Occurrence, feeding ecology, and population structure of two dolphin species, *Tursiops aduncus* and *Delphinus delphis*, off the Wild Coast of South Africa

Thesis submitted in fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY
of
RHODES UNIVERSITY

by

MICHELLE CAPUTO

Supervised by Professor William Froneman

March 2019

Abstract

Dolphins are apex predators and their movements, foraging activities and population dynamics play an important role in shaping their environment. Understanding their occurrence, movement patterns, and trophic ecology is essential to their conservation, especially as they are considered sentinel species. The Wild Coast of South Africa's Eastern Cape, is characterized by the annual sardine (*Sardinops sagax*) run, which serves as an important foraging event for apex predators, including Indo-Pacific bottlenose (*Tursiops aduncus*) and long-beaked common dolphins (*Delphinus delphis*). Despite the ecological significance of this event, no dedicated surveys for these species have previously been conducted in this area. The main objectives of this research were to: investigate long-term occurrence of dolphins during the sardine run to determine if there have been any changes over the past 19 years, as has been predicted from common dolphin dietary investigations and anecdotal evidence; to determine short-term occurrence and movement patterns of selected inshore delphinids within the area, which is characterized by three marine protected areas (MPAs); and to use stable isotope analyses to determine trophic relationships and population structure of bottlenose and common dolphins within the region. Long-term data consisted of 131 opportunistic aerial surveys conducted between May and July over the period 1996 to 2014. Results from these surveys indicate that common dolphins, typically associated with sardines, decreased significantly in average group size over the study period (p=0.0343). Bottlenose dolphins, demonstrated no such trend (p=0.916). For both species, greater majority (> 70% of total counts) of sightings were made inside the MPAs. Short-term boat-based surveys were conducted three times a year between June 2014 and December 2016, contributing to a total of 47 days of surveys divided into three locations: Amathole, Hluleka, and Pondoland, each containing a MPA. Density and group size data were analyzed for both species and photographic identification analysis was performed for photographs of bottlenose dolphin dorsal fins. Results indicate that animal and sighting density did not differ temporally (bottlenose dolphin: sighting density – p=0.398, individual density –p=0.781; common dolphin: sighting density –p=0.472, individual density – p=0.204). Environmental factors (sea surface temperature, depth, substrate, and distance from shore) appeared to have limited effect on individual and sighting density and group size for both species ($p>0.05$). Photographic identification of bottlenose dolphins resulted in 2149 individuals, with a 11.8% resighting rate, with the highest resighting rate within the Pondoland MPA (16.1%). The resighting count did not differ temporally between monthly survey based on generalized linear models ($p=0.866$), but did differ between study areas ($p<0.0001$). These results provide the first evidence of the occurrence of both species of dolphin off the Wild Coast, as they were sighted in this region in all survey months. There was no trend in density based on temporal or environmental factors, which suggests other factors are influencing their occurrence. Resightings of bottlenose dolphins within the area suggest that there is some degree of residency, though the majority of animals were only sighted on a single occasion and there was no plateau in the discovery curve. A total of 256 biopsy samples (bottlenose dolphins =128; common dolphins=128) were collected during boat-based surveys. Bottlenose dolphin samples were also collected from adjacent areas to the southwest (Algoa Bay, n=22) and northeast (KwaZulu-Natal (KZN), n=20) of the Wild Coast to investigate similarities and differences between these areas. Despite a high degree of niche overlap between the two species (41%), common dolphins fed with a broader niche (standard ellipse area probability 0.89) than bottlenose dolphins in the summer and a narrower niche in the winter (probability 0.94). There was a clear spatial variation in the diet of bottlenose dolphins along the coast, with individuals from Algoa Bay and Amathole demonstrating 0% niche overlap with individuals from KZN, but the mechanism for these differences remains unclear as other species from South African waters demonstrate a strong southwest to northeast gradient in nitrogen for the Eastern Cape coastline. This research provides valuable baseline information regarding dolphins off the Wild Coast of South Africa, which remained largely unknown. My results indicate that bottlenose dolphins may be more resident in the Wild Coast than previous predicted, and confirm that common dolphins are highly mobile in this area.

Acknowledgements

The Wild Coast, aptly named, was an adventure from the start. Thank you to my wonderful colleague, Dr. Thibaut Bouveroux, for facing this adventure with me head on (even through near-death experiences), and for your excellent advice, positivity, and support throughout my project. To my brave and trustworthy skippers, Juan Greeff and Lindelwe Machane as well as Morven Maclean and Anthony Opperman, thank you for keeping us safe in this dangerous environment and for introducing me to the most beautiful area in South Africa. This project would not have been possible without the hard work of my excellent team: Titus Shaanika, Eduard Drost, Ross-Lynne Weston, Simone Fick, Marie Leboutte, Alejandra Vargas, Ilanda Greeff, Professor Carminita Frost and her research group, Renee Koper, and all the Eastern Cape Parks and Tourism Agency (ECPTA) rangers for their help in the surf and at sea. Thank you to Dr. Leszek Karczmarski for the loan of his biopsy gun. A special thanks to Megan van der Bank from the ECPTA for her bravery, support, and guidance and thank you to Dr. Stephanie Plön for her contributions to this research. Thank you to the University of Pretoria's Stable Isotope Laboratory, and specifically Dr. Grant Hall, for conducting the stable isotope analysis.

Financial support was provided by PetroSA for fuel and equipment costs, Rhodes University for laboratory costs and analyses, and the ECPTA, providing us with boats and skippers, as well as accommodation in their amazing nature reserves during our study. My bursary was funded by the National Research Foundation, and thanks to them for giving me the opportunity to study in this beautiful country.

This project would not have been possible without the unwavering support of my supervisor, Professor William Froneman, who was an endless source of wisdom and encouragement throughout this process. Thank you for always having my back, no matter the circumstance. Thank you to Rhodes University staff and administration for helping me to navigate academics in a foreign country.

Studying abroad comes with its own set of challenges, which I was only able to navigate thanks to the support of my family and friends. Thank you to my parents, Tullio and Mary Anne Caputo, for pushing me to follow my passion to the other side of the world. I know it has not been easy to be so far apart, but I truly appreciate your relentless encouragement and your strength, pushing me to be an ambitious, independent, and adventurous woman. This research would not have been possible without you in so many ways. To my family back home, thank you for putting in the effort to stay tight knit, for picking me up when I was feeling down, and celebrating small victories with me. I am so grateful to the friends I have met in South Africa, who have truly made it feel like home, welcoming me and providing the support system I needed to get through the challenges of this project. And to the friends back home, for continually providing encouragement for all these years, no matter how far apart we may be.

I met my loving partner, Anthony Harris, along this journey and he had no idea what he was getting into but has taken it all in stride. To Anthony, I’ve been inspired by your own dedication and passion in your profession, and would not have been able to complete this work without your support and encouragement. There were long field trips apart, and challenges along the way, but you truly have been my teammate through everything and I could not have done it without you. Thank you also to our mum, Bertha Harris, for all your kindness and support.

This project literally almost killed me … twice. The support of all the people mentioned above helped me to persevere and I am forever grateful for their encouragement throughout this experience. Special mention to the doctors and nurses at Greenacres hospital, where I completed this thesis. What a “Wild” ride it has been. Thank you

Preface

Each chapter in this thesis is stand-alone, and has been published or submitted for publication to local and international peer review journals. As such, there may be some repetition in the introductory sections of the chapters and each chapter includes a reference section. This project formed part of a larger and ongoing research project led by Dr. Stephanie Plön from Nelson Mandela University which investigates cetacean ecology in the Eastern Cape province of South Africa, under research permit from the Department of Environmental Affairs: RES2014/56, RES2015/14, RES2016/57.

Table of Contents

List of Figures

List of Tables

Chapter 1: General Introduction

Dolphins and other apex predators, are considered sentinels in marine ecosystems, providing an indication of the health and richness of habitats (Wells *et al.* 2004). Their distribution and abundance are often linked to the distribution and abundance of their prey and predators (Bowen 1997; Peddemors and Cockcroft 1997; Heithaus and Dill 2002; Jefferson et al. 2008; Rosel et al. 2009; Möller et al. 2010), indicating areas of high/low productivity based on their movement patterns and habitat use. As such, changes in dolphin abundance and distribution can be useful in monitoring long-term changes to ecosystems with changing climate and increased anthropogenic impacts on the marine environment (Ross 2000; Wells et al. 2004; Bossart 2006; Moore 2008).

The South African government has recently recognized the importance of the marine sector for future economic development (Department of Science and Technology 2008; National Planning Commission 2011; Department of Environmental Affairs 2014), investing in research and infrastructure in this sector (Department of Science and Technology 2008; Treasure et al. 2013) and including specific marine objectives in the 10-year plan and 2030 objectives document (Department of Science and Technology 2008; National Planning Commission 2011). Both the 10-year plan and 2030 objectives identify marine resources as key for future economic growth and poverty alleviation, recognizing the importance of understanding and conserving this resource (Department of Science and Technology 2008; National Planning Commission 2011). Main objectives outlined by the National Planning Commission include monitoring and mitigating the impacts of climate change along the South African coastline and Southern Ocean to conserve ocean resources (National Planning Commission 2011; Department of Environmental Affairs 2014). Baseline data and monitoring programs are central to achieving this objective (National Planning Commission 2011). The lack of research funding historically has contributed to gaps in our knowledge of the marine environmental in South African territorial waters (Treasure et al. 2013).

1.1 Species Overview

1.1.1 Tursiops aduncus

Tursiops are found worldwide in all oceans with the exception of the polar regions (Reeves et al. 2002; Jefferson et al. 2008) and have been declared 'data deficient' (Hammond et al. 2012). To date two species have been identified: Indo-Pacific bottlenose dolphin (*T. aduncus*) found in South Africa, off east Africa, Australia, Asia, the Solomon Islands, and New Caledonia, and the common bottlenose dolphin (*T. truncatus*) found throughout the worlds' oceans (Jefferson et al. 2008). It has been suggested that a third species occurs in Australian waters (Charlton-Robb et al. 2011), though this remains unconfirmed (Perrin et al. 2011).

The Indo-Pacific bottlenose dolphin can be distinguished from the common bottlenose dolphins by appearance as they are generally smaller with spotted ventral patterns and shorter beaks (Reeves et al. 2002; Natoli et al. 2004), and they are usually found in coastal habitats (Ross et al. 1989; Reeves et al. 2002). The coastal *T. aduncus* usually travel in groups of less than 20 animals and are considered highly mobile (Reeves et al. 2002; Rosel et al. 2009). Their diet can vary widely, consisting of schooling, demersal, and reef fishes as well as cephalopods, mainly squid (Reeves et al. 2002; Jefferson et al. 2008). In South African territorial waters, their preferred habitat is nearshore (within 1km of the coast), in shallow waters (<30m depth) (Ross 1984; Ross et al. 1989; Cockcroft et al. 1990, 1991; Findlay et al. 1992). This coastal habitat puts them at high risk of anthropogenic influences, such as bycatch in the KwaZulu-Natal (KZN) shark nets, established to protected people from shark attacks at popular beaches, and pollution (Ross et al. 1989; Cockcroft et al. 1990, 1991; Natoli et al. 2008; Dudley and Cliff 2010). Additionally, increasing coastal development may lead to increased disturbance and habitat degradation.

In both bottlenose dolphins species, group size varies daily (Shane et al. 1986) and exhibits a fission-fusion grouping pattern, whereby associations between individuals vary in space and time to maximize their fitness by increasing survival or reproductive success (Smolker et al. 1992; Connor et al. 2000, 2011; Mann et al. 2000; Moller et al. 2002; Stensland et al. 2003; Gowans et al. 2007; Connor and Krützen 2015). The main drivers to group living include environmental factors which concentrate animals in specific regions, protection against predators, and improved foraging abilities due to cooperative feeding strategies (Stensland et al. 2003; Gowans et al. 2007). Additionally, associations between individuals have been observed to improve the communication and social learning between animals (Gygax 2002), improve mating success of adult males (Mann et al. 2000; Krützen and Sherwin 2004), and increase calving rates (Mann et al. 2000). Potential costs of living in large groups are competition for food resources (Heithaus and Dill 2002; Lodi and Monteiro-Neto 2012), transfer of pathogens and ectoparasites between individuals potentially leading to epizootics (Connor et al. 2000; Chivers et al. 2007; van Bressem et al. 2009; Ebensperger et al. 2012), dominance and competition between males for access to reproductive females (Connor and Krützen 2015), or a higher probability of being detected by a predator (Hebblewhite and Pletscher 2002).

In southern African coastal waters, *Tursiops aduncus* are widely distributed and their distribution, genetic, and general ecology have been documented in KZN waters (Cockcroft et al. 1991; Cockcroft et al. 1990; O’Donoghue et al. 2010a,c; Photopoulou et al. 2011; Natoli et al. 2004). In this area, it has been hypothesized that there is a resident stock and a migratory stock (present in the winter months) (Cockcroft et al. 1991; Goodwin et al. 1996). Other studies on *T. aduncus* in South Africa include population estimates at selected sites along the south-eastern seaboard, including Plettenberg Bay, and Algoa Bay as well as during the annual sardine run off the Wild Coast of South Africa (Ross et al. 1989; Phillips 2006; Reisinger & Karczmarski 2009). Due to the highly mobile nature of these animals, the lack of research on movement between areas along the coast, site fidelity, and population connectivity/structure presents a large gap in our knowledge of their presence and ecology in South African waters.

Figure 1.1: Adult bottlenose dolphin (*Tursiops aduncus*) from off the Wild Coast, South Africa (Photo by: Dr. Thibaut Bouveroux)

1.1.2 Delphinus delphis

The genus *Delphinus* can be divided into the long-beaked and short-beaked (*D. delphis*) types, though their classification remains controversial (Natoli et al. 2006; Amaral et al. 2012). Long-beaked common dolphins (referred to hereafter as common dolphin) are found in waters of South Africa, as well as other tropical to warm-temperate waters worldwide (e.g. Australia, South America, Japan, etc.) (Reeves et al. 2002; Jefferson et al. 2008; Natoli et al. 2006, see Figure 1.2). These animals have been 'data deficient', (Hammond et al. 2008). Common dolphins have a near-shore distribution, staying further offshore than *Tursiops,* and can travel in relatively large groups compared to other species of delphinids in South African marine waters (Reeves et al. 2002; Jefferson et al. 2008).

Common dolphins are considered one of the most gregarious cetacean species (Evans 1994; Reeves et al. 2002) as they occur in large groups of 50-400 animals on average worldwide, with superpods of several thousand animals reported (Evans 1994; Reeves et al. 2002). These animals are often found in large groups feeding cooperatively on schooling fishes (Gowans et al. 2007; Ambrose et al. 2013). It is thought that the large groups also afford common dolphins increased protection from predators (Acevedo-Gutierrez 2002; Gowans et al. 2007). In South Africa, large groups have been found along the Wild Coast area, with upwards of 500 animals in a single group (O'Donoghue et al. 2010b, a, c).

In South African waters, aerial survey data suggest year-round distribution of common dolphins in Eastern Cape waters with seasonal migration off the Wild Coast into KwaZulu-Natal waters during the annual sardine run (Cockcroft & Peddemors 1990; O'Donoghue et al. 2010a,c; Ross et al. 1989). Cockcroft and Peddemors (1990) suggest that animals remain between the coastal cities of Port Elizabeth and East London for most the year in lower relative densities, only travelling northward into the Wild Coast during the winter, where anecdotal evidence suggests that their densities increase. Typically, common dolphins feed on schooling fishes, and they are found feeding on large numbers of schooling sardines which occur along the Eastern Cape coast during the austral winter (Cockcroft and Peddemors 1990; Reeves et al. 2002; Jefferson et al. 2008; O'Donoghue et al. 2010b, a). Though research suggests diets of common dolphins in South Africa have shifted with changes in the sardine run, animals continue to migrate along the Wild Coast to KZN waters during the austral winter (Ambrose et al. 2013).

Figure 1.2: Adult common dolphin (*Delphinus delphis*) from off the Wild Coast, South Africa (Photo by: Dr. Thibaut Bouveroux)

1.1.3 Dolphin population structure and feeding ecology,

Defining population structure for marine mammals is often difficult as these animals are highly mobile within their preferred habitats and there are limited obvious physical barriers in the marine environment (Avise 1994; Krützen and Sherwin 2004). Specifically for delphinids and other cetaceans, the mobile nature of these animals, along with a lack of obvious barriers to gene flow, make defining populations challenging (Avise 1994; Krützen and Sherwin 2004; Mendez et al. 2011). Understanding population structure of delphinids is important for conservation and the management of species (Krützen and Sherwin 2004; Mendez et al. 2007; Möller et al. 2010; Mirimin et al. 2011). This has led to various approaches (e.g. Browning et al. 2014; Quérouil et al. 2013; Pinela & Borrell 2010), which consider that genetic structure, though important in identifying panmitic populations, may not be sufficient in separating sub-populations or sub-groupings given the potential for large geographical separations between genetically similar animals (Mendez et al. 2007). Investigations of habitat and resource specialization of dolphin groups can help differentiating sub-populations or sub-groupings in local areas where genetically similar animals exhibit differing feeding strategies (Barros et al. 2010; Mirimin et al. 2011; Mendez et al. 2013). These different strategies can be determined using analysis of stable isotopes (Best, P., Schell 1996; Pauly and Trites 1998; Walker and Macko 1999; Hooker and Iverson 2001; Herman and Burrows 2005; Budge et al. 2006; Marcoux et al. 2007; Knoff et al. 2008; Thiemann et al. 2009; Newsome et al. 2010; Pinela and Borrell 2010; Browning et al. 2014a).

Stomach content analysis remains an important methodology in assessing feeding ecology of cetaceans (e.g. Kaiser 2012; Ambrose et al. 2013; Rossman et al. 2015a); however, increasingly, researchers are using stable isotope analysis to compliment stomach content analyses (Newsome et al. 2010; Pinela and Borrell 2010; Kiszka et al. 2010; Bisi et al. 2013). Using stable isotopes of prey and predators, researchers can determine the proportion of a predators diet is comprised of which prey, which will represents a longer feeding time period than the snapshot of stomach content (which represents approximately 1-2 feeding events) and without the bias of digestion rates (Newsome et al. 2010). However, where a prey isotope values are unknown, stable isotope analyses can still be useful in investigating feeding habitat, based on geographical gradients in isotope signatures (Graham et al. 2010; Magozzi et al. 2017), and in defining sub-populations or groupings based on similar feeding ecology (Newsome et al. 2010; Kiszka et al. 2012; Browning et al. 2014a).

Stable isotope analysis is typically used to gain insight into the trophic level of predators and sources of primary production in the environment, with recent evidence that nutrients move on a fine enough scale to provide data regarding habitat selection (Newsome et al. 2010). Isotope signatures, specifically here δ^{15}N and δ^{13}C found in skin samples, provide information on the trophic level and habitat use of dolphins (see Newsome et al. 2010). Nitrogen increases by approximately 3.5‰ with each trophic level in skin samples, allowing researchers to identify prey preference where prey isotope values are available (Post 2002). Carbon can also be used to indicate habitat, as δ^{13}C is enriched in inshore environment compared to offshore (see Newsome et al. 2010). It is important to note that stable isotopes have been found to take from 3 weeks – 3 months to travel to the outer layer of skin; therefore, signatures do not reflect the feeding ecology at the time of sampling (Post 2002; Newsome et al. 2010; Browning et al. 2014b).

Understanding the baseline isotopic values, or signatures at the primary producer level, is important in stable isotope analyses as these values will be reflected in predator diet (Graham et al. 2010; Magozzi et al. 2017). In South African waters, there is not only a strong offshore-inshore gradient in δ^{13}C (Hill et al. 2006), but a longitudinal gradient in δ^{15}N with depletion from southwest to northeast (Van Der Lingen and Miller 2017). Both of these gradients need to be taken into account when investigating stable isotope ratios as they can help in defining feeding habitat, and connectivity between animals (Graham et al. 2010; Magozzi et al. 2017). Where animals are highly mobile, I expect that these gradients will not be visible in the isotope data. Conversely, if animals are more resident, I would expect to see distinct isotope signatures which follow these gradients. Investigating the stable isotope results in South African waters without taken these gradients into account, could lead to over-interpretation as similarities and differences in signatures could be related to geographic influences rather than trophic ecology.

Stable isotope analyses, which investigate the ratio of isotopes in various tissues of an animals body, have been increasingly used in population structuring studies as an additional tool to assess fine-scale population structuring (Marcoux et al. 2007; Barros et al. 2010; Browning et al. 2014a). For many delphinid species, movements are predominantly related to distribution of food resources, with animals following prey movements (Browning et al. 2014a). Comparing isotope signatures between animals and the environmental parameters of the area can help to define fine-scale groupings in genetically similar individuals (Browning et al. 2014; Wilson et al. 2013; Barros et al.

2010; Pinela & Borrell 2010; Kiszka et al. 2010; Newsome et al. 2010; Quérouil et al. 2013). A recent study by Louis et al. (2018) suggest that genetic similarity may be less important in determining dolphin associations than similarities in ecology, specifically feeding ecology. As such, evaluating isotopic niche of dolphins can help to determine social groupings (Louis et al. 2018).

Like stable isotope analyses, photographic identification techniques, along with mark-recapture methods, are commonly used by researchers in cetacean research. These methods allow us to investigate cetacean distribution, site fidelity, social structure, habitat use, abundance, and population demographics (e.g. Neumann et al. 2002; Balmer et al. 2008; Smith et al. 2013; Urian et al. 2015; Zanardo et al. 2016; Mason et al. 2016). By using natural, long-lasting markings on the dorsal fin of dolphins, such as nicks and notches, researchers can identify individuals (Wells and Scott 1999; Würsig and Jefferson 1999; Urian et al. 2015). With the increasing affordability of digital cameras and sophistication in photo processing software, researchers are able to photograph large numbers of animals for each group, even checking on photograph quality in the field, and improving on these photographs in the laboratory (Markowitz et al. 2003; Urian et al. 2015). Once individuals are identified, researchers can use mark-recapture models to investigate population abundance (Urian et al. 2015); however, this requires sufficient survey effort over large temporal scales and the capturing of the majority of the individuals from an area (Urian et al. 2015). Should effort not be sufficient, photographic identification is still useful to investigate residency rates and site fidelity.

1.2 Study site

Despite a growing body of knowledge on dolphins in South African waters, the region off the Wild Coast of the Eastern Cape remain largely unstudied. The Wild Coast is a 300km stretch of coastline in the Eastern Cape (S32 º45.646’ to S31° 04.282' and E28 16.783’ to E30° 13.276') (Figure 1.3). Historically, this area has been vulnerable socio-economically, representing one of the poorest areas in South Africa (Dicken 2010; Myeza et al. 2010; Van Der Lingen et al. 2010). The lack of adequate infrastructure has hindered development. One of the key features of the marine environment of the Wild Coast is the annual sardine run which attracts large numbers of apex predators, to the region during the austral winter (i.e. June – August) (O'Donoghue et al. 2010 a,b; Van Der Lingen et al. 2010). The event contributes to substantial inflow of money into the regions through ecotourism (Dicken 2010; Van Der Lingen et al. 2010).

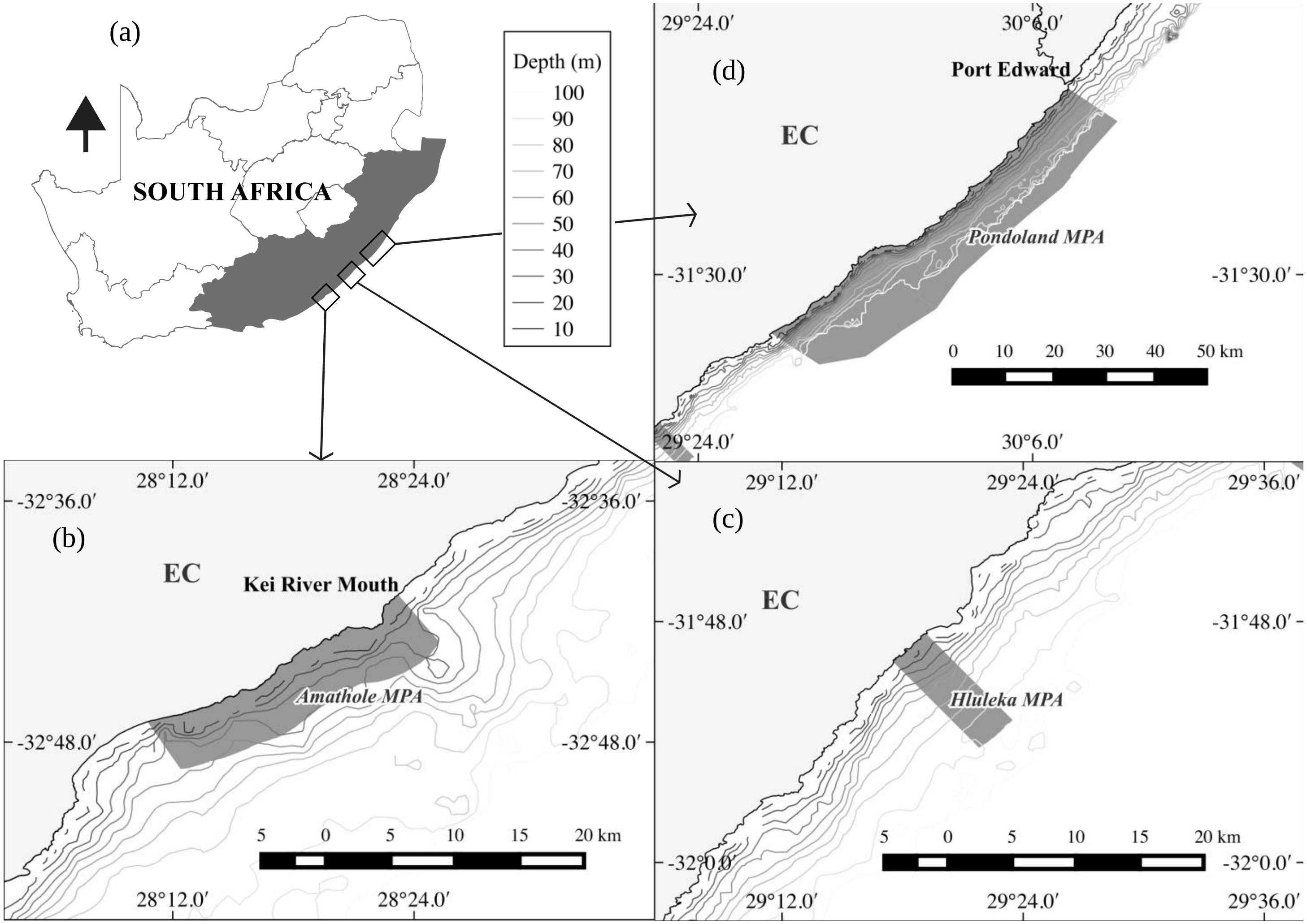


Figure 1.3: Map of the entire Wild Coast area (a) in South Africa, including three smaller study areas where boat-based studies were conducted: (b) Amathole, (c) Hluleka, and (d) Pondoland.

1.2.1 Oceanography of the Wild Coast

The waters off the Wild Coast are largely influenced by the warm Agulhas Current, which flows southward at high velocities and is the predominant current along the east coast of South Africa (Roberts et al. 2010; Lutjeharms et al. 2000, see Figure 1.3). The current travels at velocities of ≈1.5 m/s on average and has an average temperature of 22˚C (O'Donoghue et al. 2010; Lutjeharms 2006; Lutjeharms et al. 2000; Roberts et al. 2010). The continental shelf along the Wild Coast is narrow, generally extending to the 100 m contour, and smooth, which controls the trajectory of the Agulhas Current, making it stable year round (O'Donoghue et al. 2010; Lutjeharms 2006; Lutjeharms et al. 2000; Roberts et al. 2010). The proximity of the Agulhas Current to the coastline contributes to the current having a large influence on physical processes of the inshore waters (Roberts et al. 2010). The current is particularly close to shore in the Pondoland area, near an eddy formed at Port St. Johns and Waterfall Bluff (Roberts et al. 2010). South of Port Alfred, the shelf widens and the Agulhas Current starts to move offshore and continues along the Agulhas Bank (Lutjeharms et al. 2000; Lutjeharms 2006; O'Donoghue et al. 2010c; Roberts et al. 2010).

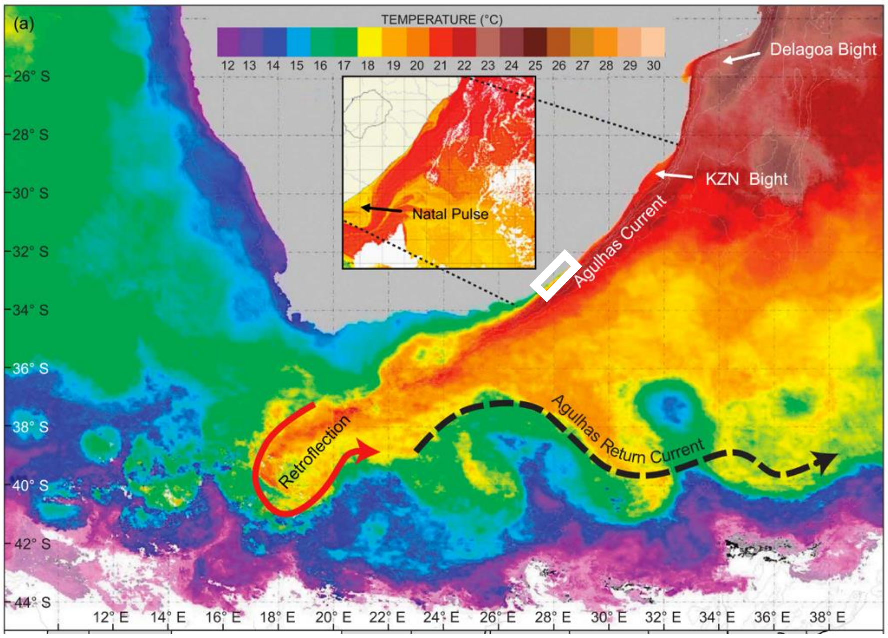


Figure 1.4: Satellite image of the oceanographic environment off the coast of South Africa, demonstrating the flow of the Agulhas Current along the south-eastern coastline of southern Africa, KZN=Kwa-Zulu Natal (from Roberts et al. 2010). Wild Coast is indicated by a white outlined box.

1.2.2 The annual sardine run

Sardines are usually present in water temperatures of approximately 20˚C, which makes the Wild Coast a poor sardine habitat due to the dominant warm-water Agulhas Current; however, the sardine run has been documented in this area since the late 19th century (Van Der Lingen et al. 2010). Much research has been done to identify the mechanisms that bring sardines to the area annually during the winter months, with an increasing amount of evidence on the presence of cooler water countercurrents during the winter months, which run inshore of the Agulhas Current at Port Alfred, East London, Port St. Johns, and Durban (Roberts et al. 2010; Schumann & Brink 1990; O'Donoghue et al. 2010; Lutjeharms 2006; Fréon et al. 2010). Roberts et al. (2010) suggest that these countercurrents run between Algoa Bay and Durban on a quasi-permanent and transient basis, which was hypothesized in previous research, but not confirmed (Schumann and Brink 1990; Armstrong et al. 1991). The main barrier to northward movement of sardines is the narrowing of the shelf at Port St. Johns and Waterfall Bluff, which causes the Agulhas Current to move inward; however, there is much evidence to suggest that cool water eddies in this area and the Durban eddy further north-east provides a gateway, which allows the sardines to move up the coast into KZN waters (Schumann and Brink 1990; Armstrong et al. 1991; Roberts et al. 2010). Also of potential importance to sardine movement are the wind and current driven small-scale processes occurring nearshore (Roberts et al. 2010).

With sardines moving into the Wild Coast area following cold water currents moving northward in winter, a number of apex predators also take advantage of this food resource, such as sharks, gannets, and cetaceans (O'Donoghue et al. 2010a,b,c; Fennessy et al. 2010; Dudley & Cliff 2010; Roberts et al. 2010). Bottlenose and common dolphins have been documented during the sardine run, and follow the sardines as they travel northward (O'Donoghue et al. 2010a,b,c; Ross et al. 1989; Cockcroft & Peddemors 1990). Numerous studies have suggested a change in the extent and magnitude of the sardine run since the early 2000s (Young and Cockcroft 1994; Dudley and Cliff 2010; O'Donoghue et al. 2010b, a; Van Der Lingen et al. 2010). More recent studies on the diet of common dolphin species occurring along the Wild Coast have indicated that these changes are also influencing the predator diet (Ambrose et al. 2013). It remains unclear how the sardine run may be affected by changing climatic conditions, but concern exists about increasing water temperatures posing a threat to the northward migration of this species (Perry et al. 2005).

Previous research on delphinid distribution in the waters off the south-east coast have focused largely on the sardine run off KZN given the abundance of animals seen during this time (Ross et al. 1989; Cockcroft et al. 1991; Cockcroft et al. 1990; Cockcroft & Peddemors 1990; O'Donoghue et al. 2010a,c; Karczmarski et al. 2000). Aerial surveys along the Wild Coast showed no evidence of "preferred areas" for bottlenose dolphins during the annual sardine run (Ross et al. 1989). However, in KZN five "preferred areas" were identified for the species during the sardine run (Cockcroft et al. 1991). Wild Coast surveys also indicate that common dolphins are found at a greater distances offshore than bottlenose dolphins during the sardine run (Ross et al. 1989). To date there is limited information on the presence or distribution of delphinids off the Wild Coast outside the period of the sardine run, and no boat-based research on these animals along the Wild Coast.

1.3 Eastern Cape Parks Board MPAs and protection of coastal resources

Marine Protected Areas (MPAs) are a management regime used worldwide for conservation of marine resources (Halpern 2003). Marine Protected Areas include areas of limited or closed access to fishing, and other anthropogenic influences (Gubbay 1995; Hoyt 2005; Pomeroy et al. 2005; Edgar et al. 2007, 2014). For many marine species this protection affords them the opportunity to recover from overexploitation (Gubbay 1995; Halpern 2003; Pomeroy et al. 2005; Edgar et al. 2007, 2014). Due to the high mobility of cetaceans, the effectiveness of MPAs for conservation of these species has been questioned (Hoyt 2005; Gormley et al. 2012; Bearzi 2012). However, increasing evidence suggests that with research, implementation, monitoring and active management, MPAs can be effective in protecting cetacean species (Hoyt 2005; Gormley et al. 2012; Bearzi 2012).

Hoyt (2005) provides an overview of requirements for MPAs and how to effectively manage them for marine mammal species. Of interest is the emphasis on research as key to the understanding of where and how MPAs can be effective for cetaceans (Hoyt 2005; Bearzi 2012). Hoyt (2005) suggests that monitoring of temporal and spatial migration, behaviour, and diet over several years is key to identifying home ranges and critical habitats for these animals. He further suggests that understanding the distribution of prey species can be important in identifying these 'hot-spots' for cetaceans and that an ecosystem approach, taking into consideration the full array of interactions within an ecosystem, is necessary in MPA management (Hoyt 2005). Many examples worldwide highlight the validity of Hoyt's (2005) emphasis on research, with several examples where researchers proposed extension or movement (either seasonal or permanent) of an MPA based on cetacean distribution adjacent or outside of existing MPAs (Gnone et al. 2011; Silva et al. 2012; Gormley et al. 2012; Bearzi 2012; Wilson et al. 2014). In migration corridors, and on feeding or breeding grounds, flexible MPAs that open and close when animals are present may be the most effective management strategy (e.g. Australia's Great Barrier Reef Marine Protected Area) (see review in Hoyt 2005). Though empirical studies demonstrating improvement to populations due to MPAs are only recently becoming more common (e.g. Gormley et al. 2012), protected areas are considered important management tools, especially when they are supported by long-term monitoring and adaptable management regimes (Gubbay 1995; Hoyt 2005; Pomeroy et al. 2005; Edgar et al. 2007, 2014). Successfully managed MPAs can influence ocean health of areas outside MPAs, which is especially important to highly mobile animals, such as delphinids (Gubbay 1995; Pomeroy et al. 2005; Edgar et al. 2007, 2014).

Four MPAs have been established along South Africa's Wild Coast to protect coastal species; from south to north these are: 1) Amathole MPA, 2) Dwesa/Cwebe MPA, 3) Hluleka MPA, and 4) Pondoland MPA. Given the lack of detailed knowledge of delphinid distribution along this coast, their effectiveness as conservation areas for delphinids remains unknown. Monitoring spatial and temporal distribution and habitat of this area is needed to inform managers regarding the use of MPAs by delphinids (as per Hoyt 2005).

1.4 Research Aims/Objectives

The aim of the current project is to examine the distribution and population structure of cetaceans along the poorly studied region of the Wild Coast of South Africa. The main research objectives are to: 1) determine the long and short- term occurrence of *T. aduncus*, and *D. delphis* (previously listed as in relation to selected environmental parameters (e.g. depth, temperature, distance from shore, and substrate), both seasonally and geographically, and to identify possible 'hotspots' off the Wild Coast, both during and outside the period of the sardine run; 2) examine fine-scale movement patterns of dolphins between the MPAs administered by ECPTA to inform management and conservation plans using photographic identification methods; 3) examine population structure and, and feeding ecology of the two species using stable isotopes.

The current lack of understanding of the delphinid populations off the Wild Coast and their connectedness to animals found in the neighbouring areas off KZN and western EC limits our understanding of their movement along the South African coastline, which is essential to the long-term conservation and management of these populations or stocks. Information gained from the present study will be fed back to ECPTA to inform management decisions along that coast, particularly for the MPAs. This is important considering pending oil and gas exploration along the entire coast of South Africa, which furthers the need for baseline distribution studies to inform exploration and monitor changes in behaviour and distribution (Environmental Resources Management Southern Africa Ltd. Ref. 0194759, for Impact Africa's submitted application for Exploration Rights in Transkei/Algoa area of the Eastern Cape). Additionally, the expected increase of tourism to the Wild Coast may cause a potential disturbance to the cetaceans. The current project will also start a photographic identification catalogue for the Wild Coast, which will form the basis for monitoring delphinid distribution and movement in the area. In addition, educational workshops for the local community and visitors to the ECPTA alike will be designed and implemented in collaboration with ECPTA.

1.5 Thesis overview

The current thesis consists of three data chapters and a final discussion chapter as per below:
Chapter 2 investigates the long-term occurrence of cetaceans along the Wild Coast during the annual sardine run in the austral winter, providing a baseline for the following chapters. In this chapter, aerial survey data of cetacean sightings taken over a period of 19 years is analyzed to assess changes in the number of animals and sightings of cetaceans over the study period. This chapter addresses objective (1) in part, as it provides long-term occurrence of delphinids and changes over time.

Chapter 3 presented the main findings of short-term data from boat-based surveys in three areas off the Wild Coast to examine temporal and spatial occurrence, density, and residency of dolphins from 2014-2016 during three months a year (February, June, and November). This chapter addresses objectives (1) and (2) as it provides short-term occurrence of delphinids and their movements, and habitat use from 2014-2016.

Chapter 4 employs stable isotope (carbon and nitrogen) analyses to assess the spatial and temporal patterns in trophic relationships and population structure of bottlenose dolphins and common dolphins along the Wild Coast and adjacent areas. I investigate how trophic niche overlaps between the two species, and for each species by study site and temporally. This chapter addresses objective (3) as it investigates feeding ecology and trophic niche of delphinids.

Chapter 5 provides a summary of the main research findings of the current study and discusses how these results contribute to our understanding of the ecology of common and bottlenose dolphins and the development and implementation of management strategies in south-eastern South Africa, with suggestions for future directions.

1.6 References

Acevedo-Gutierrez A (2002) Group behavior. In: Perrin W, Wursig B, THewissen J (eds) Encyclopedia of Marine Mammals. San Diego: Academic Press, San Diego, pp 537–544

Amaral AR, Jackson JA, Möller LM, Beheregaray LB, Manuela Coelho M (2012) Species tree of a recent radiation: the subfamily Delphininae (Cetacea, Mammalia). Mol Phylogenet Evol, 64:243–253.

Ambrose S, Froneman P, Smale M, Cliff G, Plön S (2013) Winter diet shift of long-beaked common dolphins (Delphinus capensis) feeding in the sardine run off KwaZulu-Natal, South Africa. Mar Biol 160:1543–1561. doi: 10.1007/s00227-013-2208-6

Armstrong M, Chapman P, Dudley S, Hampton I, Malan P (1991) Occurrence and population structure of pilchard Sardinops ocellatus, round herring Etrumeus whiteheadi and anchovy Engraulis capensis off the east coast of southern Africa. South African J Mar Sci 11:227–249.

Avise J (1994) Molecular markers, natural history and evolution. Chapman and Hall, Inc., New York

Balmer BC, Wells RS, Nowacek SM, Nowacek DP, Schwacke LH, McLellan WA, Scharf FS, Rowles TK, Hansen L, Spradlin T, Pabst DA (2008) Seasonal abundance and distribution patterns of common bottlenose dolphins (ursiops truncatus) near St . Joseph Bay, Florida, USA. J Cetacean Res Manag 10:157–167.

Barros NB, Ostrom PH, Stricker CA, Wells RS (2010) Stable isotopes differentiate bottlenose dolphins off west-central Florida. Mar Mammal Sci 26:324–336. doi: 10.1111/j.1748-7692.2009.00315.x

Bearzi M (2012) Cetaceans and MPAs should go hand in hand: A case study in Santa Monica Bay, California. Ocean Coast Manag 60:56–59. doi: 10.1016/j.ocecoaman.2011.12.019

Best, P., Schell DM (1996) Stable isotopes in southern right whale (Eubalaena australis) baleen as indicators of seasonal movements, feeding and growth. Mar Biol 124:483–494.

Bisi TL, Dorneles PR, Lailson-Brito J, Lepoint G, Azevedo ADF, Flach L, Malm O, Das K (2013) Trophic relationships and habitat preferences of delphinids from the southeastern Brazilian coast determined by carbon and nitrogen stable isotope composition. PLoS One 8:8–15. doi: 10.1371/journal.pone.0082205

Bossart GD (2006) Marine mammals as sentinel species for oceans and human health. Oceanography 19:134–137.

