

**Mapping cetacean distribution in the Western Cape
to explore potential range shifts
in light of climate change**

by

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SUMMARY

The southern tip of South Africa is characterised by two major current systems, each of which is associated with its own species. The southwest coastal waters represent the limit of the local or global distribution ranges of four of the eight cetacean species that most frequently occur in the area. The goal of the present study was to determine the fine scale distribution of these species and subsequently investigate which environmental factors influence and possibly limit their current distribution ranges.

The current study was focused around the Cape Peninsula, the south-western tip of South Africa, where one of the strongest thermal gradients in the southern Benguela occurs. The waters surrounding the Cape Peninsula, including False Bay which lies on the eastern side of the Peninsula, fall within the transition zone between the Benguela Current and Agulhas Current and are subject to high seasonal variety in mean sea surface temperature. Surveys with conducted in the waters ranging from Table Bay on the west coast to Cape Hangklip, the eastern tip of False Bay.

Sightings data were collected from dedicated boat-based surveys conducted over a two-year period. Dedicated surveys resulted in over 3 000 kilometres of searching for animals and in the detections of all eight species. The effective southern range end of Heaviside's dolphins (*Cephalorhynchus heavisidii*) was redefined as Hout Bay on the western side of the Peninsula, as encounters were absent further south than this. Dusky dolphins (*Lagenorhynchus obscurus*) are likely restricted from moving farther east of Cape Point, the southern tip of the Peninsula, by a combination of the warmer waters present in False Bay with changes in prey type and availability. Humpback dolphins (*Sousa plumbea*) were frequently encountered in False Bay showing a clear westward range expansion since reports in the early 1990s, possibly a result of tracking warmer sea surface temperatures within the bay. A further westward expansion is possibly limited by cooler temperatures and the presence of steep rocky shores in the south-western corner of False Bay as humpback dolphins prefer habitats with sandy bottom types. Common dolphins (*Delphinus delphis*) were encountered throughout the study area. Their distribution range is most likely determined by the movements of their prey and less influenced by water temperature as they are recorded in both warm and cooler waters. Two migratory whale species, southern right whales (*Eubalaena australis*) and humpback whales

(Megaptera novaeangliae), were recorded in shallow, coastal waters throughout the study area, whereas the non-migratory Bryde's whale (*Balaenoptera brydei*) was seen predominantly in False Bay in slightly deeper waters.

Species distribution models were built using the occurrence data to investigate relationships between the spatial occurrence of a species and its surrounding environment. The models predicted a strong influence of temperature and chlorophyll concentration on the distribution of Heaviside's and dusky dolphins on the west coast. All models indicated depth as the most influential factor driving humpback dolphin distribution, while suitable habitat for common dolphins and bottlenose dolphins was primarily influenced by water temperatures slightly offshore.

Changing oceanographic conditions have direct impacts on the distribution and availability of prey species, which in turn affects the movement patterns of cetaceans. Increases in water temperature are of particular concern for cool water limited species such as those in the Benguela Ecosystem, especially for the endemic Heaviside's dolphin which are subject to range reduction in response to changing oceanographic conditions.

Keywords: *cetaceans, climate change, common dolphins, dusky dolphins, Heaviside's dolphins, ensemble modelling, humpback dolphins*

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CHAPTER 1: GENERAL INTRODUCTION TO CLIMATE CHANGE AND CETACEANS IN THE WESTERN CAPE

ABSTRACT

The South African coastline is considered a global hotspot for marine biodiversity, which is associated with the wide range of oceanographic conditions caused by the confluence of cool upwelling and warmer nutrient poor currents. The waters off South Africa are home to over 40 cetacean species. At least four dolphin species have their global or local distribution ranges end around the Cape Peninsula, an area of significant biogeographic and oceanographic change along the South African coast. This makes for an interesting and unique study area, especially in the face of shifting oceanographic conditions such as increasing water temperature as a result of global climate change. The aim of the current study was to investigate which environmental factors influence or possibly limit the distribution ranges of those cetaceans which can frequently be seen off the south-western coast of South Africa. The project goals were to map the current patterns of whale and dolphin distribution around the Cape Peninsula and subsequently identifying areas of suitable habitat using modelled predicted distribution ranges of each species.

INTRODUCTION

Global climate change

The ocean plays an important role in regulating the Earth's climate (Hoegh-Guldberg and Bruno 2010). However, the size, complexity, and difficulty in taking measurements and compiling data in marine environments has led to a poor understanding on climate change impacts in marine environments compared to terrestrial ecosystems. Of the papers published on the rate of- and changes caused by global climate change, only 5% focus specifically on the changes within the marine environment (Hoegh-Guldberg and Bruno 2010).

