicated research surveys (Bazaruto, Mozambique and Durban, South Africa)

For each survey region:

i. the locations (GPS coordinates) where humpback whale groups were encountered per survey day was illustrated;

ii. the humpback whale groups encountered over the survey period was described according to the number of individuals and the social organisation classes represented in each. The social organisation classes included the following seven categories of whale groups (following Morete *et al.*, 2007): single adult (1AD); two adults (DYADS); three adults (TRIO); more than three adults (TRIO+); mother and calf (MOC); a mother, calf and one escort (MOCE); a mother, calf and more than one escort (MOCE+). Escorts are adult male whales accompanying mother/calf groups (Glockner-Ferrari & Ferrari, 1985; Medrano *et al.*, 1994; Morete *et al.*, 2007).

iii. survey effort was measured for each day as the total survey duration (decimal hours) recorded for that day.

iv. a group encounter rate (*GER*) was calculated for each survey day according to the following equation:

$$\boldsymbol{GER} = \frac{\textbf{number of groups encountered}}{\textbf{survey effort (decimal hours)}}$$

v. a unique fluke image collection success rate (%) (*UF*) was calculated for each survey day according to the following equation:

$$\boldsymbol{UF} = \frac{\textbf{number of individual flukes photographed}}{\textbf{number of individual whales encountered}} \times \mathbf{100}$$

2.7.2 The C1 sub-stock photo-identification catalogue

The proportion of fluke images in the catalogue was depicted for each:

i. overall photographic quality category;

ii. overall fluke distinctiveness category; and

iii. photographic data collection region.

Chi square analyses were performed to determine if there were significant differences in the proportions of fluke images in the catalogue between the overall photographic quality categories.

The number of fluke images collected per month was presented for each year's data and each photographic data collection region, respectively. However, temporal and spatial seasonal migration aspects of the C1 humpback whale sub-stock could not accurately be evaluated from this data since no effort data was available for the historic fluke image dataset to support such investigation. Due to the limitations presented by the lack of effort data, seasonality trends could not be statistically evaluated.

2.7.3 Photographic matching

2.7.3.1 Within-year matches

The occurance interval of all the within-year matched individual humpback whales was measured as the maximum resighting interval of the whale, which was calculated as the time interval (number of days) between the first encounter date (first fluke images capture date of the individual) and the last encounter date (last fluke image capture date of the individual) in a calendar year. The sub-stock's levels of short-term site fidelity to the south-eastern African coast was assessed by analysing the percentage of within-year matches encountered and re-encountered within the same region. Information on the intra-seasonal migration linkages and pathways displayed by the sub-stock was determined as the percentage of matches obtained between two pairs of regions.

2.7.3.2 Between-year matches

A re-encounter rate (*RER*) (%) was calculated for each year represented in the catalogue that contained between-year matched fluke images, as the proportion of between-year re-encounter fluke images per total number of fluke images within the same year, according to the following equation:

$$\boldsymbol{RER} = \frac{\textbf{number of re} - \textbf{encounter fluke images}}{\textbf{total number of fluke images}} \times \mathbf{100}$$

The sub-stock's levels of long term site fidelity to the south-eastern African coast was determined by evaluating:

i. the maximum duration (years) between the encounter and re-encounter dates of the between-year matched individuals; and

ii. the percentage of between-year matches obtained with the same encounter and re-encounter region.

Information on the long-term sub-region migration connectivity and migration pathways followed by the humpback whale C1 sub-stock was determined as the percentage of between-year matches obtained between pairs of regions.

2.8 Characteristics of individual humpback whale flukes identified within the C1 sub-stock

For each photographic data collection region, chi-square analyses was conducted to determine whether there was a significant difference in:

i. the proportion of individual whales with different fluke colouration types; and

ii. the proportion of individual whales with different fluke distinctiveness categories.

For each fluke colouration type, a chi-square analysis was conducted to determine whether there was a significant difference in the proportion of individuals with the associated fluke type between regions (*e.g.,* proportions of individuals with fluke type 1: SC vs ES vs EN vs MS vs MC; *etc.*). The same chi-square analysis was conducted for each fluke distinctiveness category (*e.g.,* proportions of individuals with non-unique flukes: SC vs ES vs EN vs MS vs MC; *etc*.).

CHAPTER 3 RESULTS

3.1 Humpback Whale Photo-identification Data Collection

3.1.1 Opportunistic surveys on commercial BBWW

Table 3.1 illustrates a summary of information obtained from the commercial BBWW surveys conducted off Durban and St Lucia, South Africa. Eleven trips were accompanied in 2018, for a total survey duration of 17.79 hours), and five trips in 2019 (for a total survey duration of 8.34 hours) off the coast of Durban (Table 3.1). Unique fluke images were collected for eight humpback whales encountered during these surveys (three in 2018 and five in 2019). Eight whale watch trips (for a total survey duration of 16.18 hours) were undertaken during October off the coast of St Lucia, where unique fluke images were collected for five humpback whales encountered over the survey period.

Table 3.1 A summary of information obtained from the commercial BBWW opportunistic surveys conducted off Durban (2018 and 2019) and St Lucia (2019) (sd = standard deviation).

SURVEY REGION	SURVEY YEAR	SURVEY MONTH	NUMBER OF TRIPS	TOTAL SURVEY EFFORT (DECIMAL HOURS)	MEAN (sd) SURVEY EFFORT PER TRIP (DECIMAL HOURS)	NUMBER OF UNIQUE FLUKES CAPTURED
DURBAN	2018	JULY	1	1.48	-	0
		AUGUST	6	9.52	1.59 (0.05)	2
		SEPTEMBER	3	5.22	1.74 (0.29)	0
		OCTOBER	1	1.57	-	1
	TOTAL	**-**	**11**	**17.79**	**-**	**3**
	2019	JULY	3	5.17	1.7 (0.15)	4
		AUGUST	2	3.17	1.6 (0.03)	1
	TOTAL	**-**	**5**	**8.34**	**-**	**5**
ST LUCIA	2019	OCTOBER	8	16.18	2.0 (0.08)	3
	TOTAL	**-**	**8**	**16.18**	**-**	**3**

3.1.2 Dedicated research surveys

3.1.2.1 Bazaruto, Mozambique

Six days were dedicated in September 2018 to conduct photo-identification research on humpback whales off the Bazaruto Archipelago, Mozambique; however, only four days provided weather conditions suitable for research. The weather and sighting conditions were comparable across the survey days. Figure 3.1 illustrates the survey area and locations where humpback whale groups were encountered during the survey. Twenty-one humpback whale groups were encountered over the entire survey period, where all (excluding the mother/calf pairs) were travelling in a southern direction.

The survey was initially planned to be conducted between the 20 m and 120 m isobaths to the east of the Bazaruto Archipelago Islands; however, the range of the survey area was extended to the 500 m isobath (some 20 km offshore of the islands) when the *R/V Angra Pequena* was used on 14 September.

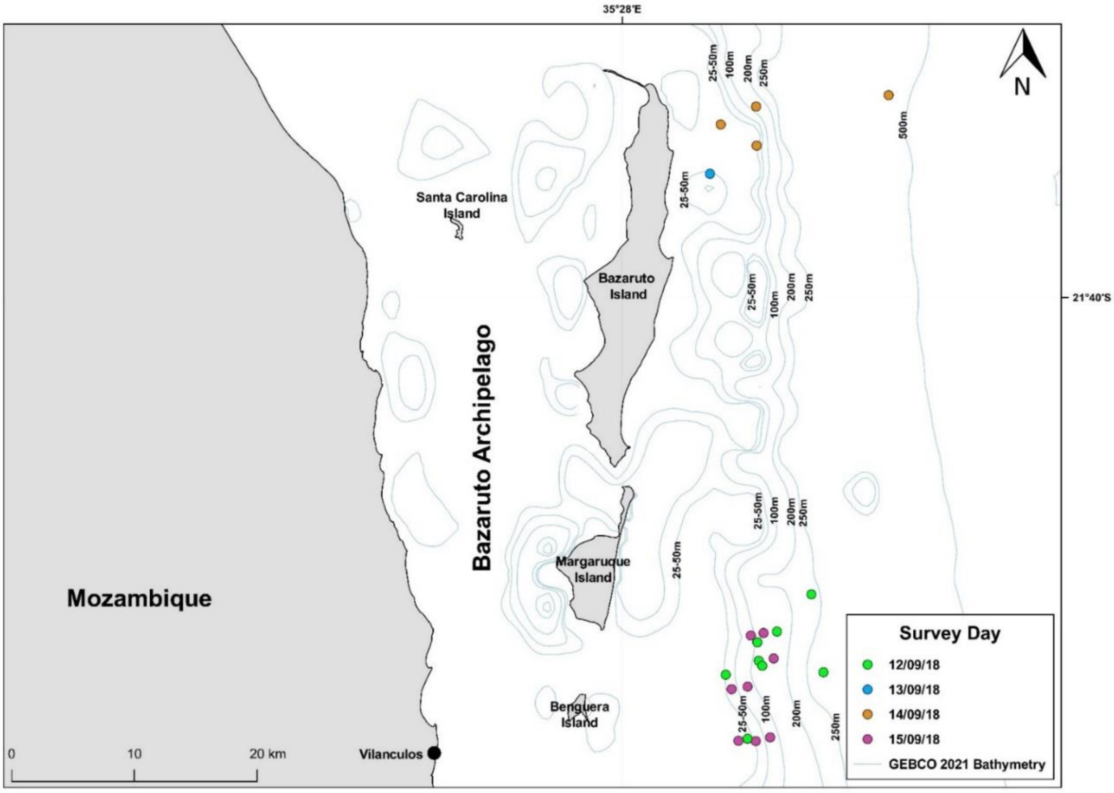


Figure 3.1 A map illustrating the survey area and localities of humpback whale groups encountered daily during the 2018 dedicated research off Bazaruto.

Figure 3.2 shows the frequencies of the sizes and social groupings of the humpback whale groups encountered over the 2018 Bazaruto dedicated research survey period. Humpback whale group sizes ranged from one to seven individuals, with an overall mean group size of 2.5 (sd = 1.5) individuals for the entire survey period. Groups comprising two individuals were most common (8 groups), of which two were MOC, and six were DYADS. Five 1AD groups were encountered. Of the 5 groups comprising three individuals, three were TRIO groups, and two were MOCE groups. Three groups comprised four or more individuals, one MOCE+ group, and two TRIO+ groups.

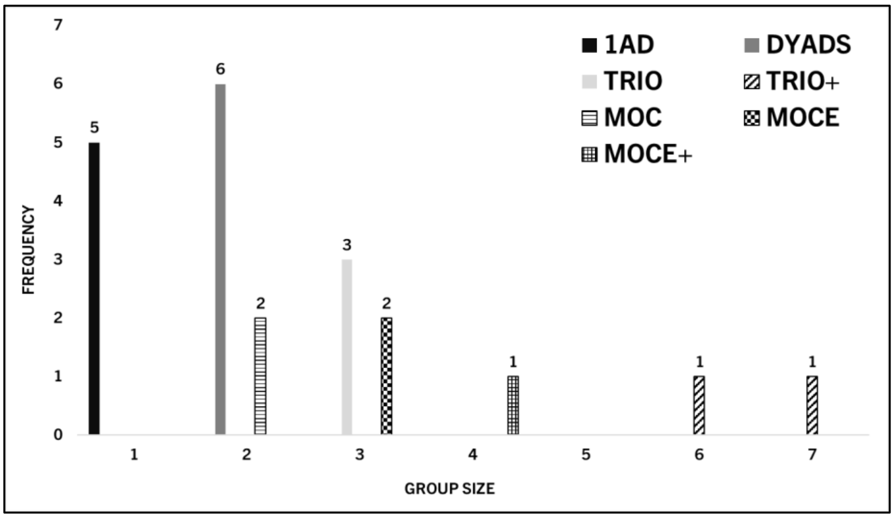


Figure 3.2 The frequency of the sizes and social groupings of humpback whale groups encountered during the 2018 Bazaruto dedicated research survey period (1AD = 1 adult; DYADS = two adults; TRIO = three adults; TRIO+ = more than three adults; MOC = mother/calf pair; MOCE = mother/calf pair and one escort; MOCE+ = mother/calf pair and more than one escort).

Table 3.2 provides a summary of information obtained during the 2018 Bazaruto dedicated research survey. Similar results were obtained on 12, and 15 September when the *MMF-RIB* was used, during which the highest effort was performed (6.0 h and 4.8 h, respectively), and the highest number of humpback whale groups were encountered (eight groups on each of these days). The *GER*'s observed on these days (1.3 and 1.7 groups per hour, respectively) were comparable and the highest for the survey period. Relatively high numbers of individuals were encountered on these days (17 and 20 individuals, respectively), where mean group sizes of 2.1 (sd = 0.8) and 2.5 (sd = 0.7) individuals were observed, respectively. Fluke images were successfully collected for 10 (*UF* = 59%) and 12 (*UF* = 60%) of the individuals encountered on these days, respectively.

The least effort was performed on 13 September (1.75 h) when the *R/V Angra Pequena tender* was used, and one individual was encountered, reflecting the low *GER* attained (0.6 groups per hour). A fluke image was successfully collected for the individual whale encountered on this day (*UF* = 100%).

When the *R/V Angra Pequena* was used on 14 September, the survey effort was moderate (3.43 h), during which the second highest number of groups were encountered (four groups), and a high *GER* was also attained (1.2 groups per hour). Relative high numbers of individuals were also encountered on this day (n = 15), irrespective of the lower numbers of groups encountered compared to 12 and 15 September. The mean group size observed on this day was 3.8 (sd =

2.8) individuals. Fluke images were collected for all the individuals encountered on this day (*UF* = 100%).

The average *UF* for the entire four-day survey was 71.7%, where unique (individual) fluke images were collected for 38 of the 53 individuals encountered.

Table 3.2 A summary of information obtained from the 2018 Bazaruto dedicated research survey (sd = standard deviation.

SURVEY DATE	SURVEY VESSEL	SURVEY EFFORT (DECIMAL HOURS)	NUMBER OF GROUPS ENCOUNTERED	GROUP ENCOUNTER RATE (GER)	MEAN (sd) GROUPS SIZE	NUMBER OF INDIVIDUALS ENCOUNTERED	NUMBER OF UNIQUE (INDIVIDUAL) FLUKE IMAGES COLLECTED	UNIQUE FLUKE IMAGE COLLECTION SUCCESS RATE (%)
12/09/18	*MMF-RIB*	6.0	8	1.3	2.1 (0.8)	17	10	59
13/09/18	*R/V Angra Pequena tender*	1.75	1	0.6	1.0 (0.0)	1	1	100
14/09/18	*R/V Angra Pequena*	3.43	4	1.2	3.8 (2.8)	15	15	100
15/09/18	*MMF-RIB*	4.8	8	1.7	2.5 (0.7)	20	12	60
TOTAL	-	**15.98**	**21**	-	**2.5 (1.5)**	**53**	**38**	-

3.1.2.2 Durban, South Africa

The *R/V Phakisa* was available for 14-days (the last seven days in July and the first seven days in August) in 2019 for conducting photo-identification research off Durban; however, only five days provided weather conditions suitable for research (4 days in July and one day in August). Figure 3.3 illustrates the survey area and locations where humpback whale groups were encountered during the survey. Thirty-five humpback whale groups were encountered between the 20 m and 200 m isobaths (between 1 and 17 km offshore), all travelling in a northern direction.

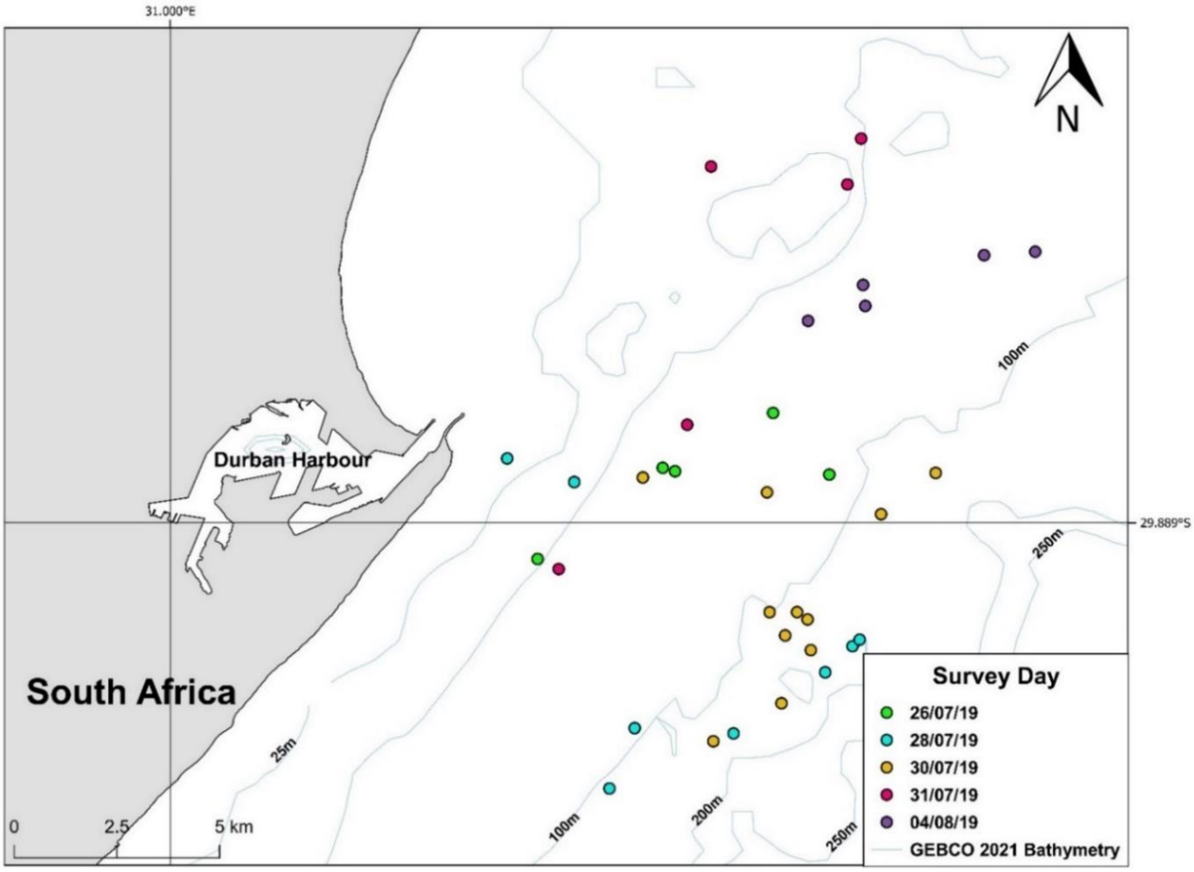


Figure 3.3 A map illustrating the survey area and localities of humpback whale groups encountered daily during the 2019 dedicated research off Durban.