Bowen WD (1997) Role of marine mammals in aquatic ecosystems. Mar Ecol Prog Ser 158:267–274.

Browning NE, McCulloch SD, Bossart GD, Worthy GAJ (2014a) Fine-scale population structure of estuarine bottlenose dolphins (Tursiops truncatus) assessed using stable isotope ratios and fatty acid signature analyses. Mar Biol 1307–1317. doi: 10.1007/s00227-014-2420-z

Browning NE, Dold C, I-Fan J, Worthy GAJ (2014b) Isotope turnover rates and diet-tissue discrimination in skin of ex situ bottlenose dolphins (Tursiops truncatus). J Exp Biol 217:214–221. doi: 10.1242/jeb.093963

Budge SM, Iverson SJ, Koopman HN (2006) Studying Trophic Ecology in Marine Ecosystems Using Fatty Acids: a Primer on Analysis and Interpretation. Mar Mammal Sci 22:759–801. doi: 10.1111/j.1748-7692.2006.00079.x

Charlton-Robb K, Gershwin L, Thompson R, Austin J, Owen K, McKechnie S (2011) A new dolphin species, the Burrunan dolphin Tursiops australis sp. Nov., endemic to southern Australian waters.

Chivers SJ, Baird RW, McSweeney DJ, Webster DL, Hedrick NM, Salinas JC (2007) Genetic variation and evidence for population structure in eastern North Pacific false killer whales (Pseudorca crassidens). Can J Zool 85:783–794. doi: 10.1139/Z07-059

Cockcroft VG, Peddemors VMV (1990) Seasonal distribution and density of common dolphins Delphinus delphis off the south-east coast of southern Africa. South African J Mar Sci 9:371–377. doi: 10.2989/025776190784378853

Cockcroft VG, Ross GJB, Peddemors VM (1990) Bottlenose dolphin Tursiops truncatus distribution in Natal’s coastal waters. South African J Mar Sci 9:1–10. doi: 10.2989/025776190784378952

Cockcroft VG, Ross GJB, Peddemors VM (1991) Distribution and status of bottlenose dolphin Tursiops truncatus on the south coast of Natal, South Africa. South African J Mar Sci 11:203–209. doi: 10.2989/025776191784287538

Connor R, Krützen M (2015) Male dolphin alliances in Shark Bay: changing perspectives in a 30-year study. Anim Behav Special is:223–235.

Connor R, Wells R, Mann J, Read AJ (2000) The bottlenose dolphin: social relationships in a fission-fusion society. In: Mann J, Connor R, Tyack P, Whitehead H (eds) Cetacean societies: Field studies of dolphins and whales. University of Chicago Press, New York, pp 91–126

Connor R, Watson-Capps J, Sherwin W, Krützen M (2011) A new level of complexity in the male alliance networks of Indian Ocean bottlenose dolphins. Biol Lett 7:623–626.

Department of Environmental Affairs (2014) White paper on national environmental management of the ocean.

Department of Science and Technology (2008) Innovation towards a knowledge- based economy: Ten-year plan for South Africa.

Dicken ML (2010) Socio-economic aspects of boat-based ecotourism during the sardine run within the Pondoland Marine Protected Area, South Africa. African J Mar Sci 32:405–411. doi: 10.2989/1814232X.2010.502642

Dudley SF, Cliff G (2010) Influence of the annual sardine run on catches of large sharks in the protective gillnets off KwaZulu-Natal, South Africa, and the occurrence of sardine in shark diet. African J Mar Sci 32:383–397. doi: 10.2989/1814232X.2010.502641

Ebensperger L, Rivera D, Hayes L (2012) Direct fitness of group living mammals varies with breeding strategy, climate and fitness estimates. A review. J Anim Ecol 81:1013–1023.

Edgar GJ, Russ GR, Babcock RC (2007) Marine protected areas. In: Connell SD, Gillanders BM (eds) Marine Ecology. Oxford University Press, pp 534–565

Edgar GJ, Stuart-Smith RD, Willis TJ, Kininmonth S, Baker SC, Banks S, Barrett NS, Becerro MA, Bernard ATF, Berkhout J, Buxton CD, Campbell SJ, Cooper AT, Davey M, Edgar SC, Försterra G, Galván DE, Irigoyen AJ, Kushner DJ, Moura R, Parnell PE, Shears NT, Soler G, Strain EMA, Thomson RJ (2014) Global conservation outcomes depend on marine protected areas with five key features. Nature 506:216–220. doi: 10.1038/nature13022

Evans W (1994) Common dolphin, white-bellied porpoise Delphinus delphis Linnaeus. In: Ridgeway S, Harrison R (eds) Handbook of Marine Mammals, Volume 5. San Diego: Academic Press, San Diego, pp 191–224

Fennessy ST, Pradervand P, de Bruyn P a (2010) Influence of the sardine run on selected nearshore predatory teleosts in KwaZulu-Natal. African J Mar Sci 32:375–382. doi: 10.2989/1814232X.2010.506988

Findlay KP, Best PB, Ross GJB, Cockcroft VG (1992) The distribution of small odontocete cetaceans off the coasts of South Africa and Namibia. South African J Mar Sci 12:237–270. doi: 10.2989/02577619209504706

Fréon P, Coetzee JC, van der Lingen CD, Connell a D, O’Donoghue SH, Roberts MJ, Demarcq H, Attwood CG, Lamberth SJ, Hutchings L (2010) A review and tests of hypotheses about causes of the KwaZulu-Natal sardine run. African J Mar Sci 32:449–479. doi: 10.2989/1814232X.2010.519451

Gnone G, Bellingeri M, Dhermain F, Dupraz F, Nuti S, Bedocchi D, Moulins A, Rosso M, Alessi J, McCrea RS, Azzellino A, Airoldi S, Portunato N, Laran S, David L, Di Meglio N, Bonelli P, Montesi G, Trucchi R, Fossa F, Wurtz M (2011) Distribution, abundance, and movements of the bottlenose dolphin (Tursiops truncatus) in the Pelagos Sanctuary MPA (north-west Mediterranean Sea). Aquat Conserv Mar Freshw Ecosyst 21:372–388. doi: 10.1002/aqc.1191

Goodwin J, Durham B, Peddemors V, Cockcroft V (1996) Genetic variation in the bottlenose dolphin Tursiops truncatus along the Kwazulu/Natal coast, South Africa. African J Mar Sci 17:225–232.

Gormley AM, Slooten E, Dawson S, Barker RJ, Rayment W, du Fresne S, Bräger S (2012) First evidence that marine protected areas can work for marine mammals. J Appl Ecol 49:474–

480. doi: 10.1111/j.1365-2664.2012.02121.x

Gowans S, Würsig B, Karczmarski L, Wursig B, Karczmarski L, Würsig B, Karczmarski L (2007) The social structure and strategies of delphinids: predictions based on an ecological framework. In: Advances in Marine Biology. ELSEVIER ACADEMIC PRESS INC, 525 B STREET, SUITE 1900, SAN DIEGO, CA 92101-4495 USA, pp 195–295

Graham BS, Koch PL, Newsome SD, McMahon KW, Aurioles D (2010) Using isoscapes to trace movements n forging behvior of top predators in oceanic ecosystems. In: West JB, Bowen GJ, Dawson TE, Tu KP (eds) Isoscapes: Understanding Movement, Pattern, and Process on Earth Through Isotope Mapping. Springer Science, pp 299–317

Gubbay S (1995) Marine protected areas — past, present and future. In: Marine Protected Areas. Springer Netherlands, Dordrecht, pp 1–14

Gygax L (2002) Evolution of group size in the dolphins and porpoises: Interspecific consistency of intraspecific patterns. Behav Ecol 13:583–590.

Halpern BS (2003) The impact of marine reserves: do reserves work and does reserve size matter? Ecol Appl 13:117–137.

Hammond P, Bearzi G, Bjørge A, Forney K, Karczmarski L, Kasuya T, Perrin W, Scott M, Wang J, Wells R, Wilson B (2008) Delphinus delphis. In: IUCN Red List Threat. Species.

Hammond P, Bearzi G, Bjørge A, Forney K, Karczmarski L, Kasuya T, Perrin W, Scott M, Wang J, Wells R, Wilson B (2012) Tursiops aduncus. In: IUCN Red List fo Threat. Species.

Hebblewhite M, Pletscher D (2002) Effects of elk group size on predation by wolves. Can J Zool 80:800–809.

Heithaus M, Dill L (2002) Feeding strategies and tactics. In: The encyclopedia of marine mammals, 2nd editio. Academic Press, San Diego, CA., pp 4114–423

Herman D, Burrows D (2005) Feeding ecology of eastern North Pacific killer whales Orcinus orca from fatty acid, stable isotope, and organochlorine analyses of blubber biopsies. Mar Ecol … 302:275–291. doi: 10.3354/meps302275

Hill J, McQuaid D, Kaehler S (2006) Biogeographic and nearshore-offshore trends in stable isotope ratios of intertidal mussels and their food sources around hte coast of southern Africa. Mar Ecol Prog Ser 318:63–73.

Hooker S, Iverson S (2001) Diet of northern bottlenose whales inferred from fatty-acid and stable-isotope analyses of biopsy samples. Can J Zool 79:1442–1454. doi: 10.1139/cjz-79-

8-1442

Hoyt E (2005) Marine Protected Areas for Whales, Dolphins and Porpoises. Earthscan, London

Jefferson T, Webber M, Pitman R (2008) Marine Mammals of the World - A Comprehensive Guide to their Identification. Academic Press/Elsevier

Kaiser S (2012) Feeding Ecology and Dietary Patterns of the Indo-Pacific Bottlenose Dollphin (Tursiops Aduncus) Off KwaZulu-Natal, South Africa. Nelson Mandela Metropolitan University

Karczmarski L, Cockcroft V, McLachlan A (2000) Indo-Pacific humpback dolphins (Sousa chinensis) in Algoa Bay, South Africa. Mar Mammal Sci 16:65–79.

Kiszka J, Oremus M, Richard P, Poole M, Ridoux V (2010) The use of stable isotope analyses from skin biopsy samples to assess trophic relationships of sympatric delphinids off Moorea (French Polynesia). J Exp Mar Bio Ecol 395:48–54. doi: 10.1016/j.jembe.2010.08.010

Kiszka J, Simon-Bouhet B, Gastebois C, Pusineri C, Ridoux V (2012) Habitat partitioning and fine scale population structure among insular bottlenose dolphins (Tursiops aduncus) in a tropical lagoon. J Exp Mar Bio Ecol 416–417:176–184. doi: 10.1016/j.jembe.2012.03.001

Knoff A, Hohn A, Macko S (2008) Ontogenetic diet changes in bottlenose dolphins (Tursiops truncatus) reflected through stable isotopes. Mar Mammal Sci 24:128–137. doi: 10.1111/j.1748-7692.2007.00174.x

Krützen M, Sherwin W (2004) Population structure in an inshore cetacean revealed by microsatellite and mtDNA analysis: bottlenose dolphins (Tursiops sp.) in Shark Bay, Western Australia. Mar Mammal … 20:28–47.

Lodi L, Monteiro-Neto C (2012) Group size and composition of Tursiops truncatus (Cetacea: Delphinidae) in a coastal insular habitat off southeastern Brazil. Biotemas 25:157–164.

Louis M, Simon-Bouhet B, Viricel A, Lucas T, Gally F, Cherel Y, Guinet C (2018) Evaluating the influence of ecology, sex and kinship on the social structure of resident coastal bottlenose dolphins.

Lutjeharms J (2006) The Agulhas Current. Springer-Verlag, Berlin

Lutjeharms JRE, Valentine HR, Ballegooyen RC Van (2000) The hydrography and water masses of the Natal Bight , South Africa. Cont Shelf Res 20:1907–1939.

Magozzi S, Yool A, Vander Zanden HB, Wunder MB, Trueman CN (2017) Using ocean models to predict spatial and temporal variation in marine carbon isotopes. Ecosphere 8:1–20. doi:

10.1002/ecs2.1763

Mann J, Connor R, Barre LM, Heithaus M (2000) Female reproductive success in bottlenose dolphins (Tursiops sp.): life history, habitat, provisioning, and group-size effects. Behav Ecol 11:210–219.

Marcoux M, Whitehead H, Rendell L (2007) Sperm whale feeding variation by location, year, social group and clan: evidence from stable isotopes. Mar Ecol Prog Ser 333:309–314. doi: 10.3354/meps333309

Markowitz TM, Harlin AD, Würsig B (2003) Digital photography improves efficiency of individual dolphin identification. Mar Mammal Sci 19:217–223. doi: 10.1111/j.1748-7692.2003.tb01103.x

Mason S, Salgado Kent C, Donnelly D, Weir J, Bilgmann K (2016) Atypical residency of short-beaked common dolphins (Delphinus delphis) to a shallow, urbanized embayment in south-eastern Australia. R Soc Open Sci 3:160478. doi: 10.1098/rsos.160478

Mendez M, Rosenbaum HC, Bordino P (2007) Conservation genetics of the franciscana dolphin in Northern Argentina: population structure, by-catch impacts, and management implications. Conserv Genet 9:419–435. doi: 10.1007/s10592-007-9354-7

Mendez M, Subramaniam a, Collins T, Minton G, Baldwin R, Berggren P, Särnblad a, Amir O a, Peddemors VM, Karczmarski L, Guissamulo a, Rosenbaum HC (2011) Molecular ecology meets remote sensing: environmental drivers to population structure of humpback dolphins in the Western Indian Ocean. Heredity (Edinb) 107:349–61. doi: 10.1038/hdy.2011.21

Mendez M, Jefferson T a, Kolokotronis S-O, Krützen M, Parra GJ, Collins T, Minton G, Baldwin R, Berggren P, Särnblad A, Amir O a, Peddemors VM, Karczmarski L, Guissamulo A, Smith B, Sutaria D, Amato G, Rosenbaum HC (2013) Integrating multiple lines of evidence to better understand the evolutionary divergence of humpback dolphins along their entire distribution range: a new dolphin species in Australian waters? Mol Ecol 22:5936–48. doi: 10.1111/mec.12535

Mirimin L, Miller R, Dillane E, Berrow SD, Ingram S, Cross TF, Rogan E (2011) Fine-scale population genetic structuring of bottlenose dolphins in Irish coastal waters. Anim Conserv 14:342–353. doi: 10.1111/j.1469-1795.2010.00432.x

Möller L, Valdez FP, Allen S, Bilgmann K, Corrigan S, Beheregaray LB (2010) Fine-scale genetic structure in short-beaked common dolphins (Delphinus delphis) along the East Australian Current. Mar Biol 158:113–126. doi: 10.1007/s00227-010-1546-x

Möller LM, Allen SSJ, Harcourt RRG (2002) Group characteristics, site fidelity and seasonal abundance of bottlenose dolphins Tursiops aduncus in Jervis Bay and Port Stephens, south-eastern Australia. Aust Mammal 24:11–21.

Moore SE (2008) Marine mammals as ecosystem sentinels. J Mammal 89:534–540. doi: 10.1644/07-MAMM-S-312R1.1

Myeza J, Mason RB, Peddemors VM (2010) Socio-economic implications of the KwaZulu-Natal sardine run for local indigenous communities. African J Mar Sci 32:399–404. doi: 10.2989/1814232X.2010.506991

National Planning Commission (2011) National Development Plan 2030: Our future - make it work.

Natoli A, Peddemors V, Hoelzel A (2004) Population structure and speciation in the genus Tursiops based on microsatellite and mitochondrial DNA analyses. J Evol Biol 17:363–375. doi: 10.1046/j.1420-9101.2003.00672.x

Natoli A, Cañadas A, Peddemors VM, Aguilar A, Vaquero C, Fernández-Piqueras P, Hoelzel A (2006) Phylogeography and alpha taxonomy of the common dolphin (Delphinus sp.). J Evol Biol 19:943–54. doi: 10.1111/j.1420-9101.2005.01033.x

Natoli A, Peddemors VM, Hoelzel a. R (2008) Population structure of bottlenose dolphins (Tursiops aduncus) impacted by bycatch along the east coast of South Africa. Conserv Genet 9:627–636. doi: 10.1007/s10592-007-9379-y

Neumann DR, Leitenberger A, Orams MB (2002) Photo-identification of short-beaked common dolphins *(Delphinus delphis)* in north-east New Zealand: A photo-catalogue of recognisable individuals. New Zeal J Mar Freshw Res 36:593–604. doi: 10.1080/00288330.2002.9517115

Newsome SD, Clementz MT, Koch PL (2010) Using stable isotope biogeochemistry to study marine mammal ecology. Mar Mammal Sci 26:509–572. doi: 10.1111/j.1748-7692.2009.00354.x

O’Donoghue SH, Whittington P a, Dyer BM, Peddemors VM (2010a) Abundance and distribution of avian and marine mammal predators of sardine observed during the 2005 KwaZulu-Natal sardine run survey. African J Mar Sci 32:361–374. doi:

10.2989/1814232X.2010.502640

O’Donoghue SH, Drapeau L, Peddemors VM (2010b) Broad-scale distribution patterns of sardine and their predators in relation to remotely sensed environmental conditions during the KwaZulu-Natal sardine run. African J Mar Sci 32:279–291. doi: 10.2989/1814232X.2010.501584

O’Donoghue SH, Drapeau L, Dudley SF, Peddemors VM (2010c) The KwaZulu-Natal sardine run: shoal distribution in relation to nearshore environmental conditions, 1997–2007. African J Mar Sci 32:293–307. doi: 10.2989/1814232X.2010.501587

Pauly D, Trites A (1998) Diet composition and trophic levels of marine mammals. ICES J Mar Sci 55:467–481.

Peddemors V, Cockcroft V (1997) Prey distribution and its importance for nearshore dolphins off the east coast of southern Africa. Paper SC/49/SM32, presented to the Scientific Committee of the International Whaling Commission, Bournemouth

Perrin WF, Thieleking JL, Walker WA, Archer FI, Robertson KM (2011) Common bottlenose dolphins (Tursiops truncatus) in California waters: Cranial differentiation of coastal and offshore ecotypes. Mar Mammal Sci 27:769–792.

Perry A, Low P, Ellis J, Reynolds J, Perry Allison L., Paula J. Low JRE and JDR, Perry A, Low P, Ellis J, Reynolds J (2005) Climate change and distribution shifts in marine fishes. Science 308:1912–1915.

Phillips G (2006) Bottlenose dolphins (Tursiops aduncus) in Plettenberg Bay, South Africa: Population estimates and temporal dynamics of groups. Nelson Mandela Metropolitan University, Port Elizabeth, South Africa

Photopoulou T, Best P, Hammond P, Findlay K (2011) Movement patterns of coastal bottlenose dolphins in the presence of a fast-flowing, prevailing current: shore-based observations at Cape Vidal, South Africa. African J Mar Sci 33:393–401. doi: 10.2989/1814232X.2011.637346

Pinela A, Borrell A (2010) isotope analysis reveals habitat partitioning among marine mammals off the NW African coast and unique trophic niches for two globally threatened species. Mar Ecol Prog Ser 416:295–306. doi: 10.3354/meps08790

Pomeroy RS, Watson LM, Parks JE, Cid GA (2005) How is your MPA doing? A methodology for evaluating the management effectiveness of marine protected areas. Ocean Coast Manag

48:485–502. doi: 10.1016/J.OCECOAMAN.2005.05.004

Post D (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703–718.

Quérouil S, Kiszka J, Cordeiro AR, Cascão I, Freitas L, Dinis A, Alves F, Santos RS, Bandarra NM (2013) Investigating stock structure and trophic relationships among island-associated dolphins in the oceanic waters of the North Atlantic using fatty acid and stable isotope analyses. Mar Biol 160:1325–1337. doi: 10.1007/s00227-013-2184-x

Reeves R, Stewart B, Clapham P, Powell J (2002) Guide to Marine Mammals of the World. In: National Audubon Society (ed) Guide to Marine Mammals of the World, 1st edn. Alfred A. Knopf, New York, p 527

Reisinger RR, Karczmarski L (2010) Population size estimate of Indo-Pacific bottlenose dolphins in the Algoa Bay region, South Africa. Mar Mammal Sci 26:86–97. doi: 10.1111/j.1748-7692.2009.00324.x

Roberts MJ, van der Lingen CD, Whittle C, van den Berg M (2010) Shelf currents, lee-trapped and transient eddies on the inshore boundary of the Agulhas Current, South Africa: their relevance to the KwaZulu-Natal sardine run. African J Mar Sci 32:423–447. doi: 10.2989/1814232X.2010.512655

Rosel PE, Hansen L, Hohn a a (2009) Restricted dispersal in a continuously distributed marine species: common bottlenose dolphins Tursiops truncatus in coastal waters of the western North Atlantic. Mol Ecol 18:5030–45. doi: 10.1111/j.1365-294X.2009.04413.x

Ross GJB (1984) The smaller cetaceans of the south east coast of southern Africa. Ann Cape Prov Museums 15:173–410.

Ross GJB, Cockcroft VG, Melton D a., Butterworth DS (1989) Population estimates for bottlenose dolphins Tursiops truncatus in Natal and Transkei waters. South African J Mar Sci 8:119–129. doi: 10.2989/02577618909504555

Ross PS (2000) Marine mammals as sentinels in ecological risk assessment. Hum Ecol Risk Assess 6:29–46.

Rossman S, Berens Mccabe E, Barros NB, Gandhi H, Ostrom PH, Stricker CA, Wells RS (2015) Foraging habits in a generalist predator: Sex and age influence habitat selection and resource use among bottlenose dolphins (Tursiops truncatus). Mar Mammal Sci 31:155–168. doi: 10.1111/mms.12143

Schumann E, Brink K (1990) Coastal-trapped waves off the coast of South Africa: generation propogation and current structures. J Phys Oceanogr 20:1206–1218.

Shane S, Wells R, Wursig B (1986) Ecology, behavior and social organization of the bottlenose dolphin: a review. Mar Mammal Sci 2:34–63.

Silva M a., Prieto R, Magalhães S, Seabra MI, Machete M, Hammond PS (2012) Incorporating information on bottlenose dolphin distribution into marine protected area design. Aquat Conserv Mar Freshw Ecosyst 22:122–133. doi: 10.1002/aqc.1243

Smith HC, Pollock K, Waples K, Bradley S, Bejder L (2013) Use of the robust design to estimate seasonal abundance and demographic parameters of a coastal bottlenose dolphin (Tursiops aduncus) population. PLoS One 8:e76574. doi: 10.1371/journal.pone.0076574

Smolker R, Richards A, Connor R, Pepper J (1992) Sex differences in patterns of association among Indian Ocean bottlenose dolphins. Behaviour 123:38–69.

Stensland E, Angerbjorn A, Berggren P (2003) Mixed species groups in mammals. Mamm Rev 33:205–223.

Thiemann GW, Iverson SJ, Stirling I (2009) Using fatty acids to study marine mammal foraging: The evidence from an extensive and growing literature. Mar Mammal Sci 25:243–249. doi: 10.1111/j.1748-7692.2008.00258.x

Treasure AM, Moloney CL, Bester MN, McQuaid CD, Findlay KP, Best PB, de Bruyn PJN, Dorrington R, Fagereng A, Froneman P, Grantham G, Hunt B, Meiklejohn K, Pakomov E, Roychoudhury A, Ryan P, Smith V, Chown S, Ansorge I (2013) South African research in the Southern Ocean: New opportunities but serious challenges. S Afr J Sci 109:1–4.

Urian K, Gorgone A, Read A, Al. E (2015) Recommendations for photo-identification methods used in capture-recapture models with cetaceans. Mar Mammal Sci 31:298–321.

van Bressem M-F, Raga J-A, Di Guardo G, et al. (2009) Emerging infectious diseases in cetaceans worldwide and the possible role of environmental stressors. Dis Aquat Organ 86:143–157.

Van Der Lingen CD, Miller TW (2017) Interspecific, ontogenetic, spatial and temporal variability in nitrogen and carbon stable isotope ratios of small pelagic fish off South Africa. In: South African Marine Science Symposium. Port Elizabeth, South Africa,

Van Der Lingen CD, Coetzee JC, Hutchings L (2010) Overview of the KwaZulu-Natal sardine run. African J Mar Sci 32:271–277. doi: 10.2989/1814232X.2010.501581

Walker J, Macko S (1999) Dietary studies of marine mammals using stable carbon and nitrogen isotopic ratios of teeth. Mar Mammal Sci 15:314–334.

Wells R, Rhinehart H, Hansen L, Sweeney J, Townsend F, Stone R, Casper D, Scott M, Hohn A, Rowles T (2004) Bottlenose dolphins as marine ecosystem sentinels: developing a health monitoring system. Eco-Health 1:246–254.

Wells RS, Scott MD (1999) Estimating bottlenose dolphin population parameters from individual identification and capture-release techniques. Reports Int Whal Comm 407–415.

Wilson RM, Nelson J a., Balmer BC, Nowacek DP, Chanton JP (2013) Stable isotope variation in the northern Gulf of Mexico constrains bottlenose dolphin (Tursiops truncatus) foraging ranges. Mar Biol 160:2967–2980. doi: 10.1007/s00227-013-2287-4

Wilson RM, Chanton JP, Balmer BC, Nowacek DP (2014) An evaluation of lipid extraction techniques for interpretation of carbon and nitrogen isotope values in bottlenose dolphin (Tursiops truncatus) skin tissue. Mar Mammal Sci 30:85–103. doi: 10.1111/mms.12018

Würsig B, Jefferson T a (1999) Methods of photo-identification for small cetaceans. Rep. Int. Whal. Comm. 43–52.

Young D, Cockcroft V (1994) Diet of common dolphins (Delphinus delphis) off the south-east coast of southern Africa:opportunism or specialization? J Zool 234:41–53.

Zanardo N, Parra GJ, Moller LM (2016) Site fidelity, residency, and abundance of bottlenose dolphins (Tursiops sp.) in Adelaide’s coastal waters , South Australia. Mar Mammal Sci 1–21. doi: 10.1111/mms.12335

Chapter 2: Long-term trends in cetacean occurrence during the annual sardine run off the Wild Coast, South Africa

*This chapter is modified from the published article: Caputo, M., P. W. Froneman, D. Preez, G. Thompson and S. Plön. 2017. Long-term trends in cetacean occurrence during the annual sardine run off the Wild Coast, South Africa. African Journal of Marine Science 39:83–94.

2.1 Introduction

Cetaceans are highly mobile apex predators whose distribution patterns are often linked to prey availability (Bowen 1997; Peddemors and Cockcroft 1997; Heithaus and Dill 2002; Jefferson et al. 2008; Rosel et al. 2009). Their effect on marine community function and structure as a consumer is well documented worldwide (Bowen 1997; Kiszka et al. 2010; Bowen and Iverson 2013). As such, shifts in prey abundance and distribution due to changing climate or anthropogenic influences may be reflected in cetacean movements (Bowen 1997; Wursig et al. 2002; Halpern et al. 2008; Simmonds and Elliot 2009; Ambrose et al. 2013). This change in cetacean movements as prey distribution shifts has been documented even within relatively short-term time periods (Nottestad et al. 2015), and may have top-down effects on ecosystems given the potential influence of cetaceans on marine environments (Bowen 1997; Wells et al. 2004). Long-term monitoring in essential in marine habitats to track these shifts. Such monitoring is especially important to monitor how ecologically significant events, such as the sardine run off the Wild Coast of South Africa, are changing with increased coastal development and climate change.

Despite the sardine run phenomenon there has been limited research on cetaceans off the Wild Coast, largely due to the remote and rugged nature of this coastline, which makes it relatively inaccessible for daily boat-based surveys, and due to the costs of ship-based research. Previous analyses of opportunistic aerial survey data for sardines from 1988–2005 (Port St. Johns to northern Kwa Zulu-Natal [KZN]), as well as opportunistic sightings of cetaceans from ship-based surveys in 2005 (Port Elizabeth to northern KZN) (O'Donoghue et al. 2010a, 2010c), indicate that the area near Waterfall Bluff (see Figure

2.1) had the highest sighting rate for sardines and associated predators (O'Donoghue et al. 2010a). The presence of long-beaked common dolphins *Delphinus delphis,* hereafter common dolphins, was a top predictor of sardine presence when compared with other predators (Cockcroft and Peddemors 1990; O'Donoghue et al. 2010b), which has been reported in previous research (Cockcroft and Peddemors 1990). Indo-Pacific bottlenose dolphins *Tursiops aduncus,* hereafter bottlenose dolphins, were the most frequently sighted cetaceans in the Wild Coast (O'Donoghue et al. 2010a, 2010c). Previous aerial surveys of delphinids confirm these results, with common dolphins associated with the sardines during the austral winter (Cockcroft and Peddemors 1990), whereas relatively large numbers of bottlenose dolphins are seen along the Wild Coast year-round, especially in comparison with sightings for this species from KZN (Ross et al. 1989). Additional evidence suggests that a migratory stock of bottlenose dolphins occurs along the south coast of KZN and northern Wild Coast during the sardine run, increasing both sightings and counts during the austral winter for this species (Cockcroft and Ross 1990b; Peddemors 1999; Natoli et al. 2008; O'Donoghue et al. 2010a); however, their occurrence along the entire stretch of the Wild Coast remains unknown.

No dedicated survey data have been published for mysticetes in the Wild Coast area. However, O'Donoghue et al. (2010a, 2010c,) sighted humpback whales *Megaptera novaeangliae* most frequently of the mysticete species (390 sightings), with significantly fewer Bryde's whale *Balaenoptera brydei* (15 sightings) and southern right whale *Eubalaena australis* (26 sightings) reported during sardine run. Of the mysticete species, only Bryde's whales are considered to be associated with the sardine run (O'Donoghue et al. 2010a). The large numbers of humpback whales present during the austral winter are on its migration to the feeding grounds in Antarctica and to their breeding grounds along the east coast of Africa (Findlay and Best 2011) and they have not been seen feeding on the abundant sardine prey despite their proximity to the run (O'Donoghue et al. 2010a, 2010c). The range of southern right whales has been expanding eastward, which may explain their presence along the Wild Coast during the sardine run; however, there are no data available to determine if their presence within the region is due to the presence of sardines (Best 1990a, 2007; O'Donoghue et al. 2010a, 2010c).

Although limited, there is increasing evidence that the timing and intensity of the sardine run has changed both spatially and temporally since the early 2000s (Dudley and Cliff 2010; O'Donoghue et al. 2010a, 2010b, 2010c) as reflected in changes in predator diet (Ambrose et al. 2013). However, in view of current and ongoing oil and gas exploration along the entire coast of South Africa as well as global climate change, the need for baseline distribution studies to inform exploration and monitor potential changes is evident (Environmental Resources Management Southern Africa Ltd. Ref. 0194759, for Impact Africa's submitted application for Exploration Rights in Transkei/Algoa area of the Eastern Cape).

The purpose of the present study is to examine the spatial and temporal patterns in the distribution of cetaceans along the Wild Coast area during the austral winter (i.e. May–July) to provide important information on these apex predators in an area for which limited data exist. Due to limited visibility of single animals located large distances from the aerial survey track, the aim is not to map all sightings along the continental shelf to give an absolute abundance (i.e. the actual and exact number of animals present), but rather to determine the relative abundance (i.e. numbers within sightable range of the transect) of cetaceans within sight range, to identify hot spots of activity in the coastal region, and to determine whether there have been significant changes in the past 19 years. Some of these species, such as the common dolphin, are known to be associated with the annual sardine run during the austral winter (O'Donoghue et al. 2010a, 2010b, 2010c), which means that when sardines are sighted, common dolphins are the most likely predator to be seen in the area. However, humpback and southern right whales are not thought to be associated with the run (O'Donoghue et al. 2010b) and the effect of the sardine run on the occurrence of bottlenose dolphins and Bryde's whales remains unclear, although both have some association (i.e. they have been sighted with sardines but not consistently) (O'Donoghue et al. 2010a, 2010b, 2010c). Since the 1980s, the KZN Sharks Board (KZNSB) has monitored the annual sardine run and associated predators using aerial surveys in order to manage bather protection nets off the KZN coastline to minimise associated bycatch of cetaceans during this time. Although previous analyses examined sardine and predator distribution in relation to environmental parameters (O'Donoghue et al. 2010a), in the present study I used these opportunistic surveys to ascertain whether cetacean occurrence and numbers off the Wild Coast has changed spatio-temporally, by examining trends pre- (1996–2004) and post-2005 (2005–2014). Without sardine biomass data, it is not possible to correlate changes in cetacean occurrence and sardine occurrence; however, this study will provide some insights into the environmental shifts of this region. Moreover, the study attempted to assess the importance of the marine protected areas (MPAs) established in the early 2000s off the Wild Coast region and administered by the Eastern Cape Parks and Tourism Authority (ECPTA), as a habitat for the cetaceans. Given the lack of dedicated research off the Wild Coast, the 19-year opportunistic aerial survey dataset represents a valuable resource for determining occurrence of cetaceans and evaluating long-term trends. Fine-scale analyses are limited using these data due to their opportunistic nature; however, broad-scale trends can be identified, which will provide important ecological information for this area.

2.2 Methods

2.2.1 Aerial surveys

Annual aerial surveys for sardine presence were conducted between May and July from 1996–2014 by the KZNSB. Flights were undertaken at an altitude of 250 m and at a speed of 175 km h^{-1}, following Leatherwood et al. (1982), between Durban and East London in a single-engine Cessna 206 from 1996–2004 and a twin-engine Partenavia P68 post-2004. Both models are high-wing aircraft, allowing for optimum visibility and providing the same sightability for both time-periods (Figure 2.1). For the purpose of this study, only the flights conducted between East London and the Mbizana River were considered as representative of the Wild Coast area. Data collected during those flight which were interrupted by adverse weather conditions were not included in the analysis.. As described in O'Donoghue et al. (2010a), the flight path was directly over the coastline with all observers facing seaward, two scanning from the backline of breakers seawards and two, the pilot and a data recorder, scanning offshore to a distance of approximately 10 km for secondary sightings. Despite their larger cues, secondary sightings for mysticete species are unreliable, given the difficulties in spotting an individual animal at large distances. Where there were large groups of animals, such as common dolphins, sightings farther offshore were recorded. The following environmental conditions were recorded at the beginning of each flight, and in response to any changes in conditions during the flight: atmospheric pressure, wind direction, wind speed, sea state and cloud cover. To ensure consistency, the same pilot was used throughout the duration of the data collection, with experienced members of the KZNSB staff present on all flights and all observers trained in the observation methods.

2.2.2 Sightings analysis

The KZNSB recorded the sighting data for each flight. When sighted, the cetaceans were identified to the lowest possible taxonomic level and their general location, count, behaviour and travel direction were recorded. For the purpose of this study, a group was defined as all individuals sighted within close proximity to each other (<50m) with no two individuals more than 10m from each other, moving in the same direction and engaged in the same predominant behaviour (adapted from Irvine et al. 1981; Smolker et al. 1992; Toth et al. 2011). Distance from shore and exact location were not recorded for most groups; instead, sightings were simply recorded on paper maps along a pre-drawn transect line (Figure 2.1). Where no species identification or group size was recorded, sightings were not included in further analyses. Flights were planned for favourable weather conditions (i.e. Beaufort Sea State <4) as poor sea conditions hampered observations. As sea state approached 4, the counts may have been underestimated due to poor conditions. No flying was possible under conditions of low cloud and heavy rain. For the purpose of this study, the survey area was divided into five sections, each approximately 74 km in length (Figure 2.1), to determine spatial trends, with total counts of cetacean sightings as well as mean and median group size per species calculated for each section and in total for the entire Wild Coast. Sections were demarcated based on the location of oceanographic changes or large river mouths, and also were based on survey location pre- and post-2005. The total number of kilometres surveyed per year was calculated. From 1996–2005 flights took place only in transect sections (d) and (e) (Figure 2.1), which would have influenced the overall number of sightings per section (and over the entire study period) due to unequal sampling effort. To account for this bias, the number of sightings and individuals as well as the mean group size were calculated per kilometre surveyed (not per flight/survey). When comparing between time-periods, only sections (d) and (e) were compared to ensure that numbers from other sections post-2005 would not skew the results.

For each species, the mean group size for all sightings was calculated for each year. No mixed-species groups were recorded; however, common and bottlenose dolphins and humpback whales were often sighted in the same area, but were separate groups and therefore, recorded separately. The number of sightings, as well as the mean and median group size per month (May, June, and July), per survey section ([a], [b], [c], [d], and [e]) and per time-period (divided into five- or four-year increments: A = 1996–2000; B = 2001–2005; C = 2006–2010; D = 2011–2014) were also calculated. In addition, the total number of kilometres of track-line surveyed within MPAs was calculated. The number of individuals per kilometre inside and outside MPAs was also calculated for each species pre- and post-2005, reported as the percentage of total observations falling within MPAs. As the track-line was not drawn at exact distance from shore that was surveyed, all points along a transect were projected perpendicularly from the track-line towards the coast, and any observations which would fall into MPAs (i.e. between the northern and southern border of these areas) were included in this analysis (see Figure 2.1 for MPA locations).

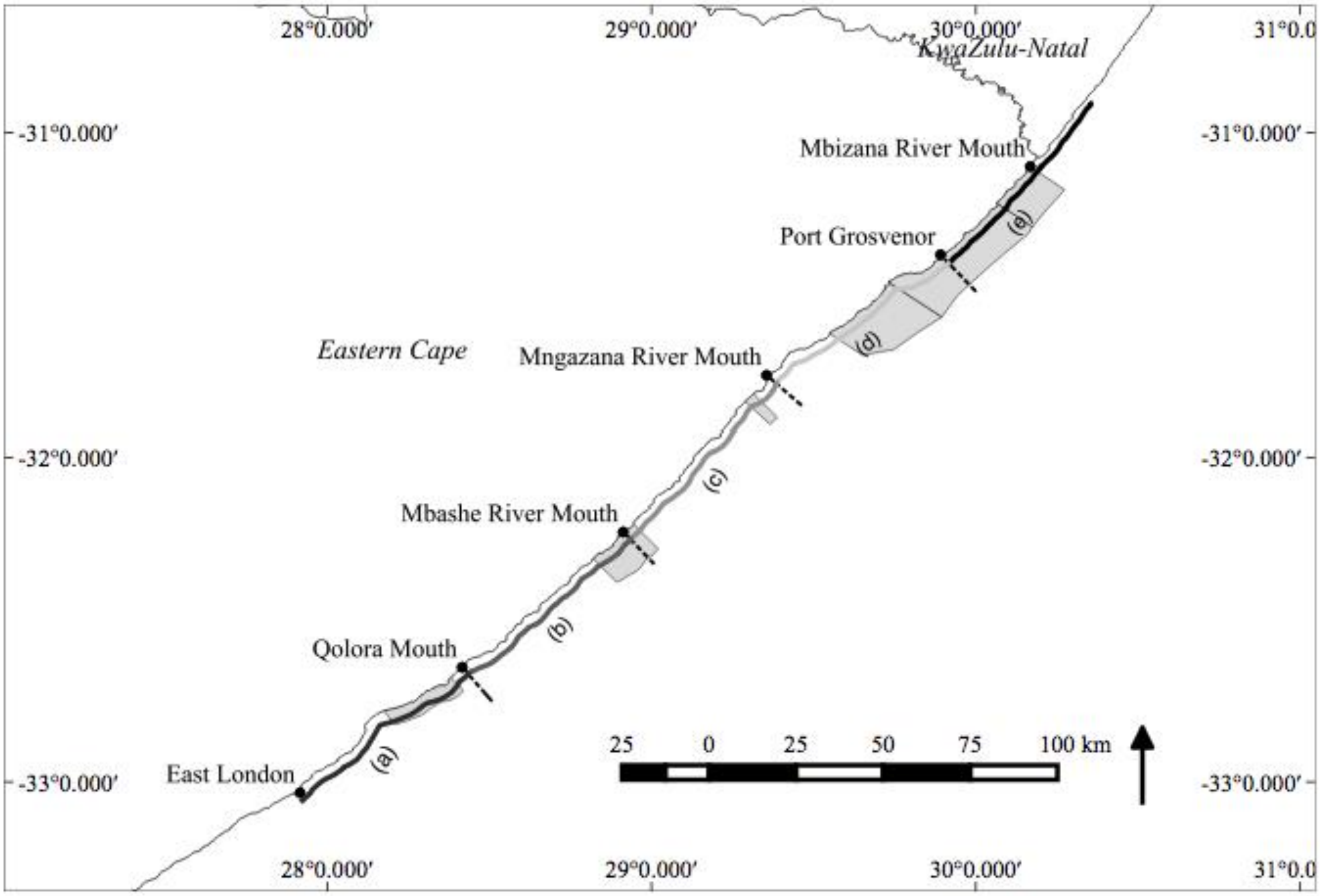


Figure 2.1: Cetacean survey track lines along the Wild Coast with five 74 km transect sections indicated: (a) East London to Qolora; (b) Qolora to Mbashe; (c) Mbashe to Mngazana; (d) Mngazana to Port Grosvenor; (e) Port Grosvenor to Mbizana River mouth. Marine protected areas (MPAs) in the region are indicated.

2.2.3 Statistical analyses

All statistical analyses were performed in R 3.1.2. As the number of sightings for Bryde's whales and southern right whales were low (n <20), they were excluded from the statistical analyses. The difference in mean group size by year was determined for each species using a linear regression. Pre- and post-2005 data were analysed separately using Kruskal-Wallis non-parametric tests to investigate differences in group size by month. For locations (d) and (e) only, the effect of location (i.e. (d) vs. (e)), time-period, and differences pre- vs post-2005 were tested for each species using Kruskal-Wallis non-parametric tests. The changes in number of individuals per kilometre, sightings per kilometre and group size by year was calculated for each species using a regression. Post-2005 data were analysed for each species separately to assess the change in group size for each survey section (i.e. a, b, c, d and e) using Kruskal-Wallis tests. The difference in mean group size inside and outside of MPAs for both pre- and post-2005 separately was tested using a Kruskal-Wallis non-parametric test. Normality was tested using plots of residuals vs fits and q-q normality plots, as well as Shapiro-Wilks normality testing. A log transformation was applied to the total number of individuals per kilometre for both bottlenose and common dolphin groups, and for sightings per kilometre for common dolphins, to achieve normality. Post-hoc testing was performed using Tukey's test. Heatmaps were generated for each species in QGIS 2.8.2.-Wien, which provide a visual representation of a kernel density analysis of sightings along a transect. Areas with high numbers of total individuals were identified along the transect by adding the total number of individuals from all groups within a set pixel size (8 km radius) and applying a quartic kernel shape to these clusters, providing a kernel density.