The physical properties of seawater (high density and specific heat) allows it to store and transport heat (Levitus et al. 2000), with a heat capacity approximately 1,000 times larger than that of the atmosphere (Bindoff et al. 2007). The ocean is essentially accumulating excess heat (Hansen et al. 1997) and has been experiencing net warming during the past 50 years (Levitus et al. 2000). Most of this heat has been stored predominantly in the ocean's upper layers (Bindoff et al. 2007). In addition to absorbing heat, the ocean acts as a carbon sink, absorbing approximately one-third of all carbon dioxide currently produced by humans, which influences ocean productivity (Behrenfeld et al. 2006) and increases the acidification of the ocean's surface layers (Bindoff et al. 2007), (Hoegh-Guldberg and Bruno 2010). The strength and direction of major current systems can also be influenced by the continual heat increase of the ocean (Bindoff et al. 2007).

These changes in the physical properties of the ocean can also have strong influences on both the distribution and abundance of marine organisms as many marine species are temperature limited. For example, changes in kelp productivity (e.g. Ling 2008, Connell and Russell 2010) and large-scale declines of coral reef systems (Hoegh-Guldberg et al. 2007) have been observed as a result of changing temperatures. Some studies show altered range shifts for previously long-term persisting kelp species and suggest significant loss of suitable habitats for future climatic conditions (Assis et al. 2016) , especially under scenarios of increasing sea surface temperature (SST). Coral reefs are biologically diverse, economically important ecosystems (Moberg and Folke 1999) which are becoming increasingly rare as a result of ocean acidification and warming seawater temperatures (Hoegh-Guldberg et al. 2007).

In the Antarctic, the abundance of krill (*Euphausia superba*) is related to ice cover, which is predicted to decrease with increasing temperatures (Trathan et al. 2003). This in turn reduces productivity and subsequently the survival of breeding sea birds, like penguins, which aren't able to move from their breeding grounds in response to changing foraging conditions (Croxall et al. 2002; Reid et al. 2005). Shrinking and early break-up of ice cover also leads to reduced feeding opportunities for polar bears (*Ursus maritimus*) which feed mainly on ice-breeding seals, resulting in declining body conditions of adult bears and poor cub survival (Regehr et al. 2006; Rode et al. 2008). Female Antarctic fur seals (*Arctocephalus gazella*) are fully dependent on krill during nursing (Reid and Arnould 1996) and a persistent 10 year period of increased SST directly resulted in reduced pup production (Forcada et al. 2005). Furthermore, reduced krill availability during summer months (Trathan et al. 2003) has been correlated to impacts on southern right whale reproductive success, where reduced feeding before conception negatively affects the output of calves during the following winter (Cooke and Rowntree 2003; Leaper et al. 2006). Other effects of global climate change include loss of suitable nesting habitats for sea turtles as a result of increasing sea water levels which erode critical egg-laying beaches (Fish et al. 2005).

Further impacts as a result of climate change include distribution shifts of commercial fish stocks as a result of warming sea temperatures (e.g. Comte and Grenouillet 2013; Perry et al. 2005) which could have severe effects on commercial fisheries as fish change their distribution ranges and community assemblages (Perry et al. 2005). In South Africa, distribution shifts of fish species like sardine (*Sardinops sagax*) was found to negatively impact the breeding success of some seabirds as their prey become less available by moving outside the feeding range of the birds (Crawford et al. 2006).

It is clear that all trophic levels within a marine ecosystem can be affected by global climate change. As marine food webs are notoriously complex, the ultimate effect of climate change on species and ecosystems is challenging to predict. Knowledge from the present-day limits of species ranges where impacts are likely to be felt first, like those dolphin species which the current project is focused on, may be helpful in assessing how marine ecosystems and top predators like dolphins will respond to environmental change.

Climate change in South Africa

The South African coast is characterised by the presence of two major current systems: the cool Benguela Large Marine Ecosystem along the Atlantic coast and the warm Agulhas Current along the Indian Ocean coast to the east (Griffiths et al. 2010; Figure 1a). There is a transition zone on the south coast where the Agulhas Current moves offshore (Figure 1a) following the continental shelf as it widens and forms the Agulhas Bank (Lutjeharms et al. 2000). The waters between Cape Agulhas and Cape Point are considered the region of overlap between the west- and south coast oceanographic regimes (Griffiths et al. 2010). The inshore component of the Benguela Current is characterized by coastal wind-driven upwelling (Figure 1a) with temperatures ranging from ~10°C to 18°C (Shannon et al. 1992). The intense upwelling on the west coast results in high biological productivity, which supports very large fish stocks (Griffiths et al. 2010). The warm Agulhas Current brings nutrient-poor tropical waters along the east coast (James et al. 2013; Figure 1c) with temperatures varying from 20° to 28°C (Griffiths et al. 2010; Schumann 1987).