The frequencies of sizes and social groupings of humpback whale groups encountered over the 2019 Durban dedicated research survey period are presented in Figure 3.4. The humpback whale group sizes ranged from one to six individuals, with an overall mean group size of 2.1 (sd = 1.1) individuals for the survey period. Groups comprising two individuals were the most common (of which all were DYADS), followed by groups comprising one individual. Two groups comprising three individuals each (both TRIO) were encountered. Three groups had four or more individuals (one MOCE+ group, and two TRIO+ groups).

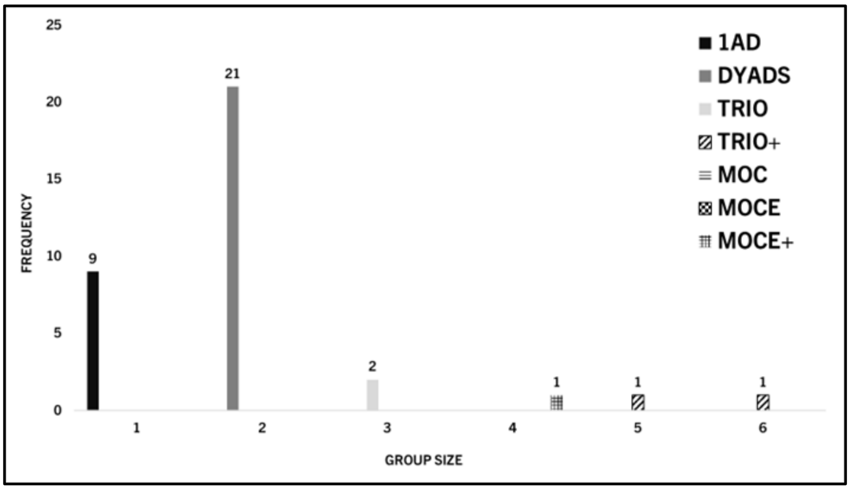


Figure 3.4 The frequency of the sizes and social groupings of humpback whale group encountered during the 2019 Durban dedicated research survey period (1AD = 1 adult; DYADS = two adults; TRIO = three adults; TRIO+ = more than three adults; MOCE+ = mother/calf pair and more than one escort).

A summary of information gathered during the 2019 Durban dedicated research survey is shown in Table 3.3. The lowest effort in terms of time was performed on 26 July (2.88 h); however, a relatively high number of humpback whale groups were encountered on this day (n = 5), resulting in the high *GER* of 1.7 groups per hour attained.

Equal efforts were performed on 28 and 31 July (4.50 h), however, a higher number of groups were encountered on 28 July (n = 9) compared to 31 July (n = 5). A *GER* of 2.0 and 1.1 groups per hour was attained on these days, respectively. The highest effort performed on 30 July and 4 August was comparable (5.8 h and 5.3 h). *GER* of 1.9 and 0.8 groups per hour was attained on these days, respectively.

Reflective of the similar number of groups encountered on 26 and 31 July and 4 August, comparable numbers of individuals were encountered (n = 8; n = 13; and n = 14, respectively). Mean group sizes of 1.6 (sd = 0.5), 2.8 (sd = 0.7) and 2.6 (sd = 1.2) were observed on these days, respectively. Relatively high numbers of individuals were also encountered on 28 July (n = 17) and 30 July (n = 20), where mean group sizes of 1.9 (sd = 1.5) and 1.8 (sd = 0.4) individuals was observed.

Considering the success of each day in obtaining unique (individual) fluke images, low *UF's* were obtained on 26, 28 and 30 July, when fluke images were collected for 13% (n = 1), 24% (n = 4) and 10% (n = 2) of the individuals encountered, respectively. Much higher *UF*'s were obtained on 31 July and 4 August, when fluke images were successfully collected for 57% (n = 8) and 77% (n = 10) of the individuals encountered, respectively. Overall, the average *UF* for the entire five-day survey was 35%, when unique (individual) fluke images were collected for 25 of the 72 individuals encountered.

Table 3.3 A summary of the information obtained from the 2019 Durban dedicated research survey (sd = standard deviation).

SURVEY DATE	SURVEY EFFORT (DECIMAL HOURS)	NUMBER OF GROUPS ENCOUNTERED	GROUP ENCOUNTER RATE (GER)	MEAN (sd) GROUPS SIZE	NUMBER OF INDIVIDUALS ENCOUNTERED	NUMBER OF UNIQUE (INDIVIDUAL) FLUKE IMAGES COLLECTED	UNIQUE (INDIVIDUAL) FLUKE IMAGE COLLECTION SUCCESS RATE (%)
26/07/19	2.88	5	1.7	1.6 (0.5)	8	1	13
28/07/19	4.5	9	2.0	1.9 (1.5)	17	4	24
30/07/19	5.8	11	1.9	1.8 (0.4)	20	2	10
31/07/19	4.5	5	1.1	2.8 (0.7)	14	8	57
04/08/19	5.3	5	0.9	2.6 (1.2)	13	10	77
TOTAL	**23.03**	**35**	**-**	**2.1 (1.1)**	**72**	**25**	**-**

3.2 Evaluation of the Photo-identification Data

The availability of temporal and spatial metadata associated with the historic fluke images is displayed in Table 3.4 and 3.5, respectively. Of the DFFE-BBWW fluke images, 98.4% had the encounter year, month, and day available, while 0.7% had only the encounter year and month available, and 1% had only the encounter year available. All the DFFE-RS and CDS fluke images had the encounter year, month, and day available. Of the MRI fluke images, 57.6% had only the encounter year information available, 40% (n = 34) had the encounter year and month available, and only 2.6% (n = 2) had the encounter year, month, and day available. All the additional commercial BBWW fluke images had the encounter year, month, and day available. The encounter GPS location (latitude and longitude) was unknown for all of the historic fluke images, however; information pertaining to the encounter coastal region and survey region/licence area was known for all.

No metadata was lacking for any of the new dataset fluke images.

Table 3.4 The availability of temporal metadata associated with the historic fluke images by contributing source, sub-divided by the method of data collection (DFFE = Department of Forestry, Fisheries, and the Environment; CDS = Centre for Dolphin Studies; MRI = Mammal Research Institute; ADDITIONAL = commercial BBWW; BBWW = boat-based whale watching; RS = research survey).

DATA SOURCE	YEAR/ MONTH/ DAY	YEAR/ MONTH (ONLY)	YEAR (ONLY)	TOTAL
DFFE-BBWW	3,181	22	31	3,234
DFFE-RS	773	-	-	773
CDS-RS	307	-	-	307
MRI-RS	2	34	49	85
ADDITIONAL-BBWW	58	-	-	58
TOTAL	4,321	56	80	4,457

Table 3.5 The availability of spatial metadata associated with the historic fluke images by contributing source, sub-divided by the method of data collection (DFFE = Department of Forestry, Fisheries, and the Environment; CDS = Centre for Dolphin Studies; MRI = Mammal Research Institute; ADDITIONAL = commercial BBWW; BBWW = boat-based whale watching; RS = research survey).

DATA SOURCE	COASTAL REGION (Y=YES; N=NO)	SURVEY REGION OR LICENCE REGION (Y=YES; N=NO)	LATITUDE/LONGITUDE UNKNOWN (NUMBER OF IMAGES)
DFFE-BBWW	Y	Y	3,234
DFFE-RS	Y	Y	773
CDS-RS	Y	Y	307
MRI-RS	Y	Y	85
ADDITIONAL-BBWW	Y	Y	58
TOTAL	-	-	4,457

Table 3.6 and 3.7 displays the number of historic and new fluke images per coastal photographic data collection region, respectively. All the DFFE-BBWW fluke images were collected within the EN region. The DFFE-RS fluke images were collected in most regions along the C1 migration corridor and breeding ground, of which three regions are in South Africa (SC, ES, EN), and one region is in Mozambique (MC). The CDS fluke images were collected within three regions, of which one region is in South Africa (SC), and two regions are in Mozambique (MS, MC). The MRI fluke images were collected in Mozambique within the MC region, and South Africa within the EN region. All the additional commercial BBWW fluke images were collected in the SC region.

The largest component of the new fluke images was collected during the Bazaruto dedicated research survey in Mozambique within the MC region (51.2%), followed by fluke images collected during the Durban dedicated research survey in South Africa, within the ES region (33.8) (Table 3.7). All the fluke images collected during the 2018 BBWW opportunistic survey were collected within the ES region, while fluke images from the 2019 opportunistic surveys were collected within the ES and EN regions.

Table 3.6 The number of historic fluke images per photographic data collection coastal region by contributing data source, sub-divided by the method of data collection (DFFE = Department of Forestry, Fisheries, and the Environment; CDS = Centre for Dolphin Studies; MRI = Mammal Research Institute; ADDITIONAL = commercial BBWW; BBWW = boat-based whale watching; RS = research survey; SC = south coast; ES = south-eastern; EN = north-eastern; MS = southern Mozambique; MC = central Mozambique).

DATA SOURCE	COASTAL REGION					TOTAL
	SC	ES	EN	MS	MC	
DFFE-BBWW	-	-	3,234	-	-	**3,234**
DFFE-RS	245	165	235	-	128	**773**
CDS-RS	161	-	-	40	106	**307**
MRI-RS	-	-	34	-	51	**85**
ADDITIONAL-BBWW	58	-	-	-	-	**58**
TOTAL	**464**	**165**	**3,503**	**40**	**285**	**4,457**

Table 3.7 The number of fluke images in the new dataset per photographic data collection coastal region by survey (BBWW = boat-based whale watching; SC = south coast; ES = south-eastern; EN = north-eastern; MS = southern Mozambique; MC = central Mozambique).

DATA SOURCE	COASTAL REGION					TOTAL
	SC	ES	EN	MS	MC	
2018 BBWW OPPORTUNISTIC SURVEYS	-	3	-	-	-	**3**
2019 BBWW OPPORTUNISTIC SURVEYS	-	5	3	-	-	**8**
2018 BAZARUTO DEDICATED SURVEY	-	-	-	-	38	**38**
2019 DURBAN DEDICATED SURVEY	-	25	-	-	-	**25**
TOTAL		**33**	**3**		**38**	**74**

For each dataset (historic and new), the proportion of fluke images per overall photographic quality score for each data collection method used (A = BBWW and B = RS) is illustrated in Figure 3.5. The largest component of the historic fluke images was of usable quality for photo-identification purposes (99%). Of the historic BBWW fluke images, the largest component of images was of good quality, followed by fair and excellent quality images. A small component of these images was of poor quality. Of the historic RS fluke images, the largest component of images was of fair and good quality, followed by relatively lower proportions of images of excellent and poor quality.

All the newly collected fluke images were of usable quality for photo-identification analyses. The largest component of the new BBWW fluke images were of excellent quality, followed by fair and good quality images. Of the new RS fluke images collected, the largest component was of excellent and good quality, followed lower proportions of fair and poor-quality images.

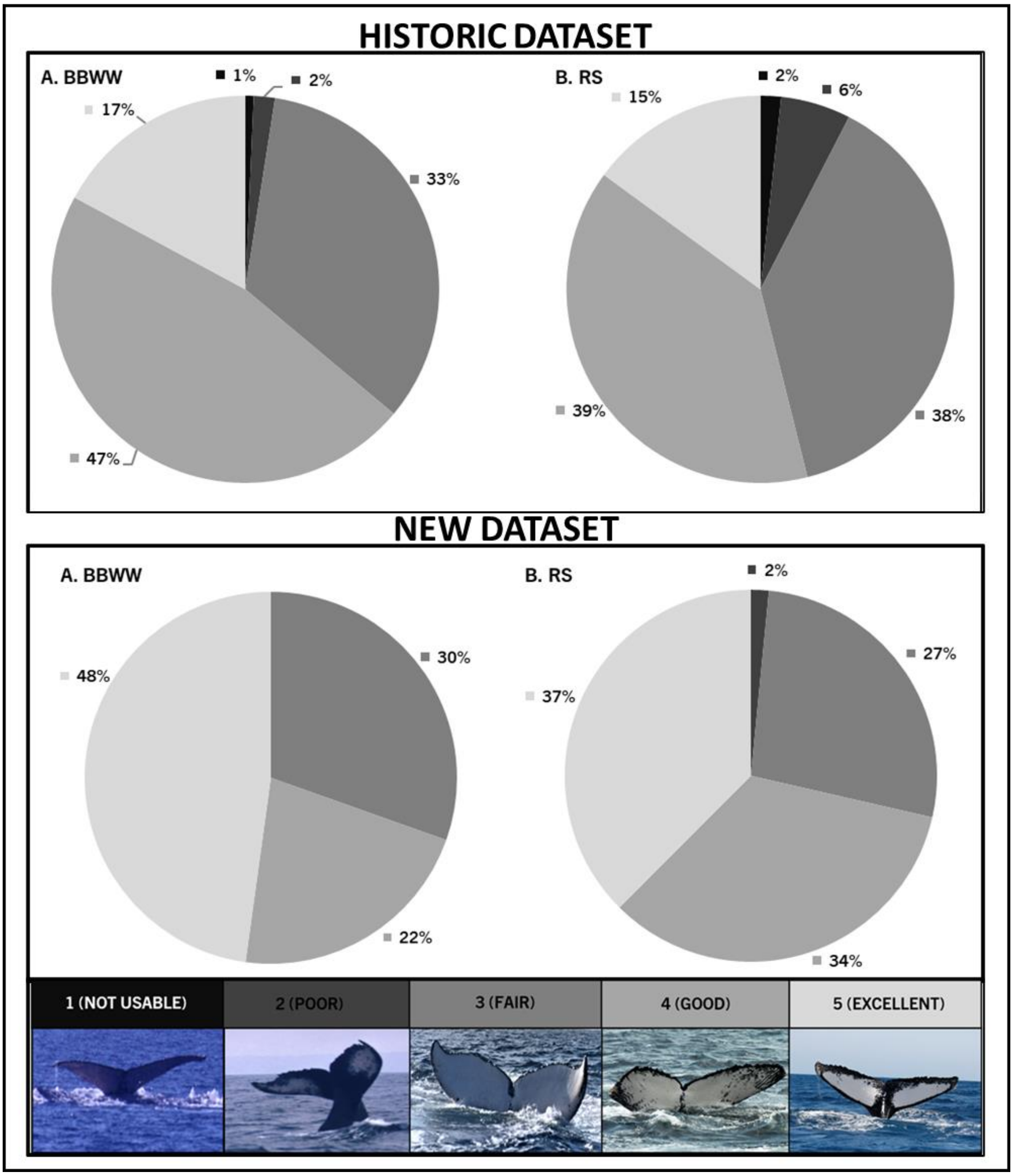


Figure 3.5 The proportion of fluke images per overall photographic quality category (example pictures below), sub-divided by the method of data collection (A = boat-based whale watching (BBWW), and B = dedicated research survey (RS) efforts) by dataset (historic and new).

3.3 A Description and Summary of the Humpback Whale C1 Sub-Stock Photo-identification Catalogue

From the historic and new datasets, 1,805 fluke images were selected for the humpback whale C1 sub-stock photo-identification catalogue; 1,731 (96%) from the historic dataset and 74 (4%) from the new dataset.

The number of fluke images (n) in the catalogue per overall photographic quality category for each fluke distinctiveness category is shown in Figure 3.6. Considering the fluke images that are not distinctive (distinctiveness category 1) (n = 701), the largest proportion are of fair quality (52.4%), followed by poor (35%), good (11.7%), and excellent (1%) quality images. Of the 741 moderately distinctive (distinctiveness category 2) fluke images, the largest proportion are of fair quality (59.1%), followed by poor (30.6%), good (7.6%), and excellent (2.7%) quality images. Of the 363 very distinctive (distinctiveness category 3) fluke images, the largest proportion are of fair quality (61.2%), followed by poor (20.4%), good (16.5%), and excellent (1.9%) quality images. Chi-square analyses revealed that there were significant differences in the proportions of fluke images in the catalogue amongst the fluke distinctiveness categories ($\chi^2 = 8.06$; $p = 0.018$), where the proportions of fluke images considered as not distinctive and moderately distinctive were significantly higher than that of very distinctive flukes, respectively (not distinctive vs very distinctive: $\chi^2 = 6.119$; $p = 0.013$ and moderately distinctive vs very distinctive: $\chi^2 = 7.23$; $p = 0.007$).

Overall, there was a significant difference in the proportions of fluke images in the catalogue amongst the overall photographic quality categories ($\chi^2 = 70.96$; $p = 0.001$), where the proportion of poor (30.2%; n = 564), fair (11.0%; n = 193) and good (57%; n = 1,027) quality images was significantly higher than that of excellent (1.9%; n = 34) quality fluke images, respectively (2 vs 5: $\chi^2 = 24.5$; $p = 0.001$, 3 vs 5: $\chi^2 = 6.231$; $p = 0.013$, 4 vs 5: $\chi^2 = 51.271$; $p = 0.001$). The proportion of good quality images was also significantly higher than that of poor ($\chi^2 = 8.379$; $p = 0.004$) and fair ($\chi^2 = 31.118$; $p = 0.001$) quality images, while poor quality images were significantly more than fair quality images ($\chi^2 = 8.805$; $p = 0.003$).