2.3 Results

2.3.1 Aerial surveys

In total, 131 aerial surveys were undertaken between 1996 and 2014, with an average of 4–5 flights per year (Table 2.1). Along the Wild Coast, 24753 km were surveyed, with significantly more ($p<0.001$, $r^2 = 0.74$) area surveyed post-2005 (20 434 km vs 4 319km). The mean distance of each survey pre-2005 was 149km, while post-2005, it was 372 km. This difference is due to flights being restricted to sections (d) and (e) from 1996-2004, and extending from (a) to (e) post-2005 (Figure 2.1). The majority of flights occurred in June (52%), with the greatest number of kilometres surveyed (12 339 km). The total number of kilometres surveys within MPAs was 90.5 km pre-2005 and 156.6 km post-2005.

Table 2.1: Aerial survey effort from 1996-2014 for flights flown over the Wild Coast of South Africa by the KwaZulu Natal Sharks Board, including the number of sightings for bottlenose dolphins (*Tursiops aduncus*, BND), common dolphins (*Delphinus delphis*, CD), and humpback whales (*Megoptera novaeanglia*, HBW).

Year	Flights	Kilometers	BND sightings	CD sightings	HBW sightings
1996	4	596	14	4	3
1997	4	596	7	4	2
1998	4	596	21	7	3
1999	2	298	9	1	0
2000	4	596	4	2	3
2001	6	894	12	2	5
2002	1	149	10	2	0
2003	3	447	17	1	0
2004	1	149	3	2	2
2005	3	1115	3	0	0
2006	6	2229	27	9	12
2007	2	743	3	6	8
2008	5	1858	11	14	13
2009	9	3344	32	18	14
2010	5	1858	17	12	44
2011	6	2229	18	8	21
2012	7	2601	14	10	31
2013	7	2601	33	4	44
2014	5	1858	13	2	37

2.3.2 Sightings analysis

In total, 630 cetacean sightings were recorded between 1996 and 2014. Bottlenose dolphins accounted for 43% of all sightings, humpback whales 38% and common dolphins 17% (Table 2.2). The remaining cetacean sightings were Bryde's whales (2%) and southern right whales (0.2%), i.e. one sighting (Table 2.2). All but one sighting of Bryde's and southern right whales were within sections (d) and (e), with the remaining sighting of Bryde's whale on the border of sections (b) and (c) (Figure 2.2).

Table 2.2: Total number of cetacean sightings from aerial survey conducted between 1996-2014, including total number of individuals, mean and median group size, and range.

Month	Distance surveyed (km)	Number of sightings	Total number of individuals	Mean group size (no.)	Median group size (no.)	Range (no.)
Tursiops aduncus Indo-Pacific bottlenose dolphin						
May	7 878.98	93	1 650	17.7	50	4–800
June	12 338.93	145	19 770	136.3	75	2–1 000
July	5 649.80	30	4 980	166.0	100	20–500
Total	24 753.12	268	32 400	120.9	60	2–1 000
Delphinus delphis Long-beaked common dolphin						
May	7 878.98	19	22 020	1 158.9	400	30–5 000
June	12 338.93	67	47 120	703.3	500	20–5 000
July	5 649.80	22	10 310	468.6	300	60–2 500
Total	24 753.12	108	79 400	735.6	500	20–5 000
Megaptera novaeangliae Humpback whale						
May	7 878.98	18	39	2.2	2	1–4
June	12 338.93	157	442	2.8	2	1–12
July	5 649.80	67	190	2.8	2	1–10
Total	24 753.12	242	671	2.8	2	1–12
Eubalaena australis Southern right whale						
May	7 878.98	0	0	0.0	0	0
June	12 338.93	0	0	0.0	0	0
July	5 649.80	1	2	2.0	2	2
Total	24 753.12	1	2	2.0	2	2
Balaenoptera edeni Bryde’s whale						
May	7 878.98	0	0	0.0	0	0
June	12 338.93	7	7	1.0	1	1
July	5 649.80	4	9	2.3	2	1–4
Total	24 753.12	11	16	1.5	1	1–4

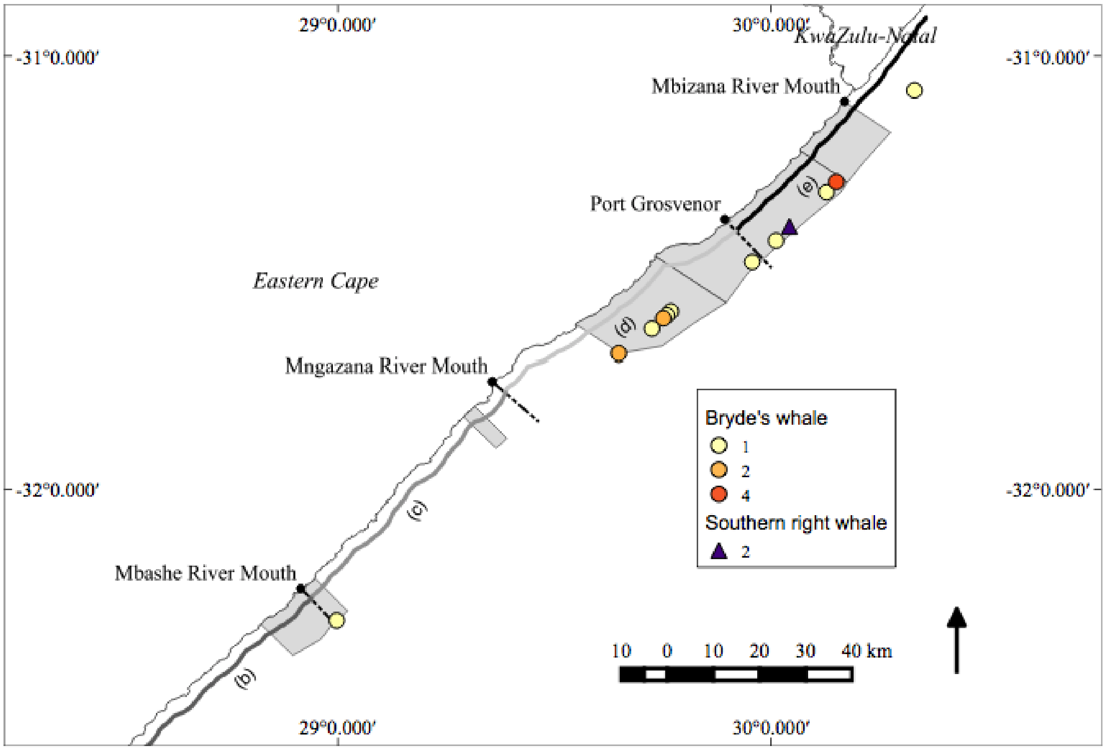


Figure 2.2: Sightings of Bryde's whales and southern right whales along the Wild Coast of South Africa, including group size. Transect sections labelled as in Figure 2.1.

The primary direction of travel for all species was north-easterly (i.e. parallel to the coast toward Durban), with 94% of humpback whales, 80% of bottlenose dolphins and 54% of common dolphins recorded as travelling in this direction. There were 20 groups which comprised both bottlenose and common dolphins. These mixed groups were recorded primarily in June (55%) between 2006 and 2010 (70%) in section (d) (50%).

The mean group size for bottlenose dolphins did not differ significantly over the period 1996–2014 (F=0.011, p=0.916); however, group size decreased significantly for common dolphins (F=5.300, p=0.034), and increased significantly for humpback whales (F=7.883, p=0.0121) (Figure 2.3). The mean group size post-2005 did not differ between years for bottlenose dolphins (F=0.427, p=0.532) or common dolphins (F=0.609, p=0.944), but showed a significant increase for humpback whales (F=9.71, p=0.0143) (Figure 2.3). Post-2005, the number of sightings per km surveyed between years did not differ significantly for either dolphin species (bottlenose: F=0.848, p=0.384; common: F=0.609, p=0.458), but did increase significantly for humpback whales (F=8.848, p=0.0178) (Figure 2.4). The number of individuals per km surveyed post-2005 did not differ significantly between years for either bottlenose dolphins (F=0.0605, p=0.811) or common dolphins (F=0.458, p=0.518, but increased significantly for humpback whales (F=18.1, p=0.00278) (Figure 2.5).

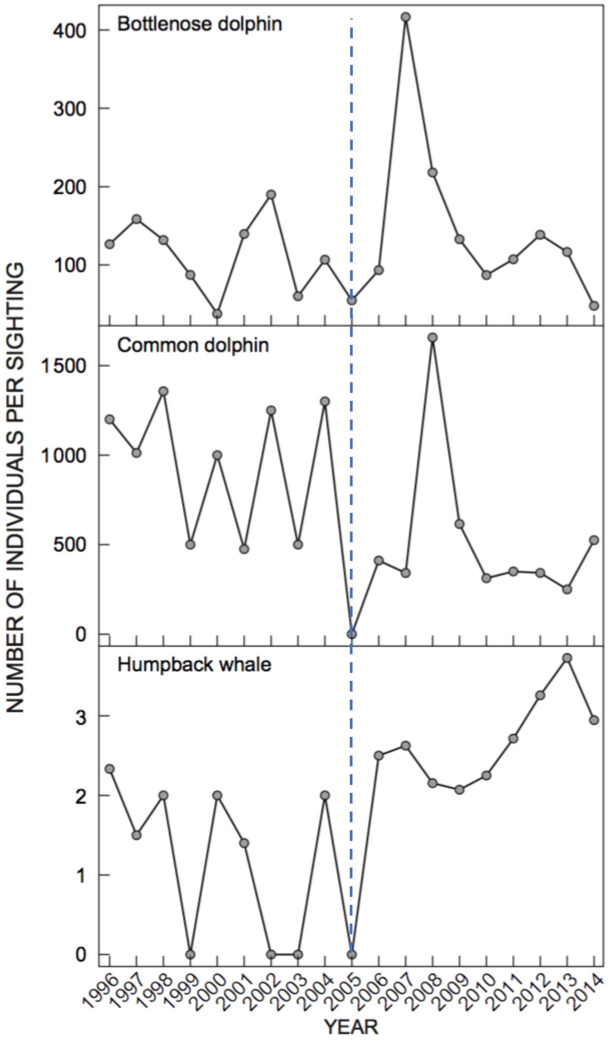


Figure 2.3: Number of individuals per sighting in each year for bottlenose dolphin, common dolphin, and humpback whales from aerial surveys conducted along the Wild Coast, South Africa between 1996 and 2014. Blue dotted line indicates 2005, where survey designed changed and additional effort was added.

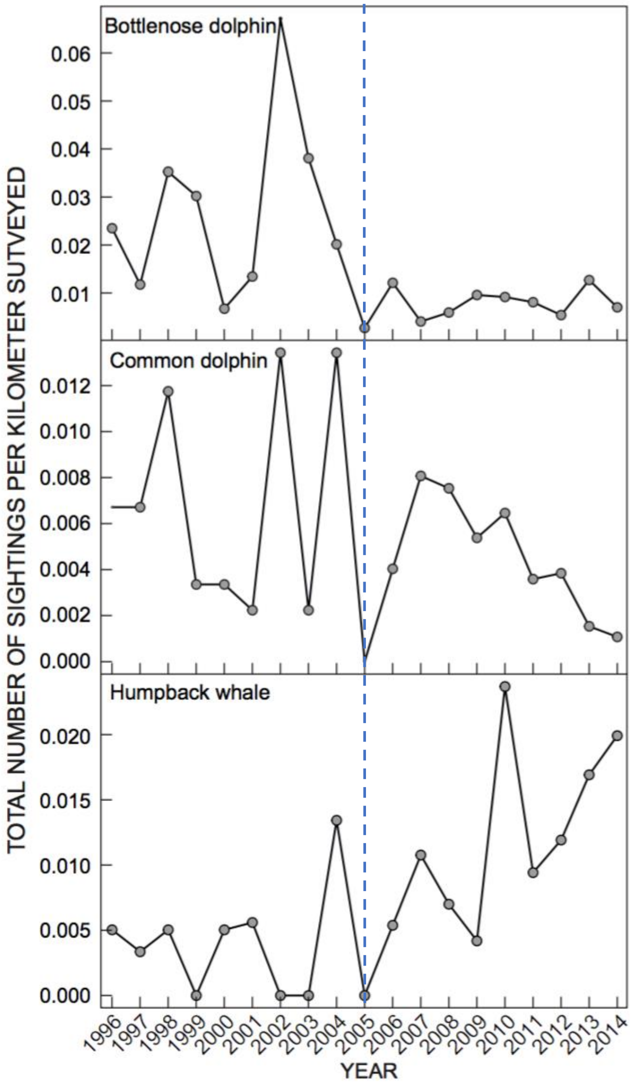


Figure 2.4: Total number of sightings per kilometre surveyed in each year, for bottlenose dolphin, common dolphin, and humpback whale from aerial surveys conducted along the Wild Coast, South Africa between 1996 and 2014. Blue dotted line indicates 2005, where survey designed changed and additional effort was added.

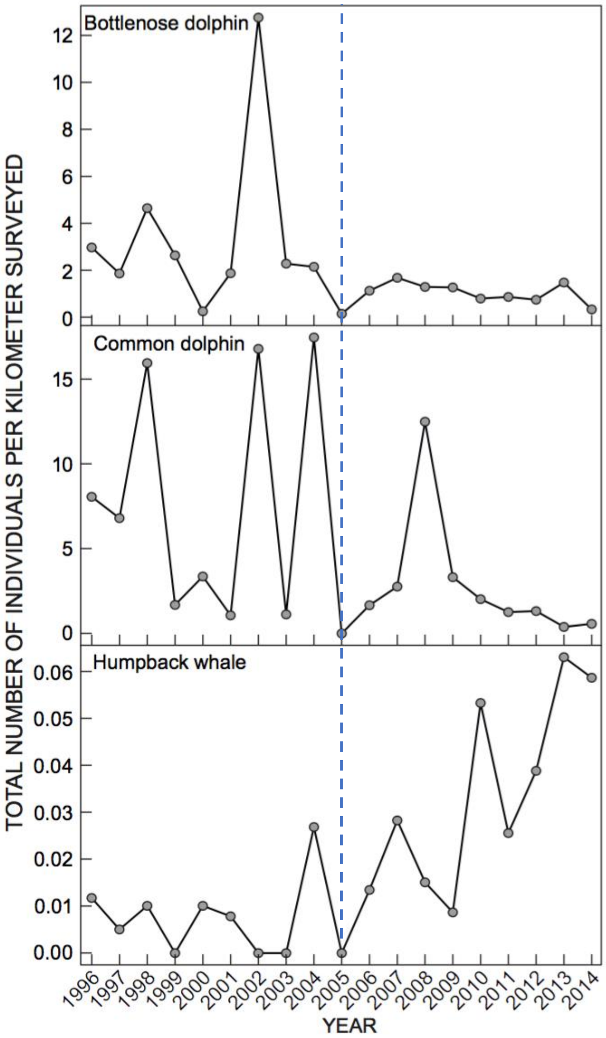


Figure 2.5: Total number of individuals per kilometre surveyed in each year, for bottlenose dolphin, common dolphin, and humpback whale from aerial surveys conducted along the Wild Coast, South Africa between 1996 and 2014. Blue dotted line indicates 2005, where survey designed changed and additional effort was added.

2.3.3 Bottlenose dolphins

Bottlenose dolphins were sighted most commonly of any species (Table 2.2), primarily in June, with a significant effect of month on group size pre-2005 ($\chi^2 = 0.977$, $p<0.001$), and significantly smaller groups in May, on average. Post-2005, there was no significant difference in group size based on month ($\chi^2 = 4.237$, $p=0.120$). For sections (d) and (e), there was no significant difference in mean group size of bottlenose dolphins between time-periods (i.e. A, B, C, and D), ($\chi^2 = 1.641$, $p=0.650$) or pre/post-2005 ($\chi^2 = 0.0314$, $p=0.859$), as well as no significant difference in mean group size between sections (d) and (e) ($\chi^2 = 1.961$, $p=0.375$) (Figure 2.6).

Post-2005, mean group size differed significantly by location (χ^2 =25.508, p<0.001), with the highest mean group size in section (a) (223.3 ind.), with section (b) (203.2 ind.) having far larger groups as well, decreasing in mean group size in a north-easterly direction along the coast (Figure 2.6, 2.7). For bottlenose dolphin sightings, 83% of sightings per kilometre were within a MPA pre-2005 and 55% post-2005, with no difference in mean group size between groups inside and outside MPAs both pre- and post-2005 (pre: χ^2 =0.00816, p=0.977; post: χ^2=4.237, p=0.120).

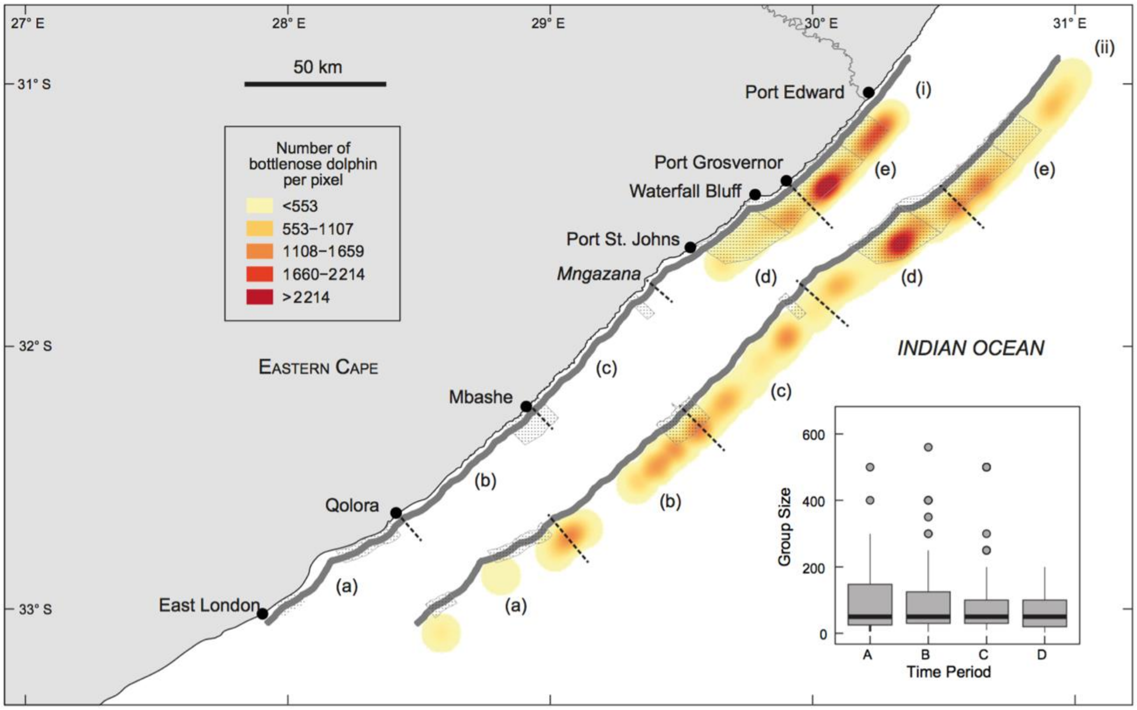


Figure 2.6: Total number of bottlenose dolphins per 8km pixel from aerial surveys conducted off the Wild Coast of South Africa, (i) pre- (only sections [d] and [e] were surveyed) and (ii) post-2005, with a plot of differences in group size in sections (d) and (e) between time-periods (A = 1996–2000; B = 2001–2005; C = 2006–2010; and D = 2011–2014). The solid line in the boxplots represents the median.

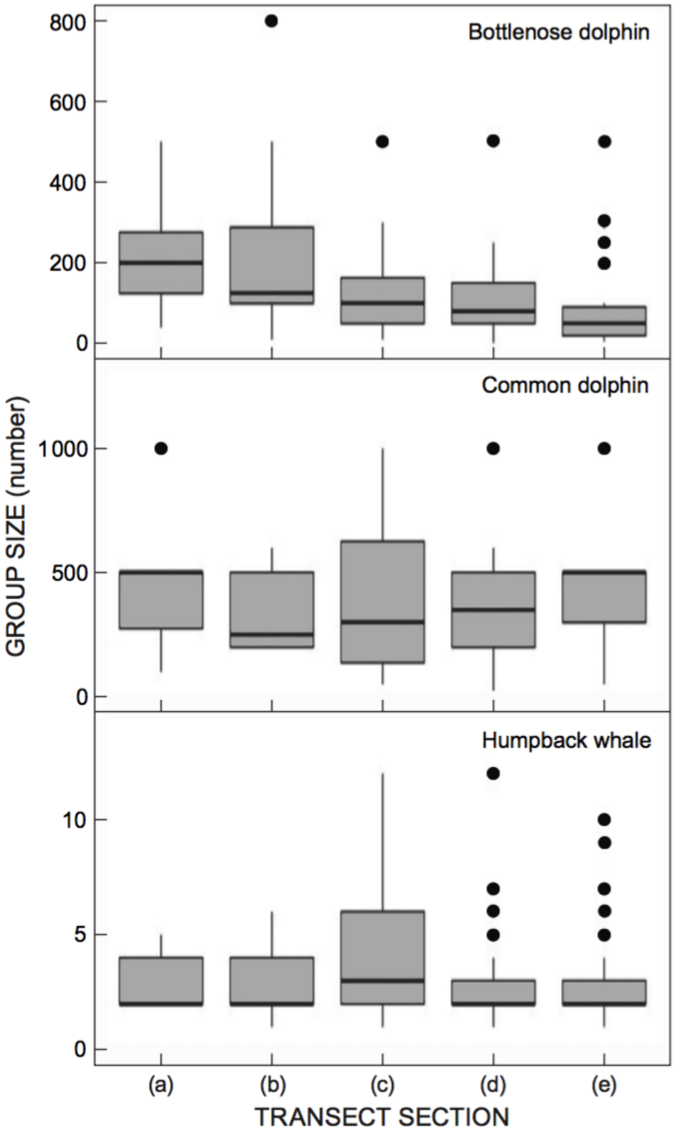


Figure 2.7: Difference in group size post-2005 between the five transect sections for three species: bottlenose dolphin; common dolphin; humpback whale sighted during aerial surveys off the Wild Coast of South Africa, with black line representing the median for each boxplot.

2.3.4 Common dolphins

Common dolphins were sighted in all three months (Table 2.2), with no significant effect of month on mean group size for either pre- or post-2005 (pre: χ^2=2.601, p=0.272; post: χ^2 = 0.763, p=0.683). For sections (d) and (e), there was a significant difference in group size between sections (χ^2 =12.988, p<0.001), with (e) having larger groups. There was also a significant difference in mean group size between time-periods A–D (χ^2 =19.143, p<0.001) for sections (d) and (e), and between pre- and post-2005 (χ^2 =18.630, p<0.001), with a decreasing mean group size over time. Between 1996 and 2000, the largest total number of individuals was sighted (52%), and the largest mean group size was recorded (1 158.3 ind.), with pre-2005 means significantly larger than post-2005 (Figure 2.8). Post-2005, there was no significant difference in mean group size by section ($\chi^2 = 6.946$, p=0.139) (Figure 2.7 and 2.8). In total, 83% of common dolphin sightings per kilometre were within MPAs pre-2005 and 73% post-2005, with no significant difference in mean group size between groups inside and outside MPAs both pre- and post-2005 (pre: $\chi^2 = 0.0662$, p=0.757; post: $\chi^2 = 3.623$, p=0.0570).

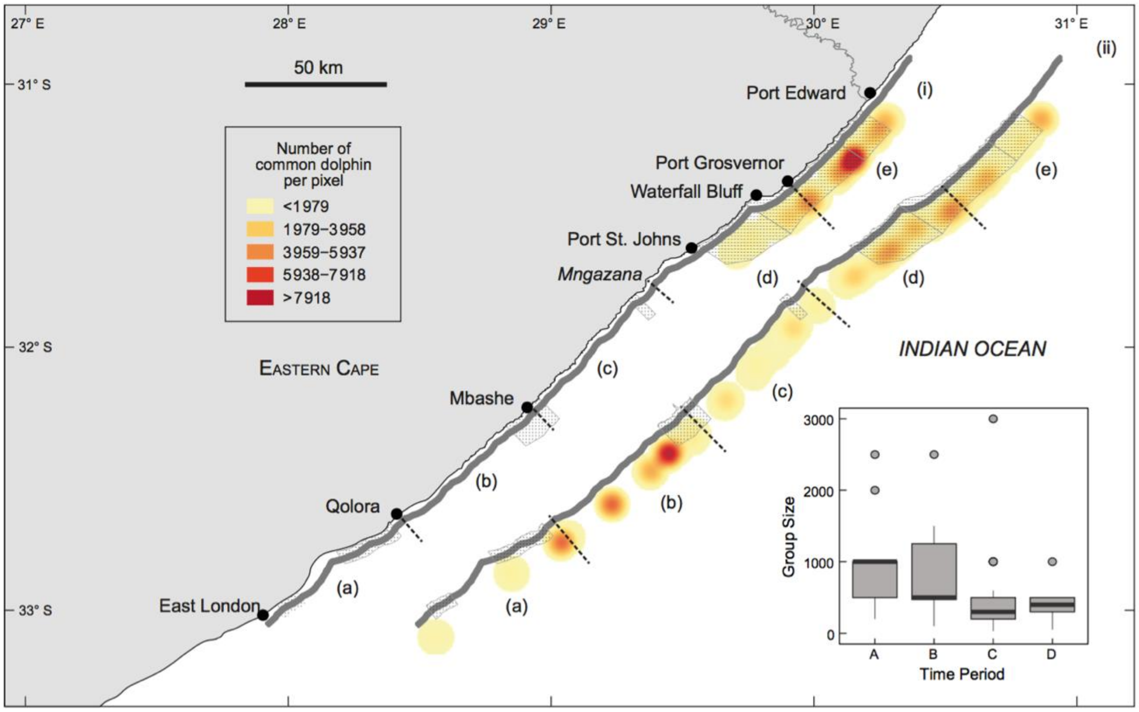


Figure 2.8: Total number of common dolphins per 8km pixel from aerial surveys conducted off the Wild Coast of South Africa (i) pre- (only sections [d] and [e] were surveyed) and (ii) post-2005, with a plot of differences in group size in sections (d) and (e) between time-periods (A = 1996–2000; B = 2001–2005; C = 2006–2010; and D = 2011–2014). The solid line on the boxplot represents the median.

2.3.5 Humpback whales

Humpback whales were sighted primarily in June (65% of sightings) (Table 2.2), with no significant difference in the mean group size between months for either pre- or post-2005 (pre: $\chi^2 = 0.420$, p=0.517; post: $\chi^2 = 1.964$, p=0.375). The highest total number of individuals recorded was in June, with July having the largest mean group size (Table 2.1). For sections (d) and (e), there was no difference in mean group size between the two sections (χ^2 =0.0246, p=0.875); however, there was a significant difference in mean group size in these two sections combined between time-periods (χ^2 =15.511, p=0.0014) and pre/post-2005 (χ^2 =5.096, p=0.0240), with an increasing trend over the study period. Between 2011 and 2014, the largest total number of individuals (55% of total sightings) and the largest mean group size (3.24 ind.) was recorded (Figure 2.9). Post-2005, there was no significant difference in the mean group size per section (χ^2 =6.946, p=0.139) (Figures 2.7 and 2.9). Pre-2005, 63% of humpback whale sightings per kilometre were within MPAs and 67% were within MPAs post-2005, with no significant difference in mean group size between groups inside and outside MPAs both pre- and post-2005 (pre: χ^2 =0.442, p=0.507; post: χ^2 =0.343, p=0.558).

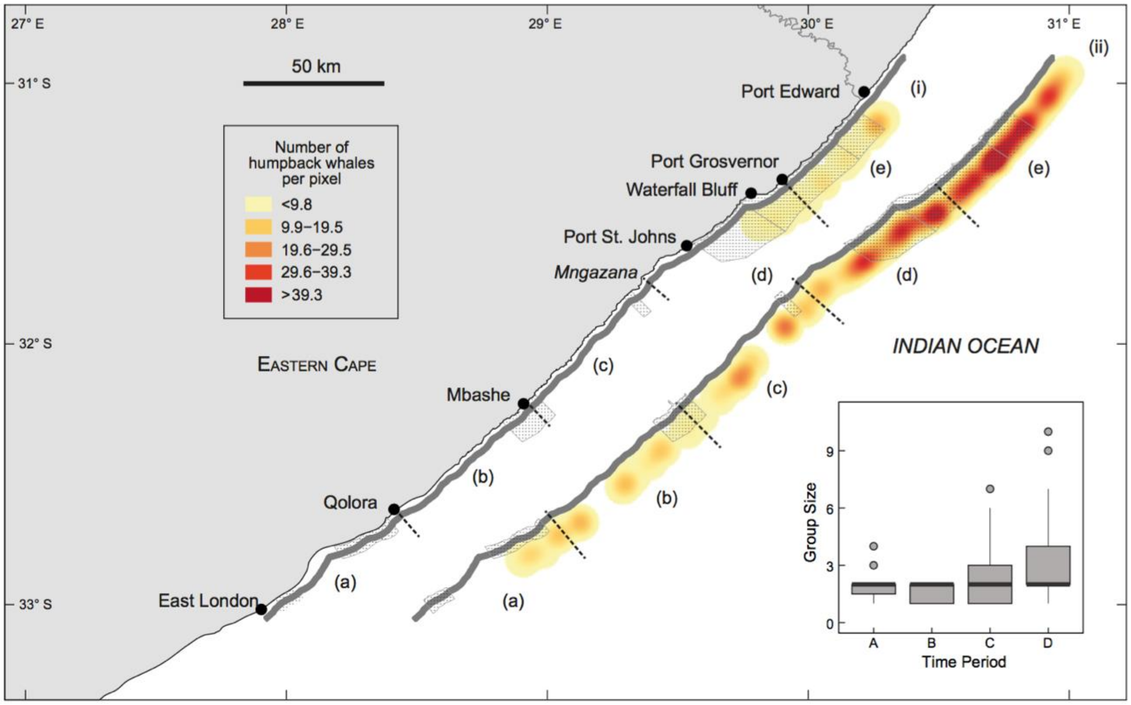


Figure 2.9: : Total number of humpback whales per 8km pixel from aerial surveys conducted off the Wild Coast of South Africa (i) pre- (only sections [d] and [e] were surveyed) and (ii) post-2005, with a plot of differences in group size in sections (d) and (e) between time-periods (A = 1996–2000; B = 2001–2005; C = 2006–2010; and D = 2011–2014). The solid line on the boxplot represents the median.

2.4 Discussion

The current study provides important information regarding cetacean occurrence in an area where limited research exists on these animals due to the remoteness and ruggedness of the coast. Common dolphin group size was shown to decrease in my study over time. Previous research suggests that common dolphin distribution and abundance is highly linked to sardine distribution and abundance (Cockcroft and Peddemors 1990; Young and Cockcroft 1994; O'Donoghue et al. 2010a, b); therefore, my finding may indicate a change in sardine occurrence, which was also found in previous research (Ambrose et al. 2013). Conversely, bottlenose dolphins did not differ in numbers temporally, which may be due to the fact that these animals are not as closely linked to sardine presence (O'Donoghue et al 2010a). Despite limitations in my methodology, including continuing surveys in Beaufort >3 which may have caused underestimation, results on humpback whale occurrence are in line with the increase in humpback whale numbers recorded in South African territorial waters (Best 2007; Findlay and Best 2011), reflected in my results as an increase in both sightings and total numbers over time. Since the exact survey path, and therefore precise location of cetacean groups, was not always available, data analysis approaches were somewhat constrained at fine scales. However, the study focused on broader scale distribution and trends, which are well captured by my analysis.

2.4.1 Bottlenose dolphins

Despite evidence that the sardine run has changed in intensity since the early 2000s (O'Donoghue et al. 2010a, 2010c; Ambrose et al. 2013), my study showed no concomitant change in bottlenose dolphin occurrence, as numbers were highest between 2006 and 2010. The number of sightings per kilometre, the total number of individuals per kilometre and the number of individuals per group did not change for both pre- and post-2005. Though changes in survey design limit my comparison between these periods, the absence of any trend in the group size during the present investigation highlights the lack of clear association between bottlenose dolphins and sardines. Bottlenose dolphins are generalist feeders in this region (Cockcroft and Ross 1990a; Kaiser 2012), and therefore more likely adaptable to changes in sardine availability, with less need for cooperative feeding in large groups (Gowans et al. 2007). A diet analysis of bottlenose dolphins from KZN revealed that sardines were not amongst the five most important prey items (Kaiser 2012). However, a resident population and a migratory stock of bottlenose dolphins have been suggested for KZN waters (Cockcroft et al. 1991; Natoli et al. 2008; O'Donoghue et al. 2010a), with migratory animals potentially coming from the Wild Coast and following the sardine run. This has been confirmed by changes in the diets of animals caught in the KZN shark nets during this time-period, although the overall main prey species remained the same and excluded sardines (Kaiser 2012), which is supported by Fennessey et al. (2010) suggesting that bottlenose dolphins feed on other prey as they move up the coast with the sardines. The increase in number of bottlenose dolphins within the study area during the sardine run (June/July), points to a migration in the area (O'Donoghue et al. 2010a, 2010c). The smaller, more numerous groups from the northern sections of the Wild Coast, contrasted with larger, less numerous groups in the southern section, could be an indication of different stocks, as suggested by previous literature (O'Donoghue et al. 2010a, c); however, these data are not conclusive and ongoing research regarding occurrence at a larger spatial scale is underway to identify longer term residency and to delineate stocks, which is important for management.

2.4.2 Common dolphins

Large numbers of common dolphins aggregate within 10 km of the coastal areas (as surveyed here) off the Wild Coast during the sardine run to feed on schooling fish (Cockcroft and Peddemors 1990; Young and Cockcroft 1994; O'Donoghue et al. 2010a, 2010c). Aerial surveys conducted by Cockcroft and Peddemors (1990) suggest that common dolphins are only present along the Wild Coast during this time only, likely in response to increased availability of sardines in the area. A key finding of the present study was that the group sizes of common dolphins decreased over time, specifically with lower numbers after 2005 (Figures 2.4, 2.8). The number of sightings per kilometre of effort did not differ, but the total number of individuals observed did decrease significantly over the study period (Figures 2.3, 2.4). The largest groups were found near Mbashe and Waterfall Bluff, areas identified by O'Donoghue et al. (2010a) to have high chlorophyll *a* concentrations, low sea surface temperatures and high abundance of sardines. As the occurrence of common dolphins along the Wild Coast is considered to be highly associated with sardines (O'Donoghue et al. 2010a), the decrease in group size of common dolphins over the duration of the study period may reflect the observed change in sardine run strength over the corresponding period (Connell 2010; O'Donoghue et al. 2010b). It is possible that the size of bait balls decreased, requiring fewer dolphins for cooperative feeding, or that the sardines moved to another area or dispersed, attracting fewer common dolphins to the Wild Coast. Another possibility is that common dolphins have changed their winter foraging behaviour in this region with little or no influence of sardine abundance in the area. Ambrose et al. (2013) demonstrated that common dolphin diet comprised mainly of mackerel from 1992 to early 2000s for KZN waters mostly likely as a result of diminished sardine availability. Anecdotal evidence from 2012, suggests that bait balls were composed primarily of mackerel, not sardine, for this year (SP unpublished data). This change in diet may have changed dolphin numbers and distribution off south-eastern Africa, which is reflected in my data as a decrease in group size.

2.4.3 Humpback whales

Humpback whales are not considered to be associated with the sardine run and there are no records of feeding activity (Best 2007; O'Donoghue et al. 2010a); however, the timing of their northward migration to breeding grounds coincides with the sardine run (Findlay and Best 2011; Findlay et al. 2017). The absence of and significant spatial pattern, strong directional movement northwards and lack of feeding behaviour observed is consistent with the area acting primarily as a migration corridor (Best 2007; Findlay et al. 2011). Humpback whale numbers in South African coastal waters have been increasing by 9.0% per year (Findlay and Best 2011), which is reflected in my results by means of an increase in group size observed in the past 4 years and an increasing number of sightings.

2.4.4 Occurrence of other whale species

Southern right whale populations have an annual increase of 6.8% in south western South Africa (Best 1990b; Brandão et al. 2010), though this may be an overestimation as some groups in some areas showed no change over the same time period (Best 1990a, 1990b). During the current investigation, only one sighting of a southern right whale was recorded over the period 1996–2014, which is unsurprising given that their distribution is predominantly in the Western Cape (Best 2007). Despite increasing sightings elsewhere along the Eastern Cape coast (Melly et al. 2017), this trend was not evident from my study.

Bryde's whales have not been studied along the Wild Coast other than the basic sighting information provided in O'Donoghue et al. (2010a). They were found to be associated with prey in the area by O'Donoghue et al. (2010c), but the small sample size here did not allow for analysis of trends. They were mostly found around Waterfall Bluff, which is where sardine concentrations were identified (O'Donoghue et al. 2010a, 2010c).

2.4.5 Marine protected areas

The highest number of cetacean sightings both pre- and post-2005 were recorded within the waters of the designated MPAs. Pre-2005, the majority of area surveyed was within MPAs; however, the largest number of sightings were still made within MPAs post-2005, when the majority of survey area was outside MPAs (57%). As common dolphins have been demonstrated to be highly associated with sardines, their distribution may be indicative of the presence of sardines (O'Donoghue et al. 2010a, 2010c). Waterfall Bluff falls within the Pondoland MPA, which extends from Port St Johns to Port Edward. The Waterfall Bluff region has been postulated as an oceanographic gate, the site of semi-permanent oceanographic eddies, where sardines move north-eastwards along the coast into KZN when the gate is open or alternatively are concentrated in this area (Roberts et al. 2010). Additionally, this area has been identified as ideal sardine habitat during the austral winter (O'Donoghue et al. 2010a), which may account for the high numbers of cetaceans found in this MPA, northward of this "gate", especially common dolphins, as they forage on these bait fishes. The current study highlights the potential importance of these MPAs to the annual sardine run and its associated predators.

2.5 Conclusions and future research

The data gathered during aerial surveys of sardine presence have provided a long-term overview of cetacean occurrence and distribution not available from any other source. In remote areas, such as the Wild Coast, where data on animal occurrence and distribution are absent and long-term systematic surveys do not exist, these datasets are useful for establishing baselines (Smultea and Jefferson 2014). With the large datasets presented here I were able to monitor both spatial and temporal trends in cetacean occurrence and assess whether the suggested change in the sardine run has had an effect on predator occurrence and distribution, specifically on delphinids.

Understanding cetacean distribution and occurrence provides important ecological information which is crucial for conservation and management. Despite the important information contained within it, many limitations exist in this dataset. Both previous research and the present study focus on the austral winter months (April–August), skewing the analysis temporally (Ross et al. 1989; Cockcroft and Ross 1990b; O'Donoghue et al. 2010a, 2010c). Additional information on animal movement would allow us to assess whether small resident groups, specifically of bottlenose dolphins, stay in relatively isolated areas, with larger migratory groups moving through the area following prey species. Without data from other times of the year it is not possible to determine the importance of the sardine run in attracting animals to the area, or identify 'resident' populations, although I can predict short-term residency. In the current analysis, no environmental data were available, as exact sighting locations were not provided. O'Donoghue et al. (2010a) identified general trends, but precisely located sightings with associated environmental data would allow us to link sightings to specific environmental trends and model the effects of climatic changes on cetaceans in this area. Additionally, long-range observations of single individuals are not reliable, which limits the results for mysticetes. Ongoing boat-based research will use information from these aerial surveys to indicate potential hotspots and provide occurrence data during the austral winter. This will allow re-evaluation of these limitations and further examination of Wild Coast populations and their connectivity with adjacent populations.

2.6 References

Ambrose S, Froneman P, Smale M, Cliff G, Plön S (2013) Winter diet shift of long-beaked common dolphins (Delphinus capensis) feeding in the sardine run off KwaZulu-Natal, South Africa. Mar Biol 160:1543–1561. doi: 10.1007/s00227-013-2208-6

Best PB (1990a) Natural markings and their use in determining calf intervals in right whales off South AFrica.

Best PB (1990b) Trends in the inshore right whale populations off South Africa, 1969-1987. Mar Mammal Sci 6:93–108.

Best PB (2007) Whales and dolphins of the southern African subregion, Cambridge. Cape Town

Bowen WD (1997) Role of marine mammals in aquatic ecosystems. Mar Ecol Prog Ser

158:267–274.

Bowen WD, Iverson SJ (2012) Methods of estimating marine mammal diets: A review of validation experiments and sources of bias and uncertainty. Mar Mammal Sci 29:719–754. doi: 10.1111/j.1748-7692.2012.00604.x

Brandão A, Best P, Butterworth D (2010) Estimates of Demographic Parameters for Southern Right Whales. Cambridge, UK

Cockcroft V, Ross G (1990a) Food and feeding of the Indian Ocean bottlenose dolphin off southern Natal, South Africa. In: Leatherwood S, Reeves R (eds) The bottlenose dolphin. San Deigo: Academic Press, pp 295–308

Cockcroft VG, Peddemors VMV (1990) Seasonal distribution and density of common dolphins Delphinus delphis off the south-east coast of southern Africa. South African J Mar Sci 9:371–377. doi: 10.2989/025776190784378853

Cockcroft VG, Ross GJB (1990b) Age, growth, and reproduction of bottlenose dolphins Tursiops truncatus from the East coast of Southern Africa. Fish Bull 88:289–302.

Cockcroft VG, Ross GJB, Peddemors VM (1991) Distribution and status of bottlenose dolphin Tursiops truncatus on the south coast of Natal, South Africa. South African J Mar Sci 11:203–209. doi: 10.2989/025776191784287538

Connell A (2010) A 21-year ichthyoplankton collection confirms sardine spawning in KwaZulu-Natal waters. African J Mar Sci 32:331–336.