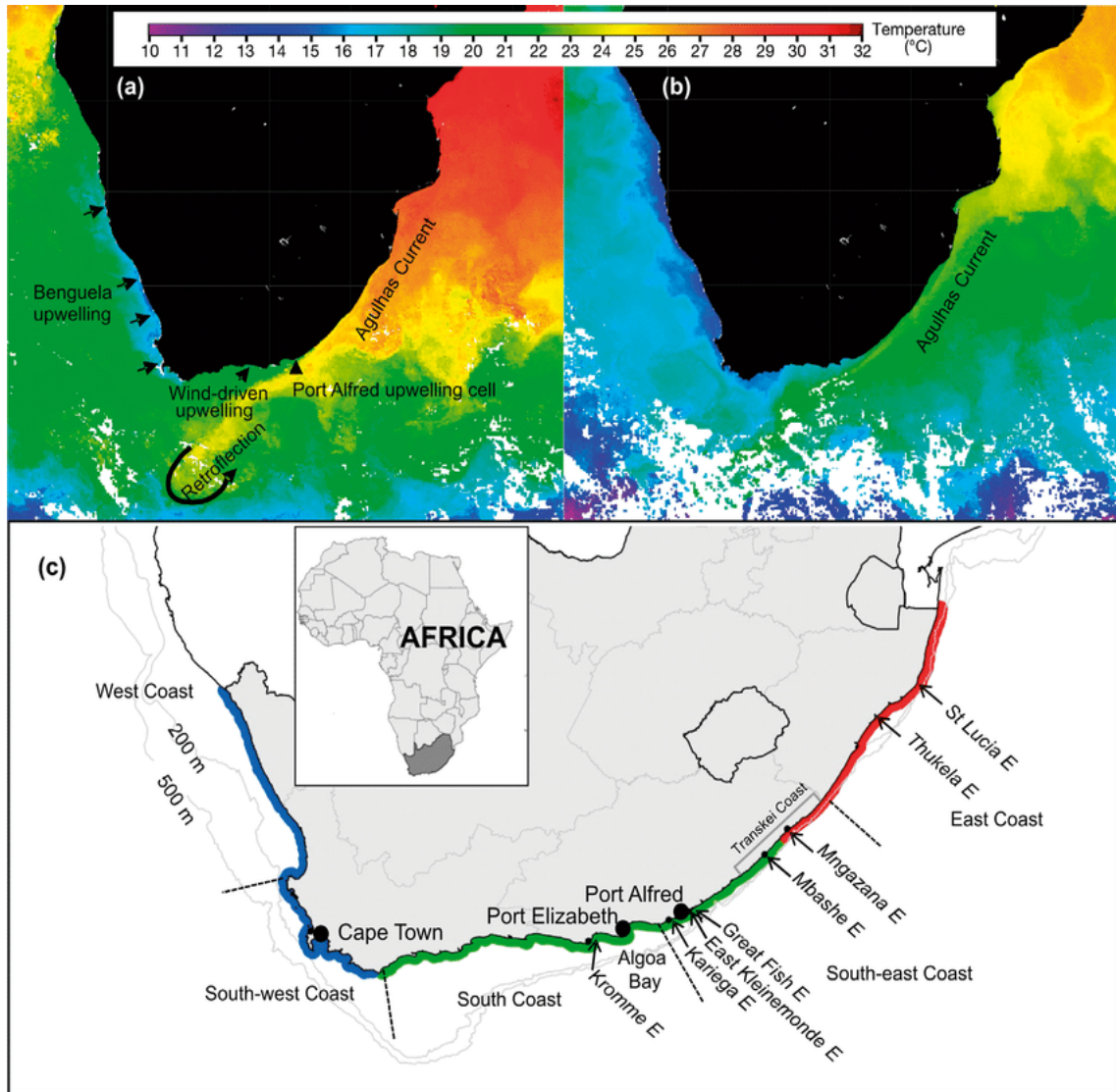


Figure 1. (a) Average sea surface temperature, derived from satellite imagery, showing the coastal upwelling region of the cool Benguela Current on the West coast of Africa (shown in blue), the warm Agulhas Current flowing down the East coast (shown in red) and the retroflection zone at the southern tip of the continent during summer, and (b) winter. (c) A map depicting the different biogeographic regions of the South African coastline, illustrating the cool-temperate waters of the West and South-west coast (blue), the warm-temperate waters of the South and South-east coast (green) and subtropical East coast (James et al. 2013).