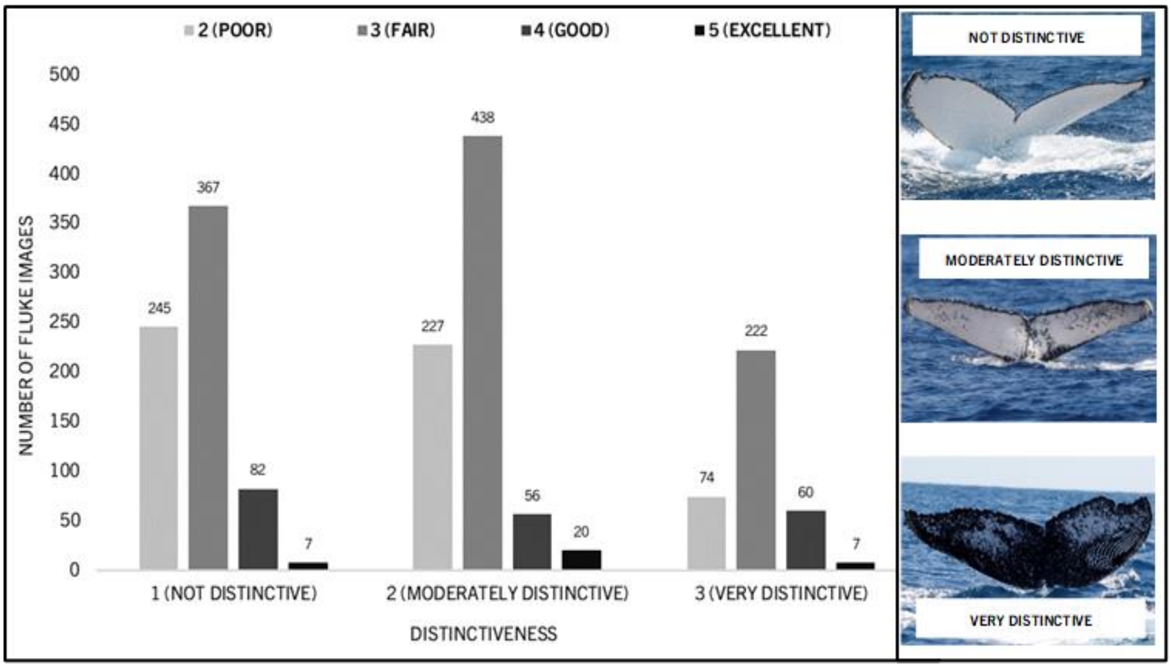


Figure 3.6 The number of humpback whale fluke images in the catalogue per overall photographic quality category, and fluke distinctiveness (displaying example images of the overall fluke distinctiveness categories).

The number of fluke images (n) in the catalogue collected within each coastal photo-identification data collection region is shown in Figure 3.7. The largest component of the catalogued fluke images was collected in the EN region (71.7%), while lower proportions were collected in the SC (12%), MC (10%), ES (3%) and MS (3%) regions.

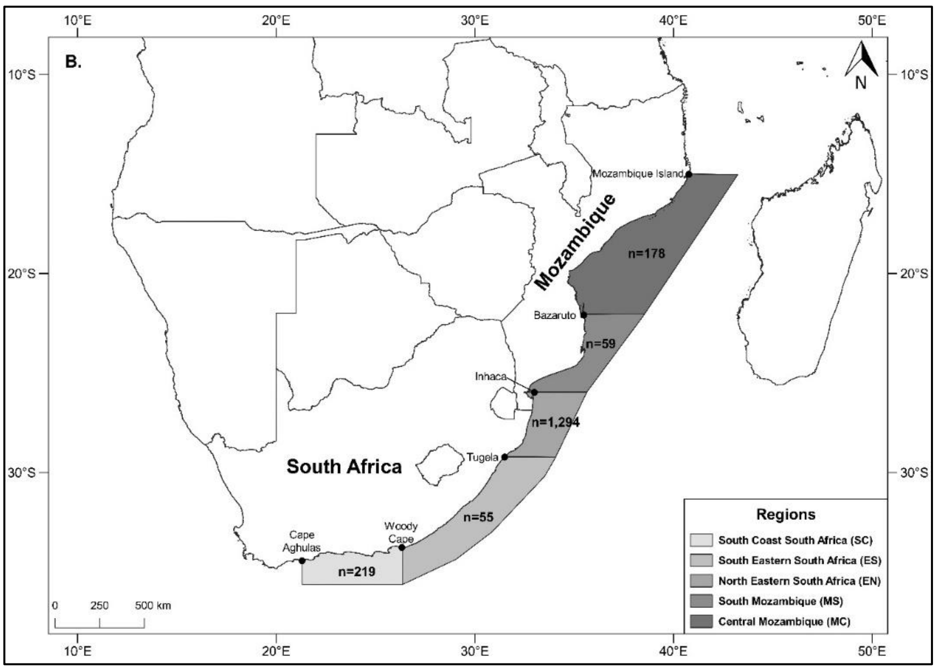


Figure 3.7 The number of fluke images in the catalogue collected within each photo-identification data collection region.

Figure 3.8 displays the number of humpback whale fluke images (n) in the catalogue by year, images source (historic and new), and the survey method used during the data collection process. The historic dataset images were collected between 1988 to 2018, excluding 1993 to 1999 and 2012, for which no fluke images were available. The largest proportion of these images were collected in 2005 (15.6%; n = 270), followed by the years 2007 (14.9%; n = 249), 2008 (14.2%; n = 246), and 2009 (13.5%; n = 234). Furthermore, 73.2% of the historic fluke images were from commercial BBWW operations (DFFE-BBWW and additional commercial BBWW combined], and 26.8% were collected through dedicated research surveys.

Regarding the new fluke images, 14.9% (n = 11) were from commercial BBWW platforms and 85.1% (n = 63) during dedicated humpback whale research surveys (Figure 3.12). These images were collected during 2018 (55.4%; n = 41) and 2019 (44.6%; n = 33).

Considering the datasets combined, the largest component of fluke images in the catalogue was collected through BBWW (70.8%; n = 1,278) efforts, and 29.2% (n = 527) were collected through dedicated scientific research surveys.

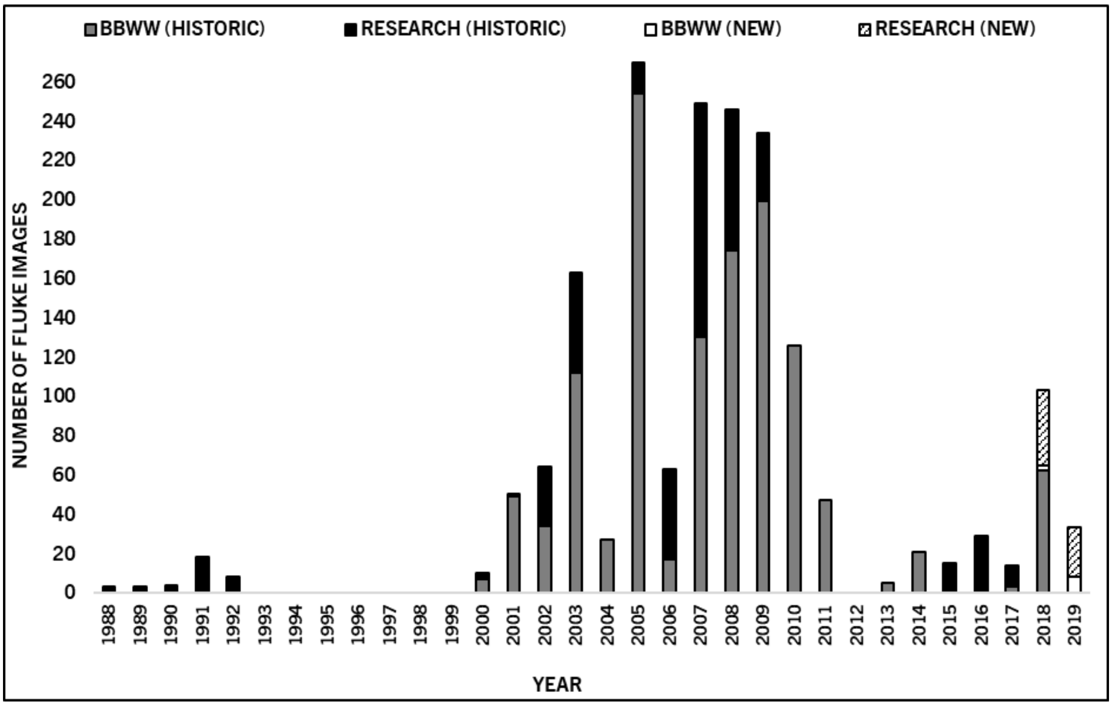


Figure 3.8 The number of humpback whale fluke images in the catalogue by year, images source (historic and new), and the survey method used during the data collection process (BBWW = boat-based whale watching).

The number of fluke images (n) in the catalogue captured per month were evaluated for each year's data (Figure 3.9). In 1988 to 1990, and 1992, fluke images were exclusively available for

July. The capture month was unknown for 94% (n = 17) of 1991's fluke images (n = 18), where the one fluke image that provided details on its capture date was collected in August. From 2000 onwards, fluke images were primarily collected between June to December. However, in 2000 and 2007, fluke images were collected from June to March of the next year. The largest proportion of the image collection years displayed one month in which a peak in fluke image collection took place (42%; n = 10), where a relatively lower proportion of the years displayed two months in which peak numbers of fluke images were collected (bimodal) (25%; n = 6). Furthermore, 42% (n = 10) of the fluke image collection years displayed an initial image collection peak in July, followed by a subsequent peak in September and October (17%; n = 4, each). The number of years that had peak image collections in August (13%; n = 3) differed by only one year from the number of years that had peak image collections in September and October, respectively.

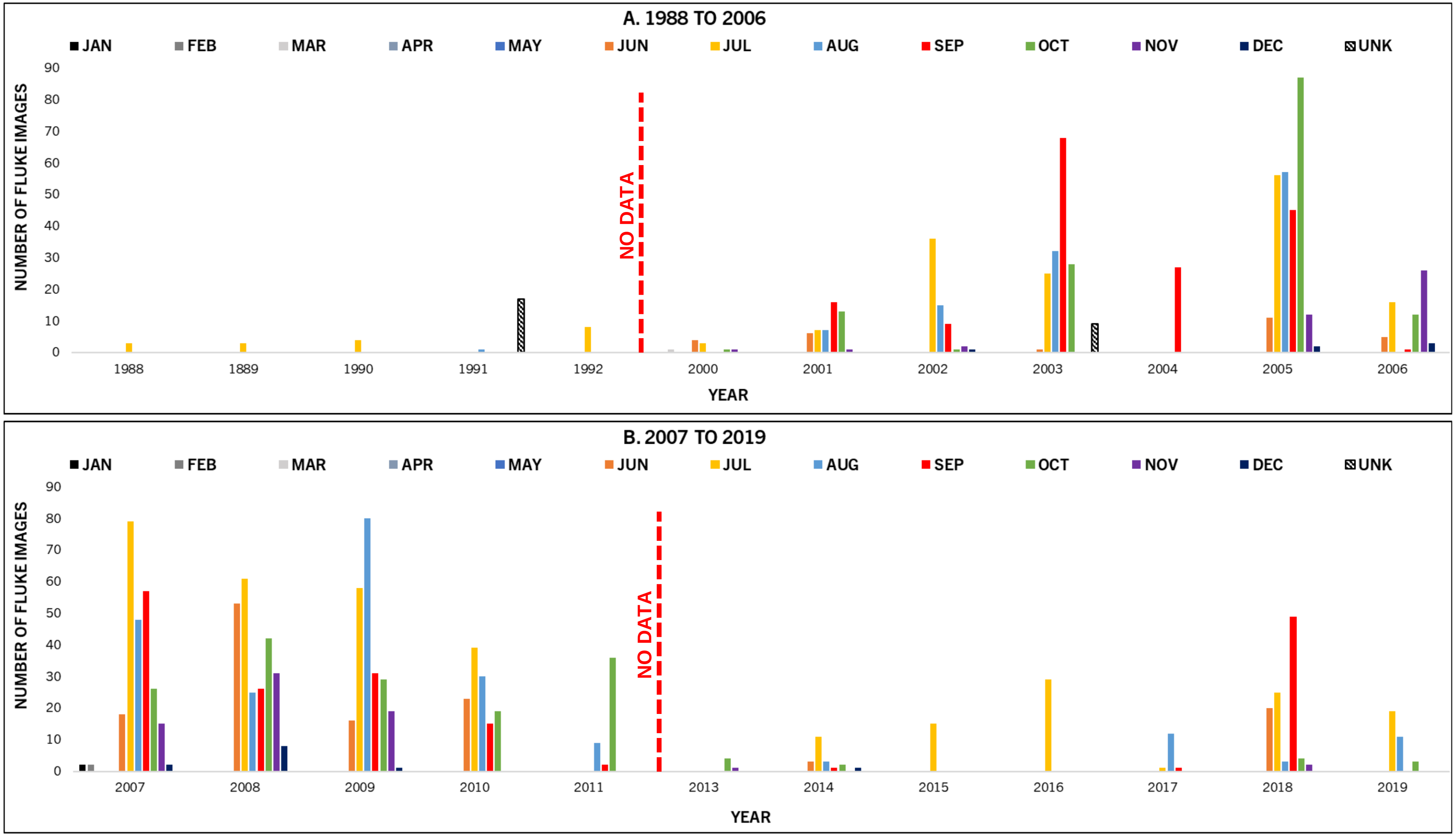


Figure 3.9 Number of humpback whale fluke images in the C1 sub-stock photo-identification catalogue captured per month between 1988 and 2019 (no data available for 1993 to 1999, and 2012.

Figure 3.10 displays the number of fluke images (n) in the catalogue captured per month within each photo-identification data collection region. Fluke images collected within the South African regions were collected across ten months (January to March and June to December). Within the SC region, fluke images were collected across ten months (excluding April and May), where the peak numbers of fluke images were collected in July and November. Fluke images were collected within the ES region between June and October, where the peak number of fluke images were collected in August. Fluke images were collected across seven months (June to December) within the EN region, where the peak number of fluke images were collected in July and October. The image capture month was unknown for nine fluke images collected within this region.

Within the Mozambique regions, fluke images were collected between July and October. In the MS region, fluke images were collected across three months (between August and October), where a peak number of images were collected in August and September. In the MC region, fluke images were collected between July and October, where peak numbers were collected in September. Lower numbers of images were collected during July, August and October.

Overall, 60% of the data collection regions displayed only one month in which peak numbers of images were collected (unimodal), while 40% displayed two months in which peak numbers of images were collected (bimodal). Furthermore, 40% of the data collection regions displayed an initial image collection peak in July, which was relatively similar to the percentage of the fluke image collection years that displayed an initial peak in July (42%).

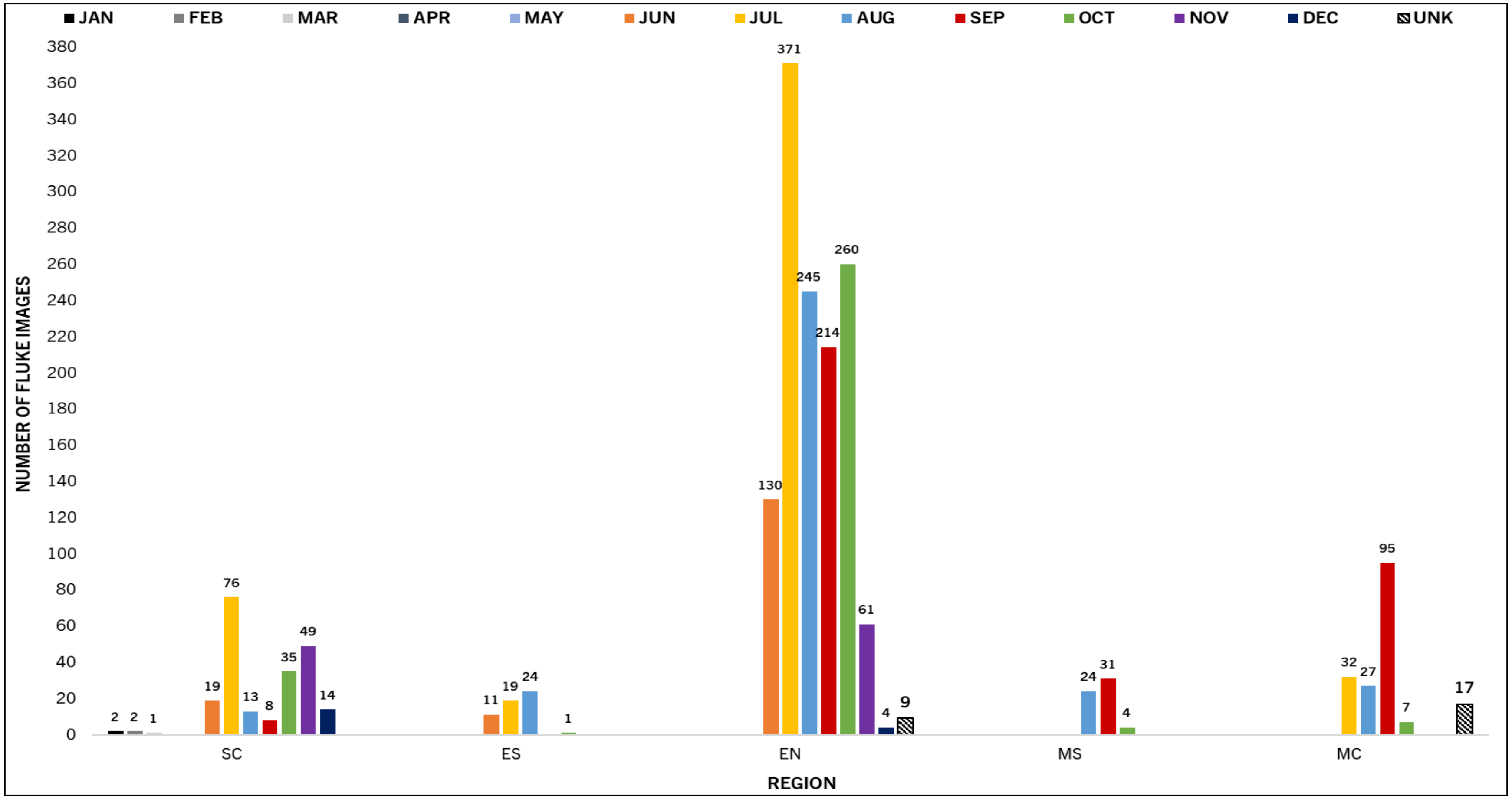


Figure 3.10 Number of humpback whale fluke images in the C1 sub-stock photo-identification catalogue captured per month within each photographic data collection coastal region (SC = south coast; ES = south-eastern; EN = north-eastern; MS = southern Mozambique; MC = central Mozambique).

3.4 Photographic Matching

3.4.1 Within-year matching

Within-year matches of fluke images were obtained for 11 individual humpback whales (Table 3.8): five (45%) matches obtained in 2005, two (18%) in 2007, two (18%) in 2008, one (9%) in 2002, and one (9%) in 2003. No within-year matches were obtained after 2008. All the within-year matched individuals were recaptured only once (seen twice) within a season.