Dudley SF, Cliff G (2010) Influence of the annual sardine run on catches of large sharks in the protective gillnets off KwaZulu-Natal, South Africa, and the occurrence of sardine in shark diet. African J Mar Sci 32:383–397. doi: 10.2989/1814232X.2010.502641

Findlay K, Best P (2011) Migrations of humpback whales past Cape Vidal, South Africa, and an estimate of the population increase rate (1988 – 2002). African J Mar Sci 33:375–392. doi: 10.2989/1814232X.2011.637345

Findlay KP, Seakamela SM, Meÿer MA, Kirkman SP, Barendse J, Cade DE, Hurwitz D, Kennedy AS, Kotze PGH, McCue SA, Thornton M, Vargas-Fonseca OA, Wilke CG (2017) Humpback whale “super-groups” – A novel low-latitude feeding behaviour of Southern Hemisphere humpback whales (Megaptera novaeangliae) in the Benguela Upwelling System. PLoS One 12:e0172002. doi: 10.1371/journal.pone.0172002

Gowans S, Würsig B, Karczmarski L, Wursig B, Karczmarski L, Würsig B, Karczmarski L

(2007) The social structure and strategies of delphinids: predictions based on an ecological framework. In: Advances in Marine Biology. ELSEVIER ACADEMIC PRESS INC, 525 B STREET, SUITE 1900, SAN DIEGO, CA 92101-4495 USA, pp 195–295

Halpern BS, Walbridge S, Selkoe KA, Kappel C V, Micheli F, D'Agrosa C, Bruno JF, Casey KS, Ebert C, Fox HE, Fujita R, Heinemann D, Lenihan HS, Madin EMP, Perry MT, Selig ER, Spalding M, Steneck R, Watson R (2008) A global map of human impact on marine ecosystems. Science 319:948–52. doi: 10.1126/science.1149345

Heithaus M, Dill L (2002) Feeding strategies and tactics. In: The encyclopedia of marine mammals, 2nd editio. Academic Press, San Diego, CA., pp 4114–423

Irvine A, Scott M, Wells R, Kaufmann J (1981) Movements and activities of the Atlantic bottlenose dolphin, Tursiops truncatus, near Sarasota, Florida. Fish Bull 79:671–688.

Jefferson T, Webber M, Pitman R (2008) Marine Mammals of the World - A Comprehensive Guide to their Identification. Academic Press/Elsevier

Kaiser S (2012) Feeding Ecology and Dietary Patterns of the Indo-Pacific Bottlenose Dollphin (Tursiops Aduncus) Off KwaZulu-Natal, South Africa. Nelson Mandela Metropolitan University

Kiszka J, Oremus M, Richard P, Poole M, Ridoux V (2010) The use of stable isotope analyses from skin biopsy samples to assess trophic relationships of sympatric delphinids off Moorea (French Polynesia). J Exp Mar Bio Ecol 395:48–54. doi: 10.1016/j.jembe.2010.08.010

Leatherwood S, Show I, Reeves R, Wright M (1982) Proposed modification of transect models to estimate population size from aircraft with obstructed downward visibility. Reports Int Whal Comm 32:577–580.

Melly B, McGregor G, Hofmeyr G, Plon S (2017) Spatio-temporal distribution and habitat preferences of cetaceans in Algoa Bay, South Africa. J Mar Biol Assoc United Kingdom 1–15.

Natoli A, Peddemors VM, Hoelzel a. R (2008) Population structure of bottlenose dolphins (Tursiops aduncus) impacted by bycatch along the east coast of South Africa. Conserv Genet 9:627–636. doi: 10.1007/s10592-007-9379-y

Nottestad L, Krafft B, Anthonypillai V, Bernasconi M, Langard L, Mork H, Ferno A (2015) Recent changes in distribution and relative abundance of cetaceans in the Norwegian Sea and their relationship with potential prey. Front Ecol Evol 2:83. doi:

10.3389/fevo.2014.00083

O’Donoghue SH, Whittington P a, Dyer BM, Peddemors VM (2010a) Abundance and distribution of avian and marine mammal predators of sardine observed during the 2005 KwaZulu-Natal sardine run survey. African J Mar Sci 32:361–374. doi: 10.2989/1814232X.2010.502640

O’Donoghue SH, Drapeau L, Peddemors VM (2010b) Broad-scale distribution patterns of sardine and their predators in relation to remotely sensed environmental conditions during the KwaZulu-Natal sardine run. African J Mar Sci 32:279–291. doi: 10.2989/1814232X.2010.501584

O’Donoghue SH, Drapeau L, Dudley SF, Peddemors VM (2010c) The KwaZulu-Natal sardine run: shoal distribution in relation to nearshore environmental conditions, 1997–2007. African J Mar Sci 32:293–307. doi: 10.2989/1814232X.2010.501587

Peddemors V (1999) Delphinids of southern Africa: A review of their distribution, status and life history. J Cetaceans Res Manag 1:157–166.

Peddemors V, Cockcroft V (1997) Prey distribution and its importance for nearshore dolphins off the east coast of southern Africa. Paper SC/49/SM32, presented to the Scientific Committee of the International Whaling Commission, Bournemouth

Rosel PE, Hansen L, Hohn a a (2009) Restricted dispersal in a continuously distributed marine species: common bottlenose dolphins Tursiops truncatus in coastal waters of the western North Atlantic. Mol Ecol 18:5030–45. doi: 10.1111/j.1365-294X.2009.04413.x

Ross GJB, Cockcroft VG, Melton D a., Butterworth DS (1989) Population estimates for bottlenose dolphins Tursiops truncatus in Natal and Transkei waters. South African J Mar Sci 8:119–129. doi: 10.2989/02577618909504555

Simmonds M, Elliot W (2009) Climate change and cetaceans: concerns and recent developments. J Mar Biol Assoc United Kingdom 89:203–201.

Smolker R, Richards A, Connor R, Pepper J (1992) Sex differences in patterns of association among Indian Ocean bottlenose dolphins. Behaviour 123:38–69.

Smultea M, Jefferson T a (2014) Changes in Relative Occurrence of Cetaceans in the Southern California Bight: A Comparison of Recent Aerial Survey Results with Historical Data Sources. Aquat Mamm 40:32–43. doi: 10.1578/AM.40.1.2014.32

Toth J, Hohn A, Able K, Gorgone A (2011) Defining bottlenose dolphin (Tursiops truncatus) stocks based on environmental, physical, and behavioral characteristics. Mar Mammal Sci 28:461–478.

Wells R, Rhinehart H, Hansen L, Sweeney J, Townsend F, Stone R, Casper D, Scott M, Hohn A, Rowles T (2004) Bottlenose dolphins as marine ecosystem sentinels: developing a health monitoring system. Eco-Health 1:246–254.

Wursig B, Reeves R, Ortega-Urtiz J (2002) “Global climate change and marine mammals” in Marine Mammals - Biology and Conservation. Kluwer Academic/Plenum Publishers, New York, NY

Young D, Cockcroft V (1994) Diet of common dolphins (Delphinus delphis) off the south-east coast of southern Africa:opportunism or specialization? J Zool 234:41–53.

Chapter 3: Into the wild – dedicated boat-based dolphin surveys off the Wild Coast of South Africa reveal the potential importance of this remote area

*Sections of this chapter regarding "group size" were adapted from the published article: Bouveroux, T., M. Caputo, P. Froneman and S. Plön. (2018). Largest reported groups for the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) found in Algoa Bay, South Africa: Trends and potential drivers. Marine Mammal Science 34(3):645-665. The analysis and results for this manuscript were completed by M. Caputo.

3.1 Introduction

Dolphins and other apex predators are considered sentinels of the health of marine ecosystems (Wells et al. 2004). As top predators, they provide a good indication of the health and richness of habitats, serving to reflect effects of changing climate or anthropogenic influences (Bowen 1997). The distribution, movement patterns, and group size of dolphins are often linked to prey availability (Bowen 1997; Peddemors and Cockcroft 1997; Heithaus and Dill 2002; Jefferson et al. 2008; Rosel et al. 2009; Möller et al. 2010). Investigations of dolphin group dynamics, occurrence, and residency are important given that there would need to be abundant and rich prey resources to sustain large groups of dolphins and/or large populations (Wells et al. 2004).

In dolphins, group size is largely determined by predation pressure, and prey availability, or a trade-off between these two factors (Wells and Scott 1999; Heithaus and Dill 2002). When group size increases for protection of individuals, especially young animals (Mann et al. 2000; Smith and Worthy 2006) or females against males (Connor et al. 2000, 2011), it may also increase the competition for resources within the group (Heithaus and Dill 2002). However, energetic gains during cooperative feeding in larger groups have been described in many delphinid species, including killer whales (*Orcinus orca*), common dolphins (*Delphinus delphis*) and spotted dolphins (*Stenella frontalis*) (Gygax 2002; Heithaus and Dill 2002).

In bottlenose dolphins (*Tursiops spp.*), group size varies daily (Shane et al. 1986) and exhibits a fission-fusion grouping pattern, where associations between individuals vary in space and time to maximize their fitness (Smolker et al. 1992; Connor et al. 2000, 2011; Mann et al. 2000; Möller et al. 2010; Connor and Krützen

2015). Coastal bottlenose dolphins (*Tursiops aduncus*) normally occur in groups of 6-60 animals on average (Wang and Yang 2009; Möller et al. 2010; James 2014; Sprogis et al. 2015), with the largest reported groups in Algoa Bay at approximately 600 animals (Bouveroux et al. 2018). This species occurs in shallow coastal waters on the continental shelf, with the largest groups generally recorded further offshore (Shane et al. 1986; Fury and Harrison 2008; Sprogis et al. 2015). In many areas across the globe, these animals are resident or semi-resident, with relatively high levels of site fidelity, despite their highly mobile nature (e.g. Zolman 2002; Balmer et al. 2008; Fury and Harrison 2008; Hwang et al. 2014).

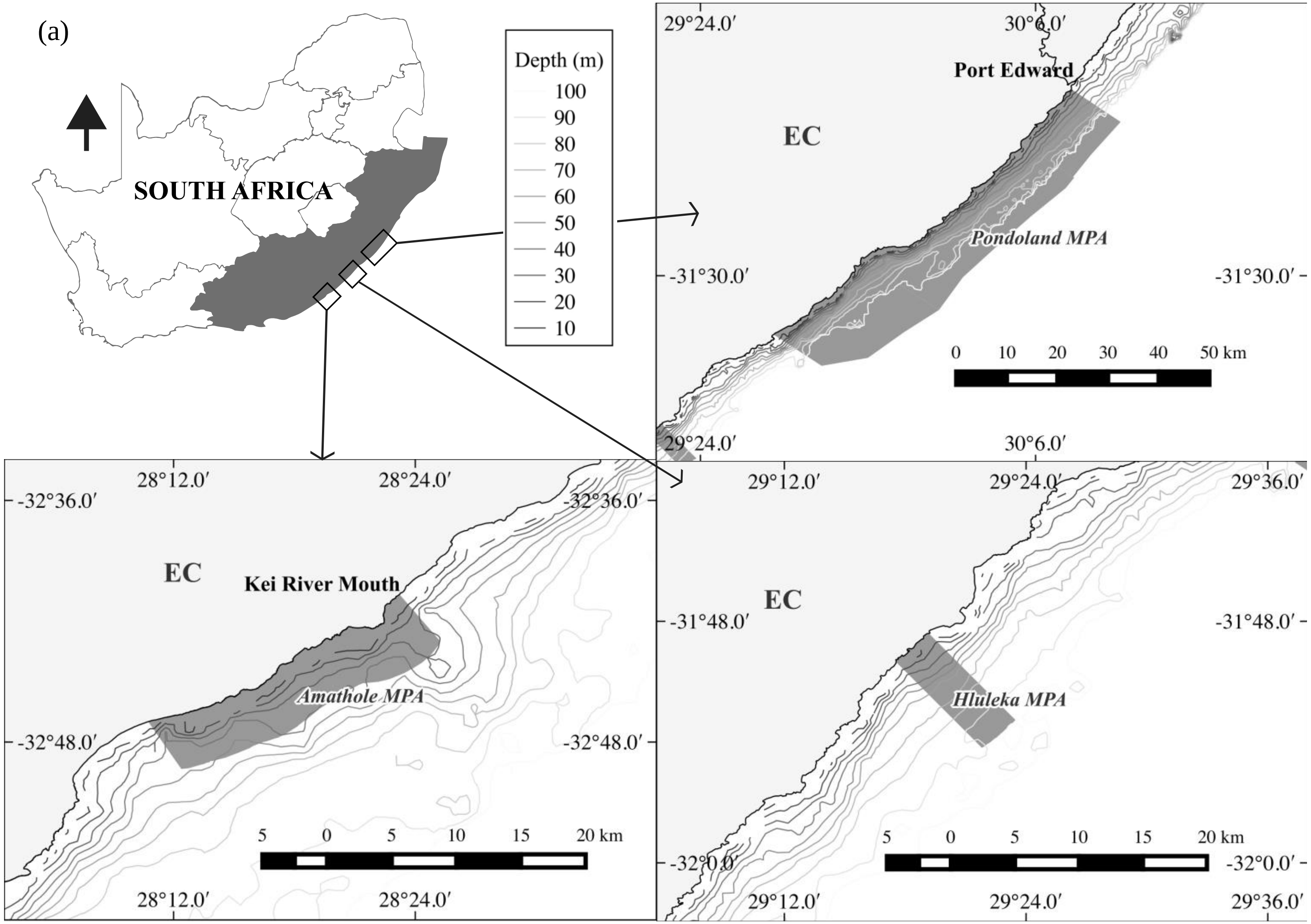
Common dolphins (*Delphinus delphis*) are considered one of the most gregarious cetacean species (Evans 1994; Reeves et al. 2002) as they occur in large groups of 50-400 animals on average worldwide (Evans 1992, Reeves *et al*. 2002). These animals feed cooperatively on schooling fishes (Ambrose *et al*. 2013), which contributes to their large group sizes. Additionally, protection from predators contributes to group size, as animals can be found in smaller numbers in areas with low predation pressure (Acevedo-Gutierrez 2002). In South Africa coastal waters, large groups have been found along the Wild Coast area, with upwards of 500 animals in a group (O'Donoghue et al. 2010b, a; Caputo et al. 2017). Globally, they are considered highly mobile animals with low residency rates and site fidelity (Evans 1994; Reeves et al. 2002; Jefferson et al. 2008).

The purpose of this study is to determine the occurrence of bottlenose and common dolphins along the Wild Coast of South Africa using boast-based surveys conducted in February, June and November over the period of 2014 – 2016. Specially, the study will use sighting data to investigate the density of these two dolphin species in the study area, including within MPAs, and to determine if any environmental variables affect their distribution. The study will also investigate whether any degree of residency occurs for bottlenose dolphins in this region, to elucidate whether the area is a migratory corridor or potentially supports a resident/semi-resident population. For bottlenose dolphins, the residency rates will be investigated using photographic identification methods. Based on previous research, it is predicted that common dolphins will only be present in the area during the June field trips and they will mostly be feeding during that time (Cockcroft and Peddemors 1990; O'Donoghue et al. 2010b, a; Caputo et al. 2017). Due to cooperative feeding on sardines in the austral winter, it is expected that the largest groups of common dolphins will be recorded in June, with colder waters having larger groups than warmer waters as sardines are a cold water species (Shane et al. 1986; Möller et al. 2002; Ambrose et al. 2013; Caputo et al. 2017). Given the sensitivity of dolphins to anthropogenic impacts, baseline studies are critical to monitoring change, especially along the Wild Coast which remains remote but is threatened by future development plans and oil and gas exploration (Wells et al. 2004; Parra et al. 2006).

3.2 Methods

3.2.1 Study Site and Data Collection

Boat-based surveys were conducted during eight field trips (i.e. trips to the field site) with 47 total survey days (i.e. days spent at sea looking for dolphins) between 2014 and 2016 in three locations along the Wild Coast of South Africa: Amathole, Hluleka, and Pondoland (Figure 3.1, see Table 3.1 for effort). These surveys areas were chosen as they give the two extremes of the south-west to north-east extent of the Wild Coast (Amathole on the southwest and Pondoland on the northeast), with a study site near the mid-section of the Wild Coast. Additionally, access to sea is limited, with no ports or formal launch sites along this coast, which limited the choice of study sites. Distance between each location is approximately: Amathole to Hluleka = 82km, Hluleka to Pondoland = 28km, Amathole to Pondoland = 100km. Each field trip was three weeks long and surveys at sea were conducted on as many days as possible during those three weeks. Two types of semi-rigid vessels were used, one 6.5m and one 9m vessel. Surveys covered approximately 2318 km of coastline, with an average of 31 km per survey and 155 km per three-week field trip, travelling in parallel transects along the 15m and 30m depth contours, alternating travel direction (i.e. northeast or southwest) on each field day at approximately 7-9 knots. During each trip to sea, logistical time constraints limited the area that could be surveyed. As this is a new area for dolphin research, the intent was to cover as much area as possible. Surveys were only conducted when weather conditions were favourable, with Beaufort <4 and swell height <2m, to maximize sightability and ensure safety of the crew.


(a)
SOUTH AFRICA
Depth (m)
100
90
80
70
60
50
40
30
20
10
29°24.0′
30°6.0′
Port Edward
EC
Pondoland MPA
-31°30.0′
0 10 20 30 40 50 km
28°12.0′
28°24.0′
-32°36.0′
EC
Kei River Mouth
Amathole MPA
-32°48.0′
5 0 5 10 15 20 km
29°12.0′
29°24.0′
29°36.0′
-31°48.0′
EC
Hluleka MPA
-32°0.0′
5 0 5 10 15 20 km

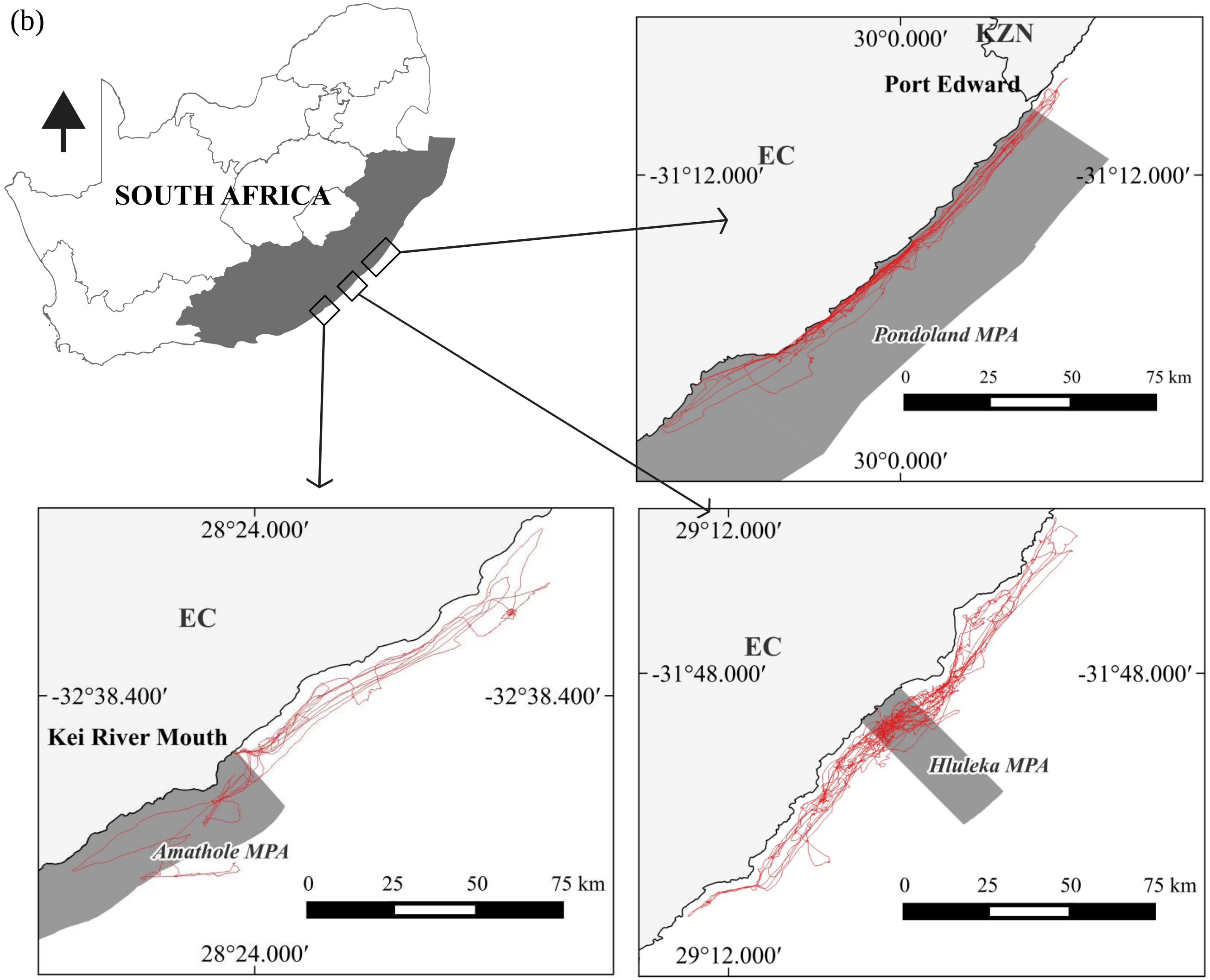


Figure 3.1: Three study areas off the Wild Coast of South Africa: Amathole, Hluleka, and Pondoland including (a) study area with depth profiles and (b) survey transects (solid red line), conducted over three years in eight different trips. Marine protected areas (MPAs) in each location are noted with a grey colouration.

Table 3.1: Survey effort for field trips off the Wild Coast of South Africa, including number of sightings, total kilometres surveyed per trip to sea and the total hours of survey effort for each trip between 2014-2016 in February (summer), June (winter), and November (summer) .

Year	Month	Location	Survey days	Sightings	Total kms	Total hours
2014	June	Amathole	5	10	229.70	15.37
2014	November	Hluleka	5	22	12.00	16.91
2015	February	Pondoland	6	18	440.60	28.23
2015	June	Pondoland	7	30	484.80	35.08
2015	November	Amathole	3	10	109.50	8.44
2016	February	Hluleka	8	30	354.90	24.84
2016	June	Hluleka	9	51	338.40	32.35
2016	November	Pondoland	4	20	235.50	20.02

Dolphin sightings were made by 4-7 observers scanning on all sides of the boat. A minimum of 1 observer was kept constant throughout the study and trained the other observers to ensure consistency of method and counts. The number of observers had no effect on the number of sightings (ANOVA: df=44, p=0.972). A group of dolphins was defined as individuals within 100m of each other engaged in similar predominant behaviours, with no two animals in the group more than 10m apart (Irvine et al. 1981). For each group, animals were approached and the following data were recorded: geographic location (determined using a hand-held Global Positioning System), time of sighting, group size (using maximum, minimum, and best estimate), group composition (adults, juveniles, and calves), and group dynamics (i.e. clumped <5m between any two animals or dispersed>5m between most individuals in the group). In smaller groups (<50 animals), an exact estimate for total number of animals was attempted by performing repeated counts. In large groups (>50 individuals), the number of animals was recorded to the nearest 10. Environmental parameters including, sea surface temperature (SST) and depth (using a depth sounder), wind direction and strength, and Beaufort Sea State (referred to as sea state) were also recorded. Additionally, the predominant behaviour of each group was recorded and updated as behaviour changed from one of five categories (as per

Shane 1990): travelling, resting, foraging, milling, or socializing (Shane 1990). If the group changed in terms of numbers or behaviour, this was recorded. The difference in number of sightings depending on sea state was significant but was not linear relationship (ANOVA: p=0.026). The sightings when sea state was greater than 4 were considered opportunistic and accounted for only 2 of the 44 sightings. Additionally, less than 7% total survey effort was in conditions with sea state exceeded 3. As such, opportunistic sightings outside of the ideal conditions were included in further analysis.

On approach, photographic identification of individuals was conducted using a Canon EOS 70D camera with a 100-400mm zoom lens. Dolphin dorsal fins have unique marks (i.e. nicks and notches) which can be used to identify individuals (Urian et al. 2015). Photographs were taken of dorsal fins, perpendicular to the animal. An attempt was made to photograph all individuals in the group, from both sides of the animals.

3.2.2 Density and group size

To account for survey effort, survey track lines were entered into *ArcMap 10.5* (ESRI® Inc., 2014) software and projected into World Geodetic System 1984, and the surveyed portion of each study area was divided into 1km x1km grid squares, with total effort (in kilometers) calculated for each grid cell using a spatial join. Bottlenose and common dolphin group sighting were plotted and the total number of sightings and animals for each species was calculated for each grid cell and corrected for effort, giving the total number of sightings per km (i.e. sighting density or encounter rate) and total number of animals per km (i.e. individual density) in each grid cell. Environmental variables were also calculated for each grid cell using a spatial junction to calculate the mean for each variable within each grid cell; these included: depth, sea surface temperature, distance to shore, and substrate type. A hotspot analysis using a quartic kernel density shaping for a 2km radius was performed *in QGIS 2.8.2-Wien* using the “heatmap” tool for each species based on both sighting and individual density, separately (Wilson et al. 2004; Natoli et al. 2004; Bearzi 2012; Alves et al. 2013).

Differences in sighting and individual densities were then compared between study areas as well as survey months, where June = winter, and November and

February = summer, using ANOVAs for each species, with Tukey's post hoc testing applied to further investigate significant differences. Using generalized linear models (GLMs), the effect of environmental variables on sighting density and individual density of bottlenose and common dolphins was investigated employing *R v 3.4* software (R Development Core Team 2017). As substrate had only one value for common dolphins, this factor was removed from the analysis. Normality was tested before ANOVAs and GLMs using Q-Q plots of residuals and fits, as well as a Shapiro-Wilks test, and response variables were log transformed where needed. All variables were assessed for collinearity as these variables can have interactive effects, and depth and distance to shore were strongly collinear (Pearson Coefficient=0.82) therefore, distance from shore was eliminated from further analysis (Zuur et al. 2009). The best models were selected through backwards stepwise deletion using the Akaike Information Criterion (AIC), with best models having delta AIC<2 (Burnham and Anderson 1992).

To determine variations in group size, positive count data were analyzed for dolphins according to the framework outlined by Zuur *et al.* (2009). Explanatory variables were assessed for collinearity. Differences in group size of dolphins was assessed against covariates using a Zero-Truncated Negative Binomial (ZTNB) Generalized Linear Model (GLM), which was fit using the '*zerotrunc'* function in the '*countreg'* package (Zuur et al. 2009; Zeileis and Kleiber 2017). Separate models were constructed where necessary to preserve sample size as logistical constraints did not warrant a balanced data set. Likelihood ratio tests (LRT) were conducted to test specific biological hypotheses between nested models. For multivariate models, global models were fitted and then followed a backward stepwise deletion process to determine the optimal model with delta AIC<2. The influence of year, austral season (June = winter, February and November = summer), predominant behavioral activity, and environmental variables (depth, SS, and sea-bottom substrate) on dolphin group size was then assessed. The number of sightings within and outside of MPAs was calculated and the mean group size within and outside of MPAs was compared using a GLM with a negative binomial distribution.

To investigate how group size varied spatially, the conversion tool "*point to raster*" in *ArcMap 10.5* was employed (ESRI® Inc., 2014). Grids cells of 1x1 km were created and the maximum and mean group size observed within each cell was calculated within the study areas (equivalent to the estimated strip scanned with the naked eye). For both density and group size analyses, the sea-bottom substrate (sandy, rocky mixed, muddy) under which dolphins were observed was obtained using a spatial junction between the data shapefile and the benthic and the coastal habitat classification shapefile provided by the South African National Biodiversity Institute (Sink et al. 2012).

3.2.3 Photographic identification and residency

Photographs were rated on distinctiveness and photo quality according to Urian et al. (1999). Distinctiveness was assessed on the number of markings on the leading and trailing edges of the dorsal fins and ranked high (D1), average (D2), or non-distinctive (D3). Photo quality was centered on focus, contrast, angle, and size of fin relative to the frame and ranked as excellent, good, or poor. Only high or average distinctiveness and excellent or good quality photos were included in further analysis (Urian et al. 1999, 2015). For common dolphins, groups were often large (>150 animals) and highly dispersed, and fins were rarely distinct enough for analysis. Due to lack of confidence in results and a low percentage of useable photographs, common dolphin data were not considered in photographic identification analysis. The photographic identification analyses were only performed on Bottlenose dolphins and considering photos that met the above criteria. Then the photos were further categorized based on location of markings on the dorsal fin and compared to previously identified individuals to determine if they were a new animal or a resighting (Urian et al. 2015). The number of animals identified as a percentage of the group size for each group was then estimated for each survey (Smith et al. 2013; Urian et al. 2015; Zanardo et al. 2016).

For each individual catalogued using photographic identification, two residency metrics were calculated 1) the number of resightings during different field trips as a ratio to total number of field trips (8 three-week field trips in total) (Simpfendorfer et al. 2011; Daly et al. 2014; White et al. 2014), and; 2) the number of days sighted as a ratio of the total number of days surveyed (47 days surveying total) (Parra et al. 2006; Zanardo et al. 2016). Resightings made on the same day were not included in the analysis (Parra et al. 2006). To group individuals by similar residency patterns, agglomerative hierarchical clustering (known as AGNES) based on these two metrics was performed using *R v 3.4* software (R Development Core Team 2017). AGNES uses a bottom-up approach to form clusters, starting at the individual level. Different hierarchical clustering methods were tested for the agglomerative coefficient with values closer to 1 suggesting a stronger clustering structure. Based on this testing, Ward's method was selected and a Euclidean dissimilarity matrix was employed (Ward 1963; Cao et al. 1997; Singh et al. 2011). AGNES results are displayed in a dendogram, showing the clusters into which, the data can be grouped.

The number of resightings per area, both within a field trip (i.e. less than 21 days apart) and from different trips (i.e. more than 21 days apart) were calculated. Resighting counts for each area and each field trip were compared using a Poisson's regression with a GLM. Additionally, the number of days between resightings for each individual were calculated both for resightings within the same field trip (i.e. time within the study area), and resightings between different field trips. The differences in time for resighting between field trips (i.e. month and year of the trip) were investigated using a Kruskal-Wallis non-parametric test, as data was non-normal. Dunn's post-hoc test for multiple pairwise comparisons was performed where needed. Resighting rates within each study area (i.e. Amathole, Hluleka, and Pondoland separately) were calculated based on the number of individuals resighted in an area as a ratio of total number of individuals seen in that area. Resightings rates for each field trip were also calculated as the number of resighted individuals as a ratio of the total number of individuals seen during that field trip. In addition, the mean number of animals resighted two or more times during different field trips in the following categories: A) same study area, B) adjacent area to the northeast, C) adjacent area to the southwest, and D) back and forth (defined as animals moving both northeast and southwest during the study) was compared using a generalized linear model with negative binomial errors. A goodness-of-fit test was employed to test the appropriateness of the negative binomial model. Normality was tested using plots of residuals and fits.

3.3 Results

Throughout the study period, a total of 47 surveys were undertaken in the three different areas (Amathole = 8, Hluleka = 22, Pondoland = 17), for a total of 2315 km of effort (see Table 3.1 for full effort summary). In total, 135 bottlenose dolphin sightings comprising an estimated 4444 animals were observed during the investigation (Table 3.1). For common dolphins, there were 47 sightings with an estimated 7965 animals observed. A total of 112 grid cells (1 km^2) containing dolphin sightings were mapped of which 19 contained both species (i.e. 17% overlap), though not concurrently. Both species were observed in waters of approximately 20 m depth on average (mean =19.77 +/- 0.9 m, median=19.1, range=3-61.7 m) and in sea surface temperatures ranging from 16.9°C to 25.4°C. The maximum distance from shore for any sighting was 3.9 km (minimum = 0.066 km) for bottlenose dolphins and 4.8 km (minimum = 0.25 km) for common dolphins. Both species were seen foraging within, on average, 1.1 km of shore (bottlenose dolphin mean=1.08+/-SD 0.75 km; common dolphin mean=1.08 +/- SD 0.51 km). For bottlenose dolphins, 59% of sightings were made within 1 km from shore and 94% were within 2 km from shore. For common dolphins, 38% of animals were seen within 1 km from shore, 42% were within 2 km from the shore, and 96% within 3 km from shore.

3.3.1 Density and group size

For bottlenose dolphins, the mean density by sighting did not vary by study area (df=2 F=0.494, p=0.612) nor did individual density (df=92, F=1.09, p=0.341; Figures 3.2 and 3.3). However, for common dolphins, the individual density was significantly different between areas (df=2, F=3.62, p=0.038) with a Tukey post-hoc test revealing that the largest difference was between Amathole (mean=17.94+/- SD 5.29 individuals/km surveyed) and Pondoland (mean=1.82+/-SD 0.628 individuals/km surveyed; df=2, p=0.032; Figure 3.4 and 3.5). Neither sighting nor individual density differed for either species between the three study months (bottlenose dolphins: sighting density – df=2, F=0.928, p=0.398, individual density – df=2, F=0.247, p=0.781; common dolphins: sighting density – df=2, F=0.767, p=0.472, individual density – df=2, F=1.66, p=0.204). No environmental factor had a significant effect on sighting density (df=2, F=0.25, p=0.91) or individual sightings (df=2, F=0.50, p=0.73) for bottlenose dolphins. The sighting density differed significantly with SST for common dolphins (df=28, F=5.20, p=0.012). Additionally, depth had a significant effect on individual density for common dolphins (df=2, F=5.75, p=0.023), with the highest density of individuals found in the deepest waters (>50m).

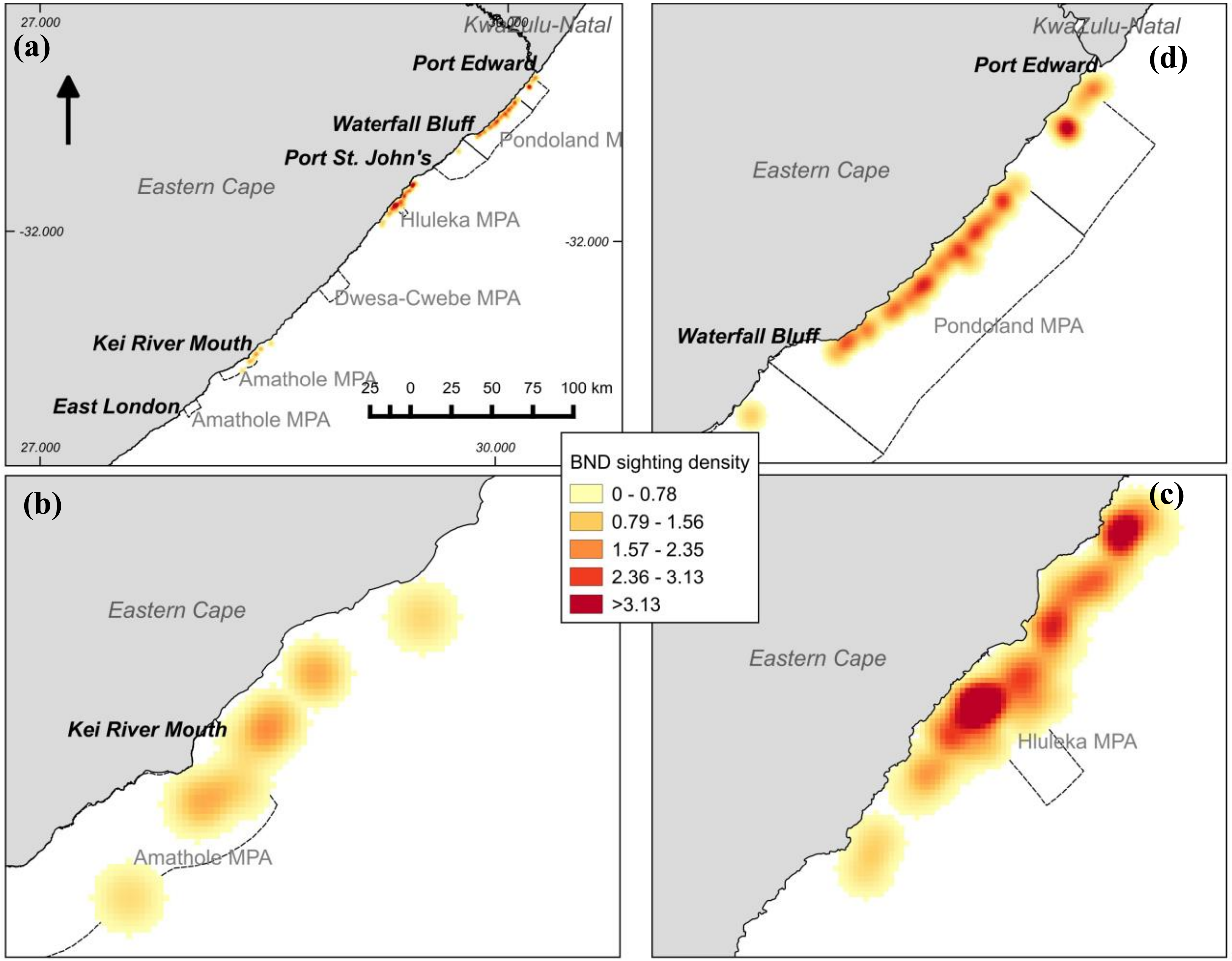


Figure 3.2: The sighting density for bottlenose dolphins (*Tursiops aduncus*) in terms of number of sightings per kilometer surveyed in each 1x1km grid, with a kernel density function applied at a 2km radius, for the entire Wild Coast of South Africa (a), and each study area separately: Amathole (b), Hluleka (c), and Pondoland (d).

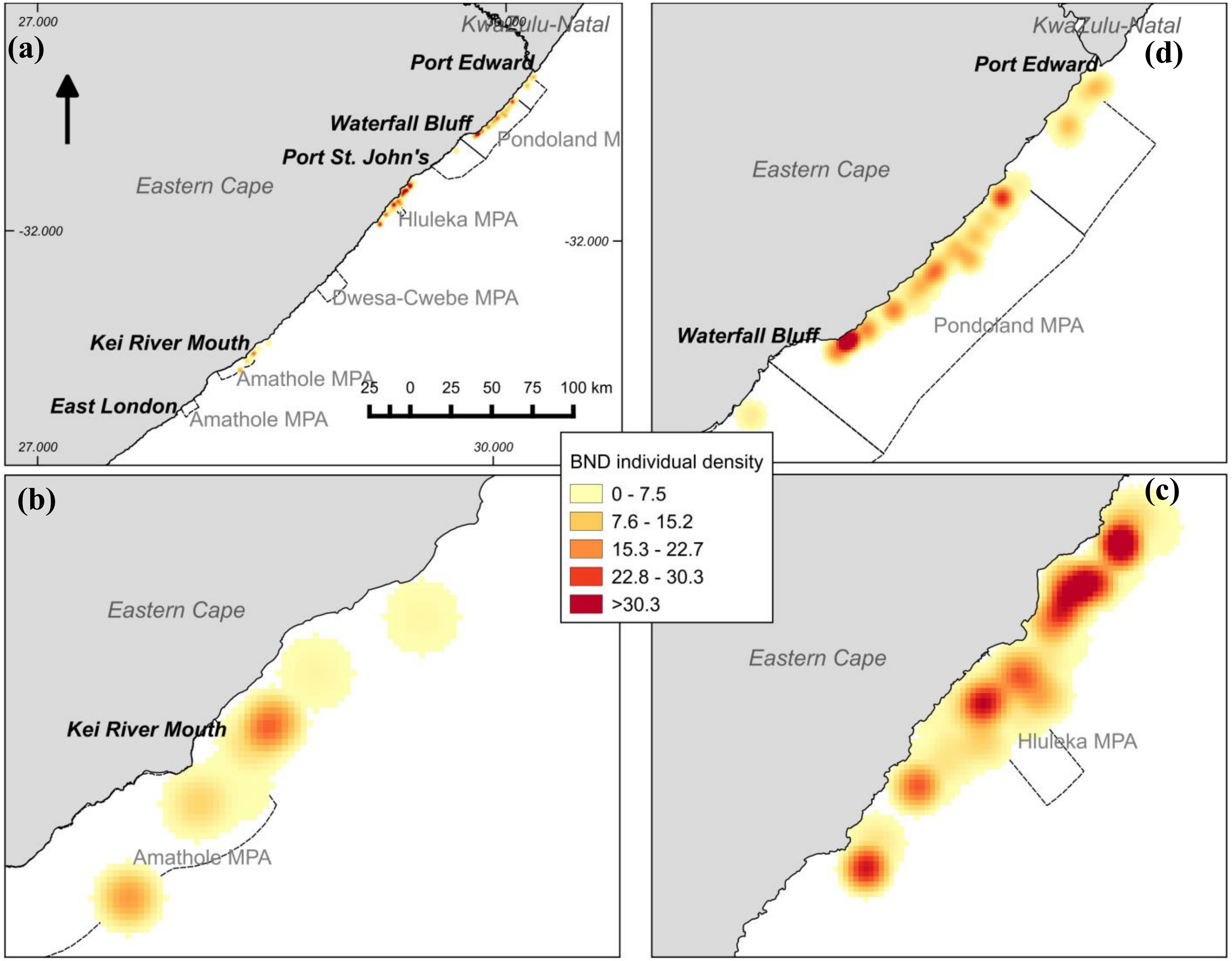


Figure 3.3: The individual density for bottlenose dolphins (*Tursiops aduncus*) in terms of the total number of animals seen per kilometer surveyed in each 1x1km grid, with a kernel density function applied at a 2km radius, for the entire Wild Coast of South Africa (a), and each study area separately: Amathole (b), Hluleka (c), and Pondoland (d).