Changes in sea surface temperatures have been recorded in the warm-water Agulhas Current, which has been reported to have warmed by as much as 0.46°C (Lloyd et al. 2012) and 1.5°C since the 1980's (Rouault et al. 2009). In contrast, the southern Benguela has experienced an increase in both the frequency and intensity of upwelling, caused by altered precipitation patterns and wind shifts which has resulted in a net cooling (Rouault et al. 2010). Changes in water temperature as a result of climate change are predicted to affect the distribution pattern of species as the preferred environmental conditions which characterise their current habitats are changing. Even small increases in water temperature (possibly as little as 2°C) could result in the disappearance of the tropical vs. subtropical barrier between the two coasts of South Africa (MacLeod 2009).

On the South African coastline, changing environmental conditions and particularly temperature, are suggested to be the limiting factor in species establishment. For example, kelp species (*Ecklonia maxima*) which previously dominated waters off the west coast have recently been recorded to spread approximately 70 km eastwards, past Cape Agulhas to inhabit the now cooler inshore waters of the south coast (Bolton et al. 2012), while the range of the warm-water associated indigenous brown mussel (*Perna perna*) has declined on the intertidal rocky shore as the species shifts eastwards away from the cooling False Bay (Mead 2011).

Environmental factors influencing the range of cetacean species

The most likely direct effect global climate change will have on marine mammals is the shifting of their distribution ranges (Learmonth et al. 2006) as animals track their preferred environmental conditions, potentially altering their local abundance (Harwood 2001). These specific distribution ranges are considered critical habitats for their survival and reproduction (Harwood 2001).

Environmental factors which influence the range of cetaceans include water temperature (Gaskin 1968), depth (Cañadas et al. 2002) and those factors which affect their prey's distribution, such as productivity. Of these factors, water temperature is thought to have the biggest influence on the geographic ranges of cetaceans (Kaschner et al. 2011) by causing

either range contraction or expansion (MacLeod 2009). The southern tip of Africa acts as a dispersal barrier between the South Atlantic and southern Indian oceans, each of which is home to markedly different dolphin species (Best 2007). Warmer waters flowing around the barrier may cause the sporadic movement of tropical cetaceans from one ocean basin to the other (Best 2007). Temperature also affects various prey species such as fish and plankton which rely on, and respond to, a specific set of environmental conditions. Changes in the abundance and/or distribution of prey species in response to sea temperature may affect the distribution range of their cetacean predators (Learmonth et al. 2006; Simmonds and Isaac 2007) or alter the grouping behaviour of dolphins as a result of decreased or changed prey availability (Lusseau et al. 2004). Additional to SST having effects on prey species, it may also influence competition between ecologically similar cetacean species (Learmonth et al. 2006; MacLeod et al. 2008)

As a result of changing temperatures, those species which readily respond to variations in their environment are predicted to change their distribution ranges in order to stay within the specific environmental conditions which represent their ecological niche. This concept is referred to as niche conservatism (Wiens and Graham 2005). Niche conservatism can be described as the tendency of a species to retain the desirable conditions of its fundamental niche over time. Species which have the ability to adapt to the changing climate and consequently shift their distribution ranges in response to changes in the environment are less likely to be negatively impacted (Wiens and Graham 2005). On the other hand, those species which cannot adapt or shift ranges due to (1) barriers (i.e. species unable to track their preferred temperatures and colonise otherwise suitable habitats due to the presence of external barriers; Simmonds and Isaac 2007), or (2) habitat degradation (i.e. species whose geographical ranges are restricted to polar zones; MacLeod 2009).