The months and regions in which the within-year matches were obtained were evaluated (Table 3.8; Figure 3.11). Among all within-year matched individuals, 64% (7 individuals) were re-encounter after one to four months, 9% (one individuals) after 10 to 30 days, and 27% (3 individual) after an interval of less than 10 days. The shortest and longest interval (days) between first and last encounter was 1 and 114 days, respectively, with a mean temporal occurrence of individuals of 43 days (sd = ± 35 days). The distance between the encounter and re-encounter region of individuals ranged from 0 to 1,200 km.

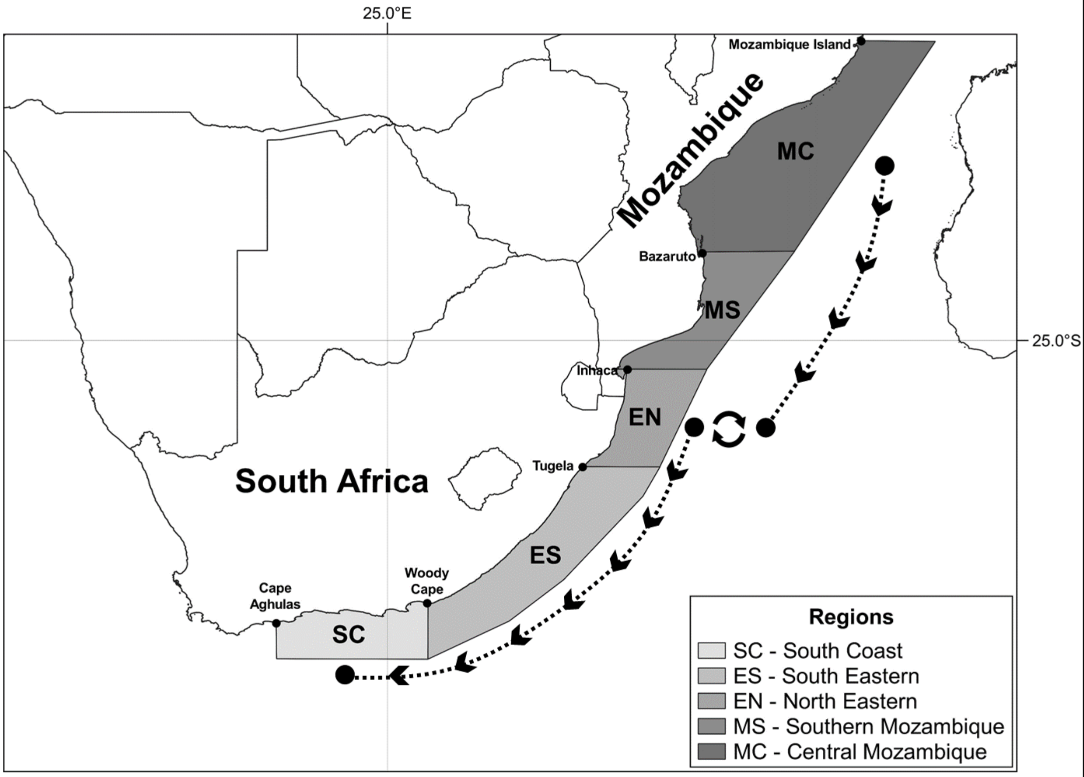
Seven (64%) matches had the same encountered and re-encountered region (EN: EN), of which six (86%) had the same encounter and re-encounter location (St Lucia: St Lucia), and one (14%) match was obtained between Richards Bay and St Lucia (some 65 km apart). Of the six matches obtained within the same location, two were encountered and re-encountered within the same month: one obtained in July (two days apart), and one in September (one day apart). Two matches were obtained between July and October (72 and 65 days apart, respectively), one between August and October (75 days apart) and another between September and October (32 days apart). The one match made between Richards Bay and St Lucia was encountered and re-encountered in July (one day apart).

Two matches were obtained between the EN and SC regions (some 1,200 km apart): one obtained between October and November (45 days apart) (2005) and another between August and December (144 days apart) (2008).

Two matches were obtained between Mozambique (MC) and South Africa (EN) (some 900 km apart), where both were encountered during September and re-encountered during October (22 and 39 days apart, respectively).

Table 3.8 Within-year match results displaying the encounter time (month) and location (area and coastal region), and the time (number of days) and distance (km) between the encounters for each match obtained.

MATCH NUMBER	ENCOUNTER YEAR	ENCOUNTER MONTH	ENCOUNTER LOCATION (AREA AND REGION)	RE-ENCOUNTER MONTH	RE-ENCOUNTER LOCATION	TIME BETWEEN ENCOUNTERS (DAYS) (MAXIMUM RECAPTURE INTERVAL)	APPROXIMATE DISTANCE BETWEEN ENCOUNTER AREAS (KM)	APPROXIMATED DISTANCE TRAVELLED PER DAY (KM/DAY)
1	2002	JULY	RICHARDS BAY (EN)	JULY	ST LUCIA (EN)	1	65	65
2	2003	SEPTEMBER	BAZARUTO (MC)	OCTOBER	ST LUCIA (EN)	22	900	40.9
3	2005	JULY	ST LUCIA (EN)	OCTOBER	ST LUCIA (EN)	72	0	
4	2005	JULY	ST LUCIA (EN)	OCTOBER	ST LUCIA (EN)	65	0	
5	2005	AUGUST	ST LUCIA (EN)	OCTOBER	ST LUCIA (EN)	75	0	
6	2005	OCTOBER	ST LUCIA (EN)	NOVEMBER	ST LUCIA (EN)	32	0	
7	2005	OCTOBER	ST LUCIA (EN)	NOVEMBER	KNYSNA (SC)	45	1,200	26.7
8	2007	JULY	ST LUCIA (EN)	JULY	ST LUCIA (EN)	2	0	
9	2007	SEPTEMBER	BAZARUTO (MC)	OCTOBER	ST LUCIA (EN)	39	900	23.1
10	2008	AUGUST	ST LUCIA (EN)	DECEMBER	KNYSNA (SC)	114	1,200	10.5
11	2008	SEPTEMBER	ST LUCIA (EN)	SEPTEMBER	ST LUCIA (EN)	1	0	



ENCOUNTER REGION		RE-ENCOUNTER REGION	TOTAL NUMBER OF MATCHES
EN		SC	2
EN		EN	7
MC		EN	2
TOTAL			11

Figure 3.11 A graphic representation and the number of within-year matches obtained from the humpback whale C1 sub-stock photo-identification catalogue, per encounter and re-encounter regions.

3.4.2 Between-year matching

Forty-eight between-year matches of fluke images representing 45 individual humpback whales were obtained (Table 3.9). Of these 45 individuals, 42 (93%) were re-encountered once (seen twice), and three (7%) were re-encountered twice (seen three times) between years.

"Re-encounter" fluke images were obtained in 50% (n = 12) of the years represented in the catalogue: 2001 to 2011 and 2018. The highest re-encounter rates were obtained in the years 2011 (8.5%), 2006 (7.9%), 2004 (7.4%), and 2001 (6%). The years 2007 to 2009 also had relative high re-encounter rates: 2007 (3.2%), 2008 (2.8%), and 2009 (4.3%). Relatively similar, but low re-encounter rates were reached in 2002 (1.6%), 2003 (1.8%), and 2010 (1.6%). The lowest re-encounter rates were reached in 2005 (0.7%), and 2018 (0.9%). Subsequently, an average between-year re-encounter rate of 3.9% was estimated.

In connection to the duration (years) between encounters, initial encounters/re-encounters ranged from single years to 18 years. Of the 42 individuals re-encountered once, 12 (28.6%) were re-encountered after one year, nine (21.4%) re-encountered after two years, and 21 (50%) re-encountered after three or more years. Only two of these individuals were re-encountered after ten or more years.

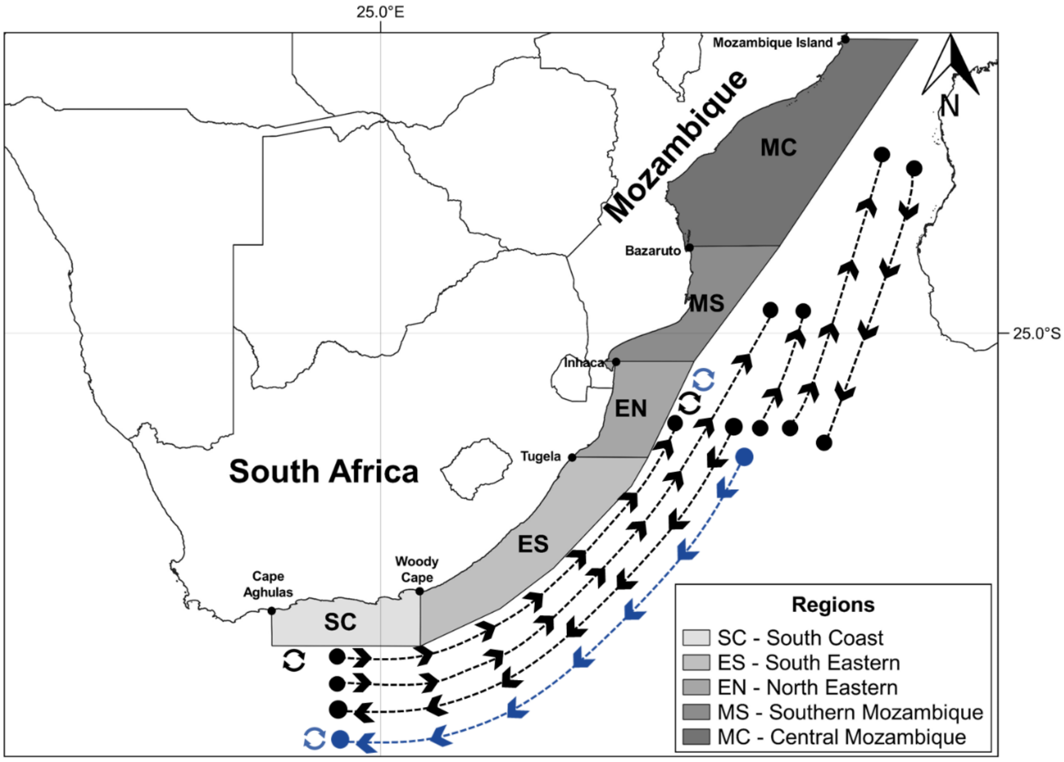
Of the three individuals re-encountered twice (seen three times), two individuals were first re-encountered one year after the initial encounter and re-encountered again 4 and 7 years after the first re-encounter, respectively (5 and 8 years from the initial encounter, respectively). The other individual was first re-encountered two years after the initial encounter and re-encountered three years after the first re-encounter (5 years from the initial encounter).

Table 3.9 Between-year matches displaying the encounter year and location area (and region), and the duration (years) and distance (km) between the encounter and re-encounter for each match obtained.

MATCH NUMBER	ENCOUNTER YEAR	ENCOUNTER REGION & LOCATION	1ST RE-ENCOUNTER YEAR	1ST RE-ENCOUNTER REGION & LOCATION	TIME BETWEEN ENCOUNTERS (YEARS)	DISTANCE BETWEEN ENCOUNTER LOCATIONS (KM)	2ND RE-ENCOUNTER YEAR	2ND RE-ENCOUNTER REGION & LOCATION	TIME BETWEEN 1ST AND 2ND RE-ENCOUNTER (YEARS)	DISTANCE BETWEEN 1ST AND 2ND RE-ENCOUNTER LOCATION (KM)
1	1988	CAPE VIDAL (EN)	2006	KNYSNA (SC)	18	1,224	-	-	-	-
2	2000	ST LUCIA (EN)	2001	ST LUCIA (EN)	1	0	-	-	-	-
3	2000	ST LUCIA (EN)	2001	ST LUCIA (EN)	1	0	-	-	-	-
4	2000	KNYSNA (SC)	2001	ST LUCIA (EN)	1	1,192	-	-	-	-
5	2001	ST LUCIA (EN)	2002	RICHARS BAY (EN)	1	66	2009	ST LUCIA (EN)	7	66
6	2001	ST LUCIA (EN)	2003	KNYSNA (SC)	2	1,192	2006	KNYSNA (SC)	3	0
7	2001	ST LUCIA (EN)	2006	ST LUCIA (EN)	5	0	-	-	-	-
8	2001	KNYSNA (SC)	2007	ST LUCIA (EN)	6	1,192	-	-	-	-
9	2001	ST LUCIA (EN)	2008	ST LUCIA (EN)	7	0	-	-	-	-
10	2001	ST LUCIA (EN)	2008	ST LUCIA (EN)	7	0	-	-	-	-
11	2002	ST LUCIA (EN)	2003	ST LUCIA (EN)	1	0	-	-	-	-
12	2002	RICHARDS BAY (EN)	2003	ST LUCIA (EN)	1	66	2007	ST LUCIA (EN)	4	0
13	2002	ST LUCIA (EN)	2004	ST LUCIA (EN)	2	0	-	-	-	-
14	2002	ST LUCIA (EN)	2005	ST LUCIA (EN)	3	0	-	-	-	-
15	2002	ST LUCIA (EN)	2007	KNYSNA (SC)	5	1,192	-	-	-	-
16	2002	RICHARDS BAY (EN)	2007	ST LUCIA (EN)	5	66	-	-	-	-
17	2002	RICHARDS BAY (EN)	2009	PONTA MAMOLI (MS)	7	258	-	-	-	-
18	2003	ST LUCIA (EN)	2004	ST LUCIA (EN)	1	0	-	-	-	-
19	2003	ST LUCIA (EN)	2007	KNYSNA (SC)	4	1,192	-	-	-	-
20	2003	ST LUCIA (EN)	2008	KNYSNA (SC)	5	1,192	-	-	-	-
21	2003	ST LUCIA (EN)	2008	KNYSNA (SC)	5	1,192	-	-	-	-
22	2004	ST LUCIA (EN)	2005	ST LUCIA (EN)	1	0	-	-	-	-
23	2004	ST LUCIA (EN)	2006	KNYSNA (SC)	2	1,192	-	-	-	-
24	2005	KNYSNA (SC)	2006	KNYSNA (SC)	1	0	-	-	-	-
25	2005	ST LUCIA (EN)	2007	ST LUCIA (EN)	2	0	-	-	-	-
26	2005	ST LUCIA (EN)	2007	ST LUCIA (EN)	2	0	-	-	-	-
27	2005	ST LUCIA (EN)	2008	KNYSNA (SC)	3	1,192	-	-	-	-
28	2005	KNYSNA (SC)	2009	PONTA MAMOLI (MS)	4	1,377	-	-	-	-
29	2005	ST LUCIA (EN)	2009	ST LUCIA (EN)	4	0	-	-	-	-
30	2005	ST LUCIA (EN)	2011	ST LUCIA (EN)	6	0	-	-	-	-
31	2005	ST LUCIA (EN)	2011	ST LUCIA (EN)	6	0	-	-	-	-
32	2006	KNYSNA (SC)	2007	KNYSNA (SC)	1	0	-	-	-	-
33	2006	KNYSNA (SC)	2008	KNYSNA (SC)	2	0	-	-	-	-
34	2006	KNYSNA (SC)	2009	PONTA MAMOLI (MS)	3	1,377	-	-	-	-
35	2006	KNYSNA (SC)	2011	ST LUCIA (EN)	5	1,192	-	-	-	-
36	2007	ST LUCIA (EN)	2008	ST LUCIA (EN)	1	0	-	-	-	-
37	2007	ST LUCIA (EN)	2009	ST LUCIA (EN)	2	0	-	-	-	-
38	2007	KNYSNA (SC)	2009	ST LUCIA (EN)	2	1,192	-	-	-	-
39	2007	ST LUCIA (EN)	2009	ST LUCIA (EN)	2	0	-	-	-	-
40	2007	BAZARUTO (MC)	2010	ST LUCIA (EN)	3	891	-	-	-	-
41	2008	KNYSNA (SC)	2009	ST LUCIA (EN)	1	1,192	-	-	-	-
42	2008	ST LUCIA (EN)	2009	ST LUCIA (EN)	1	0	-	-	-	-
43	2008	ST LUCIA (EN)	2010	ST LUCIA (EN)	2	0	-	-	-	-
44	2008	ST LUCIA (EN)	2018	BAZARUTO (MC)	10	891	-	-	-	-
45	2010	ST LUCIA (EN)	2011	ST LUCIA (EN)	1	0	-	-	-	-

Between-year matches were obtained for individuals initially encountered within the SC (n = 10), EN (n = 34), and MC (n = 1) regions (Figure 3.12). Of the 42 individuals re-encountered once (seen twice), 37 (88.1%) individuals were encountered and re-encountered in South Africa, and five (11.9%) between South African and Mozambique regions. Of the 37 South African region re-encounters, 25 (64.6%) were from the same encounter and re-encounter region (SC: SC = 3 and EN: EN = 22), while five (13.5%) re-encounters were observed between regions SC and EN, and seven (18.9%) were observed between regions EN and SC. Of the five individuals encountered and re-encountered between South African and Mozambique regions, two moved between the SC and MS regions, one moved between the EN and MS regions, one moved between EN and MC, and one moved between MC and EN.

Of the three individuals re-encountered twice (seen three times), all movements were within South Africa (EN: EN: EN = 1; EN: SC: SC = 1).



A			
ENCOUNTER REGION		1ST RE-ENCOUNTER REGION	NUMBER OF MATCHES
SC	↻	SC	3
SC	→→→→	EN	5
SC	→→→→	MS	2
EN	←←←←	SC	7
EN	↻	EN	22
EN	→→→→	MS	1
EN	→→→→	MC	1
MC	←←←←	EN	1
	TOTAL		42

B					
ENCOUNTER REGION		1ST RE-ENCOUNTER REGION		2ND RE-ENCOUNTER REGION	NUMBER OF MATCHES
EN	←←←←	SC	↻	SC	1
EN	↻	EN	↻	EN	2
		TOTAL			3

Figure 3.12 A graphic representation of the between-year matched individual humpback whales by A) 1st and 2nd encounter region (re-encountered once), and B) 1st, 2nd, and 3rd (re-encountered twice) encounter region.

3.5 Characteristics of Individual Humpback Whales and Flukes Identified within the C1 Sub-Stock

There are presently 1,746 unique humpback whale individuals recorded in this C1 sub-stock photo-identification catalogue. Of this total, 1,690 (96.8%) were encountered once, 53 (3%) were encountered twice (11 within-years, and 42 between-years), and three (0.2%) encountered three times (all between-years) (Table 3.10).

Table 3.10 Encounter frequency (number of times that individuals were encountered between 1988 and 2019).