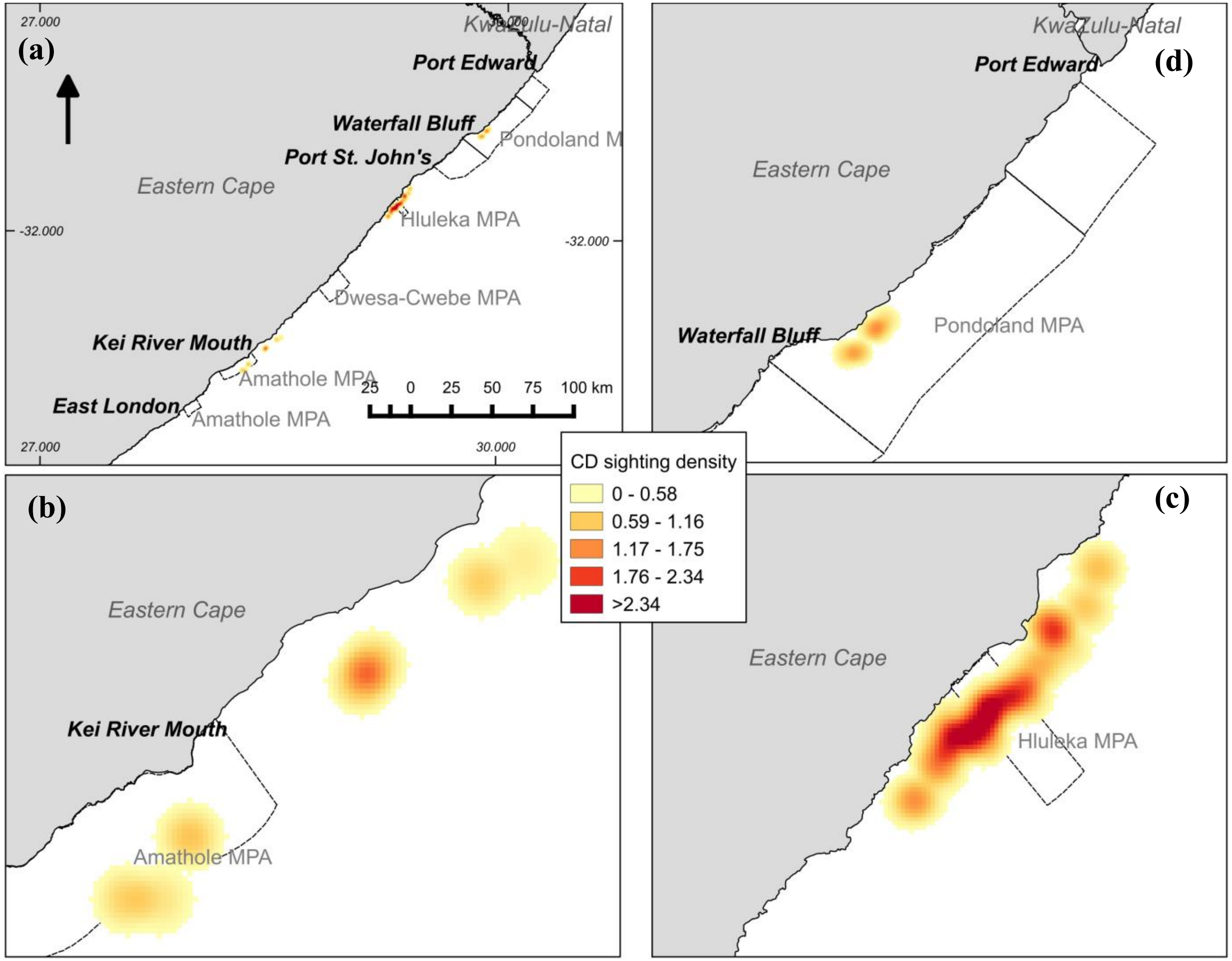


Figure 3.4: The sighting density for common dolphins (*Delphinus delphis*) in terms of number of sightings per kilometer surveyed in each 1x1km grid, with a kernel density function applied at a 2km radius, for the entire Wild Coast of South Africa (a), and each study area separately: Amathole (b), Hluleka (c), and Pondoland (d).

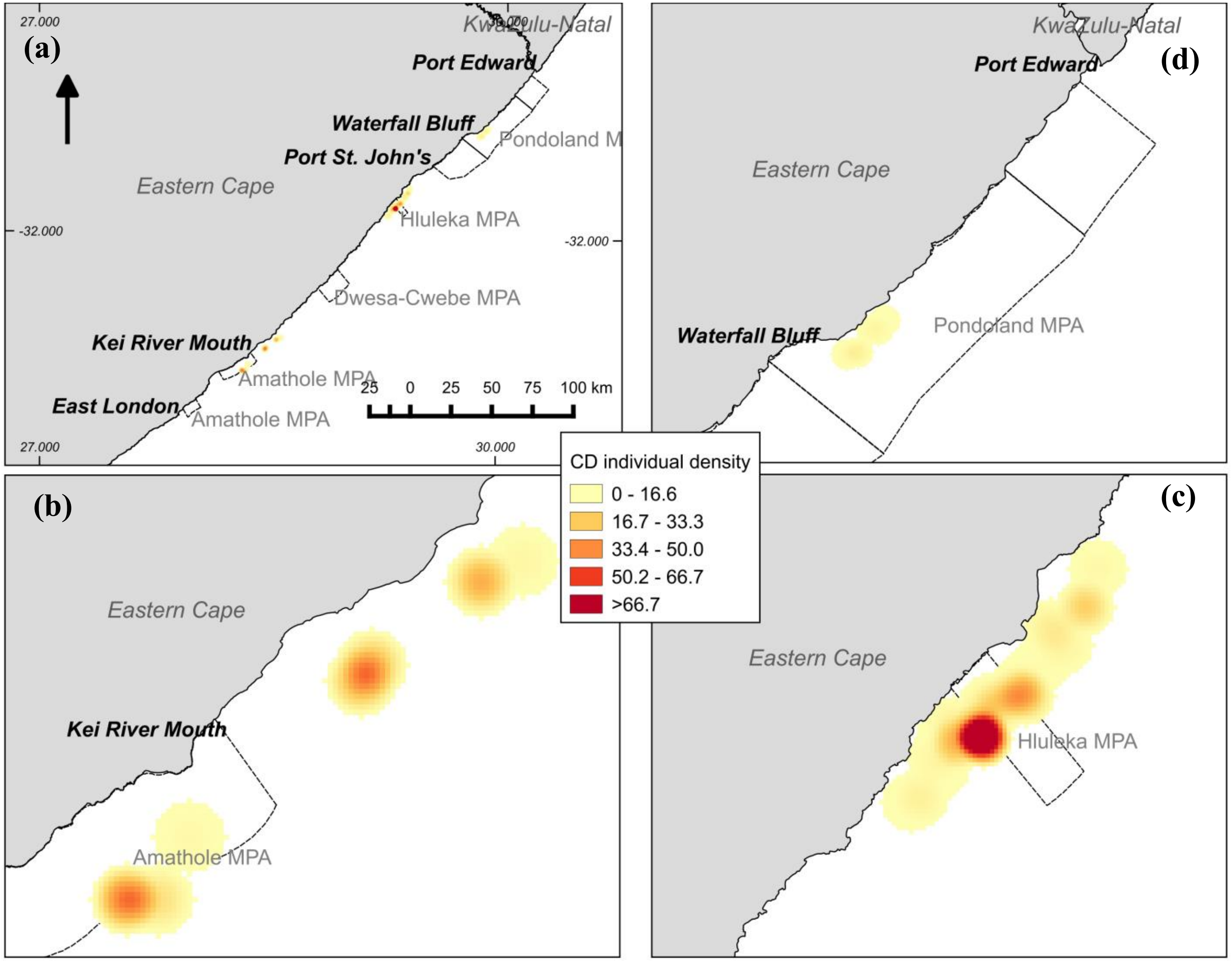


Figure 3.5: The individual density for common dolphins (*Delphinus delphis*) in terms of the total number of animals seen per kilometer surveyed in each 1x1km grid, with a kernel density function applied at a 2km radius, for the entire Wild Coast of South Africa (a), and each study area separately: Amathole (b), Hluleka (c), and Pondoland (d).

Common dolphin groups were larger than bottlenose dolphin groups over the entire study period, but not significantly (χ^2=1.21, df=1, p=0.27); common dolphin: n=50, mean=86.2+/-SD=195.74, median=27.5, range=1-1250; bottlenose dolphin n=135, mean=32.9 +/- SD=38.3, median=19, range=1-250 Figure 3.6, 3.7, and 3.8). Eighteen percent (17.8%) of the bottlenose dolphin groups comprised > 50 individuals (Figure 3.6). The maximum group size of bottlenose dolphins for each study area was 150 animals at Amathole (n=10, mean=27.7 +/- SE=10.12), 250 animals in Hluleka (n=64, mean=36.9 +/- SE=5.07) and 150 animals in Pondoland (n=61, mean=29.5 +/- SE=5.01, Figure 3.6). Group size of bottlenose dolphins did vary spatially (df=132, p=0.233). The maximum group size of common dolphins for each study area was 125 animals at Amathole (n=9, mean=55.6 +/- SE=13.3), 600 animals in Hluleka (n=34, mean=41.4 +/- SE 5.4), and 1250 animals in Pondoland (n=7, mean=55.2 +/- SE 13.4). Group size did not increase significantly over the study period for either bottlenose dolphins (df=2, p=0.4849) or common dolphins (df=1, p=0.57, Figure 3.8). For common dolphins, Pondoland had larger groups, but not significantly (df= 47, p=0.572), with an average of 186 animals per group, compared to 76 and 46 animals per group in Hluleka and Amathole, respectively (Figure 3.7).

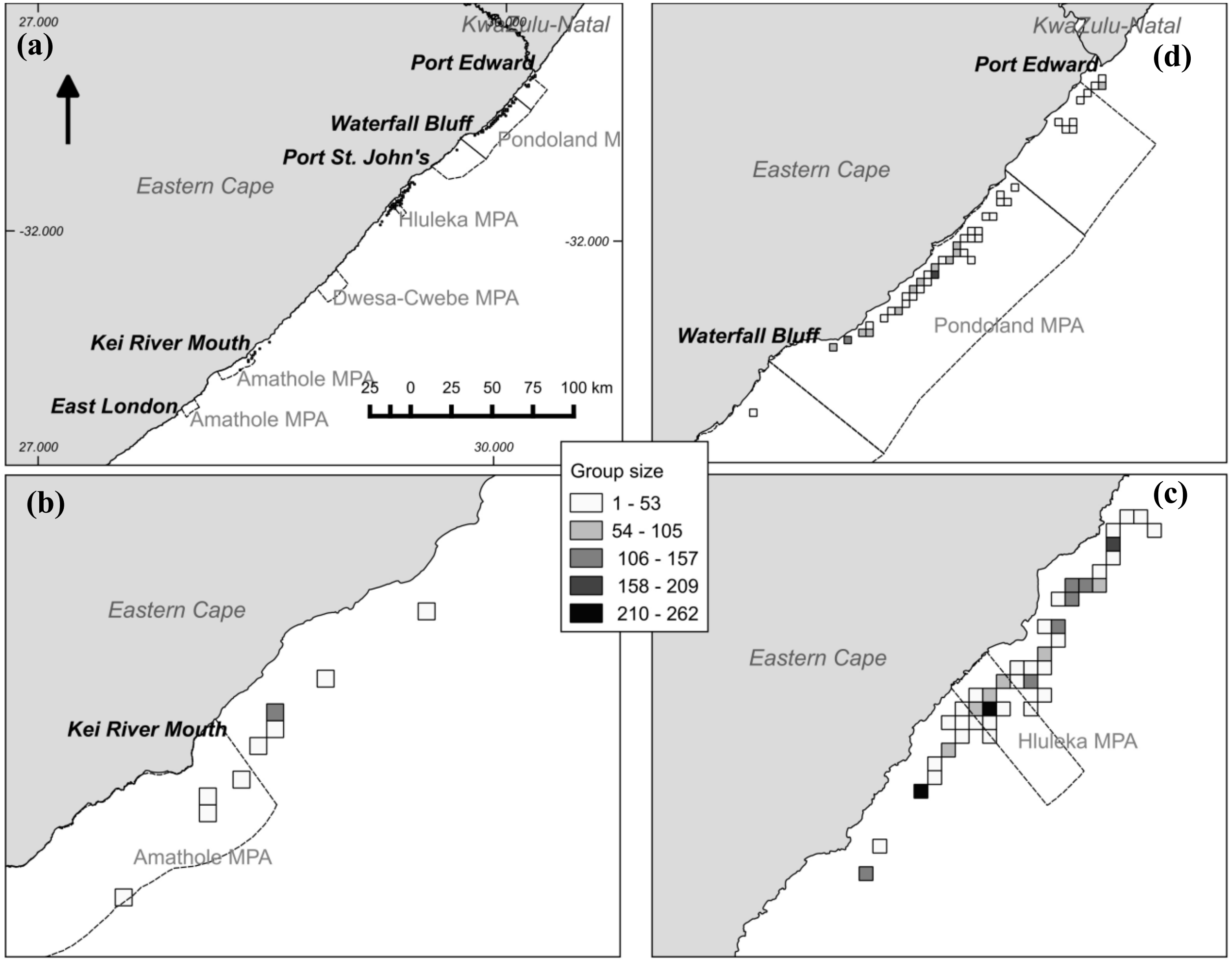


Figure 3.6: Total number of bottlenose dolphins (*Tursiops aduncus*) within each 1km x 1km grid cell from sightings over the study period, for the entire Wild Coast of South Africa (a), and each study area separately: Amathole (b), Hluleka (c), and Pondoland (d).

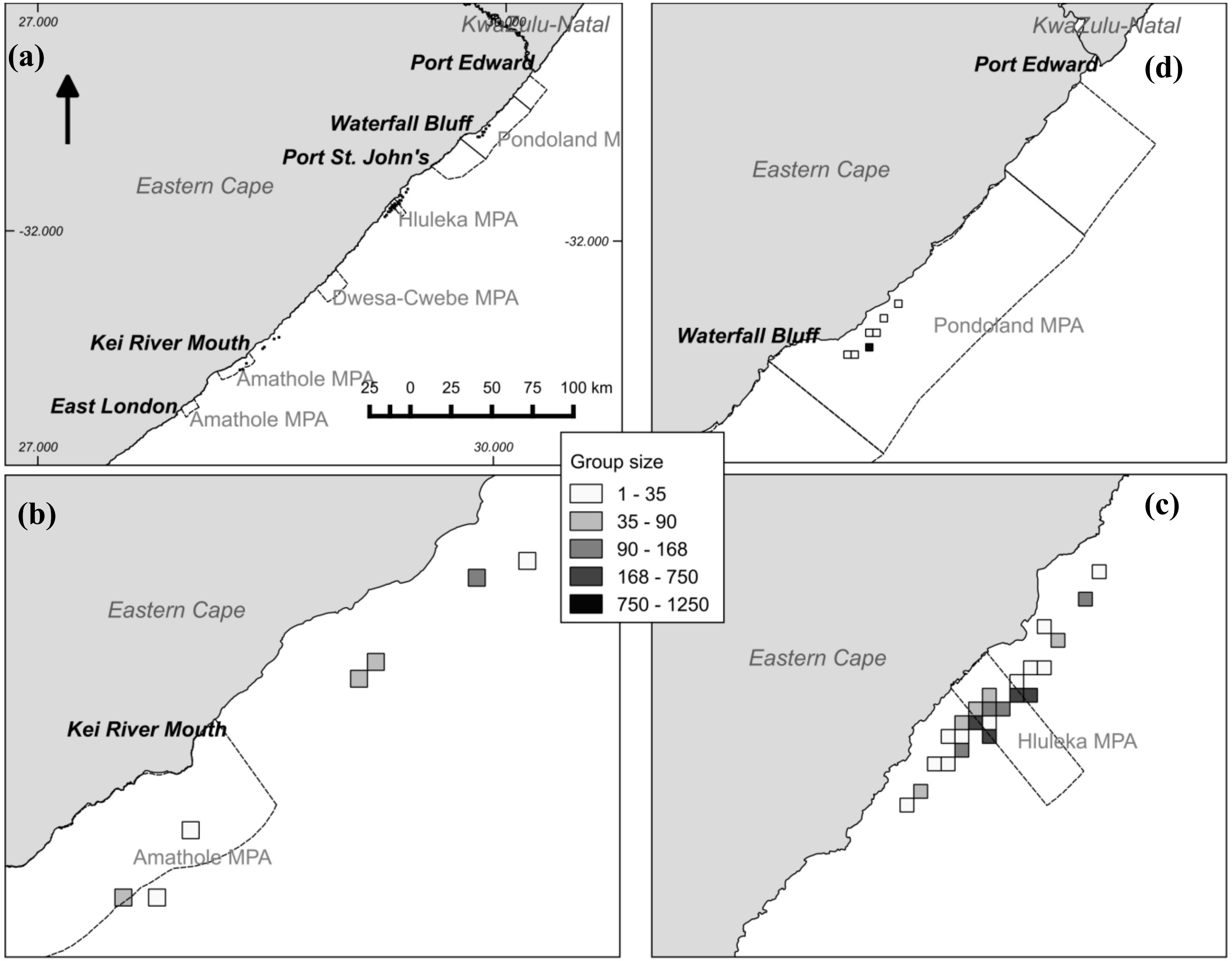


Figure 3.7: Total number of common dolphins (*Delphinus delphis*) within each 1km x 1km grid cell from sightings over the study period, for the entire Wild Coast of South Africa (a), and each study area separately: Amathole (b), Hluleka (c), and Pondoland (d).

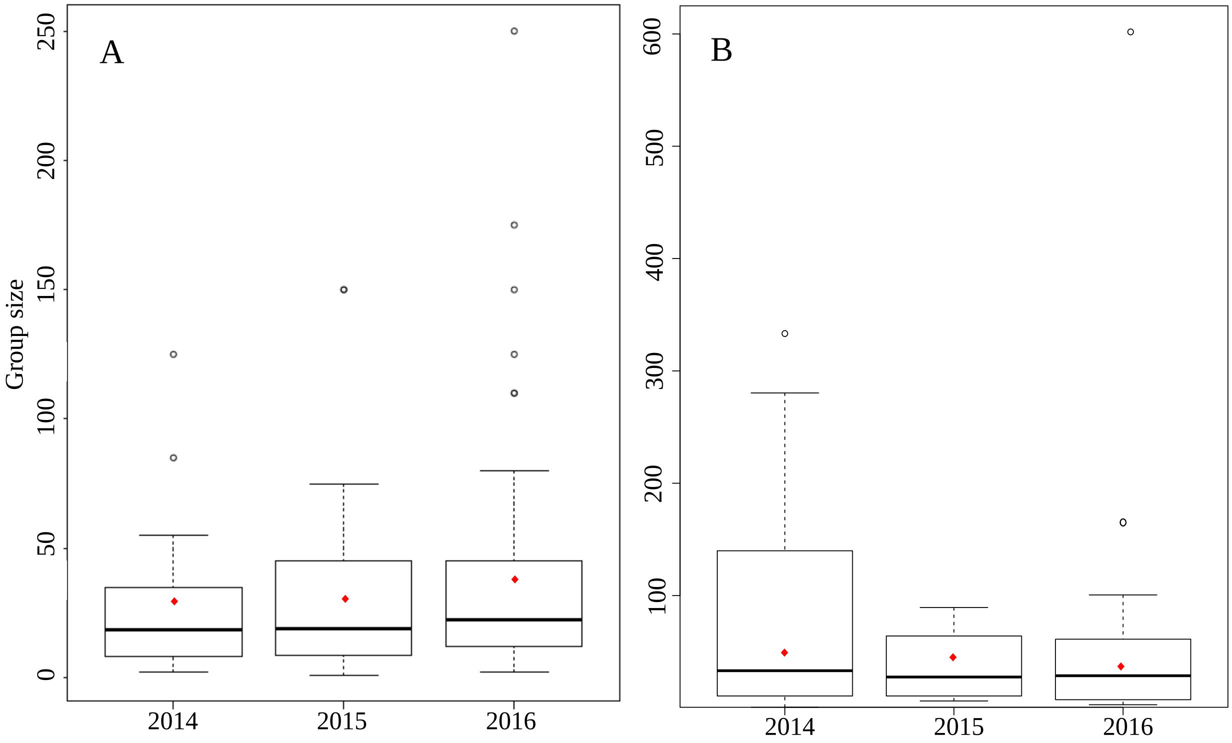


Figure 3.8: Mean (red dot) and median (black line) group size of (A) bottlenose dolphins (*Tursiops aduncus*) (n=135), and (B) common dolphins (*Delphinus delphis*) (n=47) sighted off the Wild Coast for each survey year from 2014-2015. An outlier group of 1250 common dolphins in 2015 has not been plotted.

Predominant behavior had no significant effect on group size of bottlenose dolphins (df=4, LRT=9.83, p=0.04344; Figure 3.9). The bottlenose dolphins were predominantly travelling (58.5% of the sightings) and were foraging in about 25% of the sightings. For common dolphins, there was a significant difference in group size depending on behavior (df=8, LRF=521.4, p=0.013), with the largest groups milling, foraging, and resting (milling: mean=424+/- SD 715; foraging: mean=78+/- SD 120; resting:1 group of 150 animals), and smaller groups traveling (mean=33+/- SD 144, Figure 3.9). Only one group, comprising 12 individuals, was seen socializing. When the outlier group of 1250 animals is removed from the analysis (as the group size estimate was likely inaccurate for such a large group), the average group size of animals milling dropped to 11(+/-SD 8) animals (df=8, LRT=494.2, p=0.017). Bottlenose and common dolphins were seen foraging at all locations in all in months that the surveys were conducted. When taken by location, the predominant behaviour for both species in Amathole and Pondoland was travelling (53% and 63% of sightings respectively). In Hluleka, they were predominantly seen foraging (48% of sightings).

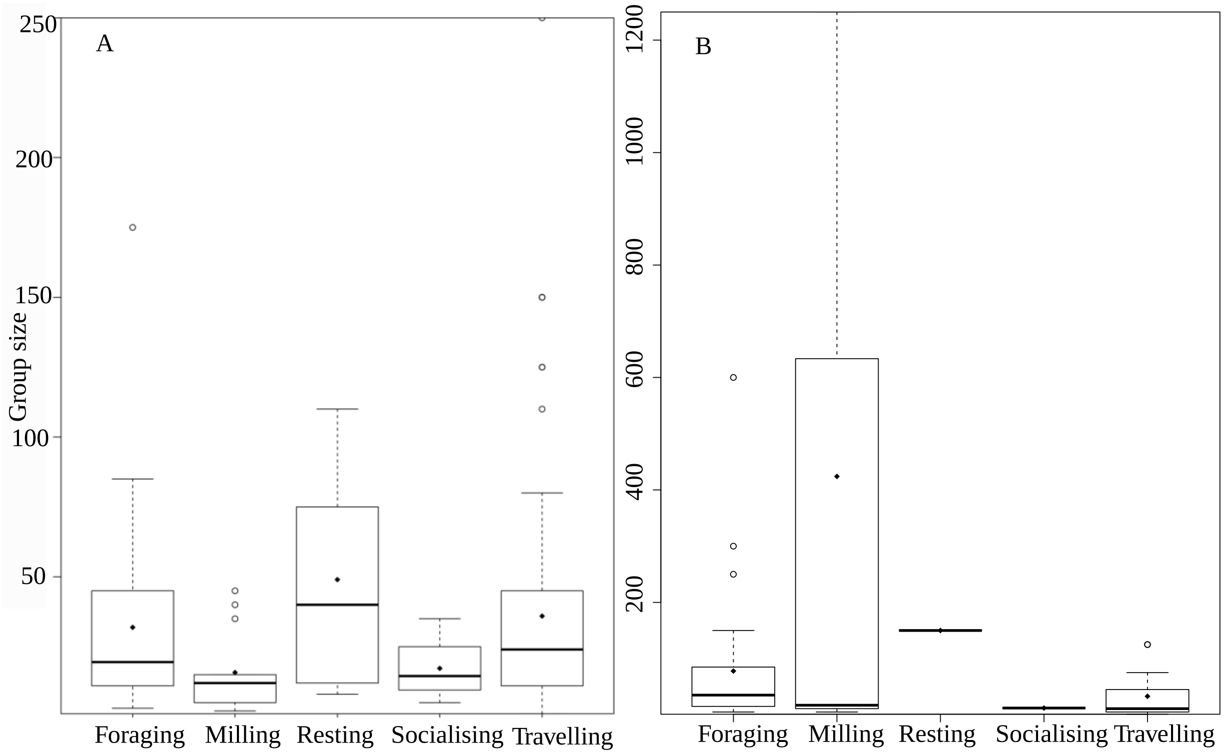


Figure 3.9: Mean (black dot) and median (black line) group size of (A) bottlenose dolphins (*Tursiops aduncus*) (n=135) and (B) common dolphins (*Delphinus delphis*) (n=47) off the Wild Coast of South Africa in each of five behavioural categories (i.e. foraging, milling, resting, socializing, and travelling).

Over the observed range of environmental variables recorded during the investigation, only the SST had a significant effect on group size for both species (bottlenose dolphins - SST: df=1, LRT=5.936, p=0.0148; depth: df=1, LRT=3.2301, p=0.0723; substrate: df=1, LRT=0.1879, p=0.6647; common dolphins – SST: df=1, LRF=5.57, p=0.018, depth: df=1, LRT=1.32, p=0.25). The majority of bottlenose dolphin groups were sighted within the three MPAs (60%). Additionally, the mean group size of the bottlenose dolphins within MPAs was higher than that recorded outside the protected areas (MPA mean=39.98+/- SE 5.19, out of MPA mean=28.21+/- SE3.01, z=2.08, p=0.038). Bottlenose dolphins within MPAs were mostly travelling (34.8%) and foraging

(14.1%). For common dolphins, 53.6% of sightings were recorded within MPAs. There were no significant differences in the group sizes of common dolphins within and outside of MPAs (MPA mean=84.87+/- SE 30.81, out of MPA mean=124.69+/- SE 48.58, z= 0.722. p=0.47).

3.3.2 Photographic identification and residency

A total of 2149 bottlenose dolphins were identified from over 10,000 photographs taken for photographic identification over 72 hours in 47 days, resulting in 3071 useable photographs (236 from Amathole, 1942 from Hluleka, and 1772 from Pondoland). A total of 459 animals were non-distinctive (D3), and numerous photographs were poor quality, both of which were not used for further analysis. There were 379 animals resighted between 2 and 7 times over the study period, when including repeat sightings within the same trip (Table 3.2). The overall, resighting rate was 11.8% for animals only sighted in different field trips (Figure 3.10). By area, Pondoland had the highest resighting rate (16.1%), followed by Hluleka (10.4%) and Amathole (2.7%). Individuals were resighted during 1-5 out of total of 47 days and during 1-5 out of 8 months. Based on the visual group size estimates during surveys, 64.9% of individuals counted in groups were identified by photographic identification, with highest identifications in Amathole (79.3%), compared with Hluleka (66.3%), and Pondoland (58.9%).

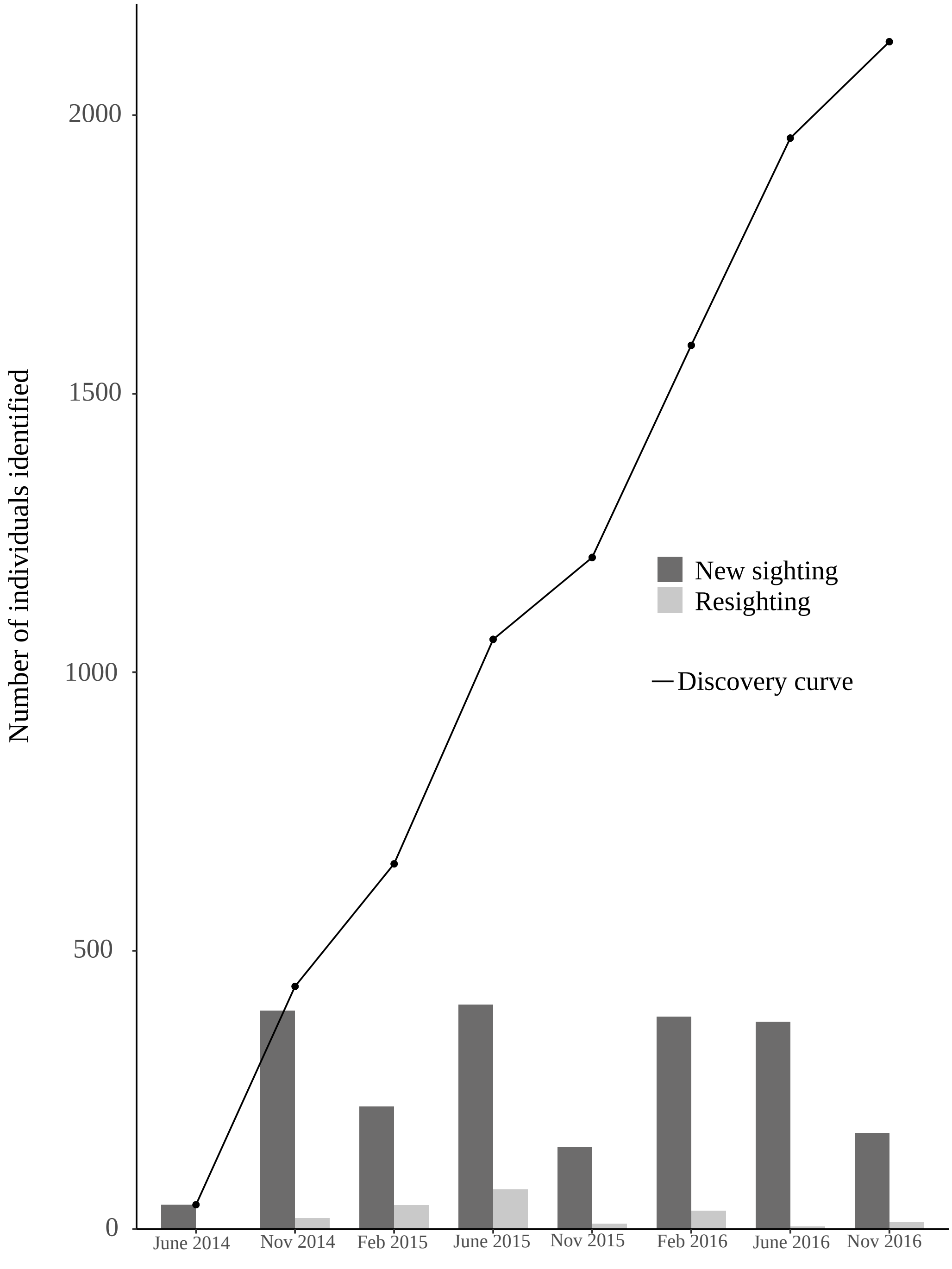


Figure 3.10: Discovery curve and number of new sightings and resightings of bottlenose dolphins (*Tursiops aduncus*) identified off the Wild Coast of South Africa, during each field trip for the duration of the study period.

Based on the dendrogram of resighting data, three clusters of individuals were identified during the investigation (Figure 3.11). Cluster 1 comprised 1832 bottlenose dolphins that were only seen during 1/47 days and 1/8 months and can be considered "occasional visitors". Cluster 2 consisted of 240 bottlenose dolphins observed 2 days and in either 1 (86 animals) or 2 (154 animals) of the months and are considered "frequent visitor". Finally, Cluster 3 comprised 77 animals which were sighted on 3-6 days and 1-5 months and are therefore, considered as "semi-resident".

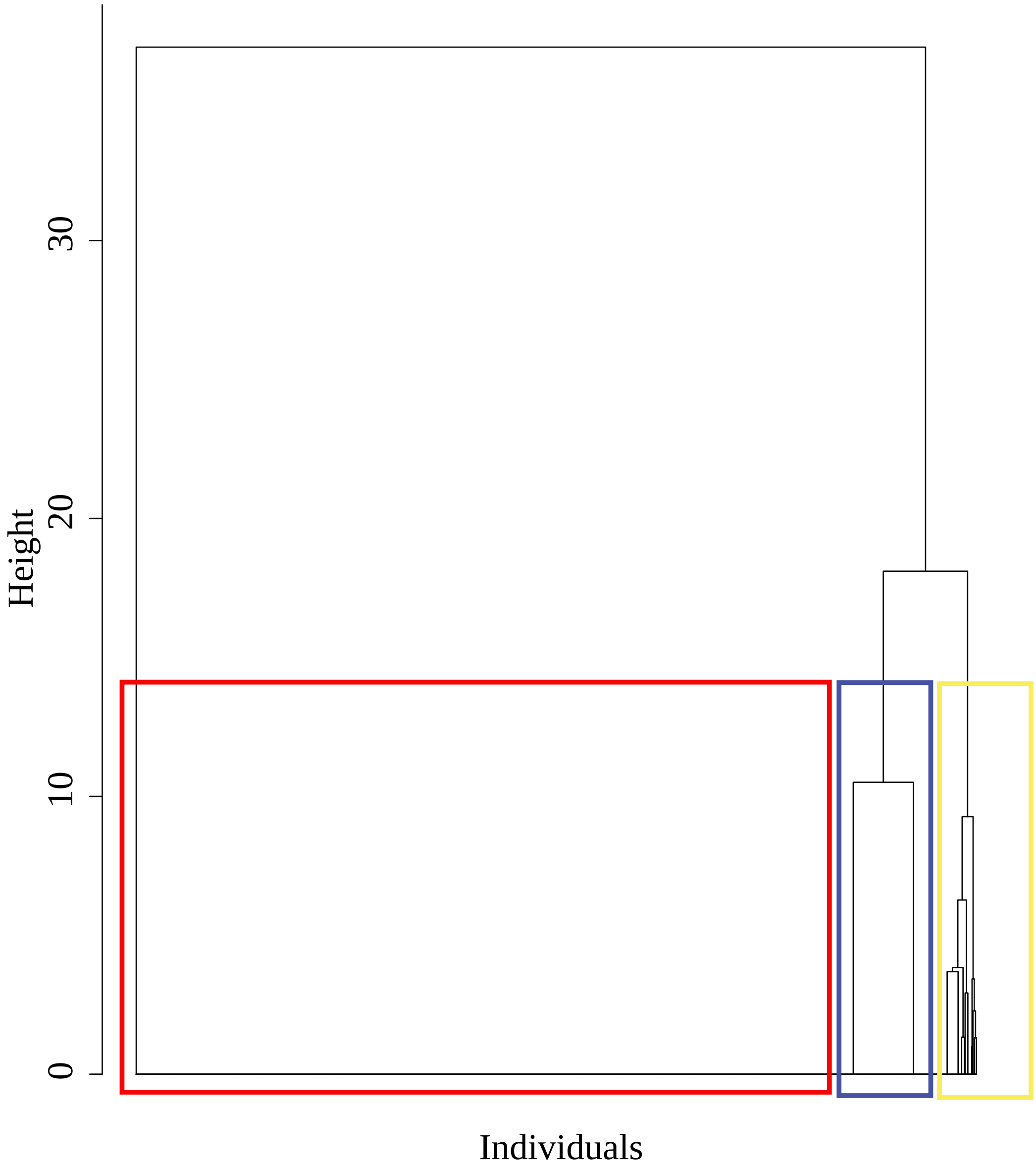


Figure 3.11: Dendogram of the agglomerative hierarchical clustering (AGNES) analysis separating clusters of bottlenose dolphins based on number of days sighted per total days surveyed and number of months seen as a ratio of total months surveyed. Three clusters represent: red = occasional visitors, yellow = frequent visitor, and blue = semi-resident.

The number of bottlenose dolphin resighted within the same field trip ranged from 2-7, with an average of 2.7+/-SD2.7 days (median=1.75, range=1-16) between sightings/resightings (Table 3.2). There were significantly more dolphins resighted 2 and 3 times (χ^2 =15.8, df=7 p=0.007) within a single field trip. Dunn's post-hoc testing revealed that there were significantly more animals sighted 2 times than any other number (χ^2=15.8 p<0.05), with animals also sighted 3 times more than 4,5,6, or 7 times (χ^2=15.8, p<0.05). There were also significantly more animals resighted within a field trip in Hluleka and Pondoland compared to Amathole (χ^2=2.08, df=2, p<0.0001), though Amathole had lower survey effort. There were significantly more animals (df=7, p<0.0001) resighted during later field trips: June 2015, and February, June and November 2016 (Table 3.2, Figure 3.10 and 3.12). The number of days between resightings within one three-week field trip (i.e. in a single location during a single year) varied from 0-16, with no significant difference in the number of days between sightings depending on location, Amathole, Hluleka, or Pondoland (df=2, χ^2=2.1, p=0.35) (Table 3.2).

In total, 254 animals were resighted between field trips (Figure 3.12). The number of bottlenose dolphin resightings between field trips ranged from 2-5 sightings per individuals, with significantly more (χ^2=63.26, df=3, p<0.0001) animals seen 2 times (79.9% of individuals) (Figure 3.13). On average, 453.4+/-172.7 days (median=453, range=88-705) passed between resightings, with significantly more days between sightings 3-4, and 4-5 (χ^2=9.05, df=3, p=0.029) (Table 3.2). Between field trip sightings only occurred from June 2015 onward (Table 3.2), as all previous resightings were within a field trip. The number of animals resighted during November 2015 was the lowest (5), significantly lower than the other field trips (df=4, p<0.0001). The majority of resightings occurred in Hluleka and Pondoland (Amathole=5, Hluleka=121, and Pondoland=128), with a significantly lower number of resightings in Amathole (df=2, p<0.0001) (Figure 3.12). There was no difference in the number of days between sightings for these three study locations (df=2, χ^2=0.56, p=0.75) (Table 3.2).

Between study areas, "A" (i.e. resightings within the same area) was significantly higher than the other categories (χ^2=20.816, p=0.0001) with a mean number of individuals of 27.5+/-9.4, as compared to “B” = 3.22+/-1.34, “C” = 4.00+/-1.84, and “D” = 1.25 (Figure 3.13). There was no significant difference in the number of individuals in the other three categories (B, C, and D) (χ^2=2.4019, p=0.30091). In Hluleka, 51.0% percent of resightings within the same study site (i.e. “A”) were during different field trips, while 48.9% were during the same trip. Six animals were sighted during all three trips to Hluleka. Most animals resighted within Pondoland were sighted within the same trip 2-5 times (56.5%), with 14 animals resighted in all three field trips to Pondoland. Five resightings between different trips occurred in Amathole, with the majority of resightings in this area coming from the same field trip (70.6%). Twenty-nine percent of individuals resighted in the same study area were seen both in the same field trip and in subsequent trips.

Table 3.2: Time in days between bottlenose dolphin (*Tursiops aduncus*) resightings both within a field trip, and between field trips, for eight field trips to the Wild Coast, South Africa, including mean+/-SD, median, and range for each trip.

Field Trip	Location	N	Mean +/-SD (days)	Median (days)	Range (days)
			Within field trip		
June 2014	Amathole	2	3.0+/-1.4	3	2 – 4
November 2014	Hluleka	6	3.3+/-3.2	3	0 – 7
February 2015	Pondoland	12	6.1+/-5.2	7	0 – 16
June 2015	Pondoland	107	5.2+/-4.2	4	0 – 13
November 2015	Amathole	10	2.8+/-3.6	0	0 – 7
February 2016	Hluleka	65	2.3+/-3.0	1	0 – 9
June 2016	Hluleka	45	6.1+/-4.8	8	0 – 13
November 2016	Pondoland	47	1.1+/-1.6	0	0 – 6
			Between field trips		
June 2015	Pondoland	73	26.7+/-44.3	114	92 – 371
November 2015	Amathole	5	246.4+/-109.5	173	154 – 368
February 2016	Hluleka	46	420.5+/-129.3	460	93 – 611
June 2016	Hluleka	75	288.0+/-198.9	358	88 – 705
November 2016	Pondoland	55	496.9+/-125.2	527	165 – 650

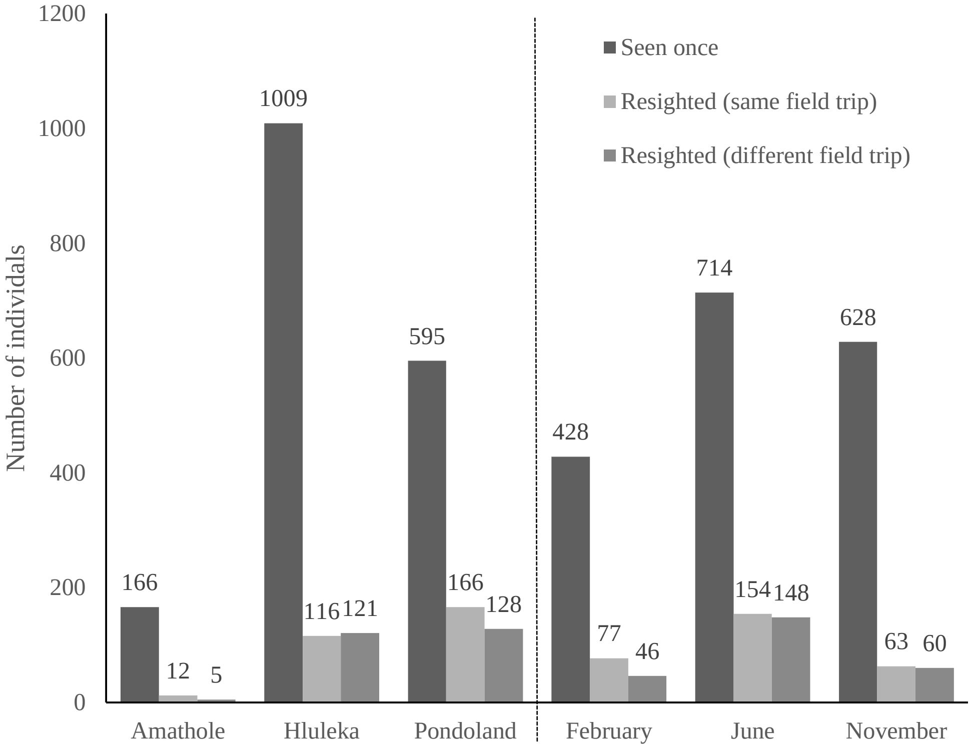


Figure 3.12: Number of individual bottlenose dolphins (*Tursiops aduncus*) seen once, resighted within a field trip (i.e. within 21 days), and resighted on one or more subsequent field trips off the Wild Coast of South Africa.