NUMBER OF TIMES ENCOUNTERED	NO MATCHES	WITHIN-YEAR MATCHES	BETWEEN-YEAR MATCHES	TOTAL
1	1690	-	-	**1690**
2	-	11	42	**53**
3	-	-	3	**3**
TOTAL	**1690**	**11**	**45**	**1746**

The proportions of individual humpback whales identified within each region by fluke colouration type are shown in Figure 3.13. Overall, individuals with a type 1 fluke colouration type significantly more prevalent in all the regions, comprising a total of 45% of the individuals, followed by individuals with type 2 (18%), 5 (15%), 3 (12%), and 4 (9%) fluke colouration.

In the SC region, individuals with a type 1 fluke colouration made up the largest proportion of the individuals encountered (46%), followed by individuals with a type 2 (18%), 5 (14%), 4 (13%), and 3 (9%) fluke colouration. A chi-square analysis revealed that the proportion of individuals with a type 1 fluke colouration was significantly larger than the proportions of individuals with a type 2, 3, 4 and 5 fluke colouration, respectively (1 vs 2: $\chi^2 = 12.3$; p = 0.001, 1 vs 3: $\chi^2 = 24.9$; p = 0.001, 1 vs 4: $\chi^2 = 18.5$; p = 0.001, 1 vs 5: $\chi^2 = 17.1$; p = 0.001).

In the ES region, individuals with a type 1 fluke colouration made up the largest proportion of the individuals encountered (47%), followed by individuals with a type 5 (18%), 2 (16%), 3 (13%), and 4 (5%) fluke colouration. A chi-square analysis revealed that the proportions of individuals with a type 1 fluke colouration was significantly larger than the proportion of individuals with a type 2, 3, 4 and 5 fluke colouration, respectively (1 vs 2: $\chi^2 = 15.3$; p = 0.001, 1 vs 3: $\chi^2 = 19.3$; p = 0.001, 1 vs 4: $\chi^2 = 33.9$; p = 0.001, 1 vs 5: $\chi^2 = 12.9$; p = 0.001).

In the EN region, individuals with a type 1 fluke colouration made up the largest proportion of the individuals encountered (42%), followed by individuals with a type 2 (22%), 5 (14%), 3

(12%), and 4 (11%) fluke colouration. A chi-square analysis revealed that the proportions of individuals with a type 1 fluke colouration was significantly larger than the proportion of individuals with a type 2, 3, 4 and 5 fluke colouration, respectively (1 vs 2: $\chi^2 = 6.3$; p = 0.01, 1 vs 3: $\chi^2 = 18.1$; p = 0.001, 1 vs 4: $\chi^2 = 16.7$; p = 0.001, 1 vs 5: $\chi^2 = 14.0$; p = 0.001).

In the MS region individuals with a type 1 fluke colouration made up the largest proportion of the individuals encountered (46%), followed by individuals with a type 3 (16%), equal proportions of individuals with a type 2 and 5 (14% each), and individuals with a type 4 (9%) fluke colouration. A chi-square analysis revealed that the proportions of individuals with a type 1 fluke colouration was significantly larger than the proportion of individuals with a type 2, 3, 4 and 5 fluke colouration, respectively (1 vs 2: $\chi^2 = 17.1$; p = 0.001, 1 vs 3: $\chi^2 = 14.5$; p = 0.001, 1 vs 4: $\chi^2 = 24.9$; p = 0.001, 1 vs 5: $\chi^2 = 17.1$; p = 0.001).

In the MC region, individuals with a type 1 fluke colouration made up the largest proportion of the individuals encountered (42%), followed by individuals with a type 2 (20%), 5 (16%), 3 (14%), and 4 (8%) fluke colouration. A chi-square analysis revealed that the proportions of individuals with a type 1 fluke colouration was significantly larger than the proportion of individuals with a type 2, 3, 4 and 5 fluke colouration, respectively (1 vs 2: $\chi^2 = 7.8$; p = 0.001, 1 vs 3: $\chi^2 = 14.0$; p = 0.001, 1 vs 4: $\chi^2 = 23.1$; p = 0.001, 1 vs 5: $\chi^2 = 11.7$; p = 0.001).

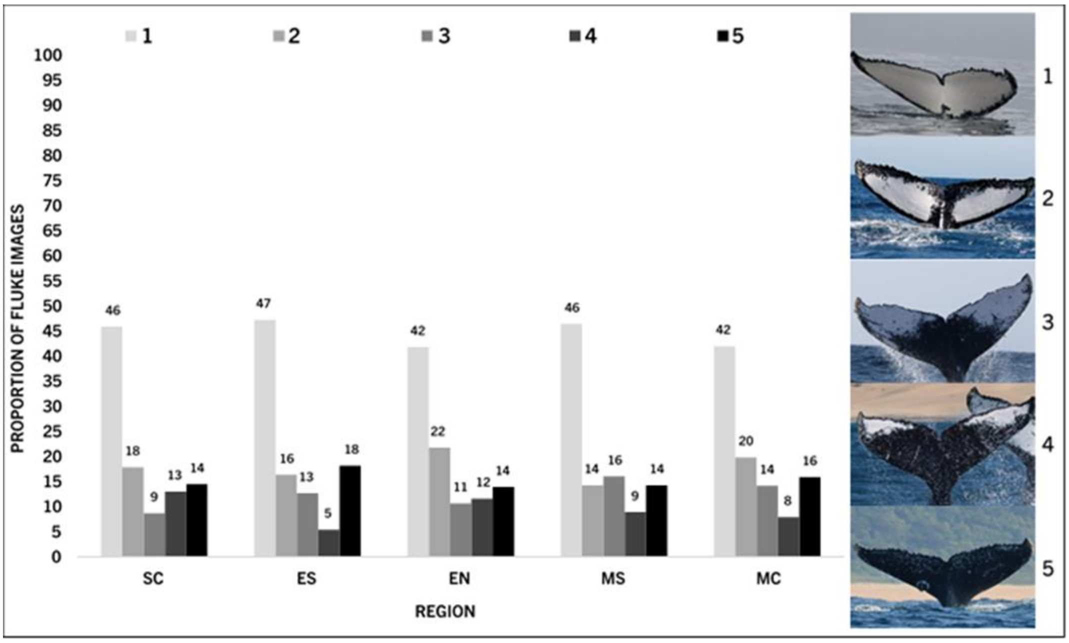


Figure 3.13 The proportion (%) of individual humpback whales identified within the C1 sub-stock by fluke type (1 = 0 - 20% black; 2 = 20 - 40% black; 3 = 40 - 60% black; 4 = 0 - 80% black; and 5 = 80 - 100% black) by photographic data collection region (SC = south coast, ES = south-eastern, EN = north-eastern, MS = southern Mozambique, MC = central Mozambique).

The proportions of individual humpback whales identified within each region by fluke distinctiveness are presented in Figure 3.14. Overall, individuals with non-distinctive flukes (distinctiveness category 1) were more prevalent in all the regions, comprising a total of 42% of the individuals, followed by individuals with moderately unique (distinctiveness category 2) (36%), and very distinctive (distinctiveness category 3) (23%) flukes. A Chi square analysis indicated that individuals with non-distinctive flukes (distinctiveness category 1) were significantly more common than individuals with a very distinctive (distinctiveness category 3) flukes (1 vs 3: χ^2 = 5.6; p = 0.02), however; not significantly more that individuals with moderately distinctive (distinctiveness category 2) flukes (1 vs 2: χ^2 = 0.46; p = 0.5). Individuals with moderately distinctive flukes were also not significantly more common than individuals with very distinctive flukes (2 vs 3: χ^2 = 2.8; p = 0.09).

In the SC region, individuals with non-distinctive flukes (distinctiveness category 1) made up the largest proportion of the individuals encountered (47%), followed by individuals with moderately distinctive (distinctiveness category 2) (30%), and very distinctive (distinctiveness category 3) flukes (22%). A chi-square analysis indicated that individuals with non-distinctive flukes (distinctiveness category 1) were significantly more than individuals with a very distinctive (distinctiveness category 3) flukes (1 vs 3: χ^2 = 9.1; p = 0.003), however; not significantly more that individuals with moderately distinctive (distinctiveness category 2) flukes (1 vs 2: χ^2 = 3.75; p = 0.5). Individuals with moderately distinctive flukes were also not significantly more common than individuals with very distinctive flukes (2 vs 3: χ^2 = 1.2; p = 0.27).

In the ES region, individuals with non-distinctive flukes (distinctiveness category 1) made up the largest proportion of the individuals encountered (40%), followed by individuals with moderately distinctive (distinctiveness category 2) (33%), and very distinctive (distinctiveness category 3) flukes (27%). A chi-square analysis indicated that there was no significant difference in the proportions of individuals with different levels of fluke distinctiveness within this region (χ^2 = 2.5; p = 0.28).

In the EN region, individuals with moderately distinctive flukes (distinctiveness category 2) made up the largest proportion of the individuals encountered (44%), followed by individuals with non-distinctive (distinctiveness category 1) (38%), and very distinctive (distinctiveness category 3) flukes (18%). A chi-square analysis indicated that the proportion of individuals with non-distinctive flukes (distinctiveness category 1) and moderately distinctive (distinctiveness category 2) flukes did not differ significantly (χ^2 = 0.44; p = 0.5), however; individuals with non-distinctive flukes and moderately distinctive flukes were more common than individuals with very distinctive flukes, respectively (1 vs 3: χ^2 = 7.1; p = 0.008, 2 vs 3: χ^2 = 10.9; p = 0.001).

In the MS region, individuals with non-distinctive flukes (distinctiveness category 1) made up the largest proportion of the individuals encountered (45%), followed by individuals with moderately distinctive (distinctiveness category 2) flukes (36%), and very distinctive (distinctiveness category 3) flukes (20%). A chi-square analysis indicated that there was not a significant difference between the proportions of individuals with non-distinctive and moderately distinctive flukes (χ^2 = 1.0; p = 0.31), however; individuals with non-distinctive flukes and moderately distinctive flukes were more common than individuals with very distinctive flukes, respectively (1 vs 3: χ^2 = 9.6; p = 0.002, 2 vs 3: χ^2 = 4.6; p = 0.03).

In the MC region, individuals with non-distinctive flukes (distinctiveness category 1) made up the largest proportion of the individuals encountered (40%), followed by individuals with moderately distinctive (distinctiveness category 2) (35%), and very distinctive (distinctiveness category 3) flukes (26%). A chi-square analysis indicated that there was not a significant difference between the proportions of individuals with different levels of fluke distinctiveness categories within this region (χ^2 = 2.9; p = 0.22).

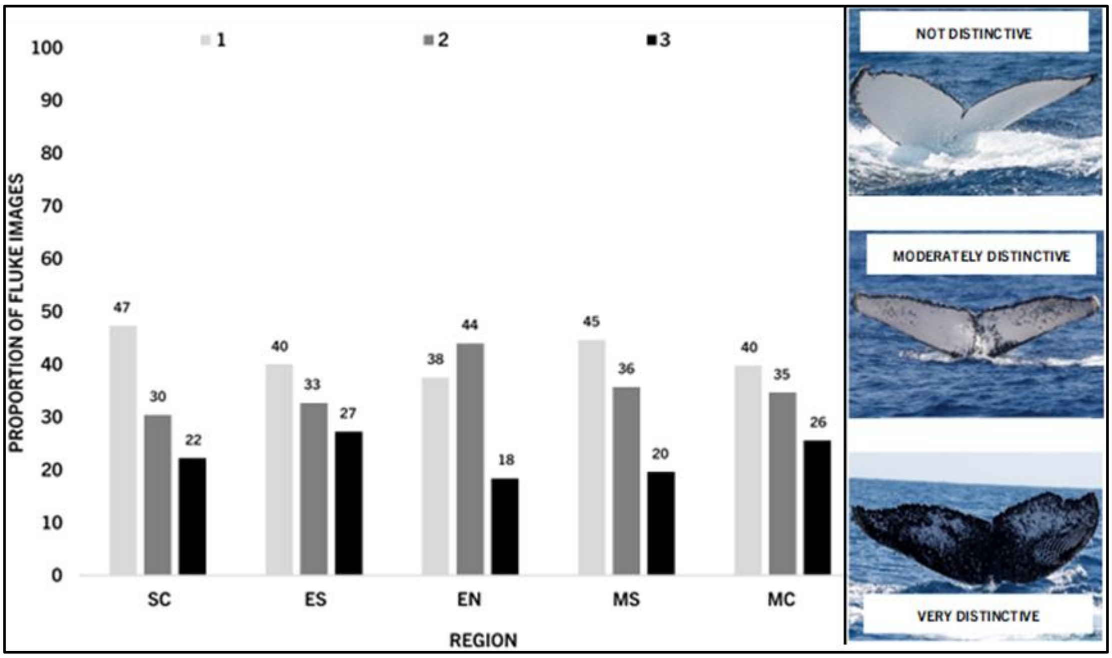


Figure 3.14 The proportion (%) of individual humpback whales identified within the C1 sub-stock by fluke distinctiveness (1 = not distinctive; 2 = moderately distinctive; 3 = very distinctive), by photographic data

collection region (SC = south coast, ES = south-eastern, EN = north-eastern, MS = southern Mozambique, MC = central Mozambique).

CHAPTER 4 DISCUSSION

4.1 Overview

In recent years, the capacity of photo-identification methodology to provide information on temporal and spatial movement patterns of humpback whales has significantly enhanced our understanding of the species migration patterns and interactions with their environment through important migration routes. This novel information ultimately plays key roles in evaluating how populations are structured, providing intrinsic knowledge needed for the successful conservation and management of the species.

The key research issues motivating the execution of this Study imputed to the fact that information on the intra-regional migration patterns and migration fidelity trends of humpback whales associated with the south-eastern African C1 sub-stock is limited and outdated. Additionally, the intra-regional stock structure and the role of this sub-stock on the overall functioning of the C breeding stock is poorly understood. Furthermore, no single photo-identification catalogue has previously been developed for the C1 sub-stock. The development of such a catalogue was therefore highly beneficial to address the key research issues presented in this work and will hereafter act as a valuable tool to address future research questions surrounding the population dynamics of the C1 sub-stock, including those related to the estimate of population or stock growth rate and abundance.

In this Chapter, the results are discussed in the context of four key aspects of the Study, namely:

the photo-identification data collection processes,

the photo-identification data,

the photo-identification catalogue, and

the photo-identification analyses performed with the catalogue data.

Each section is discussed in terms of the key aims and objectives of each, and the strengths and limitations of the results in terms of their capacity to address the key research subjects under investigation.

4.2 Photo-identification Data Collection

The results obtained from the opportunistic and dedicated surveys provide valuable information on humpback whales wintering along the respective survey regions and highlights potential focus areas for future research purposes.

4.2.1 Data collection on commercial BBWW platforms

In contrast to the extensive financial requirements associated with the utilisation of independent research vessels, especially over extended temporal and spatial scales, scientists have increasingly been taking advantage of inexpensive alternative resources, such as platforms of opportunity (PoP) from which dedicated research can be conducted (Williams, 2003; Evans & Hammond 2004; Kiszka *et al*. 2007; Moura *et al*. 2012; Sahri *et al.,* 2020). The use of PoP's is especially beneficial for the investigation and monitoring of cetacean species such as humpback whales (Williams, 2003; Williams *et al.,* 2006; Palacios *et al.,* 2012; Hupman *et al.,* 2015; Vinding *et al.,* 2015; Currie *et al.,* 2018). Commercially operated tour vessels, such as commercial BBWW vessels, are frequently approached for scientific data collection on cetacean species in marine environments (Hammond *et al.,* 1990; Würsig & Jefferson, 1990; Hauser *et al.,* 2006). These platforms have been proven to be invaluable in the long-term and broad-scale monitoring of cetacean populations globally (Evans, 1980; Evans, 1992; Bristow et al., 2001; Tonachella et al., 2012), and has been used in numerous studies focusing on various aspects of cetacean ecology and biology (e.g., Robbins & Mattila, 2000; Williams, 2003; Hauser et al., 2006; Vinding et al., 2015; Moura et al., 2012). Given the cost-effectiveness of using commercial BBWW PoP's for scientific data collection, their utilization in this study was especially beneficial for assisting in the collection of new humpback whale photo-identification data required for this study.

The fluctuating number of commercial BBWW trips accompanied off Durban in 2018 and 2019 is due to inconsistent space availability on the vessels throughout the whale-watching seasons. In contrast, commercial BBWW trips off St Lucia exclusively took place during October, with the number of trips attended primarily influenced by weather conditions, since a "ride-along" opportunity was secured on each whale watching excursion taking place over the survey period.

Although results obtained from the two regions are not directly comparable, similarities were apparent. Based on historic whaling catch and sighting records (*e.g.,* Gambell *et al.,* 1985; Best & Surmon, 1974; Tønnessen & Johnsen, 1982; Best, 1994; Findlay, 2001), shore-based sighting and acoustic records (*e.g.,* Findlay & Best, 1996b; Findlay *et al.,* 2011a), aerial survey records (*e.g.,* Findlay, 1989) and ship-based research records (Gambell *et al.,* 1975), peak densities of humpback whales are known to pass through these two regions *en route* their annual migration to and from their northern wintering ground off Mozambique between May and October. Even though these surveys were conducted during peak humpback whale migration months, the success of photo-identification data collection was surprisingly low in both regions. This low data collection success may be attributed to limitations associated with the use of commercial BBWW platforms for scientific research data collection. Such limitations may include, *inter alia,* trip lengths, restrictions on the temporal and spatial coverage conceivable during each whale watching excursion (Isojunno *et al.,* 2012; Vinding *et al.,* 2015), license agreements surrounding the type of scientific data permitted to be collected from such vessels (Hammond *et al.,* 1990), protocols and restrictions surrounding the vessels' movement towards, around, and away from the animals, as well as restrictions on the maximum distance that vessels are permitted to approach animals (Vinding *et al.,* 2015). Furthermore, the non-randomised temporal and spatial nature of commercial BBWW trips may lead to substantial variation in survey effort in terms of total survey duration and distance covered during each opportunistic survey, leading to potential biases in the total time spent with each group of animals, as well as unequal sampling opportunities between different social organisation groups of animals. Such biases can lead to several additional biases in data collection, including unequal capture probability of individuals (Perkins *et al.,* 1984, 1985; Hammond *et al.,* 1990; Evans & Hammond, 2004; Dickinson *et al*. 2010; Isojunno *et al.,* 2012). Additionally, variation in individual fluking behaviour could have also attributed to the level of success of obtaining fluke images, which within itself can lead to biases, for example in abundance estimation using mark recapture methodology (Hammond, 1986; Edds & Macfarlane, 1987; Kaufman *et al.,* 1987; Calambokidis *et al.,* 1990; Straley, 1990; Cerchio, 1998) or varying sighting success because of inconsistent weather conditions (Findlay & Best, 1996a), amongst others.