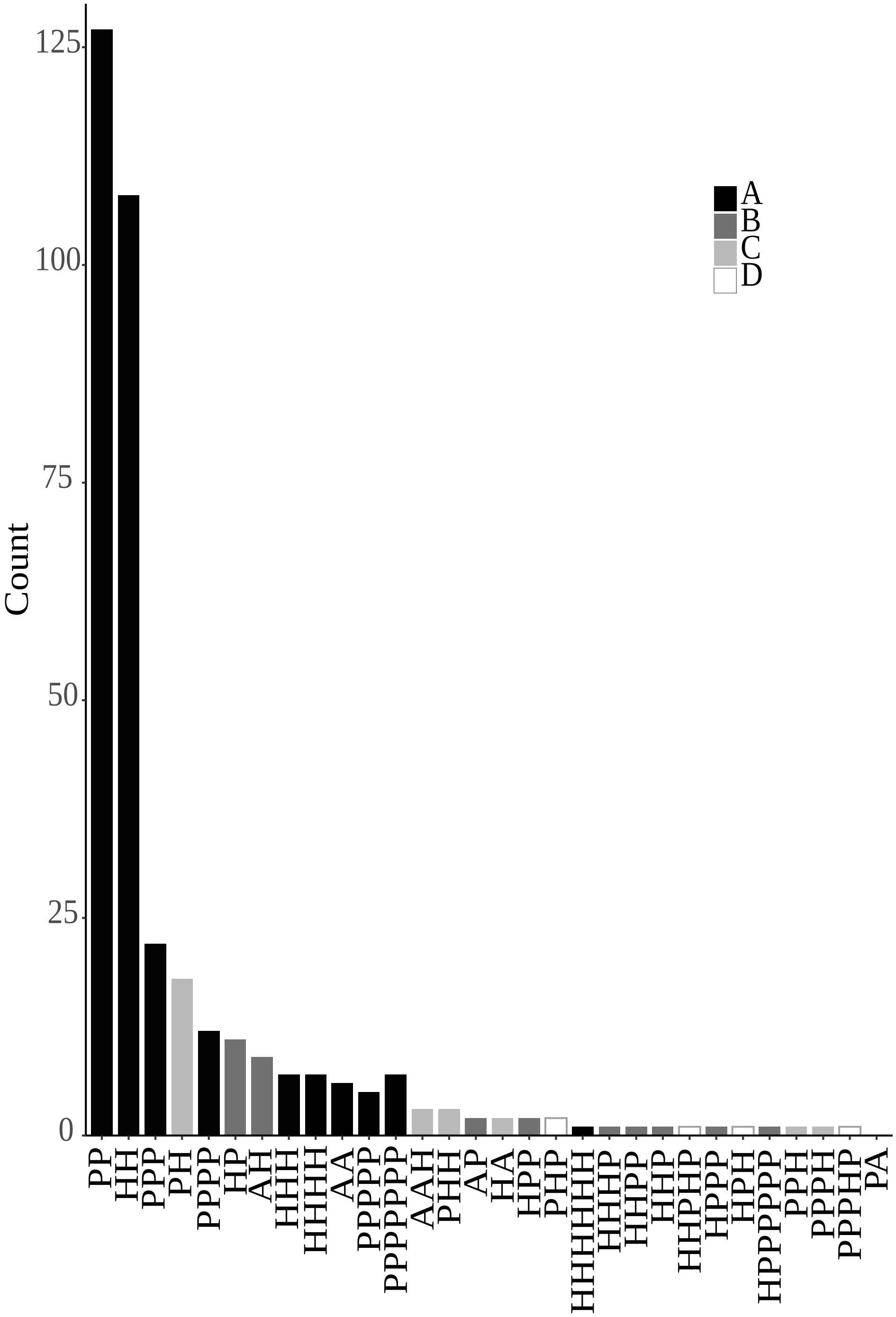


Figure 3.13: Resightings of bottlenose dolphins (*Tursiops aduncus*) from three study areas (A=Amathole, H=Hluleka, and P=Pondoland) off the Wild Coast in four different categories: A) resighted in the same area, B) resighted to the northeast of first sighting, C) resighted to the southwest of first sighting, D) back and forth movement. Where there are multiple locations, letters (i.e. A, H, and P) are listed in order of sightings.

3.4 Discussion

3.4.1 Density and group size

Contrary to previous predictions (Ross et al. 1989; Cockcroft and Peddemors 1990; Young and Cockcroft 1994), both bottlenose and common dolphins were observed during all field trips off the Wild Coast (Cockcroft and Peddemors 1990; O'Donoghue et al. 2010b). This finding is unexpected and suggests that their presence in this area is not merely a function of the sardine run as previously suggested (Cockcroft and Peddemors 1990). The continual presence of both dolphin species within the area suggests that there is sufficient prey available outside of the sardine run to sustain the large number of dolphins within the study area (Wells et al. 2004). Additionally, all observations of animals foraging were done within 1 km of shore, similar to findings from previous research (O'Donoghue et al. 2010b; Roberts et al. 2010), highlighting the important of the inshore area off the Wild Coast as a habitat for both dolphin species. It should be pointed out, however, that the investigated was restricted to shallow coastal waters within 3km of the shoreline and that oceanographic conditions greatly limited the survey effort. Thus, only inshore cetacean species were considered.

High sighting density for bottlenose dolphins occurred in Pondoland throughout the coastal area of the MPA, with a high density of both species found near Waterfall Bluff, an important area oceanographically during the sardine run as a cold-water cyclonic eddy forms here during that time (Roberts et al. 2010). My research was limited to the inshore areas, which biases the environmental data, as it will all be within inshore habitats; therefore, comparisons and hotspots interpretations are taken as representing only hotspots in my specific survey area. In Hluleka, both species were mainly sighted in the relatively small MPA with a high density of animals occurring here. Additionally, animals in Hluleka were predominantly seen foraging, indicating that this area may be highly productive. O'Donoghue et al. (2010b) also reported the highest encounter rate for bottlenose dolphins in the Hluleka area, but additional research is needed to confirm this "hotspot". As with previous studies (O'Donoghue et al. 2010c), common dolphins were found in high densities in Amathole and Hluleka. These results provide further evidence that the inshore waters around the Hluleka MPA are sufficiently productive to sustain a high density of animals and that the Amathole area as a whole is a hotspot for common dolphins. These results must be viewed with caution as the survey effort in each MPA and at each location differed, with specifically lower effort in Amathole. More consistent effort in all three locations would allow further interpretation of the similarities or differences along the coastline.

In agreement with studies conducted locally and internationally (Cockcroft and Peddemors 1990; Peddemors 1999; Jefferson et al. 2008), the highest density for common dolphins were recorded in deeper offshore waters, with one large group comprising up to 1250 individuals. As previous research was based on aerial surveys, search effort extended further offshore than in this study (Cockcroft and Peddemors 1990; O’Donoghue et al. 2010b, a), and those studies found that common dolphins were more frequently sighted in deeper waters and these groups were significantly larger than those within 1km of the shore (O’Donoghue et al. 2010b). The present study found no link between sighting density with depth. It is possible that with boat-based surveys, the larger number of common dolphin groups reported in previous research (Cockcroft and Peddemors 1990; O’Donoghue et al. 2010b, a) were present in the un-surveyed offshore area. O’Donoghue et al. (2010a) recorded the large majority (95% at least) of bottlenose sightings within 1km from shore, which suggests that the surveys have likely captured the greater majority of bottlenose dolphins present during sampling, despite relatively low effort and a steep discovery curve.

As expected, common dolphin group sizes were larger than bottlenose groups within the study area. That said, the large groups of bottlenose dolphins reported here (250 animals in Hluleka) are some of the largest ever reported globally (Möller et al. 2002; Stensland and Berggren 2007; Wang and Yang 2009; Sprogis et al. 2015), although the values are similar to other areas in South Africa (Phillips 2006; Reisinger and Karczmarski 2010). When calves were present, groups were significantly larger, which has been previously documented elsewhere in the world, potentially to reduce predation risk and for socialization (Campbell and Defran 2002; Möller et al. 2002; Gibson and Mann 2008). For both species, mean and maximum group size was lower than reported from aerial surveys conducted between 1988-2005 by O’Donoghue et al. (2010 a,b). Specifically, for common dolphins, the maximum group size reported here (1250) was substantially lower than reported by O’Donoghue et al. (2010a) (5000 individuals), though differences between survey methods may influenced the counts. Given that in KZN the diet of this species has shifted away from sardines (Ambrose et al. 2013), the smaller mean and maximum group size numbers found during this study may be as a result of a change in common dolphin behaviour with a change in the sardine run over the past 10 years, though other mechanisms may also be at work (O’Donoghue et al. 2010b; Ambrose et al. 2013)..

Contrary to my predictions that group size for common dolphin would increase during the sardine run for cooperative feeding, there was no spatial trend in the maximum group size for either dolphin species, with larger groups occurring independent of depth. Also, group size was not influenced by season, area, behaviour, or any of the environmental variables measured (except SST) and larger groups were not more dispersed or clumped, suggesting that other mechanisms, such as prey availability and predator avoidance may be driving group size. Both species showed increasing group size with decreasing SST, as seen in previously in this area (O’Donoghue et al. 2010b). Research conducted in South African waters on shark predation has provided clear evidence of shark attacks and bites on bottlenose dolphins (Cockcroft et al. 1989; Cockcroft 1991). In KZN, marine mammals, especially dolphins, are the primary prey of large sharks (> 2.5 m total length) (Cliff et al. 1989). Due to their smaller size, common dolphins are susceptible to predation from large sharks and killer whales (Heithaus 2001), although research on shark diet in South Africa has focused on bottlenose and Indo-Pacific humpback (*Sousa plumbea*) dolphins in KZN (Cockcroft et al. 1989; Cockcroft 1991). Another potential mechanism for large group size is prey availability, however the absence of dedicated fish surveys throughout the year within the region limit the understanding of the importance of this mechanism. From previous research, common dolphins were highly associated with sardines during all winter months (May – July) and were considered the predator whose distribution was the most highly linked with sardine distribution (O’Donoghue et al. 2010b). However, both species were seen feeding during all months surveyed in the present study. Given that these large groups of dolphins exist in a number of locations in South Africa (Bouveroux et al. 2018.; James 2014), this coastline must be rich enough to support large numbers of animals year-round.

3.4.2 Photographic identification and residency

The majority of bottlenose dolphins identified off the Wild Coast were only recorded on a single occasion, which is in agreement to a previous study conducted in the adjacent area of Algoa Bay (south-west of the Wild Coast)(Reisinger and Karczmarski 2010) and provides evidence of large, highly mobile populations off the south-eastern coast of South Africa. However, the discovery curve did not reach an asymptote (Figure 3.10), which suggest that the effort was not sufficient to capture all individuals in the region. This is similar to the study from Algoa Bay, which had a similar discovery curve (Reisinger and Karczmarski 2010). In the Algoa Bay study, despite similar effort and an increasing discovery curve, more than 1500 individuals were identified in 54 surveys days, resulting in a population estimate of over 28,000 animals (Reisinger and Karczmarski 2010). Given that off the Wild coast, 2149 animals were identified in 47 survey days, with a higher resighting rate (11.8% in Wild Coast vs. 8.3%, in Algoa Bay), I would expect a similarly large population estimate, especially as this area is open with no barriers to movement (Reisinger and Karczmarski 2010). With the current data set, these population estimates are not possible due to lack of sufficient effort. Whether the Algoa Bay and Wild Coast animals form part of the same population is unknown and should be investigated by comparison of photographic identification catalogues; however, given their highly mobile nature, and the openness of the coastline, migration between the two areas would likely occur. Initially, it was predicted that the sardine run may present an opportunity for mixing of individuals from adjacent areas as they move into the Wild Coast area to feed, but the absence of an increase in individual and sighting density or group size during the austral winter has provided some indication to refute this prediction, but this needs to be tested further with considerable increase in effort throughout the year.

Low resighting rates compared to studies of bottlenose dolphins conducted elsewhere in the world (Möller et al. 2002; Gnone et al. 2011; Hwang et al. 2014; Sprogis et al. 2015; Zanardo et al. 2016), limit the interpretation of the results in this region, as further sampling effort is required to ensure that all individuals are capture. However, the Wild Coast had a higher resighting rate (11.8%) than the adjacent population in Algoa Bay (8.3%) (Reisinger and Karczmarski 2010). In open or exposed coastlines like the

Wild Coast, mobile species are expected to have lower site fidelity than in protected shallow bays (Defran and Weller 1999; Hwang et al. 2014). In the currently study, the resighting of individuals within the same study area over the entire study period (3.5 years), and the number of animals resighted within the same three-week study period, provide some indication that future research on residency of these animals is necessary (Möller et al. 2002; Zolman 2002; Zanardo et al. 2016). Unexpectedly, the arrival of sardines did not coincide with new resightings, though the highest number of both new and resighted animals was recorded in June 2015 during the sardine run (Figure 3.10). The number of resightings was largest in later trips, as well as the number of days between sightings, which is as expected. Over a year passed between resightings on average, which could indicate high mobility in this region. However, the resighting of individuals within a study area more than 2 weeks after the initial sighting is interesting, and further indicates the need for long-term monitoring of residency rates in this region.

Result of the cluster analysis suggests that the majority of bottlenose dolphins are non-resident in the area and can therefore, be considered “occasional visitors”. The back and forth movement of some animals between Pondoland and Hluleka indicates movement between study sites (Figure 3.13), and the ability to survey both areas during the same time-period would be useful in determining the range of semi-resident animals. In large groups of over 50 individuals, being certain that all individuals have been photographed is nearly impossible, and photographic effort was increased to maximize the number of individuals captured. Despite this effort, only just over half the estimated number of bottlenose dolphins sighted were identified in Pondoland and Hluleka. The non-identified animals include unmarked individuals and poor quality photos, but an increase in both survey and photographic effort should increase the percentage of identifiable animals in each group.

3.4.3 Conclusion

This study provides evidence of the occurrence and partial residency of bottlenose and common dolphins in the coastal waters of the Wild Coast off the coast of South Africa. This result is in contrast to previous studies which suggested that dolphins migrate into the area to coincide with the annual sardine run (Ross et al. 1987; Cockcroft and Peddemors 1990; Young and Cockcroft 1994; O'Donoghue et al. 2010b, a). The presence of the dolphins outside of the austral winter suggests that the coastal waters provide sufficient food to sustain these top predators at other times of year. Logistical constraints limited my ability to conduct research within the three MPAs over the same time period, and thus the data should be viewed with caution as they represent only a snapshot. More intensive survey effort is required to better understand the population demographics of dolphins within the area, especially for photographic identification as the discovery curve did not reach an asymptote. Future studies should focus on further understanding of the mechanisms underpinning the occurrence and habitat use by dolphins in this area. Site fidelity is challenging to assess from my data, and will be difficult to investigate given with adverse weather, at sea conditions, and the openness of the coastline. Increased sampling effort over a smaller geographic area would allow for a better understanding of site fidelity and population size estimates. However, this first boat-based study has demonstrated the importance of this previously unknown area as a habitat for common and bottlenose dolphins, and provides valuable baseline data for future monitoring.

3.5 References

Acevedo-Gutierrez A (2002) Group behavior. In: Perrin W, Wursig B, THewissen J (eds) Encyclopedia of Marine Mammals. San Diego: Academic Press, San Diego, pp 537–544

Alves MDDO, Schwamborn R, Borges JCG, Marmontel M, Costa AF, Schettini CAF, Araújo ME De (2013) Aerial survey of manatees, dolphins and sea turtles off northeastern Brazil: Correlations with coastal features and human activities. Biol Conserv 161:91–100. doi: 10.1016/j.biocon.2013.02.015

Ambrose S, Froneman P, Smale M, Cliff G, Plön S (2013) Winter diet shift of long-beaked common dolphins (Delphinus capensis) feeding in the sardine run off KwaZulu-Natal, South Africa. Mar Biol 160:1543–1561. doi: 10.1007/s00227-013-2208-6

Balmer BC, Wells RS, Nowacek SM, Nowacek DP, Schwacke LH, McLellan WA, Scharf FS, Rowles TK, Hansen L, Spradlin T, Pabst DA (2008) Seasonal abundance and distribution patterns of common bottlenose dolphins (ursiops truncatus) near St . Joseph Bay, Florida, USA. J Cetacean Res Manag 10:157–167.

Bearzi M (2012) Cetaceans and MPAs should go hand in hand: A case study in Santa Monica Bay, California. Ocean Coast Manag 60:56–59. doi: 10.1016/j.ocecoaman.2011.12.019

Bouveroux T, Caputo M, Froneman P, Plon S (2018) Largest reported groups for the Indo-Pacific bottlenose dolphin (Tursiops aduncus) found in Algoa Bay, South Africa: Trends and potential drivers. Mar Mammal Sci 34:645–665.

Bowen WD (1997) Role of marine mammals in aquatic ecosystems. Mar Ecol Prog Ser 158:267–274.

Burnham K, Anderson D (1992) Data-based selection of an appropriate biological model: the key to the modern data analysis. In: McCullough D, Barret R (eds) Wildlife 2001: Populations. Elsevier Science Publishers, London, England, pp 16–30

Campbell GBB, Defran R (2002) Bottlenose dolphins (Tursiops truncatus) in Turneffe Atoll , Belize: occurrence, site fidelity, group size, and abundance. Aquat Mamm 28:170–180.

Cao Y, Bark A, Williams W (1997) A comparison of clusteringmethods for river benthic community analysis. Hydrobiologia 347:24–40.

Caputo M, Froneman PW, Preez D, Thompson G, Plön S (2017) Long-term trends in cetacean occurrence during the annual sardine run off the Wild Coast , South Africa. African J Mar Sci 39:83–94. doi: 10.2989/1814232X.2017.1304451

Cliff G, Dudley S, Davis B (1989) Sharks caught in the protective gill nets off Natal, South Africa. The great white shark Carcharodon carcharias (Linnaeus). African J Mar Sci 8:131–144.

Cockcroft V (1991) Incidence of shark bites on Indian Ocean hump-backed dolphins (Sousa plumbea) off Natal, South Africa.

Cockcroft V, Cliff G, Ross J (1989) Shark predation on Indian Ocean bottlenose dolphins Tursiops truncatus off Natal, South Africa. South African J Zool 24:305–310.

Cockcroft VG, Peddemors VMV (1990) Seasonal distribution and density of common dolphins Delphinus delphis off the south-east coast of southern Africa. South

African J Mar Sci 9:371–377. doi: 10.2989/025776190784378853

Connor R, Krützen M (2015) Male dolphin alliances in Shark Bay: changing perspectives in a 30-year study. Anim Behav Special is:223–235.

Connor R, Wells R, Mann J, Read AJ (2000) The bottlenose dolphin: social relationships in a fission-fusion society. In: Mann J, Connor R, Tyack P, Whitehead H (eds) Cetacean societies: Field studies of dolphins and whales. University of Chicago Press, New York, pp 91–126

Connor R, Watson-Capps J, Sherwin W, Krützen M (2011) A new level of complexity in the male alliance networks of Indian Ocean bottlenose dolphins. Biol Lett 7:623–626.

Daly R, Smale MMJ, Cowley PDP, Froneman PWP, Daly R, Smale MMJ, Cowley PDP, Froneman PWP (2014) Residency patterns and migration dynamics of adult bull sharks (Carcharhinus leucas) on the east coast of southern Africa. PLoS One 9:e109357. doi: 10.1371/journal.pone.0109357

Defran R, Weller D (1999) Occurrence, distribution, site fidelity, and school size of bottlenose dolphins (Tursiops truncatus) off San Diego, California. Mar Mammal Sci 15:366–380.

Evans W (1994) Common dolphin, white-bellied porpoise Delphinus delphis Linnaeus. In: Ridgeway S, Harrison R (eds) Handbook of Marine Mammals, Volume 5. San Diego: Academic Press, San Diego, pp 191–224

Fury C, Harrison P (2008) Abundance, site fidelity and range patterns of Indo-Pacific bottlenose dolphins (Tursiops aduncus) in two Australian subtropical estuaries. Mar Freshw Res 59:1015–1027.

Gibson QA, Mann J (2008) The size, composition and function of wild bottlenose dolphin (Tursiops sp.) mother-calf groups in Shark Bay, Australia. Anim Behav 76:389–405. doi: 10.1016/j.anbehav.2008.01.022

Gnone G, Bellingeri M, Dhermain F, Dupraz F, Nuti S, Bedocchi D, Moulins A, Rosso M, Alessi J, McCrea RS, Azzellino A, Airoldi S, Portunato N, Laran S, David L, Di Meglio N, Bonelli P, Montesi G, Trucchi R, Fossa F, Wurtz M (2011) Distribution, abundance, and movements of the bottlenose dolphin (Tursiops truncatus) in the Pelagos Sanctuary MPA (north-west Mediterranean Sea). Aquat Conserv Mar

Freshw Ecosyst 21:372–388. doi: 10.1002/aqc.1191

Gygax L (2002) Evolution of group size in the dolphins and porpoises: Interspecific consistency of intraspecific patterns. Behav Ecol 13:583–590.

Heithaus M, Dill L (2002) Feeding strategies and tactics. In: The encyclopedia of marine mammals, 2nd editio. Academic Press, San Diego, CA., pp 4114–423

Heithaus MR (2001) Predator-prey and competitive interactions between sharks (order Selachii) and dolphins (suborder Odontoceti): a review. J Zool London 253:53–68.

Hwang A, Defran RH, Bearzi M, Maldini D (2014) Coastal Range and Movements of Common Bottlenose Dolphins (Tursiops truncatus) off California and Baja California , Mexico. Bull South Calif Acad Sci 113:1–13.

Irvine A, Scott M, Wells R, Kaufmann J (1981) Movements and activities of the Atlantic bottlenose dolphin, Tursiops truncatus, near Sarasota, Florida. Fish Bull 79:671–688.

James B (2014) Natural and human impacts on habitat use of coastal delphinids in the Mossel Bay area, Western Cape, South Africa. University of Pretoria

Jefferson T, Webber M, Pitman R (2008) Marine Mammals of the World - A Comprehensive Guide to their Identification. Academic Press/Elsevier

Mann J, Connor R, Barre LM, Heithaus M (2000) Female reproductive success in bottlenose dolphins (Tursiops sp.): life history, habitat, provisioning, and group-size effects. Behav Ecol 11:210–219.

Möller L, Valdez FP, Allen S, Bilgmann K, Corrigan S, Beheregaray LB (2010) Fine-scale genetic structure in short-beaked common dolphins (Delphinus delphis) along the East Australian Current. Mar Biol 158:113–126. doi: 10.1007/s00227-010-1546-x

Möller LM, Allen SSJ, Harcourt RRG (2002) Group characteristics, site fidelity and seasonal abundance of bottlenose dolphins Tursiops aduncus in Jervis Bay and Port Stephens, south-eastern Australia. Aust Mammal 24:11–21.

Natoli A, Peddemors V, Hoelzel A (2004) Population structure and speciation in the genus Tursiops based on microsatellite and mitochondrial DNA analyses. J Evol Biol 17:363–375. doi: 10.1046/j.1420-9101.2003.00672.x

O'Donoghue SH, Whittington P a, Dyer BM, Peddemors VM (2010a) Abundance and distribution of avian and marine mammal predators of sardine observed during the 2005 KwaZulu-Natal sardine run survey. African J Mar Sci 32:361–374. doi: 10.2989/1814232X.2010.502640

O'Donoghue SH, Drapeau L, Peddemors VM (2010b) Broad-scale distribution patterns of sardine and their predators in relation to remotely sensed environmental conditions during the KwaZulu-Natal sardine run. African J Mar Sci 32:279–291. doi: 10.2989/1814232X.2010.501584

Parra GJ, Corkeron PJ, Marsh H (2006) Population sizes, site fidelity and residence patterns of Australian snubfin and Indo-Pacific humpback dolphins : Implications for conservation. Biol Conserv 129:167–180. doi: 10.1016/j.biocon.2005.10.031

Peddemors V (1999) Delphinids of southern Africa: A review of their distribution, status and life history. J Cetaceans Res Manag 1:157–166.

Peddemors V, Cockcroft V (1997) Prey distribution and its importance for nearshore dolphins off the east coast of southern Africa. Paper SC/49/SM32, presented to the Scientific Committee of the International Whaling Commission, Bournemouth

Phillips G (2006) Bottlenose dolphins (Tursiops aduncus) in Plettenberg Bay, South Africa: Population estimates and temporal dynamics of groups. Nelson Mandela Metropolitan University, Port Elizabeth, South Africa

Reeves R, Stewart B, Clapham P, Powell J (2002) Guide to Marine Mammals of the World. In: National Audubon Society (ed) Guide to Marine Mammals of the World, 1st edn. Alfred A. Knopf, New York, p 527

Reisinger RR, Karczmarski L (2010) Population size estimate of Indo-Pacific bottlenose dolphins in the Algoa Bay region, South Africa. Mar Mammal Sci 26:86–97. doi: 10.1111/j.1748-7692.2009.00324.x

Roberts MJ, van der Lingen CD, Whittle C, van den Berg M (2010) Shelf currents, lee-trapped and transient eddies on the inshore boundary of the Agulhas Current, South Africa: their relevance to the KwaZulu-Natal sardine run. African J Mar Sci 32:423–447. doi: 10.2989/1814232X.2010.512655

Rosel PE, Hansen L, Hohn a a (2009) Restricted dispersal in a continuously distributed marine species: common bottlenose dolphins Tursiops truncatus in coastal waters of the western North Atlantic. Mol Ecol 18:5030–45. doi: 10.1111/j.1365-

294X.2009.04413.x

Ross GJB, Cockcroft VG, Butterworth DS (1987) Offshore distribution of bottlenosed dolphins in Natal coastal waters and Algoa Bay, eastern Cape. South African J Zool 22:50–56.

Ross GJB, Cockcroft VG, Melton D a., Butterworth DS (1989) Population estimates for bottlenose dolphins Tursiops truncatus in Natal and Transkei waters. South African J Mar Sci 8:119–129. doi: 10.2989/02577618909504555

Shane S (1990) Comparison of bottlenose dolphin behavior in Texas and Florida, with a critique of methods for studying dolphin behavior. In: Leatherwood S, Reeves R (eds) The Bottlenose Dolphin. Academic Press, San Diego, pp 245–265

Shane S, Wells R, Wursig B (1986) Ecology, behavior and social organization of the bottlenose dolphin: a review. Mar Mammal Sci 2:34–63.

Simpfendorfer C, Yeiser B, Wiley G, Poulakis P, Stevens P, Heupel M (2011) Environmental influences on the spatial ecology of juvenile smalltooth sawfish (pristis pectinata): Results from acoustic monitoring. PLoS One 6:e16918.

Singh W, Hjorleifsson E, Stefansson G (2011) Robustness of fish assemblages derived from three hierarchical agglomerative clustering algorithms performed on Icelandic groundfish survey data. J Mar Sci 68:189–200.

Sink K, Holness S, Harris L (2012) National Biodiversity Assessment 2011: Technical Report. Volume 4: Marine and Coastal Component. South African National Biodiversity Institute, Pretoria, South Africa

Smith HC, Pollock K, Waples K, Bradley S, Bejder L (2013) Use of the robust design to estimate seasonal abundance and demographic parameters of a coastal bottlenose dolphin (Tursiops aduncus) population. PLoS One 8:e76574. doi: 10.1371/journal.pone.0076574

Smith HR, Worthy G a J (2006) Stratification and intra- and inter-specific differences in fatty acid composition of common dolphin (Delphinus sp.) blubber: implications for dietary analysis. Comp Biochem Physiol B Biochem Mol Biol 143:486–99. doi: 10.1016/j.cbpb.2005.12.025

Smolker R, Richards A, Connor R, Pepper J (1992) Sex differences in patterns of association among Indian Ocean bottlenose dolphins. Behaviour 123:38–69.

Sprogis K., Raudino H., Rankin R (2015) Home range size of adult Indo-Pacific bottlenose dolphins (Tursiops aduncus) in a coastal and estuarine system is habitat and sex-specific. Mar Mammal Sci 32:287–308. doi: 10.1111/mms.12260

Stensland E, Berggren P (2007) Behavioural changes in female Indo-Pacific bottlenose dolphins in response to boat-based tourism. Mar Ecol Prog Ser 332:225–234.

Urian K, Hohn A, Hansen L (1999) Status of the photo-identification catalog of coastal bottlenose dolphins of the western North Atlantic: Report of a workshop of catalog contributors.

Urian K, Gorgone A, Read A, Al. E (2015) Recommendations for photo-identification methods used in capture-recapture models with cetaceans. Mar Mammal Sci 31:298–321.

Wang J, Yang A (2009) Indo-Pacific bottlenose dolphin (Tursiops aduncus). In: Perrin W, Wursig B, Thewissen J (eds) Encyclopedia of Marine Mammals, 2nd edn. Academic Press, Amsterdam, pp 602–608

Ward J (1963) Hierarchical grouping to optimize an objective function. Am Stat Assoc 58:236–244.

Wells R, Rhinehart H, Hansen L, Sweeney J, Townsend F, Stone R, Casper D, Scott M, Hohn A, Rowles T (2004) Bottlenose dolphins as marine ecosystem sentinels: developing a health monitoring system. Eco-Health 1:246–254.

Wells RS, Scott MD (1999) Estimating bottlenose dolphin population parameters from individual identification and capture-release techniques. Reports Int Whal Comm 407–415.

White J, Simpfendorfer C, Tobin A, Heupel M (2014) Spatial ecology of shark-like batoids in a large coastal embayment. Environ Biol 97:773–786.

Wilson B, Reid RJ, Grellier K, Thompson PM, Hammond PS (2004) Considering the temporal when managing the spatial: a population range expansion impacts protected areas-based management for bottlenose dolphins. Anim Conserv 7:331–338. doi: 10.1017/S1367943004001581

Young D, Cockcroft V (1994) Diet of common dolphins (Delphinus delphis) off the south-east coast of southern Africa:opportunism or specialization? J Zool 234:41–53.

Zanardo N, Parra GJ, Moller LM (2016) Site fidelity, residency, and abundance of bottlenose dolphins (Tursiops sp.) in Adelaide's coastal waters , South Australia. Mar Mammal Sci 1–21. doi: 10.1111/mms.12335

Zeileis A, Kleiber C (2017) Count data regression. R Packag. version 0.2-0

Zolman E (2002) Residence patterns fo bottlenose dolphins (Tursiops trucatus) in the Stono River estuary, Charleston County, South Carolina, U.S.A. Mar Mammal Sci 18:879–892.

Zuur A, Leno E, Walker N, Saveliev A, Smith G (2009) Mixed effects models and extensions in ecology with R. Springer, New York

Chapter 4: Foraging ecology and population structure of *Tursiops aduncus* and *Delphinus delphis* along the Wild Coast, South Africa inferred using stable isotope analysis

*This chapter was modified by the article submitted for publication to PLOS-One which has been peer reviewed: Caputo, M., S. Plön, Bouveroux, M. van der Bank, and P.W. Froneman. Submitted. Foraging ecology and population structure of *Tursiops aduncus* and *Delphinus delphis* along the Wild Coast, South Africa inferred using stable isotope analysis. PLOS-One.

4.1 Introduction

As top predators, dolphins play an important role in ecosystems, transporting nutrients between habitats and shaping marine communities with their foraging activities (Wells et al. 2004). Understanding foraging ecology of these animals is critical for conservation and management of habitats and resources, and in monitoring anthropogenic impacts (Barros et al. 2010; Kiszka et al. 2014; Rossman et al. 2015b). Stomach content analysis from bycaught or stranded animals is frequently used to examine the feeding ecology of dolphins (e.g. Kaiser 2012; Ambrose et al. 2013; Di Beneditto and Monteiro 2015; Rossman et al. 2015a). Gut content analyses, however, only provide short-term insights (one feeding event), which may be biased due to differential digestion rates of various prey (Pierce and Boyle 1991). Additionally, fish otoliths and squid beaks digest relatively slowly, which can also bias interpretation (Bowen and Iverson 2012). Given these limitations, stable isotope analysis has become increasingly employed, both on its own and as compliment to stomach content studies, to investigate trophic ecology of dolphins (Pinela and Borrell 2010; Fernandez et al. 2011; Bisi et al. 2013; Wilson et al. 2013).

Research from KwaZulu Natal (KZN) on diet of long-beaked common dolphins (*Delphinus delphis)* hereafter referred to as common dolphins during the sardine run suggests that the predominant prey has shifted from sardine to mackerel since the 1990s (Ambrose et al. 2013). Their diet consists primarily of pilchard (*Sardinops ocellatus*), sardine (*Sardinops sagax*), chub mackerel (*Scomber japonicas*), elf (*Pomatomus saltatrix*), lanternfish (*gymnoscopelus bolini*), maasbanker (*trachurus delagoa*), squid

(*Loligo spp*.), flying fish (*Cheilopogon sp*.), and strepie (*Sarpa salpa*) (Sekiguchi et al. 1992; Young and Cockcroft 1994; Ambrose et al. 2013). From a study on KZN animals, Indo-Pacific bottlenose dolphins (*Tursiops aduncus*), hereafter referred to as bottlenose dolphins diet consists primarily of cuttlefish (*Sepia sp*.), piggy (*Pomadasys olivaceum*), maasbanker (*Trachurus delagoa*), mackerel (*Scomber japonicas*), squid *(Loliga sp*.), and pandora (*Pagellus bellotti natalnesis*) (Kaiser 2012). Isotope signatures from dolphins in KZN, showed a 9% overlap in the diet of bottlenose and common dolphins during the sardine run (Browning et al. 2014c), with a significant difference in mean values for nitrogen isotopes from these animals, but no such difference between carbon values (Browning et al. 2014c). Common dolphins are typically found further offshore than bottlenose dolphins; however, the similarity in carbon values found by Browning et al. (2014a) in KZN waters was attributed to their movement nearshore to coincide with the sardine run. This is consistent with stomach content analyses from the area (Sekiguchi et al. 1992; Young and Cockcroft 1994; Ambrose et al. 2013). Additionally, Browning et al. (2014a) found that bottlenose dolphin isotope signatures did not differ between KZN and Plettenberg Bay (southwest of Algoa bay) animals. Further understanding of the connectivity of animals along the south-eastern coastline is critical to conservation and management in this area.

Stable isotope analysis has been widely employed to assess the trophic ecology of a variety of predators in both inshore and offshore marine ecosystems (Burton and Koch 1999; Borrell et al. 2013)**.** Predator stable isotope composition, specifically carbon ($\delta\ C^{13}$) and nitrogen ($\delta\ N^{15}$) ratio, reflects those of their prey, providing a method of determining predator feeding ecology in terms of feeding habitat (carbon) and trophic level (nitrogen). Enrichment in isotopic ratios per trophic level is considered to be 3.5‰ for $\delta^{15}N$, and 0.4‰ for $\delta^{13}C$ on average (Post 2002); however, research from a variety of species in South African waters suggests that this could be an over-estimation in this region, especially for top predators (Van Der Lingen and Miller 2011). Stable isotope analyses provide a wealth of information, including trophic position and niche, resources partitioning, as well as spatial and temporal changes in diet, as there is a strong inshore – offshore gradient in these signatures (Newsome et al. 2010; Jackson et al. 2011). Recent studies have shown that even within relatively close geographic proximity, animals can show differentiation in these trophic signatures, allowing researchers to identify sub-groupings, which is important for management decisions (Burton and Koch 1999; Barros et al. 2010; Bisi et al. 2013; Borrell et al. 2013; Wilson et al. 2013). Additionally, basal isotope signatures from the bottom of the food chain can vary spatially (Cherel and Hobson 2007; Graham et al. 2010; Van Der Lingen and Miller 2014), providing information on predator foraging habitat, movement, and residency

The concept of ecological niche was first introduced by Grinnell (1917) to define an organisms' role and position in a community based on their behaviour (Grinnell 1917). This definition has subsequently been adapted and expanded upon by researchers, recognizing that an organisms' niche is largely controlled by both prey and predators, and interactions with its environment (Elton 1927; Hutchinson 1957; Odum 1959; Weatherley 1963). Furthermore, the issues arising from overlapping niches between organisms, and resource partitioning are well understood (Hutchinson 1957; Schoener 1974), and these concepts are widely used in ecological research (e.g. Parra 2006; Fernandez et al. 2011; Kaiser 2012; Browning et al. 2014a). With recently developed statistical methods, such as SIBER (Stable Isotope Bayesian Ellipse in R) (Jackson et al. 2011), researchers can use trophic niche of organisms to gain insights into the population dynamics as well as spatial and temporal trends in trophic ecology of animals. It is also useful in assessing in resource partitioning between species (e.g. Parra 2006; Fernandez et al. 2011; Browning et al. 2014a).

The purpose of this study is to investigate the trophic ecology of bottlenose and common dolphins off the Wild Coast of South Africa. The main goals are to determine the trophic relationships between these two species, and to explore the short-term spatial and temporal patterns in their foraging ecology. The investigation will also evaluate the similarities/differences in isotope values between these animals and those from two adjacent communities, Algoa Bay and KZN, which lie to the southwest and northeast of the Wild Coast, respectively. If the Wild Coast is indeed a migratory corridor, one would expect similar trophic signatures for dolphins along the entire stretch of the Wild Coast in comparison with Algoa Bay and KZN animals. Complete turnover rate for isotopes of metabolic tissues in *Tursiops trucatus* has been found to be 104.40+/-35 days for carbon and 205.8+/-84.49 for nitrogen (Giménez et al. 2016), which may limit the interpretation of seasonal dietary fluctuations. Thus, seasons reported here reflect only time of sample collection. This research will also provide baseline isotope signatures to be compared in any future monitoring of changes in dolphin diet which may reflect changes in environmental conditions.

4.2 Methods

4.2.1 Study Area

The study was conducted along the south-eastern coast of South Africa (S29º35.344’ E31 º80.722’). The predominant current in this region is the Agulhas Current, which (velocities > 2.5 m/s) flows in a south westerly direction along the continental shelf (Roberts et al. 2010). Algoa Bay is a relatively shallow bay (< 70 m) with approximately 90km of coastline, ranging in temperatures from approximately 17-21ºC with periodic upwelling events reducing temperatures to below 13ºC (Goschen and Schumann 2011). This area is known to support large groups of bottlenose dolphins (*Tursiops aduncus*), with sightings of common dolphins (*Delphinus delphis*) throughout the year (Bouveroux et al. 2018.; Ross et al. 1987; Reisinger and Karczmarski 2010; Melly et al. 2017).

The Wild Coast is a dynamic stretch of coastline in South Africa’s Eastern Cape, from East London to Port Edward (Fig 1). The continental shelf narrows in this area, which increases the influence of the Agulhas Current on the coastal environment (Roberts et al. 2010). This narrowing also concentrates coastal species inshore, including seasonally large aggregations of sardines, *Sardinops sagax,* during May and July. These fish shoal in the shallow coastal waters attract a large number of apex predators, including, predatory fish, sharks and cetaceans (Lutjeharms et al. 2000; O’Donoghue et al. 2010b; Roberts et al. 2010; Caputo et al. 2017).

Oceanographic conditions along the KwaZulu-Natal (KZN) coastline differ from northeast to southwest, largely dependent on the width of the continental shelf. The lower and mid sections of the south coast of KZN are similar to the Wild Coast in that the continental shelf is narrow, bringing the fast flowing, warm waters of the Agulhas Current within 5km of the shore (O’Donoghue et al. 2010c; Roberts et al. 2010). In the upper section of the south coast, a large semi-permanent eddy called the Durban Eddy greatly affects the oceanography, occasionally switching the current in a northerly direction (O'Donoghue et al. 2010b; Roberts et al. 2010). This region is considered a transition zone between the southern and northern sections of the KZN coast, as in the north currents are dominated primarily by wind rather than the Agulhas Current, due to the widening of the continental shelf in this area (O'Donoghue et al. 2010b; Roberts et al. 2010). Slightly lower water temperatures in the north result in increased chlorophyll *a* concentrations in this area relative to the south section of the KZN coast (O'Donoghue et al. 2010b; Roberts et al. 2010).

(a)

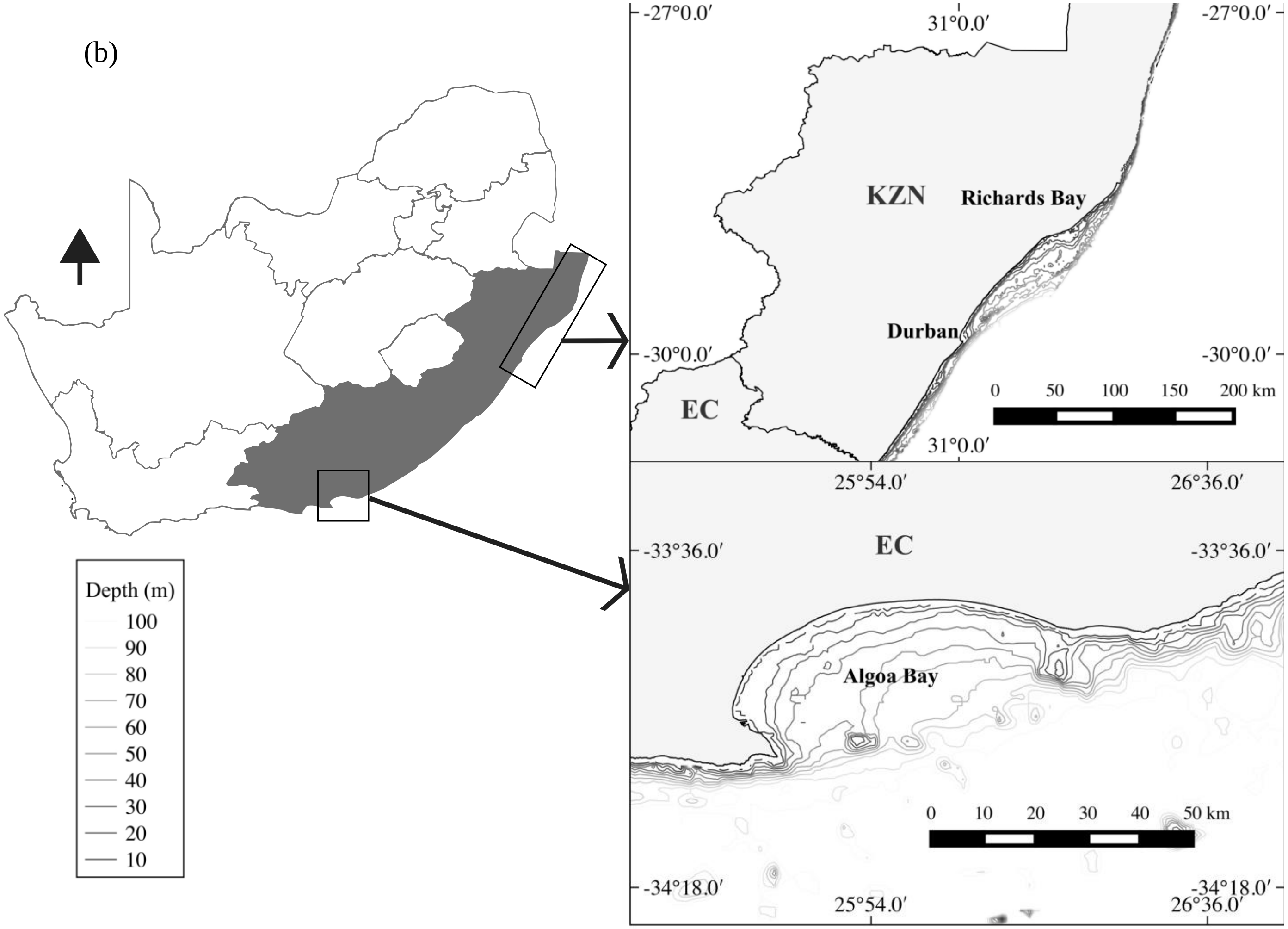


Figure 4.1: Maps of the three coastal areas where samples were taken: (a) the Wild Coast and (b) the KwaZulu Natal coast and Algoa Bay, including bathymetry.