4.2.2 Data collection during dedicated research surveys

While the primary objective of the dedicated research surveys was to collect new humpback whale fluke images for inclusion in the C1 sub-stock photo-identification catalogue, additional invaluable information pertaining to the occurrence of humpback whales off Bazaruto, Mozambique, and Durban, South Africa, were attained.

a) Bazaruto, Mozambique

Information on the movement and distribution of humpback whales along the Mozambique coastline is limited. However, based on records from previous humpback whale research conducted on this coastline (*e.g.*, Findlay *et al.,* 1994; Best *et al.,* 1998; Findlay *et al.,* 2011b; Banks, 2013), the relatively high number of humpback whale groups encountered over this brief survey period was expected. The direction of travel recorded for the humpback whale groups encountered over the survey was also foreseeable, as the southern migration of humpback whales in this region generally occurs from the beginning of September when individuals start their seasonal migration to high latitude feeding grounds (Findlay *et al.,* 1994; Best *et al.,* 1998; Banks, 2013).

Regular observations of sets of blows and surface behaviours', including breaching, tail lobbing, and flipper slapping, indicated that regions outside the survey's proposed range contained high densities of humpback whales. Several authors have recorded similar observations (*e.g.,* Findlay *et al.,* 1994; Findlay *et al.,* 2011b; Banks, 2013). Consequently, since the *R/V Angra Pequena* has high seakeeping abilities, and is custom designed for conducting offshore marine research, humpback whale research was conducted at offshore distances beyond the survey's initial proposed range when this vessel was used.

During humpback whale research conducted in this same region during August and September 1991 (Findlay *et al.,* 1994) and 2003 (Findlay *et al.,* 2011), maximum group sizes of five individuals were recorded, with mean group sizes of 1.92 (sd = 0.75) and 1.7 (sd = 0.73) individuals, respectively. It is noteworthy that these records are slightly lower than the observations made during this survey. Furthermore, a comparatively higher mean group size of 3.36 (SE = 0.26) individuals has also previously been recorded in this region (Banks, 2013). Regarding social organisation, the present research findings are consistent with Findlay *et al.* (1994, 2011), where singletons and DYADS made up the greatest proportion of the sightings recorded in this region during this survey period. The less frequent number of TRIO, TRIO+, MOCE, and MOCE was expected, as it has been suggested that humpback whale groups consisting of one to two individuals are the most frequent group size observed during migration (Brown & Corkeron, 1995; Findlay *et al.,* 1996b). There were remarkably high activity levels in the large TRIO+ groups, which are believed to be males competing for sexual access to a single mature female (Tyack & Whitehead, 1983; Clapham *et al.,* 1992). Escort humpback whales in the presence of a cow-calf pair (MOCE and MOCE+) are believed to be mature males seeking access to a female that may come into postpartum oestrus where ovulation occurs immediately following the birth of a new-born humpback whale calf (Glockner-Ferrari & Ferrari, 1990).

b) Durban, South Africa

Current knowledge on the past occurrence of humpback whales within the historic Durban whaling grounds, which is based on information obtained from historic whaling catch and sighting records (*e.g.,* Harmer, 1929, 1931; Matthews, 1937; Mackintosh, 1942; Tønnessen & Johnsen, 1982; Wray & Martin, 1983; Gambell *et al.,* 1975; Best & Ross, 1989; Findlay, 2001), distribution records (*e.g.,* Olsen, 1914; Bannister & Gambell, 1965), and records from aerial surveys (*e.g.,* Findlay, 1989; Findlay & Best, 2016), shore-based sighting and acoustic surveys (*e.g.,* Findlay & Best, 1996b; Findlay *et al.,* 2011a), and ship-based research surveys (*e.g.,* Gambell *et al.,* 1975), suggests a bimodal seasonal abundance of humpback whales in this region. Whales have been observed to be present between May and November, with peaks in densities of northward and southward travelling whales observed towards the end of July, and mid to late September, respectively. Subsequently, the relatively high numbers of humpback whale groups encountered over this research period were anticipated. Furthermore, the direction of travel recorded for the humpback whales encountered over this survey period align with the northward migration period suggested for this region. The fact that the humpback whale groups encountered during this survey period was located between 1 and 17 km offshore (between the 25 m and 200 m isobaths) suggests that these were groups travelling within the near-shore migration stream *en route* to the northerly winter breeding grounds situated within southern and central Mozambique (Findlay & Best, 2006; Findlay *et al.,* 2011a, b).

The maximum and mean group sizes of humpback whales observed during this survey period (Figure 3.7) compares favourably to previous observations made in this region (Findlay & Best, 2006, 2016). Off Cape Vidal (located some 300 km to the north of Durban), Findlay & Best (2006) recorded a maximum group size of six individuals, with a mean group size of 2.3 (sd = 0.2) individuals during northward migration, while Findlay & Best (2016) recorded a maximum group size of five individuals, with a mean group size of 1.8 (sd = 0.9) individuals off Durban. Regarding social organisation, it has been suggested that the timing of northward migration varies between different reproductive or age class segregations of humpback whales, following the order of lactating females and immature males/females in the first months, followed by mature males and females during the middle months, and resting and pregnant females in the last months (Chittleborough, 1965; Dawbin, 1966). Additionally, Brown & Corkeron (1995) revealed that variation also occurs in pod size during different months of the northward migration, where the first months are dominated by pod sizes of three or more individuals, followed by pairs dominating the middle period, and singletons being dominant towards the last months. Considering the months during which this survey took place, and if humpback whales associated with the C1 sub-stock follow the same northward migration pattern suggested by these authors, it would be expected that pairs of mature males/females and singletons would be the dominant social organisation of humpback whale groups present throughout the survey period of this study (Chittleborough, 1965; Dawbin, 1966; Brown & Corkeron, 1995).

4.2.3 Efficiency of the Survey Vessels used for Photo-identification Data Collection

Although the aim of this study was not to evaluation of the efficiency of survey vessels in conducting photo-identification research, these data collecting survey allowed for the opportunity to provide some suggestions on the efficiency of the vessel used in this study, to consider in future similar studies.

It has widely been suggested that the characteristics of a vessel may influence the efficiency of data collection (Katona *et al.*, 1979; Leonori *et al.*, 2012; Williamson *et al.*, 2016). A wide range of vessels has been identified as adequate for sufficiently conducting photo-identification research on humpback whales, including small rigid inflatable boats (RIB) and fibreglass skiffs (5-10 m) powered by outboard engines, Trimaran (14 m), and auxiliary ketch boats (16 m) (Katona *et al.*, 1979; Hammond *et al.*, 1990; Würsig *et al.*, 1990; Matthews *et al.*, 2001; Ritter, 2010; Titova *et al.*, 2018). Although larger vessels are often efficient in conducting such research activities, smaller vessels are often preferred as these are more manoeuvrable, allow for closer encounters, and permit the photographing of the animals' features at lower angles (Katona *et al.*, 1979; Würsig *et al.*, 1990).

Results obtained during the Bazaruto research survey follows these suggestions to some extent. On days when the *MMF-RIB* was used, comparable results regarding the number of humpback whale groups encountered, *GER*, and *UF* was obtained. The high *GER* and the success in capturing fluke images when this vessel was used was also expected, since RIBs are most often used for cetacean photo-identification research (Katona *et al.*, 1979; Hammond *et al.*, 1990). When the *R/V Angra Pequena* was used, a much higher *UF* was obtained compared to when the *MMF-RIB* was used, demonstrating the capability and efficiency of using the *R/V Angra*

Pequena to conduct photo-identification research on humpback whales; however, more research on this vessel is required to make accurate conclusions. The *R/V Angra Pequena* tender was used significantly lesser than the other vessels so that sufficient information could not be collected to make reliable comparisons to the other survey days or provide comments on the efficiency of the vessel to conduct photo-identification research. The use of such small vessels is however unlikely to be as efficient as larger, more manoeuvrable vessels with greater seakeeping capabilities.

Furthermore, the *R/V* Phakisa, a custom-designed 14.5 meters Legacy-Catamaran, which was used for the Durban dedicated survey, provided a stable platform with a high vantage point, enabling sufficient photo-identification data collection.

4.3 The Photo-identification Data

Due to the inherited nature of the historic dataset, several important aspects of the data were questionable, particularly its value and capability to provide the necessary information required to address the key research issues under investigation. Consequently, the investigation of the quality of the fluke images in terms of the extent of detail they display, and the obtainability of the metadata associated to these images were essential for this study. Since two different data collection methods were used for the initial acquisition of the historic fluke images, the dataset was categorized into two sub-datasets (BBWW and RS). Subsequently, assumptions surrounding the value of the data associated with each sub-dataset were unique and individually evaluated.

Scientists require access to a range of additional information pertaining to each individually identifiable image (the image metadata), for photo-identification analyses to be successful (Rosel *et al.,* 2011; Pollicelli *et al.,* 2017). It is advised that such image metadata should be suitable for usage in a wide array of photo-identification analyses, including mark-recapture, spatial and temporal distribution and migration patterns, population status and structure. Given the non-scientific nature of the historic BBWW photo-identification data, the absence of some temporal metadata pertaining to these fluke images was anticipated (Table 3.4). It is widely acknowledged that the lack of standardised data collecting strategies or well-planned study designs, sampling biases, inadequate training, and insufficient knowledge and/or skills, all common characteristics of citizen science, may result to limited quality data (Paulos, 2009; Conrad & Hilchery, 2011; Burgess *et al.,* 2017; Jungblut *et al.,* 2020; Jäckel *et al.,* 2021).

Additionally, the limited temporal metadata is possibly explicable by the fact that this type of information is typically automatically recorded by digital cameras rather than film cameras, where the correct information is dependent on the device's settings being configured correctly by the person handling the equipment. The fact that a proportion of the historic BBWW fluke images lacked some spatial metadata, specifically GPS coordinates relating to the exact location at which the fluke images were captured, was also anticipated (Table 3.5). In terms of photographic data, recreational photographers often capture images of animals or their features merely for personal use, omitting to collect any additional information relating to the encounter, which may be of substantial value to science (Chase & Levine, 2016; Kent, 2017; Dudgeon *et al.*, 2019). Furthermore, the lack of spatial metadata pertaining to the data collected as citizen science during commercial BBWW excursions is partly explicable by the fact that some of these data, such as the geographic location (coordinates) associated with an individual encounter, requires a GPS, which is often not accessible to everyone. Although the metadata associated with the historic BBWW fluke images is not extensive, preventing their use in population analyses such as abundance estimates, they provided sufficient information necessary for photo-identification analyses to address our research issues.

In contrast to the BBWW fluke images, it was surprising that not all the historic RS fluke images had complete temporal and spatial metadata associated with them. Scientific research generally follows a rigorous methodology, where data collection efforts are systematically planned and conducted by knowledgeable and skilled professionals using a standardised data-collection protocol (Rubinstein & Sluis, 2013; Çaparla & Dönmez, 2016). Therefore, it was expected that all the RS fluke images would have accurate recordings of the encounter date (year, month, and day) and location (coastal/survey region, bay, position reference, if not coordinates) available.

Nevertheless, information on the capture year and month were known for over 98% of the historic fluke images, where the spatial metadata pertaining to each historic fluke image provided sufficient information on the coastal and survey region at which the images were captured. Subsequently, the collection of available metadata pertaining to the historic dataset fluke images exhibits adequate information to allow for the acquisitions of information on the seasonal temporal and spatial migration patterns, and site fidelity patterns of the humpback whale C1 sub-stock through photo-identification analyses.

The quality of photographs has demonstrated to be an imperative factor determining the utility of the information relating to an individual's natural markings (such as the colouration patterns, trailing edge peaks and notches, and scarification patterns on humpback whales' flukes), where a decrease in quality makes the accurate recognition of individually marked animals challenging (Katona *et al.,* 1979; Gowans & Whitehead, 2001; Friday *et al.,* 2000; Stevick *et al.,* 2001; Marshall & Pierce, 2012). The evaluation of the images' quality is therefore strongly advised to ensure equal probabilities in individual recognition in all photo-identification analyses. The fact that the majority of the historic BBWW fluke images were of usable quality was not surprising (Figure 3.5). Although the quality of citizen science data is considerably more variable than scientific research data, several studies have identified that it is often of sufficient quality for research purposes (Crall *et al.*, 2011; Wiggins *et al.,* 2011; Bonter & Cooper, 2012; Moyer-Horner *et al.,* 2012; Kosmala *et al.,* 2016; Aceves-Bueno *et al.,* 2017). Furthermore, the relatively high percentage of usable quality fluke images represented within the RS data collection was expected, since this type of data is most often collected by scientific professionals with some level of experience in research-specific data collection techniques. The overall relatively high quality of fluke images contained in the historic dataset validates the value of the data in terms of their use in photo-identification analyses (Figure 3.5).

4.4 The Photo-identification Catalogue

With the novel multiregional photo-identification catalogue developed as part of this study, it was possible to obtain a more detailed understanding of the distribution, movement and breeding behaviour patterns, and the population structure of the humpback whales that utilize the south-easter African coast as a migration corridor and winter breeding ground.

One particularly valuable aspect of this catalogue is the extent of sufficient quality fluke images it contains (Figure 3.6). Images that portray the distinctive characteristics of humpback whales' flukes adequately is imperative for obtaining key information required for conducting successful photo-identification analyses. The predominantly fair to excelled quality of the catalogue images portraying individuals with non-distinctive flukes enables successful photo-identification (Figure 3.6). Since the flukes portrayed by these images were either entirely black or white with no noticeable distinctive markings or scars and with relatively smooth trailing edge patterns with only a few peaks and notches, the relatively high photographic quality allowed for clearer visibility of fluke details, decreasing the probability of obtaining false matches with these images. Although some of the catalogue images representing individuals with non-distinctive flukes were of poor quality, leading to a higher probability of falsely matching (Stevick *et al.,* 2001), they contained sufficient detail to unmistakably identify the individuals they represent. The high quality of the catalogue images portraying individuals with moderately- and very-distinctive flukes also considerably reduces the probability of falsely matching the fluke images they represent.

Another vital factor that has been considered to influence the accurate identification of individuals from photo-identification data is the stability of the natural markings over time (Carlson *et al.,* 1990; Dufault & Whitehead, 1995; Stevick *et al.,* 2001; Vincent *et al.,* 2001). Evidence suggests that drastic changes in humpback whales' fluke pigmentation only occur in the transitions between the juvenile life stage and adulthood, and most significantly in calves with darker fluke colouration (Carlson *et al.,* 1990; Stevick *et al.,* 2001). Based on this knowledge, it was assumed that the identification of humpback whales represented in this catalogue would not be severely influenced by variability in fluke features, as no fluke images of calves or juveniles were included, which significantly increased the probability of obtaining true matches.

To obtain accurate information on the distribution and migration patterns of humpback whales, it is essential to gain a comprehensive understanding of their movement over broad temporal and spatial scales. The large component of citizen science data represented in this catalogue as the historic BBWW fluke image collection (Figure 3.8), demonstrates the value of exploiting opportunistic data for filling data gaps arising from the limitations of traditional scientific research. Opportunistic data collections, such as cetacean observation and photo-identification data produced by citizen science during activities such as land- or boat-based whale watching, collectively often extend over broad temporal and spatial scales, frequently beyond ranges achievable through traditional scientific research (Brossard *et al.,* 2005; Dickinson *et al.,* 2012; Cigliano *et al.,* 2015; Embling *et al.,* 2015; Kent, 2017; Earp & Liconti, 2020; Kelly *et al.,* 2020; Sandahl & Tøttrup, 2020). Citizen science data has especially been useful for the monitoring of cetacean species such as humpback whales and has extensively been used in obtaining information on the spatio-temporal migration and distribution patterns (Bruce *et al.,* 2014; Vinding *et al.,* 2015; Lodi & Tardin, 2018; Lotriet, 2018; Valani *et al.,* 2020), abundance (Tonachella *et al.*, 2012; Currie *et al.*, 2018), population growth rate (Pirotta *et al.*, 2020), stock structure (Mwango'mbe *et al.,* 2021), and habitat use (Pierce *et al.,* 2010; McCulloch *et al.,* 2021) of the species. The fact that no citizen science data, specifically commercial BBWW fluke images, is represented in this catalogue for the 20th century is explicable by fact that no archived photo-identification data collections were seemingly available, neither provided by any of the historic data sources for this period. It should be noted that citizen science forms part of an important regulation for commercial BBWW operations in the study area. As a component of licence agreements, commercial BBWW companies operating along the South African coastline are required to provide the Department of Forestry, Fisheries and the Environment (DFFE) with any scientific data collected during excursions. Such data include, *inter alia*, photo-identification and sighting data, although such data collections are not a prerequisite of operations (Turpie *et al.,* 2005; IWC, 2018, DFFE, 2021). However, the lack of availability or absence of BBWW citizen science photo-identification data for the 20th century might lie in the fact that formal commercial whale watching activities in South Africa only began after 1990 (Hoyt, 1995; Findlay, 1997; Hoyt, 2001; Turpie *et al.*, 2005), after which the first formal regulation of the industry was instituted under the Marine Living Resources Act (Act No.18 of 1998) much later towards the end of the century. Consequently, the requirements for submitting scientific data collected during commercial BBWW expeditions were inexistent prior to the establishment of this formal regulation.

Regarding this catalogues' scientific research data component, the relatively low availability of fluke images pre-21st century could be attributed to several factors. Some are related to challenges associated with photo-identification as a research method, such as:

a) difficulties in data collecting attributing to limited financial resources, inadequate or lack of appropriates skills, technical limitations, and poor or complete lack of knowledge or the understanding of animal behaviour;

b) lack of knowledge on appropriate data compilation, management, analysis, and interpretation;

c) institutional limitations and restrictions pertaining to the capturing and sharing of data; and

d) unavailability of data sharing platforms.