4.2.2 Sample Collection

Boat-based surveys were conducted off three Eastern Cape Parks and Tourism Agency (ECPTA) reserves along the Wild Coast of South Africa between June 2014 and July 2016 in three different sampling areas: Amathole, Hluleka, and Pondoland located within Marine Protected Areas (MPAs) (Figure 4.1a). The surveys took place over three weeks each in June (winter), overlapping November/December (summer), and overlapping both February/March (summer) each year when sea conditions were Beaufort 3 or less (see Table 3.1 for survey effort). Surveys were conducted along the 15m and the 30m contours, northeast or southwest of the launch site on each alternate trip. When animals were sighted, their geographic position was recorded using a Garmin GPS; a visual estimate of group size was taken continually during the sighting; group behaviour was recorded (travelling, socializing, foraging, resting, mating); and photographs were taken using a Canon E0S70D with a 100-400mm lens). Biopsy sampling was conducted off the Wild Coast, with additional tissue samples taken from animals bycaught in shark nets in KwaZulu-Natal waters (Fig 4.1b). Biopsy samples were taken from adult bottlenose and common dolphins using a modified .22 rifle designed by Pneudart for veterinary capture, with an adjustable pressure valve (Krutzen et al. 2002). Additional surveys and biopsy sampling were also conducted in Algoa Bay along the 10m contour each month from July 2015 to July 2016 (Figure 4.1b). Biopsy sampling was attempted for all sightings in order to get samples from as many different groups as possible. All samples were divided into winter (May – September) and summer (November– March) seasons (Table 4.1).

Skin samples from KZN waters were obtained from animals taken as bycatch in the shark nets permanently deployed by KZN Sharks Board (see Cliff and Dudley 1992, 2011 for details of the shark nets). These animals are assumed to be representative of the normal healthy population given that they were bycaught and not stranded (Lane et al. 2014). Animals were immediately frozen upon collection from nets, and no decayed animals were chosen for this study to ensure the quality of the samples (as per Lane et al. 2014).

4.2.3 Stable isotope analysis

Tissue samples were separated into blubber and skin, with only the skin being analyzed for stable isotopes. Skin was frozen at -80 ºC until analysis. Skin samples were dried at 60ºC for 48h to remove any water and subsequently ground into a fine powder using a macerator.

Aliquots of approximately 0.6 to 0.7 mg (tissues) were weighed into tin capsules that were pre-cleaned in toluene (Bligh and Dyer 1959).

Isotopic analysis was undertaken by Dr. Grant Hall on a Flash EA 1112 Series coupled to a Delta V Plus stable light isotope ratio mass spectrometer via a ConFlo IV system (all equipment supplied by Thermo Fischer, Bremen, Germany), housed at the Stable Isotope Laboratory, Mammal Research Institute, University of Pretoria.

A laboratory running standard (Merck Gel: $\delta^{13}C$ = -20.57‰, $\delta^{15}N$=6.8‰, C%=43.83, N%=14.64) and blank sample were run after every 12 unknown samples. All results are referenced to Vienna Pee-Dee Belemnite for carbon isotope values, and to air for nitrogen isotope values. Results are expressed in delta notation on a per mille scale using the standard equation:

$$\delta X(‰) = [(R_{sample}/R_{standard}-1]x1000$$

where: X= ^{15}N or ^{13}C and R represents $^{15}N/^{14}N$ or $^{13}C/^{12}C$, respectively. Analytical precision was <0.14‰ for $\delta^{13}C$ and <0.09‰ for $\delta^{15}N$. The carbon to nitrogen ratio was also calculated. When C:N > 4, the effect of differences in lipids within a tissue can significantly bias isotope analyses (Post et al. 2007). The values from this study were between 3.5-4 as no chemical washing of lipids was done. As such, a correction factor was applied where C:N>3.5, as per Post et al. (2007) to remove this bias as follows:

$$\delta^{13}Ccorrected = \delta^{13}Cuntreated - 3.32 + 0.99x\ C:N$$

4.2.4 Data analysis

Data analysis was performed in the R statistics platform (v. 3.2.2). A generalized linear model was performed to test the effects of species, year, location, and season on both the mean $\delta^{13}C$ and $\delta^{15}N$ signatures, as well as the interactions between these explanatory variables. The best models were selected through backwards stepwise deletion using the Akaike Information Criterion (AIC), with best models having delta AIC<2. As there was significant interaction between variables, additional analysis was necessary as per below.

As there were significant differences for both isotopes between species, these were analyzed separately. For each species separately, the difference in mean $\delta^{13}C$ and $\delta^{15}N$ signatures between locations (including Algoa Bay and KZN, where applicable) was tested using an ANOVA (Analysis of Variance). The difference between summer and winter for each isotope was compared for each species using an ANOVA including all samples (Wild Coast and Algoa Bay/KZN). Where there was a significant effect of season, data was separated by season and tested for effects of location using an ANOVA.

To examine the differences between bottlenose and common dolphin $\delta^{13}C$ and $\delta^{15}N$ isotopes for Wild Coast samples only, ANOVAs were performed for each location (i.e. Amathole, Hluleka, and Pondoland) separately, and each season (i.e. summer and winter) separately due to interactive and main effects found in GLM analyses. All data were tested for normality using Shapiro-Wilks tests and Q-Q plots, and log and reciprocal transformations were performed where applicable. With transformation, all data was normal. Post-hoc testing was performed using Tukey's HSD.

Niche width was calculated for each species, for each location, and during each time-period using SIBER (Stable Isotope Bayesian Ellipses in R) metrics in the R statistics platform (v. 3.2.2) (Jackson et al. 2011; Team and R Core Team 2017). Bayesian ellipses were calculated using 10^4 repetitions to ensure accuracy (Jackson et al. 2011). Given the differences in sample sizes, I employed the small sample size corrected ellipses when comparing between groups (known as SEAc), which is appropriate for all sample sizes (Jackson et al. 2011). Differences in SEAc between groups were compared using the SIBER model to determine the probability that one was significantly larger or smaller than another, with values ranging from 0 to 1. The overlap in SEAc between locations was calculated for each species using the overlap function in SIAR with a step function of 1 (Jackson et al. 2011). Additionally, the overlap between the two species was calculated in total, and for each location and season.

4.3 Results

A total of 256 biopsy samples were collected from the Wild Coast sites comprising 128 bottlenose and 128 common dolphin samples. An additional 22 bottlenose dolphin samples were collected from Algoa Bay and 20 from KZN. Eleven common dolphin samples were obtained from KZN (Table 4.2). Bottlenose dolphins were observed foraging during 26.5% of sightings, and common dolphins were foraging during 64.7% of sightings, with foraging activities observed for both species at all times of year. Prey were observed during foraging activities, but species was unknown.

Models of δ^{13}C revealed significant differences between species (t=-4.23, df=254, p<0.0001) and locations (t=-3.41, df=254, p<0.0001), as well as interactive effects between species and location (t=4.29, df=254, p<0.0001) and year (t=-2.23, df=254, p<0.0001). The best model for δ^{15}N included only the location explanatory variable; however other acceptable models included species and season. There were no interactive effects in this model, and main effects revealed significant differences in mean δ^{15}N between species (F=10.1, df=254, p=0.002), with no effect of location (F=1.733, df=253, p=0.18) or season (F=1.265, df=254, p=0.26). Given the differences between species for both isotopes and significant interactive effects in mean δ^{13}C models, additional analysis were undertaken for each species separately, and between species for each location and season separately.

Table 4.1: Mean carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values for bottlenose dolphin (*Tursiops aduncus*, BND) and common dolphin (*Delphinus Delphis*, CD) from the Wild Coast of South Africa.

Location	Year	Season	*n*	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Bottlenose dolphins (*Tursiops aduncus*)					
Amathole	2014	Winter	5	-14.33+/-0.46	12.79+/-0.47
Amathole	2015	Summer	4	-14.09+/-0.28	12.92+/-0.39
Hluleka	2014	Summer	15	-15.00+/-0.32	12.22+/-0.42
Hluleka	2016	Summer	20	-14.69+/-0.25	12.51+/-0.61
Hluleka	2016	Winter	30	-14.95+/-0.31	12.24+/-0.81
Pondoland	2015	Summer	26	-15.25+/-0.42	12.36+/-0.53
Pondoland	2015	Winter	28	-15.14+/-0.42	12.06+/-0.78
Algoa Bay		Summer	14	-14.09+/-0.73	13.93+/-0.73
Algoa Bay		Winter	8	-14.13+/-0.57	14.04+/-0.73
KZN		Summer	9	-15.40+/-0.37	12.02+/-0.36
KZN		Winter	5	-15.24+/-0.35	11.98+/-0.36
Common dolphins (*Delphinus delphis*)					
Amathole	2014	Winter	16	-14.49+/-0.33	12.58+/-0.46
Amathole	2015	Summer	12	-14.78+/-0.16	11.71+/-0.37
Hluleka	2014	Summer	20	-15.34 0.31	12.19+/-0.44
Hluleka	2016	Summer	22	-15.29+/-0.48	11.93+/-0.72
Hluleka	2016	Winter	38	-14.74+/-0.42	11.99+/-0.70
Pondoland	2015	Summer	5	-15.24+/-1.09	12.49+/-1.19
Pondoland	2015	Winter	15	-14.99+/-0.37	11.67+/-0.61
KZN		Summer	1	-15.23	11.86
KZN		Winter	5	-14.64+/-0.50	12.22+/-0.77

4.3.1 Bottlenose dolphins

For bottlenose dolphins, there was a significant difference between locations for mean $\delta^{13}C$ (F=38.9, df=165, p<0.0001) and $\delta^{15}N$ (F=27.99, df=165, p<0.0001) (Figure 4.2a and b). Post-hoc testing revealed that for $\delta^{13}C$, Algoa Bay was significantly different (Tukey HSD, p<0.01) from all sites. There was also a significantly difference in $\delta^{13}C$ (Tukey HSD, p<0.0001) between Amathole and Pondoland. Post-hoc testing of $\delta^{15}N$, showed significant differences (Tukey HSD, p<0.001) between all sites, with the exceptions of Algoa Bay-Amathole, and Pondoland-KZN. There was no significant difference in $\delta^{13}C$ values between summer and winter for bottlenose dolphins (F=1.47, df=162, p=0.74); however, $\delta^{15}N$ was significantly higher in winter (F=1.44, df=162, p=0.04, summer mean = 12.50+/-0.88‰, winter mean = 12.52 +/-

0.88‰). When each location was analyzed separately, neither $\delta^{13}C$ or $\delta^{15}N$ was significantly different between summer and winter ($p>0.05$). Niche analysis between study locations revealed that Algoa Bay bottlenose dolphins had the largest niche area (SEAc=,1.10), significantly larger than any other site (Amathole SEAc=0.53, Hluleka SEAc=0.67, Pondoland SEAc=0.79, KZN SEAc=0.62) (0.68 – 0.99 probability) (Figure 4.2c). Algoa Bay had 0% overlap with any other site, except Amathole, where the overlap was <0.00001. Amathole did not overlap with either Pondoland or KZN, and overlapped only by 1.6% with Hluleka.

4.3.2 Common dolphins

There was a significant difference between locations for $\delta^{13}C$ (F=5.56, df=135, $p=0.001$, Figure 4.3a). Post-hoc test revealed that Amathole was significantly different from both Hluleka (Tukey HSD, $p<0.001$) and Pondoland (Tukey HSD, $p=0.016$). No other locations were significantly different in $\delta^{13}C$ values. There was no significant difference in $\delta^{15}N$ (F=1.31, df=135, $p=0.27$) between locations (Figure 4.3b). There was a significant difference in $\delta^{13}C$ values between summer (-15.20+/-0.49‰) and winter (-14.73+/-0.42‰) for all common dolphin samples (F=35.44, df=133, $p<0.0001$); however, $\delta^{15}N$ was not significantly different between the two seasons (F=0.13, df=133, $p=0.72$). When each location was analyzed separately, there was a significant increase in $\delta^{13}C$ in summer at Amathole ($p=0.01$) and Hluleka ($p<0.0001$). Additionally, Amathole had an increase in $\delta^{15}N$ in winter ($p<0.0001$). All other locations showed no differences between seasons for either isotope ($p>0.05$). Niche analysis between study locations revealed that Pondoland had the largest niche area (SEAc=1.19), significantly larger than both Amathole (SEAc=0.44, 0.99 probability) and Hluleka (SEAc=0.94, 0.96 probability) (Figure 4.3c). KZN was larger than both Amathole and Hluleka (SEAc, 1.14, >0.91 probability), and Hluleka was larger than Amathole (>0.90 probability). Hluleka, Pondoland, and KZN were highly overlapped (>80%), with a 22.7 – 36% overlap with Amathole.

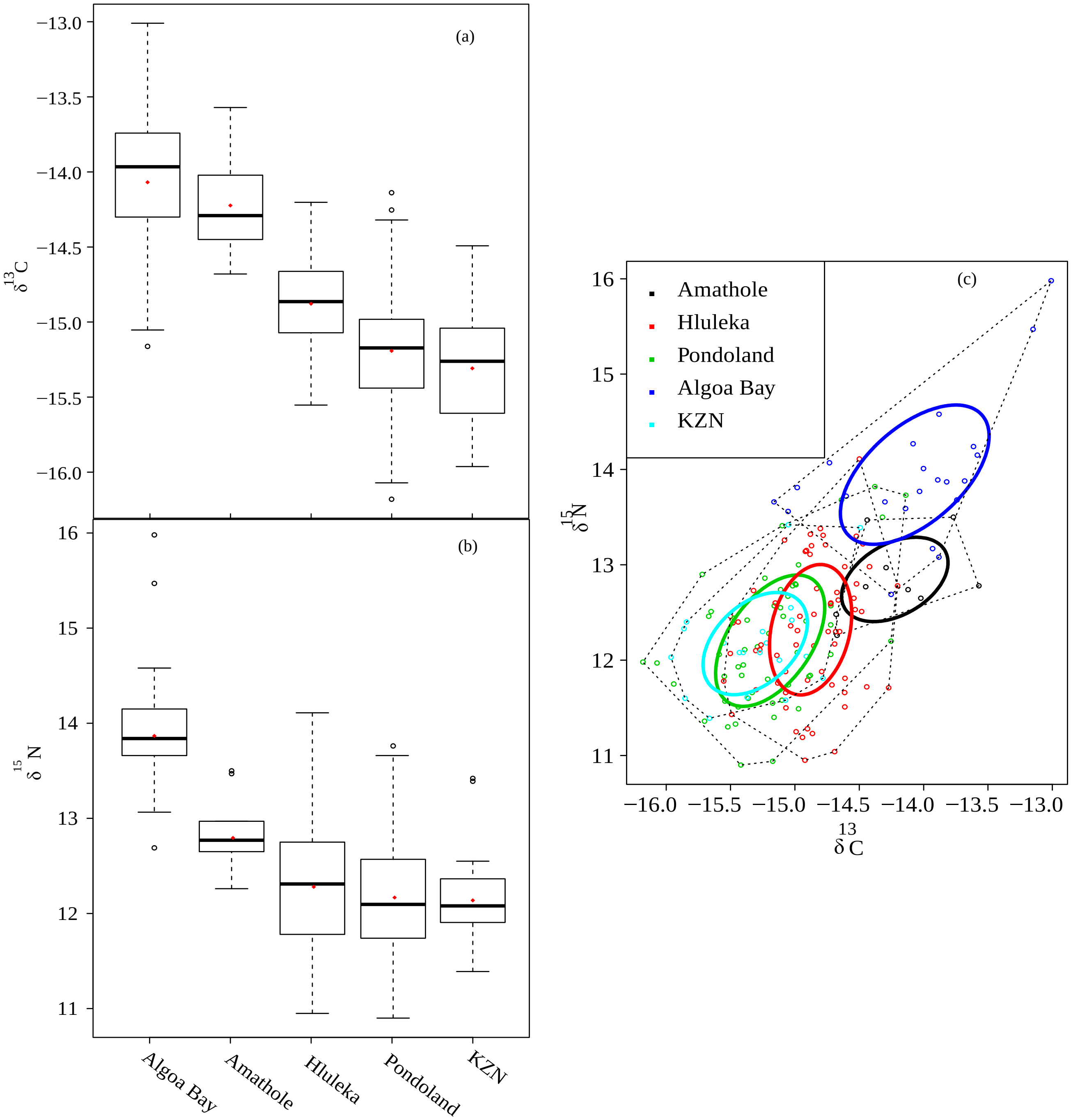


Figure 4.2: Mean (red dot) and median (black line) (a) carbon $\delta^{13}C$ and (b) nitrogen $\delta^{15}N$ isotope values for bottlenose dolphin (*Tursiops aduncus*) samples taken from five different location off southeastern South Africa, including (c) trophic niche of each location represented by stable isotope Bayesian ellipses

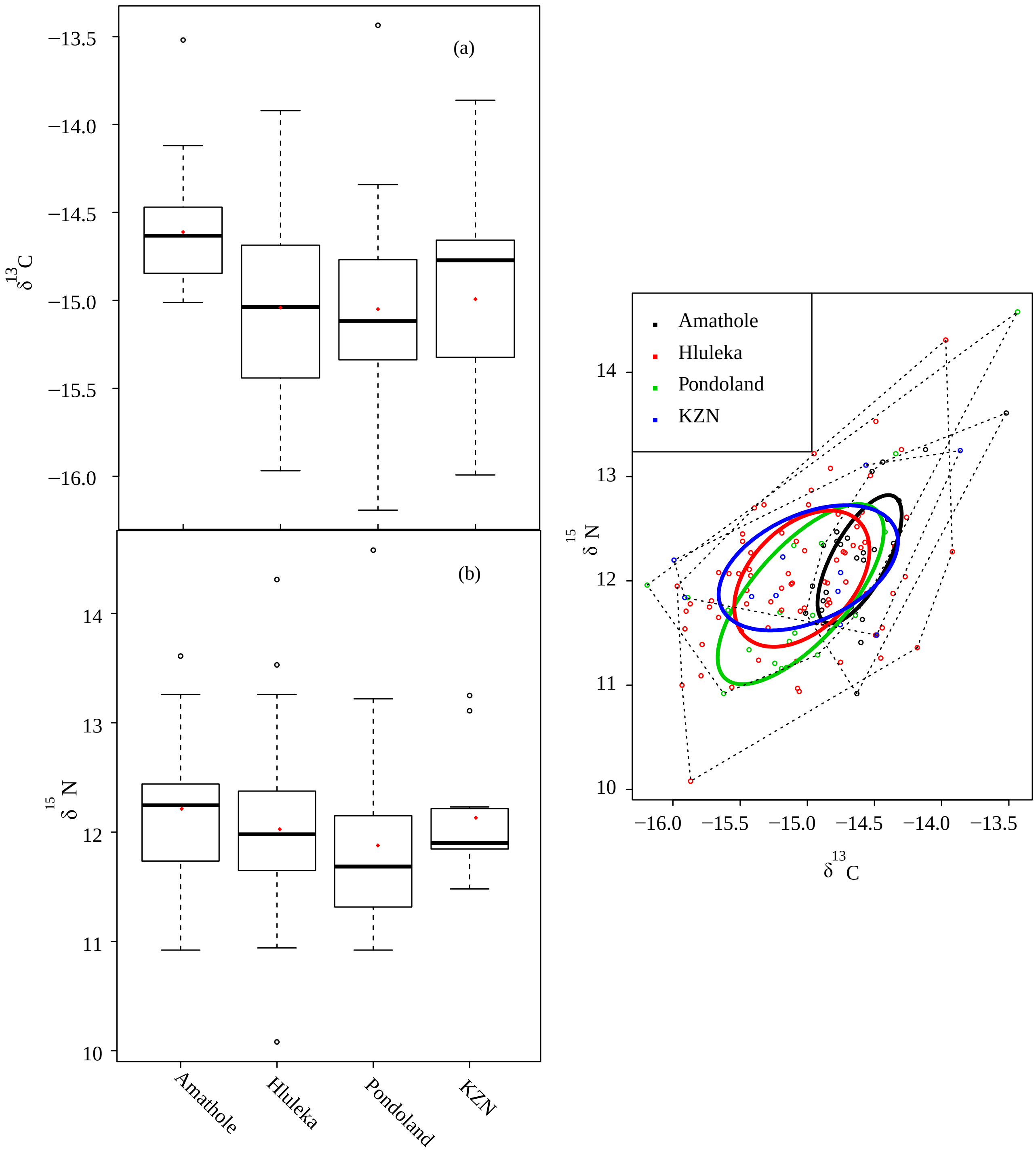


Figure 4.3: Mean (red dot) and median (black line) (a) carbon δ^{13}C and (b) nitrogen δ^{15}N isotope values for common dolphin (*Delphinus delphis*) samples taken from five different location off southeastern South Africa, including (c) trophic niche of each location represented by stable isotope Bayesian ellipses.

4.3.3. Bottlenose vs. common dolphin

Given the differences between locations and seasons found within a species, the differences between species for each location and season were analyzed separately. For Amathole, there was a significant difference between species in both $\delta^{13}C$ (F=9.85, df=35, p=0.003) and $\delta^{15}N$ (F=8.68, df=35, p=0.006), with bottlenose dolphins having significantly higher isotope values (Table 4.2). Similarly, both $\delta^{13}C$ (F=6.84, df=143, p=0.01) and $\delta^{15}N$ (F=7.23, df=143, p=0.008) differed significantly at Hluleka with bottlenose dolphins being enriched for both isotopes (Table 4.2). At Pondoland, neither the $\delta^{13}C$ (F=1.06, df=72, p=0.31) nor the $\delta^{15}N$ (F=0.058, df=72, p=0.06) differed between the species (Table 4.2). In summer, bottlenose dolphins had significantly higher $\delta^{13}C$ (F=8.36, df=122, p=0.005) and $\delta^{15}N$ (F=12.86, df=122, p<0.001) values (Table 4.2). In winter, common dolphins had significantly higher $\delta^{13}C$ (F=11.42, df=130, p<0.001) values, with no difference in the $\delta^{15}N$ (F=1.37, df=130, p=0.24) between the two species (Table 4.2). In terms of trophic niche, bottlenose and common dolphin trophic niche was highly overlapped in Hluleka and Pondoland (51.7% and 45.7% respectively) relative to their overlap at Amathole (10.6%). Common dolphin trophic niche area was significantly larger in both Hluleka (common dolphin SEAc=0.94, bottlenose dolphin SEAc=0.67) and Pondoland (common dolphin SEAc=1.19, bottlenose dolphin SEAc=0.79) (>0.90 probability); however, bottlenose had a larger niche area in Amathole (common dolphin SEAc=0.44, bottlenose dolphin SEAc=0.53) (0.86 probability). Seasonally, these two species overlapped most in summer (47.7% vs. winter 34.5%, Figure 4.4), with common dolphin having a larger niche area in summer (0.87 probability) and bottlenose dolphin having a larger niche area in winter (0.95 probability).

Table 4.2: Mean $\delta^{13}C$ and $\delta^{15}N$ (+\-sd) isotopes for bottlenose and common dolphin samples collected in three location off the Wild Coast of South Africa, and in two seasons.

	Bottlenose dolphin		Common dolphin	
	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Amathole	-14.22+/-0.39	12.85+/-0.41	-14.61+/-0.31	12.21+/-0.60
Hluleka	-14.88+/-0.32	12.32+/-0.68	-15.04+/-0.50	12.02+/-0.65
Pondoland	-15.19+/-0.42	12.21+/-0.63	-15.05+/-0.60	12.03+/-0.68
Summer	-14.95+/-.047	12.41+/-0.54	-15.20+/-0.5	12.02+/-0.65
Winter	-14.98+/-0.42	12.21+/-0.79	-14.73+/-0.42	12.05+/-0.70

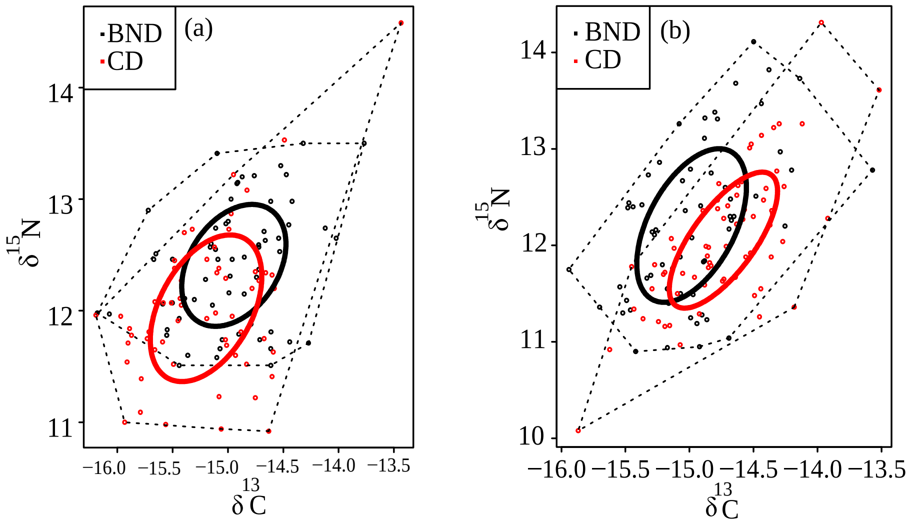


Figure 4.4: Niche area, represented as stable isotope Bayesian ellipses, for bottlenose dolphins (BND, *Tursiops aduncus*) and common dolphins (CD, *Delphinus delphis*) from the Wild Coast of South Africa in both (a) summer (May-September) and (b) winter (November-March).

4.4 Discussion

Dolphins are highly mobile and widespread with complex residency patterns which makes long-term monitoring difficult, particularly in remote areas (Graham et al. 2010). The oceanographic conditions off the Wild Coast further restrict research in this region as access to sea is challenging and few, if any, samples from stranded animals are available. Given these difficulties, the current research, though limited, provides important baseline data for elucidating dolphin life history patterns in this region and for monitoring future conditions. Additionally, the use of stable isotope analysis here contributes not only to our knowledge of dolphin trophic ecology in this region, but to baseline stable isotope values for these delphinids in this region (Van der Lingen and Miller 2011; Van Der Lingen and Miller 2014; Magozzi et al. 2017).

Previous isotope research in South African waters has shown several gradients, which are important in interpreting the results of this study (Hill et al. 2006; Van der Lingen and Miller 2011; Van Der Lingen and Miller 2011, 2014, 2017). For δ^{13}C, distinct nearshore-offshore gradients were observed in mussels and their prey, with nearshore environments being enriched in carbon (Hill et al. 2006). These cross-shelf differences were also observed during isotopic investigations on a variety of species from both nearshore and offshore areas, with depleted $\delta^{13}C$ in the offshore species (Van Der Lingen and Miller 2011). Hill et al. (2006) noted an increase in primary producer $\delta^{13}C$ during the austral summer; therefore, higher values were expected for summer if animals were feeding in the same area in both seasons. In the present study, common dolphins showed enriched values for $\delta^{13}C$ during the winter, with values for bottlenose dolphins <0.4‰ different, despite statistical significance between the two species. If the environment favours higher $\delta^{13}C$ in summer, the enrichment observed for common dolphins in winter months is likely larger than modelled as it was not considering the changes in basal isotopic values. This enrichment may be linked with the sardine run, as common dolphins are thought to move nearshore to feed on this prey during the austral winter (Cockcroft and Peddemors 1990; Young and Cockcroft 1994; O'Donoghue et al. 2010a, b). However, it is important to note that despite research indicating an average isotopic turnover rate in skin at 1 week to 1 month for *Tursiops truncatus* (Browning et al. 2014b), more recent research, suggests that turnover rates can be substantially slower (104.40+/-35 days for carbon and 205.8+/-84.49 for nitrogen) (Giménez et al. 2016). It is therefore possible that the results obtained in the present study reflect "spring" feeding activity (i.e. March-May).

Significant gradients have been found in $\delta^{15}N$ for South African waters, with enrichment from northeast to southwest (i.e. longitudinally) in both primary producers and fish isotope ratios (Hill et al. 2006; Van der Lingen and Miller 2011; Van Der Lingen and Miller 2017). Carbon ratios also show this longitudinal gradient, in addition to the nearshore-offshore gradient, in investigations of primary producers (Hill et al. 2006). For Wild Coast dolphins, this gradient was observed in bottlenose dolphins, as mean $\delta^{15}N$ were significantly higher in Algoa Bay than other locations, with a decreasing trend in mean $\delta^{15}N$ in a northeasterly direction. Whether the enrichment in $\delta^{13}C$ observed for bottlenose dolphins in southwestern sites is as a result of the longitudinal gradient or the nearshore-offshore gradient remains unclear; however, it is likely that the longitudinal gradient is the more likely explanation in this case, as this was distinct for $\delta^{15}N$ as well. For common dolphins, this gradient was less visible in the data, which could be interpreted as increased movement through the region, resulting in less distinct signatures for each of the study location. This could indicate that bottlenose dolphins are more resident in this region than common dolphins, though additional sampling effort would be needed to confirm this prediction.

For the sardine species found in this region (i.e. *Sardinops sagax*), the longitudinal gradient in $\delta^{15}N$ was found to be significant, with $\delta^{15}N$ values in the Wild Coast area reduced by approximately 2‰ from west coast sardines, averaging $\delta^{15}N$ values of 9-11‰ (Van Der Lingen and Miller 2017). In Algoa Bay, these values increase to >11‰ (Van Der Lingen and Miller 2017). Given an enrichment factor of 3.5‰ at each trophic level (Post 2002), dolphins feeding solely on sardines should have $\delta^{15}N$ value of approximately 12.5-14.5‰. Bottlenose dolphins from Algoa Bay, Amathole, and Hluleka had $\delta^{15}N$ values >12.5‰; however, these were not significantly different between summer and winter for these locations. It is likely that these higher values are more closely related to the isoscape (i.e. values at the base of the food chain), rather than as a result of feeding behaviour. The $\delta^{15}N$ values for common dolphins in Amathole and Pondoland were higher than 12.5‰. These values were significantly different at Amathole, with an increase in winter potentially indicating a change in diet, though whether this is because of sardines, or as dolphins move further inshore here, as demonstrated by a significant increase in their $\delta^{13}C$, remains unclear. However, in interpreting these results, it is important to keep in mind that previous research for other species suggested that a 3.5‰ enrichment factor per trophic level may be overestimated for top predators in South African waters (Van Der Lingen and Miller 2011), and that a mixed species diet, including species of lower trophic position, may reduce the overall isotope signatures of predators (Van der Lingen and Miller 2011; Van Der Lingen and Miller 2014).

The high percentage of isotopic niche overlap between bottlenose and common dolphins along the Wild Coast observed during this investigation (41%) is in contrast to the 9% overlap recorded for KZN waters from stable isotope analyses (Ambrose et al. 2013; Browning et al. 2014c), suggesting that off the Wild Coast region, these two species are feeding in similar habitats in the Wild Coast. Bottlenose dolphins had a higher mean $\delta^{15}N$ than common dolphins at all locations. This could be for a variety of reasons, including the inshore offshore gradient in nitrogen signatures, the larger size of bottlenose dolphins which allows them to feed on larger prey, or their preference for feeding in the enriched inshore environments. The difference between these two species in $\delta^{15}N$ was less than 3.5‰, suggesting that the enrichment for bottlenose dolphins does not equate to an increased trophic level. During summer, common dolphins demonstrated a larger trophic niche area than bottlenose dolphins. Given the strong inshore-offshore gradient in stable isotope values recorded along the South African coastline

(Hill et al. 2006), this increase in the trophic niche area observed for the common dolphins suggests that they may be feeding both inshore and offshore; however, common dolphins had significantly higher $\delta^{13}C$ than bottlenose dolphins during winter but not in $\delta^{15}N$, indicating movement inshore as carbon increases along an offshore-inshore gradient. Thus, they may be feeding at a similar trophic level, in carbon enriched waters. By contrast, in summer, common dolphins had significantly lower $\delta^{13}C$ than bottlenose dolphins, suggesting that common dolphins may be moving further offshore, potentially focusing on more variety of prey given that they also had a larger niche area. The overlap in trophic niche of these two species was highest in summer (outside the sardine run period), which refutes the prediction that common dolphins are pelagic feeders that would only overlap in diet with bottlenose during the winter (Cockcroft and Peddemors 1990; O'Donoghue et al. 2010b, a) and suggests that they feed in this area at other times of year.

4.4.1 Dolphin feeding ecology

In KZN waters, gut content analysis indicates that bottlenose dolphins are generalist feeders with the majority of their diet consisting of teleost fishes and cephalopods (Cockcroft and Ross 1990a; Kaiser 2012). Long-term data suggest that there have been no changes in their main prey items since 1985 and no shift in trophic level since the 1970's (Kaiser 2012). Unfortunately, long-term datasets on prey availability are not available for the Wild Coast area, but findings from KZN suggest possible stability in the fish assemblages along this section of the coastline (Kaiser 2012). Results of the stable isotope analysis indicate a seasonal difference with enriched $\delta^{15}N$ values in summer months, suggesting that they are feeding on prey at a higher trophic position during this time, though the difference remains less than one trophic level.

Stable isotope signatures have increasingly been employed to determine fine-scale population structure and connectivity of delphinids, specifically bottlenose dolphins (Barros et al. 2010; Wilson et al. 2013; Kiszka et al. 2014; Browning et al. 2014a). Even within relatively close geographical areas, stable isotope signatures have been useful in identifying populations/sub-populations for bottlenose dolphins (Barros et al. 2010; Worthy et al. 2011; Borrell et al. 2013). The results reveal that the southwestern (Amathole) bottlenose dolphins are differentiated from northeastern animals (Hluleka, Pondoland, and KZN) as there was no overlap in trophic niche between these groups, with further differentiation moving southwesterly.

Additionally, Algoa Bay animals are feeding on a much larger trophic area, with larger ranges for both carbon and nitrogen. This suggests that they feed on prey from varied trophic levels and habitats. Research limited to KZN waters showed genetic separation of bottlenose dolphins between north and south coast populations, with a potential migratory stock in the south coast KZN during the sardine run (Goodwin et al. 1996; Natoli et al. 2008). Therefore, evidence suggests that there is fine-scale population structuring occurring in the area despite relative proximity of groups and lack of barriers to movement. This was not expected, and there is no evidence that a migratory population occurs along the entire Wild Coast. The similarities between Hluleka, Pondoland, and KZN animals suggest movement of animals between these areas or similarities in the basal isotopic signatures of these areas. A recent study suggested that the common dolphin diet has shifted from sardine to chub mackerel (*Scomber japonicus*) in KZN coastal waters over the past two decades (Ambrose et al. 2013). However, over the corresponding period, no change in their stable isotope signatures was recorded (Ambrose et al. 2013). Although common dolphins are considered oceanic, the enriched δ^{13}C values observed during the summer months at Amathole and Hluleka suggest that they are feeding in the enriched δ^{13}C nearshore waters off the Wild Coast outside of the sardine run (Burton and Koch 1999; Hill et al. 2006) .

Globally, common dolphins are known to follow sardine distribution, with these prey moving both offshore and inshore, largely following changes in temperature (Marçalo et al. 2015; Ball et al. 2017). It was previously thought that this was also occurring off the Wild Coast (Cockcroft and Peddemors 1990; O'Donoghue et al. 2010b). However, unlike other areas of the globe, the sardines off the Wild Coast, a cold-water species, are restricted to cold water counter-currents flowing inshore during the austral winter (Fréon et al. 2010; Roberts et al. 2010). This cold water is restricted to the inshore area due to the narrowing of the continental shelf here, which brings the fast-flowing warm Agulhas Current nearshore (Roberts et al. 2010). Despite this seasonal influx of sardines, in the present study, common dolphins were sighted, and feeding, off the Wild Coast during both seasons, which indicates that other mechanisms may influence their presence in the area, perhaps reflecting the availability of alternative prey species

Given the generally large groups of common dolphins observed in South African waters and the highly mobile nature of this species (Cockcroft and Peddemors 1990; Evans 1994), defining populations is often difficult. Results of the current investigation revealed that there was considerable overlap in trophic niche in all the study locations, including Amathole and KZN, suggesting widespread movement and a lack of fine-scale population structuring. It is, however, worth noting that mean $\delta^{13}C$ values and, to a lesser extent mean $\delta^{15}N$ values, of common dolphins increased in a southwesterly direction, paralleling those observed for bottlenose dolphins.

4.4.2 Conclusion

In the present study, sample size was not always the same between two groups, and some areas had limited samples to analyze; however, stable isotope analyses have become increasingly sophisticated, allowing for investigations of isotopic niche and resource partitioning despite these limitations in the data set (Jackson et al. 2011). Jackson et al. (2011) demonstrated that unlike previously used Convex Hull methods (Layman et al. 2007), ellipses calculated using SIBER are unbiased to sample size and use a Bayesian inference to remove the influence of differing sample sizes (Jackson et al. 2011). With a lack of information on prey species composition from the area, traditional stable isotope analysis, including contribution of each prey type to diet, are not possible here (Newsome et al. 2010; Jackson et al. 2011). Indeed, I cannot conclusively say from stable isotopes whether difference and similarities in ellipse area are a result of animals feeding on the same prey, or on different prey at the same trophic level. However, the data to contribute valuable evidence to support previous research on other species which suggested a southwest to northeast gradient in basal isotope signatures (Hill et al. 2006; Van Der Lingen and Miller 2017). Gathering baseline stable isotopes data is critical for delphinid ecology, especially for areas where researchers lack access to location specific prey samples and where stranded animals are not available for stomach content analysis (Graham et al. 2010; Magozzi et al. 2017). Therefore, this study is important in providing baseline data on the southwest-northeast gradient, specifically for the Wild Coast area.

Much of the research on the feeding ecology of dolphins from South Africa has been based on stomach contents and skin/tooth isotope samples taken from animals bycaught in the KZN shark nets, with only a limited number of biopsy samples taken in KZN (Cockcroft and Ross 1990a; Young and Cockcroft 1994; Ambrose et al. 2013; Browning et al. 2014c). This study extends the knowledge south-westerly along the coastline, and highlights how the feeding ecology of these animals' changes over space and time, providing evidence of sub-groupings or sub-populations for bottlenose dolphins, though further investigations are required to confirm this hypothesis. Further research should focus on population structuring and connectivity using genetic methods, and on continuing surveying and sampling of these animals with increased sampling effort throughout the year. These results have implications for marine conservation and management along the southeastern coast of South Africa, especially for marine spatial planning given the fine-scale structuring of bottlenose dolphin populations.

4.5 References

Ambrose S, Froneman P, Smale M, Cliff G, Plön S (2013) Winter diet shift of long-beaked common dolphins (Delphinus capensis) feeding in the sardine run off KwaZulu-Natal, South Africa. Mar Biol 160:1543–1561. doi: 10.1007/s00227-013-2208-6

Ball L, Shreves K, Pilot M, Moura AE (2017) Temporal and geographic patterns of kinship structure in common dolphins (Delphinus delphis) suggest site fidelity and female-biased long-distance dispersal. Behav Ecol Sociobiol 71:123. doi: 10.1007/s00265-017-2351-z

Barros NB, Ostrom PH, Stricker CA, Wells RS (2010) Stable isotopes differentiate bottlenose dolphins off west-central Florida. Mar Mammal Sci 26:324–336. doi: 10.1111/j.1748-7692.2009.00315.x

Bisi TL, Dorneles PR, Lailson-Brito J, Lepoint G, Azevedo ADF, Flach L, Malm O, Das K (2013) Trophic relationships and habitat preferences of delphinids from the southeastern Brazilian coast determined by carbon and nitrogen stable isotope composition. PLoS One 8:8–15. doi: 10.1371/journal.pone.0082205

Bligh EG, Dyer WJ (1959) A rapid method of total lipid extraction and purification. Can J Biochem Physiol 37:911–917.

Borrell A, Velasquez Vacca A, Pinela AM, Kinze C, Lockyear CH, Vinghi M, Aguilar A (2013) Stable isotopes provide insight into population structure and segregation in eastern north Atlantic sperm whale. PloSOne 8:e82398.

Bouveroux T, Caputo M, Froneman P, Plon S (2018) Largest reported groups for the Indo-Pacific bottlenose dolphin (Tursiops aduncus) found in Algoa Bay, South Africa: Trends and potential drivers. Mar Mammal Sci 34:645–665.

Bowen WD, Iverson SJ (2012) Methods of estimating marine mammal diets: A review of validation experiments and sources of bias and uncertainty. Mar Mammal Sci 29:719–754. doi: 10.1111/j.1748-7692.2012.00604.x

Browning NE, McCulloch SD, Bossart GD, Worthy GAJ (2014a) Fine-scale population structure of estuarine bottlenose dolphins (Tursiops truncatus) assessed using stable isotope ratios and fatty acid signature analyses. Mar Biol 1307–1317. doi: 10.1007/s00227-014-2420-z

Browning NE, Dold C, I-Fan J, Worthy GAJ (2014b) Isotope turnover rates and diet-tissue discrimination in skin of ex situ bottlenose dolphins (Tursiops truncatus). J Exp Biol 217:214–221. doi: 10.1242/jeb.093963

Browning NE, Cockcroft VG, Worthy G (2014c) Resource partitioning among South African delphinids. J Exp Mar Bio Ecol 457:15–21. doi: 10.1016/j.jembe.2014.03.016

Burton R, Koch P (1999) Isotopic tracking of foraging and long-distance migration in northeastern Pacific pinnipeds. Oecologia 119:578–585.

Caputo M, Froneman PW, Preez D, Thompson G, Plön S (2017) Long-term trends in cetacean occurrence during the annual sardine run off the Wild Coast , South Africa. African J Mar Sci 39:83–94. doi: 10.2989/1814232X.2017.1304451

Cherel Y, Hobson KA (2007) Geographical variation in carbon stable isotope signatures of marine predators: A tool to investigate their foraging areas in the Southern Ocean. Mar Ecol Prog Ser 329:281–287. doi: 10.3354/meps329281

Cliff G, Dudley SFJ (1992) Protection against shark attack in South Africa, 1952-90. Aust J Mar Freshw Res 43:263–72.

Cliff G, Dudley SFJ (2011) Reducing the environmental impact of shark-control programs : a case study from KwaZulu-Natal , South Africa. Mar Freshw Res 62:700–709.

Cockcroft V, Ross G (1990) Food and feeding of the Indian Ocean bottlenose dolphin off southern Natal, South Africa. In: Leatherwood S, Reeves R (eds) The bottlenose dolphin. San Deigo: Academic Press, pp 295–308

Cockcroft VG, Peddemors VMV (1990) Seasonal distribution and density of common dolphins Delphinus delphis off the south-east coast of southern Africa. South African J Mar Sci 9:371–377. doi: 10.2989/025776190784378853

Di Beneditto APM, Monteiro LR (2015) Isotopic niche of two coastal dolphins in a tropical marine area: specific and age class comparisons. J Mar Biol Assoc United Kingdom 96:1–6. doi: 10.1017/S0025315415001095

Elton C (1927) The Animal Community. In: Animal Ecology. pp 1–15

Evans W (1994) Common dolphin, white-bellied porpoise Delphinus delphis Linnaeus. In: Ridgeway S, Harrison R (eds) Handbook of Marine Mammals, Volume 5. San Diego: Academic Press, San Diego, pp 191–224

Fernandez R, Garcia-Tiscar S, Santos MB, Lopez A, Martinez-Cedeira JA, Newton J, Pierce GJ (2011) Stable isotope analysis in two sympatric populations of bottlenose dolphins Tursiops truncatus: Evidence of resource partitioning? Mar Biol 158:1043–1055. doi: 10.1007/s00227-011-1629-3

Fréon P, Coetzee JC, van der Lingen CD, Connell a D, O'Donoghue SH, Roberts MJ, Demarcq H, Attwood CG, Lamberth SJ, Hutchings L (2010) A review and tests of hypotheses about causes of the KwaZulu-Natal sardine run. African J Mar Sci 32:449–479. doi: 10.2989/1814232X.2010.519451

Giménez J, Ramírez F, Almunia J, Forero MG, de Stephanis R (2016) From the pool to the sea: applicable isotope turnover rates and diet to skin discrimination factors for bottlenose dolphins (Tursiops truncatus). J Exp Mar Bio Ecol 475:54–61.

Goodwin J, Durham B, Peddemors V, Cockcroft V (1996) Genetic variation in the bottlenose dolphin Tursiops truncatus along the Kwazulu/Natal coast, South Africa. African J Mar Sci 17:225–232.

Goschen W, Schumann E (2011) The physical oceanogrphic processes of Algoa Bay, with emphasis on the western coastal region.

Graham BS, Koch PL, Newsome SD, McMahon KW, Aurioles D (2010) Using isoscapes to trace movements n forging behvior of top predators in oceanic ecosystems. In: West JB, Bowen GJ, Dawson TE, Tu KP (eds) Isoscapes: Understanding Movement, Pattern, and Process on Earth Through Isotope Mapping. Springer Science, pp 299–317

Grinnell J (1917) The niche-relationships of the California thrasher. Am Ornithol Union 34:427–433.

Hill J, McQuaid D, Kaehler S (2006) Biogeographic and nearshore-offshore trends in stable isotope ratios of intertidal mussels and their food sources around hte coast of southern Africa. Mar Ecol Prog Ser 318:63–73.

Hutchinson GE (1957) Concluding Remarks. Cold Spring Harb Symp Quant Biol 22:415–427. doi: 10.1101/SQB.1957.022.01.039

Jackson A, Inger R, Parnel A, Bearhop S, Parnell A, Inger R, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R. J Anim Ecol 80:595–602.

Kaiser S (2012) Feeding Ecology and Dietary Patterns of the Indo-Pacific Bottlenose Dollphin (Tursiops Aduncus) Off KwaZulu-Natal, South Africa. Nelson Mandela Metropolitan University

Kiszka JJ, Méndez-Fernandez P, Heithaus MR, Ridoux V (2014) The foraging ecology of coastal bottlenose dolphins based on stable isotope mixing models and behavioural sampling. Mar Biol 161:953–961. doi: 10.1007/s00227-014-2395-9

Krutzen M, Barre LM, Moller M, Heithaus MR, Simms C, Sherwin W (2002) A biopsy system for small cetaceans: darting success and wound healing. Mar Mammal Sci 18:863–878.

Lane EPE, de Wet M, Thompson P, Siebert U, Wohlsein P, Plon S, Thompson P, Plon S (2014) A systematic health assessment of Indian Ocean bottlenose (Tursiops aduncus) and Indo-Pacific humpback (Sousa plumbea) dolphins, incidentally caught in the shark nets off the KwaZulu-Natal coast, South Africa. PloSOne 9:e107038. doi: 10.1371/journal.pone.0107038

Layman C, Arrington D, Montana C, Post D (2007) Can stable isotope ratios provide for community-wide measures of trophic structure? Ecology 88:42–48.

Lutjeharms JRE, Valentine HR, Ballegooyen RC Van (2000) The hydrography and water masses of the Natal Bight , South Africa. Cont Shelf Res 20:1907–1939.

Magozzi S, Yool A, Vander Zanden HB, Wunder MB, Trueman CN (2017) Using ocean models to predict spatial and temporal variation in marine carbon isotopes. Ecosphere 8:1–20. doi: 10.1002/ecs2.1763

Marçalo A, Katara I, Feijó D, Araújo H, Oliveira I, Santos J, Ferreira M, Monteiro S, Pierce GJ, Silva A, Vingada J (2015) Quantification of interactions between the Portuguese sardine purse-seine fishery and cetaceans. ICES J Mar Sci J du Cons 72:2438–2449. doi: 10.1093/icesjms/fsv076

Melly B, McGregor G, Hofmeyr G, Plon S (2017) Spatio-temporal distribution and habitat preferences of cetaceans in Algoa Bay, South Africa. J Mar Biol Assoc United Kingdom 1–15.

Natoli A, Peddemors VM, Hoelzel a. R (2008) Population structure of bottlenose dolphins

(*Tursiops aduncus*) impacted by bycatch along the east coast of South Africa. Conserv Genet 9:627–636. doi: 10.1007/s10592-007-9379-y

Newsome SD, Clementz MT, Koch PL (2010) Using stable isotope biogeochemistry to study marine mammal ecology. Mar Mammal Sci 26:509–572. doi: 10.1111/j.1748-7692.2009.00354.x

O'Donoghue SH, Whittington P a, Dyer BM, Peddemors VM (2010a) Abundance and distribution of avian and marine mammal predators of sardine observed during the 2005 KwaZulu-Natal sardine run survey. African J Mar Sci 32:361–374. doi: 10.2989/1814232X.2010.502640

O'Donoghue SH, Drapeau L, Peddemors VM (2010b) Broad-scale distribution patterns of sardine and their predators in relation to remotely sensed environmental conditions during the KwaZulu-Natal sardine run. African J Mar Sci 32:279–291. doi: 10.2989/1814232X.2010.501584

O'Donoghue SH, Drapeau L, Dudley SF, Peddemors VM (2010c) The KwaZulu-Natal sardine run: shoal distribution in relation to nearshore environmental conditions, 1997–2007. African J Mar Sci 32:293–307. doi: 10.2989/1814232X.2010.501587

Odum EP (1959) A Descriptive Population Ecology of Land Animals. Ecology 40:166–166. doi: 10.2307/1929948

Parra GJ (2006) Resource partitioning in sympatric delphinids : space use and habitat preferences of Australian snubfin and Indo-Pacific humpback dolphins. J Anim Ecol 862–874. doi: 10.1111/j.1365-2656.2006.01104.x

Pierce G, Boyle P (1991) A review of methods for diet analysis in piscivorous marine mammals. Oceanogr Mar Biol Annu Rev 29:409–486.

Pinela A, Borrell A (2010) isotope analysis reveals habitat partitioning among marine mammals off the NW African coast and unique trophic niches for two globally threatened species. Mar Ecol Prog Ser 416:295–306. doi: 10.3354/meps08790

Post D (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703–718.

Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J, Montaña CG (2007) Getting to the fat of the matter: Models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia 152:179–189. doi: 10.1007/s00442-006-0630-x

Reisinger RR, Karczmarski L (2010) Population size estimate of Indo-Pacific bottlenose dolphins in the Algoa Bay region, South Africa. Mar Mammal Sci 26:86–97. doi: 10.1111/j.1748-7692.2009.00324.x

Roberts MJ, van der Lingen CD, Whittle C, van den Berg M (2010) Shelf currents, lee-trapped and transient eddies on the inshore boundary of the Agulhas Current, South Africa: their relevance to the KwaZulu-Natal sardine run. African J Mar Sci 32:423–447. doi: 10.2989/1814232X.2010.512655

Ross GJB, Cockcroft VG, Butterworth DS (1987) Offshore distribution of bottlenosed dolphins in Natal coastal waters and Algoa Bay, eastern Cape. South African J Zool 22:50–56.

Rossman S, Berens Mccabe E, Barros NB, Gandhi H, Ostrom PH, Stricker CA, Wells RS (2015a) Foraging habits in a generalist predator: Sex and age influence habitat selection and resource use among bottlenose dolphins (Tursiops truncatus). Mar Mammal Sci 31:155–168. doi: 10.1111/mms.12143

Rossman S, Ostrom PH, Stolen M, Barros NB, Gandhi H, Stricker CA, Wells RS (2015b) Individual specialization in the foraging habits of female bottlenose dolphins living in a trophically diverse and habitat rich estuary. Oecologia 178:415–425. doi: 10.1007/s00442-015-3241-6

Schoener TW (1974) Resource Partitioning in Ecological Communities. Science 185:27–39. doi: 10.1126/science.185.4145.27

Sekiguchi K, Klages N, Best P (1992) Comparative analysis of the diets of smaller odontocete cetaceans along the coast of Southern Africa. South African J fo Mar Sci 12:843–861.

Team RC, R Core Team (2017) A language and environment for statistical computing. R Found. Stat. Comput. http://www.R-project.org/.

Van der Lingen C, Miller T (2011) Trophic dynamics of pelagic nekton in the southern Benguela Current ecosystem : calibrating trophic models with stable isotope analysis. In: Omori K, Guo X, Yoshi N, Fujii N, Handoh I, Isobe A, Tanabe S (eds) Interdisciplinary Studies on Environmental Chemistry-Marine Environmental Modeling & Analysis. TERRAPUB, pp 85–94

Van Der Lingen CD, Miller TW (2011) Calibrating trophic models of the southern Benguela with stable isotope data. In: South African Marine Science Symposium. Grahamstown, South Africa, Van Der Lingen CD, Miller TW (2014) Spatial, ontogenetic and interspecific variability in stable isotope ratios of nitrogen and carbon of Merluccius capensis and Merluccius paradoxus off South Africa. J Fish Biol 85:456–472. doi: 10.1111/jfb.12436

Van Der Lingen CD, Miller TW (2017) Interspecific, ontogenetic, spatial and temporal variability in nitrogen and carbon stable isotope ratios of small pelagic fish off South Africa. In: South African Marine Science Symposium. Port Elizabeth, South Africa,

Weatherley R (1963) Notions of niche and competition among animals, with special reference to freshwater fish. Nature 197:14–17.

Wells R, Rhinehart H, Hansen L, Sweeney J, Townsend F, Stone R, Casper D, Scott M, Hohn A, Rowles T (2004) Bottlenose dolphins as marine ecosystem sentinels: developing a health monitoring system. Eco-Health 1:246–254.

Wilson RM, Nelson J a., Balmer BC, Nowacek DP, Chanton JP (2013) Stable isotope variation in the northern Gulf of Mexico constrains bottlenose dolphin (Tursiops truncatus) foraging ranges. Mar Biol 160:2967–2980. doi: 10.1007/s00227-013-2287-4

Worthy G, Shippee S, Ostrom P, Wells R, Allen J, Barleycorn A (2011) Fine scale feeding habits of bottlenose dolphins in the western Florida panhandle as assessed by stable isotope signature analysis. 3.

Young D, Cockcroft V (1994) Diet of common dolphins (Delphinus delphis) off the south-east coast of southern Africa:opportunism or specialization? J Zool 234:41–53.

Chapter 5: Summary and conclusions

5.1 Summary

The aim of this project was to determine the spatial and temporal occurrence of dolphins off the Wild Coast of South Africa, and further to investigate their feeding ecology and movements in the area. Few studies had been conducted in Wild Coast area, and the lack of boat-based and year-round research left a gap in our knowledge of dolphin ecology along the south-eastern coastline of South Africa. Moreover, previous research has largely been skewed to the austral winter to coincide with the annual sardine run (Peddemors and Cockcroft 1997; O'Donoghue et al. 2010b, a). This study used long-term aerial and boat-based surveys (from 2014-2016) to show that both common and bottlenose dolphins occur off the Wild Coast in both winter and summer seasons, during which time they were recorded foraging. This result was unexpected as previous studies suggested that the presence both species demonstrated strong seasonality in the waters along the Wild Coast (Cockcroft and Peddemors 1990; Cockcroft et al. 1991; Peddemors and Cockcroft 1997; O'Donoghue et al. 2010a, b). The foraging year-round presence of both species of dolphin in the coastal waters of the Wild Coast suggests the area is likely more productive than previously thought and represents an important region for the dolphins. Additionally, stable isotopes results suggest the trophic niche of these two species highly overlap in this area, despite differences in preferred diet reported elsewhere along the coast (Cockcroft et al. 1990; Young and Cockcroft 1994; Ambrose et al. 2013). Previous research suggested that a migratory population of bottlenose dolphins from the Eastern Cape travelled through the Wild Coast and entered KZN waters during the sardine run (Cockcroft and Ross 1990b; Peddemors 1999; Natoli et al. 2008; O'Donoghue et al. 2010a). Results of the stable isotope analysis from this study show no overlap between the south-western and north-eastern bottlenose dolphin sampled, even in this relatively small area (<85 km) for these highly mobile animals. This suggests that fine-scale population structuring does occur in this area, despite the open nature of this coastline. By contrast, there was high niche overlap in the three regions for common dolphin suggesting movement/migration of this species. This study provides important baseline data for conservation and management of these two dolphin species in the future.

5.2 Dolphin occurrence

Aerial surveys of cetaceans are useful to examine animal distribution as they cover large areas, and may provide accurate counts as cetaceans have sightability (Dawson et al. 2008). For short-term movement and habitat use studies, boat-based research provides fine-scale patterns, and more accurate descriptions of behaviour and track changes, as well as allowing researchers to identify individuals and collect biopsy samples (Dawson et al. 2008). Both aerial and boat-based surveys were conducted during this investigation which allowed for the determination of long-term patterns, fine-scale movement, and habitat use in three of the MPAs along the coast (Chapters 3 and 4).

The sighting and individual density of both common and bottlenose dolphins appeared not to be influenced by environmental factors such as SST and depth. There was also a lack of short-term temporal trends for either species, with no seasonal changes in density. With the influx of sardines in the austral winter, it would be anticipated that their densities would increase to feed on this rich resource. No such trend was observed with no apparent seasonal trends in occurrence for both species (Cockcroft and Peddemors 1990; Cockcroft et al. 1991; Peddemors and Cockcroft 1997). Additionally, there was evidence of regional habitat use, including hotspots of dolphin occurrence, which should be investigated further to determine if these hotspots are areas of high productivity.

In the study area, bottlenose dolphin occurred in some of the largest groups ever reported globally. Coastal populations of *T. aduncus* are generally observed in groups of 6 to 60 animals (e.g. Möller et al. 2002; Stensland and Berggren 2007; Fury and Harrison 2008; Wang and Yang 2009; James 2014; Sprogis et al. 2015). Other areas with large number of individuals include the Mediterranean Sea, with up to 670 individuals identified (Gnone et al. 2011), and California, with over 200 individuals identified (Hwang et al. 2014), fewer numbers than the relatively small regions of Hluleka and Pondoland. In South African territorial waters, large groups of *T. aduncus* have occasionally been recorded (Bouveroux et al. 2018.; Ross et al. 1987; Phillips 2006; Reisinger and Karczmarski 2010). For example a group of up to 300 individuals was recorded along the south coast of KZN (Ross et al. 1987). The absence of any change in their numbers during the sardine run (Chapter 2) and presence their year-round (Chapter 3) was expected given that their distribution is not linked to sardine availability (O’Donoghue et al. 2010a). Despite some level of residency, with animals resighted primarily in the same study area as their first sighting, the larger majority of individuals were only sighted once. The number of individuals identified in this study is, however, almost double what has been reported for bottlenose dolphin outside of South Africa (Zolman 2002; Gnone et al. 2011; Hwang et al. 2014; Zanardo et al. 2016), and considerably higher than in the adjacent area, Algoa Bay (Reisinger and Karczmarski 2010). The population estimate for Algoa Bay, with approximately 1500 individuals identified, was over 20,000 animals (Reisinger and Karczmarski 2010). This suggests that large numbers of animals occur off the Wild Coast, forming huge populations. However, attempts to estimate the actual population size were unsuccessful as a result of unfavourable oceanographic conditions and limited time at sea. With large numbers of individuals in the area, the likelihood of resightings is diminished unless there is high site fidelity. Given this diminished likelihood of resightings, the 14 animals resighted in all the field trips to Pondoland are of interest, and indicate some level of site fidelity despite low overall resighting rates. However, the overwhelming number of animals that were only sighted once suggests that the majority of animals were using the area as a migratory corridor.

Common dolphin group sizes along the south-eastern coastline of South Africa have decreased since 1994 particularly post 2005 (Caputo et al. 2017). Previously, superpods of up to 5000 animals were sighted during the sardine run along the Eastern Cape coast (O’Donoghue et al. 2010a, b). The largest group observed in this three-year study was estimated to comprise 1250 individuals; however, group size estimates for this many animals are difficult and this number should be viewed with caution. It is unclear what ecological processes account for the recent decline in common dolphin group size, although it has been speculated that it could be linked to the decrease in the frequency and intensity of the annual sardine run (Fréon et al. 2010; O’Donoghue et al. 2010a; Ambrose et al. 2013), as common dolphin distribution globally has been shown to be highly linked with distribution of sardines and anchovies (Grant and Bowen 1998; Jefferson et al. 2008).

Ambrose et al. (2013) describe a shift in common dolphin diet from predominantly sardine in 1972-1992 to mackerel in 2000-2009, which they linked with changes in the sardine run. Shifts in predator diets in response to changes in prey availability (i.e. abundance or distribution) have been described for numerous terrestrial (e.g. Steenhof and Kochert 1985, 1988; Jaksic et al. 1992; Garrott et al. 2007) and aquatic species (e.g. Cairns 1987; Montevecchi

1993; Jackson et al. 2011; Olson et al. 2014). Specifically, Olson et al. (2014) describe a shift in Pacific Ocean yellowfin tuna (*Thunnus albacares*) diet over 10 years from large epipelagic fishes to an array of smaller mesopelagic species and crustaceans. Researchers concluded that this shift had resulted from broad-scale change in the food web of the eastern tropical Pacific Ocean (Olson et al. 2014), suggesting that predator ecology is important for tracking changes in the marine environment. Given that in this study, no change in total number of common dolphins occurred, it is probable that the Wild Coast area is sufficiently productive to sustain large numbers of these predators, despite any potential decline in the magnitude and extent of the sardine run.

5.3 Feeding ecology

Researchers are increasingly using stable isotope analyses to investigate the feeding ecology and fine-scale population structure in dolphin populations (Newsome et al. 2010; Barros et al. 2010; Worthy et al. 2011; Browning et al. 2014a). Traditional methods such as photographic identification may not provide sufficient information on populations given that resighting rates may be low in large populations and migratory corridors (Defran and Weller 1999). Large amount of photographic identification effort may, therefore, return results that lack ecological interpretation. Moreover, mark-recapture studies are logistically difficult, particularly in remote areas with the inability to conduct line-transect methods due to oceanographic conditions or safety precautions at sea.

Bottlenose and common dolphin were observed feeding at all times of year along the Wild Coast (Chapter 3). Moreover, results of stable isotope analysis indicate that there was a high degree of trophic niche overlap overall between the two species (Chapter 4). This result is in stark contrast to a previous study which demonstrated only a 9% overlap in their diets in the coastal water of KZN (Jefferson et al. 2008; Browning et al. 2014b). The high trophic niche overlap of the two dolphin species along the Wild Coast could be a function of the narrowing of the continental shelf in this area (Roberts et al. 2010), or the prey availability inshore, which supports both species year-round. Although there were no significant temporal differences in the trophic niche overlap between the two species, the extent of the overlap was highest during

February. This is in keeping with the lack of change in individual and sighting density over the study period from boat-based surveys.

A high degree of trophic niche overlap was observed in common dolphin from the north-eastern Wild Coast sites, and KZN, which may indicate that these animals are highly mobile in this region, as they did not show distinct isotope signatures for each sampling location. Given that globally, *Delphinus spp*. are considered highly mobile animals, capable of travelling huge distances, the movement between the study sites was not unexpected (Evans 1994; Natoli et al. 2008a). By contrast there was significant spatial differences in the stable isotope ratios of the bottlenose dolphins from Algoa Bay, demonstrating 0% overlap with the other sites. Similarly, there was only 5% niche overlap between individuals from Amathole and Hluleka. This result was supported by photographic identification analyses with only 16 resightings between Amathole and the other two sites; whereas there were 46 resightings of bottlenose dolphins between the geographically close Hluleka and Pondoland, which showed high levels of trophic niche overlap (Chapter 4). Whether this structuring exists genetically or not is unknown, but fine-scale population structuring has been found in *Tursiops spp*., even within relatively small spatial scales in numerous locations across the world (Tezanos-Pinto et al. 2009; Barros et al. 2010; Mirimin et al. 2011; Kiszka et al. 2012). Research from South Africa has suggested that there may be a resident stock in KZN with a migratory stock entering the area during the sardine run (Natoli et al. 2004). Therefore it is possible that the lack of overlap between bottlenose dolphins in the western and eastern sites may indicate two genetically distinct groups.

5.4 Marine Protected Areas

Well managed and monitored MPAs can serve to protect dolphins, despite their highly mobile nature (Bearzi 2012). The MPAs of the Wild Coast were not established/proclaimed by the ECPTA for dolphins but rather to protect important habitats and the recreational line fisheries of the region (Department of Environmental Affairs and Tourism 2004, 2011). Cetaceans occurrence could be employed to establish the ecosystem health of these MPAs (Wells et al. 2004; Hwang et al. 2014).

In this study, the majority of sightings and largest groups of both species of dolphin from long-term and short-term surveys were found within MPAs. Additionally, animals were often seen foraging in these areas, which suggests increased prey availability within these region. The increase in prey availability within the MPAs may reflect the effectiveness of these regions in sustaining fish stocks. The remoteness of the region, coupled with adverse sea conditions, restrict access to the sea and likely limits boat-based fishing in this area (Department of Environmental Affairs and Tourism 2004, 2011). In the same respect, there is limited enforcement at sea, but land-based activities are monitored and controlled (Department of Environmental Affairs and Tourism 2004, 2011). Research on the species occurrence and diversity, inside and outside of MPAs in this area would help to elucidate the mechanisms behind higher dolphin numbers within MPAs. As dolphins are considered sentinel species, whose occurrence can indicate the health of the marine environment (Wells et al. 2004), their presence in MPAs is important to managers at the ECPTA for future management plans.

5.5 Future directions and Conclusions

Population estimates based on mark-recapture analysis using photographic identification (Urian et al. 1999; Balmer et al. 2008; Smith et al. 2013; Zanardo et al. 2016) would provide valuable baseline information on the dolphins off the Wild Coast. Photographic identification is commonly used for mark recapture studies on dolphins worldwide (Urian et al. 1999; Balmer et al. 2008; Smith et al. 2013; Zanardo et al. 2016); however, the large groups of bottlenose dolphin recorded in this study make photographic identification a time-consuming process, with few resightings. Additionally, with the open coastline and difficult sea conditions which limit the number of days at sea per month, abundance estimates were not possible in this study and are likely to be difficult in the future. Additional methods are needed to investigate population ecology, including possibly molecular techniques and food web tracers (as the stable isotope and fatty acids analyses).

Genetic studies on inshore delphinids off of South Africa have largely been restricted to the north-eastern coast, largely reflecting the availability of specimens by-caught in shark nets and strandings (Natoli et al. 2004, 2008b). A larger genetic study, including samples from KZN, the Wild Coast, East London, and Algoa Bay, and further afield if possible, is needed to better understand population structure and connectivity of different dolphin species in the territorial waters along southeastern coastline of South Africa. Wild Coast samples collected here from skin biopsies are available to contribute to this research objective. This would allow researchers to determine whether the Wild Coast animals form their own separate sub-population or comprise animals from adjacent areas. It would also give information on sex ratio in groups to provide information on social structure in these large groups. As photographic identification is limited in this area because of the huge numbers of bottlenose dolphin individuals, and difficulty with common dolphin identification, genetic studies are an important resource. The isotope results suggest that the bottlenose dolphin in the western and eastern portions of the Wild Coast form sub-populations with little overlap. Whether these animals are still genetically part of a panmitic population is an important question for management and the Wild Coast may be important in the mixing of adjacent populations as a middle ground.

Fine-scale habitat mapping for the Wild Coast may help to identify preferred areas and habitats, which was not in the scope of the current study. Remotely sensed data could also contribute to this research. Anecdotally, there is extensive reef habitat inshore along the entire length of coast, but this has never been formally mapped and quantified. Given that dolphins were frequently seen foraging, this mapping would allow us to better link behaviour and movements to reefs or potential feeding areas. Additionally, linking the prey to isotope signatures to identify the main components of each species diet would give researchers further knowledge on their feeding ecology and determine the importance of sardines to these animals and the richness of the environment.

The current research provides baseline information specific to dolphins from the Wild Coast, unavailable from any other source. This information is necessary for monitoring change and understanding the importance of this area to dolphins, as it was previously thought of as a migratory corridor, used only for foraging during the austral winter. Here, I highlight that the sardine run that occurs of the Wild Coast may not be as important to dolphin occurrence and foraging ecology as previously thought, and that the area may provide rich enough prey availability to allow residency throughout the year. Despite a decrease in common dolphin groups since 2005, they still occur in the area and were seen feeding during all but one field trip. While evidence suggests that both species are highly mobile and may migrate through the area, staying only briefly; there is some indication that small groups of bottlenose dolphin may be semi-resident to the area. Despite the limitations of this study, largely related to the difficulties of conducting research in a remote area, this investigation provides important baseline data on the delphinids of the Wild Coast, and highlights that this area does have dolphins occurring and foraging outside of the sardine run, which was previously unknown. This research is a starting point for further dolphin studies along this coast, which are necessary not only for conservation of dolphin species, but to monitor changes in the ecosystem as coastal habitats are increasingly threatened from coastal development, and the Wild Coast, though remaining remote to date, has been suggested as an area for future coastal development.

5.6 Reference

Ambrose S, Froneman P, Smale M, Cliff G, Plön S (2013) Winter diet shift of long-beaked common dolphins (Delphinus capensis) feeding in the sardine run off KwaZulu-Natal, South Africa. Mar Biol 160:1543–1561. doi: 10.1007/s00227-013-2208-6

Balmer BC, Wells RS, Nowacek SM, Nowacek DP, Schwacke LH, McLellan WA, Scharf FS, Rowles TK, Hansen L, Spradlin T, Pabst DA (2008) Seasonal abundance and distribution patterns of common bottlenose dolphins (ursiops truncatus) near St . Joseph Bay, Florida, USA. J Cetacean Res Manag 10:157–167.

Barros NB, Ostrom PH, Stricker CA, Wells RS (2010) Stable isotopes differentiate bottlenose dolphins off west-central Florida. Mar Mammal Sci 26:324–336. doi: 10.1111/j.1748-7692.2009.00315.x

Bearzi M (2012) Cetaceans and MPAs should go hand in hand: A case study in Santa Monica Bay, California. Ocean Coast Manag 60:56–59. doi: 10.1016/j.ocecoaman.2011.12.019

Bouveroux T, Caputo M, Froneman P, Plon S (2018) Largest reported groups for the Indo-Pacific bottlenose dolphin (Tursiops aduncus) found in Algoa Bay, South Africa: Trends and potential drivers. Mar Mammal Sci 34:645–665.

Browning NE, McCulloch SD, Bossart GD, Worthy GAJ (2014a) Fine-scale population structure of estuarine bottlenose dolphins (Tursiops truncatus) assessed using stable isotope ratios and fatty acid signature analyses. Mar Biol 1307–1317. doi: 10.1007/s00227-014-2420-z

Browning NE, Cockcroft VG, Worthy G (2014b) Resource partitioning among South African delphinids. J Exp Mar Bio Ecol 457:15–21. doi: 10.1016/j.jembe.2014.03.016

Cairns DK (1987) Seabirds as indicators of marine food supplies. Biol Oceanogr 5:261–271.

Caputo M, Froneman PW, Preez D, Thompson G, Plön S (2017) Long-term trends in cetacean occurrence during the annual sardine run off the Wild Coast , South Africa. African J Mar Sci 39:83–94. doi: 10.2989/1814232X.2017.1304451

Cockcroft VG, Peddemors VMV (1990) Seasonal distribution and density of common dolphins Delphinus delphis off the south-east coast of southern Africa. South African J Mar Sci 9:371–377. doi: 10.2989/025776190784378853

Cockcroft VG, Ross GJB (1990) Age, growth, and reproduction of bottlenose dolphins Tursiops truncatus from the East coast of Southern Africa. Fish Bull 88:289–302.

Cockcroft VG, Ross GJB, Peddemors VM (1990) Bottlenose dolphin Tursiops truncatus distribution in Natal’s coastal waters. South African J Mar Sci 9:1–10. doi: 10.2989/025776190784378952

Cockcroft VG, Ross GJB, Peddemors VM (1991) Distribution and status of bottlenose dolphin Tursiops truncatus on the south coast of Natal, South Africa. South African J Mar Sci 11:203–209. doi: 10.2989/025776191784287538

Dawson S, Wade P, Slooten E, Barlow J a Y (2008) Design and field methods for sighting surveys of cetaceans in coastal and riverine habitats. Mamm Rev 38:19–49.

Defran R, Weller D (1999) Occurrence, distribution, site fidelity, and school size of bottlenose dolphins (Tursiops truncatus) off San Diego, California. Mar Mammal Sci 15:366–380.

Department of Environmental Affairs and Tourism (2004) Notice declaring the Pondoland Marine Protected Area under section 43 of the Marine Living Resources Act (18/1998). South africa

Department of Environmental Affairs and Tourism (2011) Submission of proposal to declare the Amathole (border) marine protected area (MPA). South Africa

Evans W (1994) Common dolphin, white-bellied porpoise Delphinus delphis Linnaeus. In: Ridgeway S, Harrison R (eds) Handbook of Marine Mammals, Volume 5. San Diego: Academic Press, San Diego, pp 191–224

Fréon P, Coetzee JC, van der Lingen CD, Connell a D, O’Donoghue SH, Roberts MJ, Demarcq H, Attwood CG, Lamberth SJ, Hutchings L (2010) A review and tests of hypotheses about causes of the KwaZulu-Natal sardine run. African J Mar Sci 32:449–479. doi: 10.2989/1814232X.2010.519451

Fury C, Harrison P (2008) Abundance, site fidelity and range patterns of Indo-Pacific bottlenose dolphins (Tursiops aduncus) in two Australian subtropical estuaries. Mar Freshw Res

59:1015–1027.

Garrott R, Bruggeman JE, Becker MS, Kalinowski ST, White P (2007) Evaluating prey switching in wolf-ungulate systems. Ecol Appl 17:1588–1597.

Gnone G, Bellingeri M, Dhermain F, Dupraz F, Nuti S, Bedocchi D, Moulins A, Rosso M, Alessi J, McCrea RS, Azzellino A, Airoldi S, Portunato N, Laran S, David L, Di Meglio N, Bonelli P, Montesi G, Trucchi R, Fossa F, Wurtz M (2011) Distribution, abundance, and movements of the bottlenose dolphin (Tursiops truncatus) in the Pelagos Sanctuary MPA (north-west Mediterranean Sea). Aquat Conserv Mar Freshw Ecosyst 21:372–388. doi: 10.1002/aqc.1191

Hwang A, Defran RH, Bearzi M, Maldini D (2014) Coastal Range and Movements of Common Bottlenose Dolphins (Tursiops truncatus) off California and Baja California , Mexico. Bull South Calif Acad Sci 113:1–13.

Jackson A, Inger R, Parnel A, Bearhop S, Parnell A, Inger R, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R. J Anim Ecol 80:595–602.

Jaksic F, Jimenez J, Castro S, Feinsinger P (1992) Numerical and functional response of predators to a long-term decline in mammalian prey at a semi-arid Neotropical site. Oecologia 89:90–101. doi: 10.1007/BF00319020

James B (2014) Natural and human impacts on habitat use of coastal delphinids in the Mossel Bay area, Western Cape, South Africa. University of Pretoria

Jefferson T, Webber M, Pitman R (2008) Marine Mammals of the World - A Comprehensive Guide to their Identification. Academic Press/Elsevier

Kiszka J, Simon-Bouhet B, Gastebois C, Pusineri C, Ridoux V (2012) Habitat partitioning and fine scale population structure among insular bottlenose dolphins (Tursiops aduncus) in a tropical lagoon. J Exp Mar Bio Ecol 416–417:176–184. doi: 10.1016/j.jembe.2012.03.001

Mirimin L, Miller R, Dillane E, Berrow SD, Ingram S, Cross TF, Rogan E (2011) Fine-scale population genetic structuring of bottlenose dolphins in Irish coastal waters. Anim Conserv 14:342–353. doi: 10.1111/j.1469-1795.2010.00432.x

Möller LM, Allen SSJ, Harcourt RRG (2002) Group characteristics, site fidelity and seasonal abundance of bottlenose dolphins Tursiops aduncus in Jervis Bay and Port Stephens, south-eastern Australia. Aust Mammal 24:11–21.

Montevecchi W (1993) Birds as indcators of changes in marine prey stocks. In: Furness R, Greenwood J (eds) Birds as monitors of environmental change. Springer, Dordrecht,

Natoli A, Peddemors V, Hoelzel A (2004) Population structure and speciation in the genus Tursiops based on microsatellite and mitochondrial DNA analyses. J Evol Biol 17:363–375. doi: 10.1046/j.1420-9101.2003.00672.x

Natoli A, Canadas A, Vaquero C, Politi E, Fernandez-Navarro P, Hoelzel A (2008a) Conservation genetics of the short-beaked common dolphin (Delphinus delphis) in the Mediterranean Sea and in the eastern North Atlantic Ocean. Conserv Genet 9:1479–1487.

Natoli A, Peddemors VM, Hoelzel a. R (2008b) Population structure of bottlenose dolphins (Tursiops aduncus) impacted by bycatch along the east coast of South Africa. Conserv Genet 9:627–636. doi: 10.1007/s10592-007-9379-y

Newsome SD, Clementz MT, Koch PL (2010) Using stable isotope biogeochemistry to study marine mammal ecology. Mar Mammal Sci 26:509–572. doi: 10.1111/j.1748-7692.2009.00354.x

O’Donoghue SH, Whittington P a, Dyer BM, Peddemors VM (2010a) Abundance and distribution of avian and marine mammal predators of sardine observed during the 2005 KwaZulu-Natal sardine run survey. African J Mar Sci 32:361–374. doi: 10.2989/1814232X.2010.502640

O’Donoghue SH, Drapeau L, Peddemors VM (2010b) Broad-scale distribution patterns of sardine and their predators in relation to remotely sensed environmental conditions during the KwaZulu-Natal sardine run. African J Mar Sci 32:279–291. doi: 10.2989/1814232X.2010.501584

Olson R, Duffy L, Kuhnert P, Galván-Magaña F, Bocanegra-Castillo N, Alatorre-Ramírez V (2014) Decadal diet shift in yellowfin tuna Thunnus albacares suggests broad-scale food web changes in the eastern tropical Pacific Ocean. Mar Ecol Prog Ser 497:157–178.

Peddemors V (1999) Delphinids of southern Africa: A review of their distribution, status and life history. J Cetaceans Res Manag 1:157–166.

Peddemors V, Cockcroft V (1997) Prey distribution and its importance for nearshore dolphins off the east coast of southern Africa. Paper SC/49/SM32, presented to the Scientific Committee of the International Whaling Commission, Bournemouth

Phillips G (2006) Bottlenose dolphins (Tursiops aduncus) in Plettenberg Bay, South Africa:

Population estimates and temporal dynamics of groups. Nelson Mandela Metropolitan University, Port Elizabeth, South Africa

Reisinger RR, Karczmarski L (2010) Population size estimate of Indo-Pacific bottlenose dolphins in the Algoa Bay region, South Africa. Mar Mammal Sci 26:86–97. doi: 10.1111/j.1748-7692.2009.00324.x

Roberts MJ, van der Lingen CD, Whittle C, van den Berg M (2010) Shelf currents, lee-trapped and transient eddies on the inshore boundary of the Agulhas Current, South Africa: their relevance to the KwaZulu-Natal sardine run. African J Mar Sci 32:423–447. doi: 10.2989/1814232X.2010.512655

Ross GJB, Cockcroft VG, Butterworth DS (1987) Offshore distribution of bottlenosed dolphins in Natal coastal waters and Algoa Bay, eastern Cape. South African J Zool 22:50–56.

Smith HC, Pollock K, Waples K, Bradley S, Bejder L (2013) Use of the robust design to estimate seasonal abundance and demographic parameters of a coastal bottlenose dolphin (Tursiops aduncus) population. PLoS One 8:e76574. doi: 10.1371/journal.pone.0076574

Sprogis K., Raudino H., Rankin R (2015) Home range size of adult Indo-Pacific bottlenose dolphins (Tursiops aduncus) in a coastal and estuarine system is habitat and sex-specific. Mar Mammal Sci 32:287–308. doi: 10.1111/mms.12260

Steenhof K, Kochert M (1985) Dietary shifts of sympatric buteos during a prey decline. Oecologia 66:6–16. doi: 10.1007/BF00378546

Steenhof K, Kochert M (1988) Dietary responses of three raptor species to changing prey densities in a natural environment. J Anim Ecol 57:37–48.

Stensland E, Berggren P (2007) Behavioural changes in female Indo-Pacific bottlenose dolphins in response to boat-based tourism. Mar Ecol Prog Ser 332:225–234.

Tezanos-Pinto G, Baker CS, Russell K, Martien K, Baird RW, Hutt A, Stone G, Mignucci-Giannoni A a, Caballero S, Endo T, Lavery S, Oremus M, Olavarría C, Garrigue C (2009) A worldwide perspective on the population structure and genetic diversity of bottlenose dolphins (Tursiops truncatus) in New Zealand. J Hered 100:11–24. doi: 10.1093/jhered/esn039

Urian K, Hohn A, Hansen L (1999) Status of the photo-identification catalog of coastal bottlenose dolphins of the western North Atlantic: Report of a workshop of catalog contributors.

Wang J, Yang A (2009) Indo-Pacific bottlenose dolphin (Tursiops aduncus). In: Perrin W, Wursig B, Thewissen J (eds) Encyclopedia of Marine Mammals, 2nd edn. Academic Press, Amsterdam, pp 602–608

Wells R, Rhinehart H, Hansen L, Sweeney J, Townsend F, Stone R, Casper D, Scott M, Hohn A, Rowles T (2004) Bottlenose dolphins as marine ecosystem sentinels: developing a health monitoring system. Eco-Health 1:246–254.

Worthy G, Shippee S, Ostrom P, Wells R, Allen J, Barleycorn A (2011) Fine scale feeding habits of bottlenose dolphins in the western Florida panhandle as assessed by stable isotope signature analysis. 3.

Young D, Cockcroft V (1994) Diet of common dolphins (Delphinus delphis) off the south-east coast of southern Africa:opportunism or specialization? J Zool 234:41–53.

Zanardo N, Parra GJ, Moller LM (2016) Site fidelity, residency, and abundance of bottlenose dolphins (Tursiops sp.) in Adelaide’s coastal waters , South Australia. Mar Mammal Sci 1–21. doi: 10.1111/mms.12335

Zolman E (2002) Residence patterns fo bottlenose dolphins (Tursiops trucatus) in the Stono River estuary, Charleston County, South Carolina, U.S.A. Mar Mammal Sci 18:879–892.