The relative scarcity of research related fluke images pre-21st century may have also been due to scarcity of whales in the area at this time (Findlay, 1989; Best, 1993), and the IWC's delay in conducting comprehensive assessments of humpback whale stocks across the Southern Hemisphere, which was only initiated after 2001. Consequently, sufficient assessments on the C1 sub-stock were only concluded in 2009 (IWC, 2010). Furthermore, although the usability of natural markings to identify individual humpback whales has been noted throughout available historical records (*e.g.,* Lillie, 1915; Matthews, 1937; Pike, 1953; Schevill and Backus, 1960), the value of identifying humpbacks' by tail fluke photographs, and the extensive information that can be obtained from such images through photo-identification analyses, have only been noted in the last three decades (Katona & Kraus, 1979; Katona *et al.*, 1979; Katona & Whitehead, 1981; Hammond *et al.*, 1990; Stevick *et al.*, 2001; Urian *et al.*, 2015). To date, only a limited number of photo-identification studies have been performed on the humpback whale C1 sub-stock (*e.g.*, Cerchio *et al.*, 2008b; Findlay *et al.*, 2011a, b; Banks, 2013; Minton *et al.*, 2016), where access to the photo-identification data collected during these studies is restricted. Furthermore, irrespective of the low availability of fluke images pre-21st century, the overall increase in the number of fluke images following this period may be attributed to technological development over time, such as digital cameras, digital platforms for files' exchange and software to compare images, amongst others. However, since photo-identification data wasn't readily available for some of the years, it is unfortunate that this catalogue is unable to represent the humpback whale C1 sub-stock over consistent temporal scales. It should therefore be noted that any temporal related population estimates derived from photo-identification analyses performed with this catalogue's data should be interpreted with caution.

Furthermore, the fact that fluke images represented in this catalogue were collected in all the photo-identification data collection regions along the coast of South Africa and Mozambique (Figure 3.9), provides an opportunity to gain novel information on the distribution and movement patterns of individuals within and between the south-eastern African migration corridor and breeding ground. It should be noted that the remarkably high percentage of fluke images collected in the EN region (Figure 3.9) was primarily due to the presence of a commercial BBWW company that has been operating in the region of St Lucia and Richards Bay since 1991. Furthermore, St Lucia is a popular tourist destination situated within iSimangaliso Wetland Park, one of South Africa's UNESCO World Heritage sites (Allen & Brennan, 2004; Lawrie & Stretch, 2011). Since notably lower numbers of fluke images and data were collected within the other photographic data collection regions (Figure 3.9), primarily due to lower research effort, these regions should be flagged as focus areas for future photo-identification research on humpback whales, especially within the ES and MS regions.

The temporal and spatial extent to which the fluke images were collected also allows for the opportunity to gain insight into the seasonal occurrence patterns of whales on the coastline. In this catalogue, the number of fluke images available for each month per year (season) may reflect the effort of data collection, however; this number may also reflect the densities of humpback whales occurring on the coast by month (Figure 3.9). However, since not all fluke images included in this catalogue could be correlated with effort, it was not feasible to use the information on the monthly number of fluke images available for each year to make valid inferences on the densities of humpback whale occurrences by month, or to conclude the months in which peak densities of humpback whales occur on the coastline. Nonetheless, it was assumed that the months in which fluke images were available provided conclusive evidence of the presence of humpback whales along the coastline during that month.

Information on the occurrence of humpback whales along the south-eastern African coastline recorded throughout the 20^{th} century indicated that whales were historically seasonally present on the coastline for approximately nine months, where the earliest annual sighting date for northward travelling whales was recorded in April, and the last annual sighting date for southward travelling whales was recorded in December (Olsen, 1914; Lea, 1919; Matthews, 1973; Rayner, 1940; Mackintosh, 1942; Dawbin, 1966; Gambell, 1976; Best & Surmon, 1974; Best, 1994; Best & Ross, 1996; Findlay & Best, 1996b; Dawbin, 1997). However, more recent research indicated a change in the seasonal occurrence period of humpback whales in the referred region to approximately 10 months, shifting the start of the northward migration from April to May (one month later) and the end of the southward migration from December to February (two months later) (Banks, 2013). Within this catalogue, the months during which fluke images were collected during the 20^{th} century falls within the historical seasonal occurrence period. Furthermore, it was assumed that the proportion of the 1991 fluke images for which the capture month was unknown was collected during August or September, as it formed part of the Findlay *et al.* (1994) dataset which was collected during a survey off the coast of southern and central Mozambique in August and September 1991. Furthermore, the months in which fluke images were collected from 2000 onwards falls within the current seasonal occurrence period of humpback whales on this coast, as suggested by Banks (2013). However, no fluke images were available for May in any of the years and could therefore not confirm that May is the first month that humpback whales start occurring on the coast in present years.

When comparing the number of humpback whale fluke images collected per month within each photographic data collection region (Figure 3.10) to more site-specific seasonal occurrence records, it appears that southward migrating humpback whales are present off the south coast of South Africa for one month longer than initially believed. Sighting records collected from Plettenberg Bay/Knysna (34°S, 23°E) from 2006 to 2008 indicated that southward migrating humpback whales were observed until mid-February (Banks, 2013). However, as shown in this catalogue, the fluke image collected in this region during March of 2000 suggest that whales are potentially present on the south coast for longer periods, although additional information is required to derive any conclusions. Furthermore, the months in which peak numbers of fluke images were collected in this region is comparable to the months during which peak encounter rates were observed by Banks (2013), which may suggest that July and November represent the months during which peaks in humpback whale densities are observed in this region during northward and southward migration, respectively.

The months in which fluke images were collected in the south-eastern data collection region coincide closely to the period during which humpback whales are expected to migrate through this region (*e.g.*, Matthews, 1937; Bannister & Gambell, 1965; Gambell *et al.*, 1975; Tønnessen & Johnsen, 1982; Wray & Martin, 1983; Findlay, 1989; Best *et al.*, 1998; Findlay, 2001; Findlay & Best, 2016).

The months in which fluke images were collected at locations along the north-eastern data collection region provide evidence that humpback whales were observed between June to December. This timeframe is one month longer than previous observations made during shore-based surveys conducted at Cape Vidal each year from 1988 and 1991, and in 2002 (Findlay, 1994; Findlay & Best, 1996a & 1996; Findlay & Best, 2006; Findlay *et al.*, 2011a). Results from these surveys suggested that humpback whales seasonally migrate past this region between June and October. However, it should be noted that the period of these surveys did not extend beyond the end of October. Since the fluke images captured within locations along the north-eastern data collection region were collected between June to December, it is possible that the period during which individuals occur within locations along the south-eastern region is longer than historically suggested, since whales that are observed within the north-eastern region during December are expected to still travel past locations along the south-eastern region during southern migration.

According to historical records of the seasonal catches of humpback whales from Linga Linga / Inhambane, Mozambique (23°47'S, 35°32'E) during the early 1900's (*e.g.,* Olsen, 1914; Lea, 1919; Best *et al.,* 1998), and boat-based and aerial surveys conducted off Ponta Mamoli (26°42'S, 32°54'E) and the Bazaruto Archipelago (21°39'S, 35°31'E) between 2006 to 2009 (Banks, 2013), humpback whales seasonally occur within their southern and central Mozambique breeding grounds between July and October. In this catalogue, the months during which fluke images were collected within the Mozambique data collection regions corresponds to the seasonal occurrence period of humpback whales suggested for these regions, since no fluke images were collected before July or after October in any of the years. Banks (2013) observed peaks in humpback whale encounter rates off the Bazaruto Archipelago during August and September, which might explain the relatively high number of fluke images collected during these months in both Mozambique data collection regions.

4.5 Photographic Matching

With photo-identification matching of the fluke images represented in the newly developed C1 sub-stock multiregional photo-identification catalogue, it was possible to obtain valuable novel information on the intra- and inter-seasonal occurrence and movement patterns of humpback whales migrating and breeding along the south-eastern African coast. However, to gain a clear understanding of the results obtained from the matching processes, and to enable the correct interpretation thereof, it is essential to consider the limitations of this photo-identification catalogue. This is particularly relevant in terms of the usefulness of the catalogue data for accurate population parameters estimation through mark-recapture analyses for which there are several assumptions that are required to be met.

One of the key assumptions of mark-recapture population estimation is that all the individuals in the population have an equal probability of being captured (Hammond, 1990; Lettink & Armstrong, 2003). Several studies reporting on the spatial and temporal migration patterns of humpback whales has revealed that their migration flow is generally structured (Dawbin, 1966, 1997; Craig *et al.,* 2003), and that the period or Julian date at which some individual whales or groups are present in certain areas is consistent between seasons; however, this period is often brief (Félix & Haase, 2001; Craig *et al.,* 2003; Cerchio *et al.,* 2005, 2008a, 2008b). Therefore, it is crucial to ensure that sampling effort spans over temporal and spatial scales representative of the entire population and migration period, and that this effort remains consistent over seasons to satisfy the "equal probability of being sampled" assumption, to avoid heterogeneous capture probabilities between seasons, and to obtain unbiased population parameter estimates through mark-recapture analyses (Felix & Haase, 2001; Cerchio *et al.*, 2005, 2008a, 2008b; Constantine *et al.*, 2012; Banks, 2013). The fact that this C1 photo-identification catalogue fluke images were obtained from several non-related sources meant that the temporal and spatial extent to which fluke images were seasonally collected by these sources were inconsistent between collection regions and years (refer to Table 3.10 and 3.11), which ultimately means that capture probabilities were unequal between individuals. Subsequently, the characteristics of the C1 photo-identification catalogue data are not considered a true representation of the sub-stock, and any population estimation obtained through mark-recapture analysis through the use thereof should be interpreted with caution. Consequently, no abundance estimation has been carried out in this study.

Another assumption of open population mark-recapture models states that marks used for identification purposes are not lost or overlooked and that all marked animals are reported on recovery. Concerns surrounding the lack of stability in animals' identifiable features or markings over time have been raised for several cetacean species, including humpback whales (Hammond, 1986, 1990; Carlson *et al.,* 1990; IWC, 1990; Blackmer *et al.,* 2000; Gowans & Whitehead, 2001; Stevick *et al.,* 2001). Potential physical changes in humpback whales' flukes, such as the increase or decrease of fluke peaks and notches or ventral fluke marks/scarification and pigmentation patterns over the animals' lifespan, may result in "tag-loss" over time or non-reporting of positive matches (Carlson *et al.,* 1990; Stevick *et al.,* 2001; Stevick *et al.,* 2011). Such tag-loss or overlooking of positive matches have the potential to cause severe bias in parameter estimates (Stevick *et al.,* 2011). Furthermore, the likelihood of lost tags or overlooked matches of individual humpback whales represented in this catalogue could have further resulted from varying image quality. This could have increased the risk of biased population parameter estimates obtained from this catalogue's fluke images.

Based on the results of the within-year matching process, the limitations of the C1 photo-identification catalogue are evident. It is possible that the temporal and spatial extent of photo-identification data collection each year influenced the number of fluke images collected in different months and regions, thereby impacting the extent to which within-year matches were obtained within/between encounter months and regions. Consequently, the within-year matching process produced unique results for each year represented in the C1 photo-identification catalogue, resulting in an inability to make unbiased comparisons between them.

Nonetheless, the 11 within-year fluke image matches obtained from 2002 to 2008 revealed valuable information regarding the intra-seasonal migration patterns and fidelity of humpback whales along the south-eastern African (Table 3.8; Figure 3.11). Since the mean re-encounter interval of the within-year matches was 42.54 days, there is evidence indicating that humpback whales are broadly seasonally present on the south-eastern African coastline for extended periods. This observation is further supported by the fact that the longest known re-encounter interval obtained for a single humpback whale was 114 days. These extended re-encounter intervals are potentially attributed to the migration of the C1 sub-stock along their migratory corridor, northwards towards their breeding grounds and southwards following the breeding season. These results are comparable to sighting intervals obtained from humpback whales photographed within three localities along the eastern Australian migration corridor and breeding range, where sighting intervals between recaptures of individuals ranged from 5-125 days (Burns *et al.,* 2014). The extended re-encounter intervals also provide evidence for a longer seasonal occurrence of humpback whales off the south-eastern African coastline compared to the occurrence patterns displayed by other humpback whale sub-stocks wintering at their respective breeding grounds within the WIO. Research on the occurrence patterns of the humpback whale C4 sub-stock off Réunion Island revealed relatively shorter mean re-capture intervals ranging from 22-29 days, where the longest period recorded for a single whale was 64 days (Dulau-Drouot *et al.,* 2012). Within-year recapture results associated with the C3 sub-stock off Antongil Bay, Madagascar, revealed much shorter mean recapture intervals compared to the results form Réunion Island, ranging from 3-8 days (Cerchio *et al.,* 2008a).

Evaluation of the spatial movements of the within-year recaptured individuals provided valuable information on the intra-seasonal site fidelity and geographic pathways used by these individuals during a migration period. The relatively high number of within-year matches obtained from fluke images collected in the north-eastern coastal region provides substantial evidence that this region is a popular site temporally visited by the C1 sub-stock during migration. The temporal occurrence of humpback whales within this region is suggested by the short re-encounter intervals obtained from the three individual whales encountered and re-encountered within the same region in the same month (in July 2002: one day apart; in July 2007: two days apart; and in September 2008: one day apart). Since the individual that moved between Richards Bay and St Lucia was encountered and re-encountered one day apart (in July 2002), and since Richards Bay is situated south of St Lucia, it is assumed that the whale was encountered during northward migration. The timing of this individuals initial encounter and re-encounter month also fall within the northward migration period of humpback whales suggested for region (Findlay, 1994; Findlay & Best, 1996b, 2006; Findlay *et al.,* 2011a). The short re-encounter intervals associated with the two individuals that were re-encountered in St Lucia during the same month (in 2007 and 2008) may suggest that these whales were using the area for resting *on route* northward and southward migration, respectively. This resting activity is not an uncommon phenomenon during migration (Chittleborough, 1953; Dawbin, 1956; Chittleborough, 1965; Jenner *et al.,* 2001; Findlay & Best, 2006; McCulloch *et al.,* 2021).

Alternatively, the extended re-encounter intervals obtained from three individuals encountered in St Lucia during July/August and re-encountered again in October may suggest that these whales were encountered and re-encountered during northward and southward migration, respectively. The months during which these individuals were encountered and re-encountered corresponds to the northward and southward migration period suggested for whales in this region (Findlay, 1994; Findlay & Best, 1996b, 2006; Findlay *et al.,* 2011a). There is also little reason to believe that these extended re-encounter intervals display continuous occupancy in the area. In the past, most of the whales that traversed this region displayed travelling behaviour, suggesting that this area is a transit station during migration rather than a destination (Findlay, 1994; Findlay & Best, 1996b, 2006; Findlay *et al.,* 2011a).

The two within-year fluke image matches of individuals attained between St Lucia (EN) and Plettenberg Bay/Knysna (SC) (some 1,200 km apart) in 2005 and 2008, respectively, provide additional evidence on the long-range coastal movement of humpback whales during migration, as well as the migration pathways used by the C1S sub-stock. The months of the first and second encounters (October/November) in which the 2005 within-year match was obtained between these two regions suggested that the individual was encountered during the southward migration period on both occasions. Since the re-encounter interval of this individual was 45 days, the approximate distance that this whale possibly could have travelled per day, if the whale maintained its course and travel speed, is around 26.7 km moving at a rate of approximately 1.1 km/h. This daily travel distance and speed is significantly lower than other southward migration rates recorded for this sub-stock. Findlay (1994) proposed an estimated average instantaneous swim speed of 5.3 km/h for southward migrating whales off Cape Vidal (situated within the EN region), acquainting to an average daily travel distance of 127.2 km if speed is maintained over a twenty-four-hour period. However, it was mentioned that these instantaneous swim speeds estimated for southward migrating whales should be interpreted with caution, since the speeds were recorded from whales travelling along a region in the fast-flowing southward moving Agulhas Current during daylight hours (Findlay, 1994; Findlay & Best, 1996a, 2006; Findlay *et al.*, 2011a; Banks, 2013). Investigations during the southward migration of humpback whales moving along the west coast of South Africa (BSB) indicated that 70% of whale groups sighted moved at net speeds of less than 1.5 km/h (Best *et al.*, 1995). Records on the movement patterns of humpback whales migrating within the Eastern Indian Ocean along the western Australian coast suggested swimming speed for travelling whales to range between 3.6 - 14.4 km/h, while slower swim speeds (<3.6 km/h) are associated with resting whales (Chittleborough, 1953; Jenner *et al.*, 2001; Jenner & Jenner, 2011). Based on the migration rates suggested by Chittleborough (1953), Best *et al.* (1995), Jenner *et al.* (2001) and Jenner & Jenner (2011), it is likely that the individual re-encountered between St Lucia and Plettenberg Bay/Knysna in 2005 was travelling and resting, explaining the longer than expected time between its encounter and re-encounter compared to if it was not resting. The encounter/re-encounter months (August/December) in which the within-year match was obtained between these two regions in 2008 suggested that the individual was encountered during northward migration and re-encountered during the southward migration. The re-encounter interval of this individual also indicated that the animal was present on the coast for a minimum of three months; this period is not impossible since humpback whales have been revealed to occur on this coastline for ten months during migration (Olsen, 1914; Lea, 1919; Rayner, 1940; Mackintosh, 1942; Dawbin, 1966; Matthews, 1973; Gambell, 1976; Best & Surmon, 1974; Best, 1994; Best & Ross, 1996; Findlay & Best, 1996b; Dawbin, 1997; Banks, 2013).

The two within-year matches of fluke images obtained between the Bazaruto Archipelago (MC) and St Lucia (EN) (in 2003: October/November; and 2007: September/October), links humpback whales breeding in central Mozambique to the migration corridor previously associated with the C1S sub-stock. The months during which these individuals were encountered/re-encountered correspond to the southward migration period for humpback whales along this coastline. Since these animals took 22 and 39 days to move between the two regions, respectively, they travelled at approximately 1.7 and 1.0 km/h, assuming they maintained their course and a continuous swim speed. These speeds also correspond to the resting travel speeds mentioned by Chittleborough (1953), Best *et al.* (1995), Jenner *et al.* (2001) and Jenner & Jenner (2011).

The 48 between-year fluke image matches obtained from 45 unique humpback whales provides valuable evidence on the long-term migration fidelity, movement patterns and intra-regional migratory linkages displayed by humpback whales utilizing the Southeast African coast as migration corridor and breeding ground (Table 3.9; Figure 3.12).

Mark-recapture analyses performed with photo-identification data has proven to be a valuable tool for obtaining re-sighting histories, evaluating site-specific annual return rates, determining re-encounter intervals, estimating the number of years that an individual was sighted, and documenting the movement of individuals between different locations (*e.g.,* Clapham *et al.,* 1993; Chaloupka *et al.,* 1999; Felix & Haase, 2001; Wedekin *et al.,* 2010; Zerbini *et al.,* 2010; Witteveen & Wynne, 2017).These population parameter estimates have especially been valuable for obtaining information on site fidelity trends displayed by individuals, enabling a better understanding of how populations are structured. The reason owing to the highly variable seasonal re-encounter rates (ranging between 0.7 - 8.5%) and the resultant relatively low mean re-encounter rate (3.9%) obtained from the between-year fluke image matching process is unclear. However, estimates of seasonal re-encounter rates have previously been shown to be influenced by several factors, including temporal and spatial variation in effort performance, population size, and variability of photographic “catchability”, which in turn is highly influenced by the variable behaviour patterns of different individuals, weather conditions, the number of photographers (Baker *et al.,* 1986; Calambokidis *et al.,* 2001; Wedekin *et al.,* 2010; Robbins *et al.,* 2011; Burns *et al.,* 2013; Witteveen & Wynne, 2017).

Nonetheless, since 50% of the between-year matched individuals were re-encountered after extended timespans of three or more years after their initial encounter and/or first re-encounter, there is sufficient evidence indicating the long-term migration fidelity of the C1 sub-stock humpback whales to the south-eastern African coastline. The remaining between-year matched individuals were re-encountered after annual (29%) and biennial (21%) periods. The idea of long-term migration fidelity is further supported by the fact that three individuals were encountered and re-encountered in three different years, where their re-encounter intervals ranged over timespans of five years (two individuals) and eight years (one individual). Based on these results, there is reason to believe that a considerably larger number of previously identified whales return to the south-eastern African coast each year; however, failure to detect any between-year re-encounters of individuals before 2000, between 2012 to 2017, and in 2019 during the image matching process could have been restricted by the low availability of fluke images available for these years.

Furthermore, the fact that 98% of the between-year matches were obtained from individuals that were initially encountered along the South African coast could be explicable by the fact that 87% of the C1 sub-stock photo-identification catalogue fluke images were collected within South African coastal regions. Additional to the nine within-year matched individuals encountered and re-encountered in South African regions during migration, the 40 individuals encountered and re-encountered within/between these same regions between different years (37 individuals seen twice; 3 individuals seen three times) provides further evidence on the usage of the South African coastal waters by the C1S sub-stock individuals during migrations. Some levels of long-term migration fidelity to Plettenberg Bay/Knysna (within the SC region) are suggested by four between-year encounters/re-encounters obtained in this area. Additionally, strong long-term fidelity to St Lucia (within the EN region) is indicated by 22 between-year encounters/re-encounters of individuals obtained in this area. Supplementary to the within-year match obtained between Richards Bay and St Lucia, four between-year re-encounters obtained between these two locations confirm that these areas form part of the migration corridor for this sub-stock. Furthermore, thirteen between-year matches (together with the one within-year match) obtained between locations within the SC region (Plettenberg Bay/Knysna) and EN region (Cape Vidal and St Lucia) confirms that these areas are used during migration.

The fact that low numbers of fluke images in the C1 sub-stock photo-identification catalogue were collected in Mozambique regions (MS and MC) (refer to Table 3.7) may have accounted for the lack of within-, and between-year encounter/re-encounter of individuals within/between sub-areas within the breeding ground. However, since humpback whales constantly move between sub-areas within breeding ground regions, individuals often only spend brief periods in some area (Mattila *et al.,* 1994; Cerchio *et al.,* 2008a, 2008b; Wedekin *et al.,* 2010; Erst *et al.,* 2011; Baracho-Neto *et al.,* 2012; Dulau-Drouot *et al.,* 2012; Witteveen & Wynne, 2017). These phenomena also may have accounted for the absence of encounters/re-encounters of individuals in Mozambique regions within/between years.

Similarly, the low number of fluke images available for the Mozambique regions could have accounted for the low numbers of between-year recaptures of individuals obtained between Mozambique and South African regions. Nevertheless, the two between-year matches obtained between Plettenberg Bay/Knysna (SC) and Ponta Mamoli (MS), one between-year match obtained between Richards Bay (EN) and Ponta Mamoli (MS), and two between-year matches obtained between St Lucia (EN) and the Bazaruto Archipelago (MC), links the migration corridor along the South African coastline to the C1S sub-stock breeding ground in southern and central Mozambique. These results confirm the migratory connection of humpback whales travelling between South Africa and Mozambique as suggested by numerous authors (*e.g.,* Olsen, 1914; Findlay, 1994; Findlay *et al.,* 1994; Best & Ross, 1996; Best *et al.,* 1998; IWC, 2000; Cerchio *et al.,* 2008b; Erst *et al.,* 2011; Banks, 2013). However, it does not necessarily indicate that these individuals belong to the C1S sub-stock breeding in southern and central Mozambique regions and may possibly be individuals associated with the C1N sub-stock breeding off northern Mozambique, Tanzania, and Kenya.

4.6 Characteristics of Individual Humpback Whales and Flukes Identified within the Humpback Whale C1 Sub-Stock

It is believed that the 1,746 individual humpback whales identified in the humpback whale C1 sub-stock photo-identification catalogue represent only a portion of the sub-stock since the last abundance estimate for this sub-stock was approximately 7,035 whales (Findlay & Best, 2006; Branch, 2006; IWC, 2010; Branch, 2011). Since this abundance estimate was calculated over a decade ago, and it is estimated that the stock annually increases at a rate ranging between 9.0% to 12.3% (Findlay & Best, 2006), the abundance estimate of 7,035 whales should be considered as the minimum size of the stock and highlights the need to re-evaluate the population to allow for a more updated estimate of the stocks' size.

Furthermore, phenotypic characteristics of animals can provide valuable insight into the geographic structure of populations (Matthews, 1937; Baker *et al.,* 1985, 1986). It is evident from historic whaling records that the body or fluke colouration patterns of humpback whales often vary between regions (Lilie, 1915; Pike, 1953; Chittleborough, 1965; Allen *et al.,* 1994; Rosenbaum *et al.,* 1995). Consequently, there has been a growing focus on the value of investigating the pigmentation pattern and the distinctive characteristics of individual humpback whales' flukes to gain information on the discreteness of breeding populations and the levels of relatedness among sub-stocks within breeding populations (Matthews, 1937; Omura, 1953; Pike, 1953; Chittleborough, 1965; Baker *et al.,* 1985, 1986; Allen *et al.,* 1994; Rosenbaum *et al.,* 1995; Elwen *et al.,*2013). Among the central and eastern North Pacific humpback whale stocks, Baker *et al.* (1985) observed a longitudinal cline in the ventral fluke pigmentation ranks of the individuals across five feeding regions, where the fluke colourations of whales feeding in the western regions were on average lighter than those feeding in the eastern regions. Presently, humpback whale populations in the Southern Hemisphere are divided into geographically discrete feeding populations which segregate to distinct breeding regions, where evidence indicates that little genetic exchange occur between these populations on feeding and breeding grounds, resulting to highly structured stocks and distinct subdivisions amongst populations (*e.g.,* Mackintosh, 1948, 1965; Chittleborough, 1965; Baker *et al.,* 1990; Clapham & Mayo, 1990; Katona & Beard, 1990; Perry *et al.,*1990; Clapham *et al.,* 1993; IWC 1998). It is also believed that the seasonal migratory summer and winter destinations and residency of this species is maternally directed (Clapham & Mayo, 1987; Baker *et al.,* 1990; Rosenbaum *et al.,* 1995). Consequently, it is assumed that the fluke colouration patterns of individual whales associated with a specific feeding stock is determined by the consolidation of pigmentation patterns exhibited by the individuals annually visiting the associated stocks' breeding region, and the level of inter-oceanic mixing that occurs between breeding sub-stocks (Baker *et al.,* 1985, 1986; Allen *et al.,* 1994; Rosenbaum *et al.,* 1995). By evaluating the distribution of the different fluke colouration types of the humpback whales identified within the C1 photo-identification catalogue across different sub-regions along the Southeast African migration corridor and breeding grounds, it is possible to determine the level of distinctiveness or similarity of individuals between these regions, thus providing valuable information on the intra-regional structure of the stock and the levels of connectivity that exist between these sub-regions. Subsequently, since over 40% of the individual humpback whales photographed in each of the sub-regions along the migration corridor and Mozambique breeding ground exhibited predominantly white (type 1) fluke colouration patterns (Figure 3.13), there is evidence proposing migration connectivity between sub-regions, and a reason to believe that individuals utilising the South African coast as migration corridor disperse to a common breeding ground off Mozambique. Moreover, these findings were comparable to results obtained by Rosenbaum *et al.* (1995), who analysed the geographic variation in fluke colouration patterns of humpback whale populations globally and revealed that individuals with lighter coloured flukes dominated the Southern Hemisphere stocks. Although the case, findings from this study does not necessarily provide conclusive evidence for the migratory connections and utilization of a common breeding ground and should be coupled with genetic evidence for more accurate representations of the movements of the C1 sub-stock. Furthermore, sampling bias in each of the regions could have affected the results, since it has previously been demonstrated that fluke colouration is often gender-specific, where males generally have lighter coloured flukes compared to females (Lillie, 1915; Matthews, 1937; Baker, 1985; Allen *et al.*, 1994; Rosenbaum *et al.*, 1995). This would especially have affected results obtained from breeding regions, where higher sampling effort in some years may have resulted to higher sampling of competitive groups, which are known to be dominated by males (Clapham *et al.*, 1992).

Additional to fluke colouration type, it has been demonstrated that variation in the distinctiveness of humpback whale flukes between regions may also provide valuable insight into the structure of populations (Steiger *et al.,* 2008; Elwen *et al.,* 2013). Although the distinctiveness of humpback whale flukes is determined according to a combination of three characteristics (see Chapter 2, Section 2.3), the presence and uniqueness of natural markings and/or scars on individual whales flukes, as a result of predation (*e.g.,* Shevchenko, 1974; Whitehead & Glass, 1985; Dolphin, 1987; Jefferson *et al.,* 1991; Mikhalev, 1997; Naessig & Lanyon, 2004; Mehta *et al.,* 2007; Steiger *et al.,* 2008; Dwyer & Visser, 2011), ship-strikes and entanglement (*e.g.,* Jensen *et al.,* 2004; Robbins & Mattila, 2004; Meÿer *et al.,* 2011), barnacle and ectoparasite attachment (*e.g.,* Olsen, 1914; Angot, 1951; Osmond & Kaufman, 1998), and bacterial, viral or fungal infections (*e.g.,* Matthews, 1978; Higgins, 2000), may vary spatially an temporally amongst populations, providing a useful indicator of levels of distinctness between oceanic populations, and the levels of connectivity between sub-stocks breeding within the same ocean (Best, 1969; Smith *et al.,* 1999; Steiger *et al.,* 2008; Elwen *et al.,* 2013). Consequently, by evaluating the distinctiveness of the individual humpback whale flukes identified in the catalogue, it was possible to obtain some information on the uniqueness and extent of natural markings and/or scars on these flukes. Furthermore, by comparing the results across sub-regions along the south-eastern African coast, it is possible to obtain information on level of intra-regional migration connectivity that occur along this coast. Subsequently, it appears that individuals identified in all sub-regions along the C1 sub-stock migration corridor and breeding grounds possess some levels of unique natural markings and/or scars (23%), while some 38% to 47% of individuals had no unique natural markings or scars present on their flukes (Figure 3.14). Irrespective of the results, information obtained from this analysis is limited, and a more in-depth evaluation on the type of scars/natural markings occurring on these flukes is required to connect individuals to specific regions more accurately, and to draw accurate conclusions on the intra-regional structure of the C1 sub-stock based on this analysis.

CHAPTER 5 CONCLUSION & RECOMMENDATIONS

This study provides valuable and novel information on several key aspects pertaining to photo-identification of the humpback whale C1 sub-stock migrating and breeding along the south-eastern African coast.

With respect to the historic dataset, the value of exploiting citizen science data to fill data gaps resulting from traditional research limitations is emphasised, and the usefulness of these datasets to represent populations over broad spatial and temporal scales is demonstrated. From the quality assessments of the historic commercial BBWW fluke images, it is possible to conclude that citizen science has the potential to produce data of sufficient quality necessary for conducting successful photo-identification analyses. In connection with the new dataset, results from the opportunistic data collecting efforts on commercial BBWW vessels raised concerns surrounding the effectiveness of the short-term use of these opportunistic platforms to collect research-specific scientific data. The efficacy of utilizing these opportunistic platforms has been questioned, particularly due to the constraints and limitations associated with their short-term use, which makes accurate and unbiased data collection difficult, regardless of the cost-effective nature of their use. In contrast, it was evident that the short-term dedicated scientific surveys conducted off Bazaruto, Mozambique, and Durban, South Africa, produced valuable results, providing conclusive evidence on the distribution and movement of humpback whales occurring off these regions. Results obtained from the dedicated survey off Bazaruto confirms that extensive numbers of humpback whales are distributed off this coast during September where southward migrating movement is evident.

The results from this survey also raised questions on the influence of some marine vessels on the efficiency of photo-identification data collection: however, more extensive research is required to make any valid conclusions. With respect to the dedicated survey conducted off Durban, results confirmed the occurrence of humpback whales off this region during July and August, where northward migrating movement is evident. Overall, the results obtained from these surveys may suggest that research-specific data collection during short-term dedicated scientific surveys is possibly more efficient compared to data collection during opportunistic surveys on commercial BBWW vessels conducted over a longer period.

One of the key outcomes of this study was the successful development of a multiregional photo-identification catalogue representing humpback whales associated with the C1 sub-stock.

During the catalogue development process, it became evident that performing image quality analyses and determining the distinctive nature of the photo-identifiable features of the individual was of high importance, particularly for equal recognition between individuals and unbiased analyses of photo-identification. Although the photo-identification data included in this catalogue represents the humpback whale C1 sub-stock over extensive temporal and spatial scales, large data gaps prevent consistent assessment and the accurate illustration of the distribution and migration patterns of this population. Through awareness-raising among research organizations, tour operators, and other marine wildlife groups on the importance of this catalogue to provide key information necessary for the successful conservation and management of this sub-stock, and by encouraging these sectors to voluntarily collect photo-identification data, it is possible to expand the temporal and spatial scope of the catalogue, thereby enabling a more accurate representation of the population. Additional to the fact that this catalogue provides a valuable non-invasive tool to obtain novel information on the distribution, migration, and structure of humpback whale populations within the WIO, it offers a valuable resource to facilitate international collaborations in humpback whale research. The maintenance and expansion of this catalogue could significantly contribute towards a better understanding of the population ecology of humpback whales throughout the Southern Hemisphere through the examination of the animal's movement patterns on small and broad scales.

Through the photographic matching of this catalogue's data, results produced conclusive evidence on the intra- and inter-seasonal movement and distribution patterns, and site fidelity of humpback whales migrating and breeding along the south-eastern African coastline. From the within-year matching results, we can infer that humpback whales travel extensive distances and use multiple regions along the South African coast within a migrating season, such as the south coast, north-eastern, and central Mozambique regions Additionally, from the within-year match results it is possible to conclude that humpback whales are broadly seasonally present on this coast for extensive periods of at least 114 days. The between-year match results provide evidence that humpback whales display long-term fidelity to the south-eastern African coastline, and that the pathway utilized by this population during migration at minimal extends between the south coast of South Africa and central Mozambique.

Furthermore, based on previous abundance estimates (Findlay & Best, 2006; Branch, 2006; IWC, 2010; Branch, 2011), it can be concluded that the photo-catalogue represents only a fraction of the individuals associated with the C1 sub-stock. However, the catalogue provides an important contribution on which future catalogues may be based. Additionally, it's evident that phenotypic characteristics, such as the colouration type and distinctiveness of humpback whale flukes may provide valuable insights into the local and broad-scale structure of populations and sub-stocks within breeding populations.

5.1 Recommendations for Future Research:

Through the long-term acquisition of information on humpback whales inhabiting the Indian Ocean, our knowledge and understanding of the species' behaviour and ecology within this region continue to expand. As a key objective of this study, extensive photo-identification techniques applied to information gathered from humpback whales seasonally utilizing the southern Western Indian Ocean have significantly enhanced our understanding and knowledge of the C Breeding Stock structure, migration, and fidelity patterns along this region. It is, however, fundamental to continue the collection of this type of data in the study area to improve our understanding of the species on several scales and to allow the tracking of population changes over time through photo-identification analysis.

Future photo-identification humpback whale research efforts planned along the Western Indian Ocean should include areas of historically poor coverage, most notably the South Coast, south-eastern, southern Mozambique, and central Mozambique regions. It is fundamental to acquire a more continuous and accurate representation of the intra-regional population structure, width and extent of the migration stream, the migration pathways utilized by these animals, and the level of connectivity between the migration and breeding area along this region. Continuous and consistent data collection efforts are therefore required to obtain an updated and accurate abundance estimate of the C1S sub-stock. It is further advised that an additional photo-identification catalogue is developed for the C1N component of the C1 sub-stock, and subsequently compared to the C1S catalogue compiled as part of this study, to determine the northern migration and breeding limits of the C1S component, the level of intermixing that occurs between the C1S and C1N sub-stock individuals, and the northern Kenya distribution limits of the C1 sub-stock.

Information on the western and southern limits of the south-eastern African migration corridor utilized by the C1 sub-stock is limited and requires further investigation. Furthermore, the photo-identification catalogue developed during this study should be evaluated against catalogues representing the other C sub-stocks breeding within the Western Indian Ocean, including the C2, C3, and C4 sub-stocks so potential matches can be detected, which will provide a better understanding of the level of exchange between these sub-regions, and the overall inter-oceanic structure of the C Breeding Stock. It is also advised that this catalogue is compared to the Antarctic Humpback Whale Catalogue, particularly photo-identification images from Management Areas II to IV, to increase our understanding of the level of connectivity between these sub-stocks' feeding and breeding grounds. The level of connectivity between the C and B Breeding Stocks is also poorly understood and should therefore be considered a focus area for future research.

Although the value of citizen science as a means of low-cost data collection has been established, the use thereof to obtain information on humpback whales occurring along the south-eastern African coastline is poor. The South African whale watching industry has evidently expanded over the last decade and should be approached more frequently in the future as a valuable source of marine science data.

Moreover, it is recommended that the information provided in this thesis should be incorporated into any future management and conservation efforts of the humpback whales occurring along this Eastern African coast, as well as any future marine special planning events.

5.2 Data Archiving

The humpback whale C1 photo-identification catalogue developed during this study has been archived with WILDOCEANS, a programme of the WILDTRUST, and Cape Peninsula University of Technology for future use.

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