Another group of species highlighted as being at high risk are those in eastern boundary current upwelling zones (Bakun et al. 2015) like the Benguela ecosystem off the west coast of South Africa. Species in this range are surrounded by a barrier of water which is warmer than that of their preferred range which makes them vulnerable to increasing sea temperatures as these increases will likely reduce the extent of the cooler water. The biggest impact of climate change on fish species is thought to be the mismatch between food availability and the larval and juvenile phase (Grémillet et al. 2008) as warmer waters can reduce plankton production

(a key food source; Bakun et al. 2015) and thus negatively impact the survival and recruitment of juvenile fish (Grémillet et al. 2008). In the northern Benguela ecosystem, a significant decline in catches of key fish species has been apparent over a three-decade period (Heymans et al. 2004). The intrusion of warmer waters from the Angolan Current down the west coast of Africa (known as the 1995 Benguela Niño), resulted in high fish mortalities and the subsequent starvation of adult seals in Namibia (Gammelsrød et al. 1998). Further anticipated effects on eastern boundary upwelling systems include changes in the intensity of upwelling as well as the poleward expansion of upwelling cells in both hemispheres. Although enhanced upwelling could result in increased nutrient enrichment, it could also lead to a reduction in phytoplankton production within an upwelling cell as mixing of the water column, driven by wind, becomes deeper (Bakun et al. 2015).

Those cetacean species whose movements are restricted by the presence of physical barriers, fall subject to habitat degradation or reside in an eastern boundary current system are predicted to be greatly affected by global climate change (GCC) as their ranges are subject to reduction (MacLeod 2009) and thus these cetaceans may face the risk of extinction (Thomas et al. 2004; Wiens and Graham 2005). Extinction risk assessments (Thomas et al. 2004) predict that species with the smallest ranges will face the greatest risk of extinction (as explained by the relationship between species' range and population size), which has implications for the conservation status of species. It is therefore critical to know the geographical area a species occupies in order to understand, and consequently predict, whether its range is likely to decline in response to GCC (MacLeod 2009).

Project goals

The present study aims to gain a better understanding of the fine scale distribution of several cetacean species which are frequently observed along the south-western Cape of South Africa. Eight cetacean species are regularly seen in the area, of which five are dolphin species and three are whales. The project goal was thus to record sightings data of these eight species to better understand and improve our knowledge of their current distribution. Data were first collected from dedicated boat-based surveys to define the spatial occurrence of each species within the waters around the southern Peninsula, specifically between Table Bay and the Cape

Hangklip region, as will be explained in Chapter two. These data were then used to identify areas of suitable habitat through predictive habitat modelling using the occurrence data recorded for each species and using a range of explanatory variables to describe the modelled habitats (Chapter three). Finally, the current distribution of species is discussed in the face of a changing climatic environment.

Cetaceans in South Africa

The South African waters are home to a high diversity of cetacean species (Elwen et al. 2011) with over 40 species occurring in the region (Best 2007). This high diversity is largely owing to the unique oceanographic features which characterise the west and east coast, each associated with its own species, with an area of overlap between St Helena Bay and Cape Agulhas (Findlay et al. 1992). Apart from southern right whales (*Eubalaena australis*), there have been no long term, year-round studies focused on the distribution and seasonal movement patterns of the cetacean species regularly seen off the south-western region of the coast (review in Elwen et al. 2011). The most recent study describing the spatial and temporal distribution patterns of several cetacean species is Vinding et al. (2015), providing the first long term data for the south-western Cape. The present study focuses on eight species of cetacean which are commonly encountered off the Western Cape, including five dolphin species – four of which have their distribution ranges end within this region (Best 2007) and three whale species.

Dusky dolphin

Dusky dolphins (*Lagenorhynchus obscurus*) were first described from the 'Cape of Good Hope' (Best 2007). The species occurs exclusively within the Benguela ecosystem within the Southern African subregion and is sympatric with the Heaviside's dolphin throughout the majority of the Benguela. However, their range extends much farther north, south and offshore than that of the Heaviside's dolphin's (Findlay et al. 1992). They are relatively small in size (~1.90 m) with little differentiation between male and female body size and can be distinguished from Heaviside's dolphin by their curved (rather than triangular) dorsal fin and

white coloured patches on the flank (Best 2007). They can be seen in groups between two to 800 individuals, with a mean of 35 animals in a group (Findlay et al. 1992). Dusky dolphins are generalist predators, feeding on a wide variety of prey including hake, mackerel and cephalopods (Sekiguchi et al. 1992). As suggested by Best (2007), these dolphins can switch their feeding behaviour between surface-, nearshore- and more pelagic schooling fish. They have not been observed to follow the same inshore-offshore movement patterns of Heaviside's dolphin, but it is suggested that their movement possibly tracks local upwelling, with large groups only being observed close to areas characterised by strong upwelling (Elwen et al. 2010). This suggests distribution patterns may be coupled to prey availability and areas of high productivity. Dusky dolphins are subject to low levels of bycatch by fisheries and there have been several reports of deaths due to net entanglement (Best 2007). Their population estimates in South Africa are currently unknown, and they are listed as 'Data Deficient' by the IUCN (www.iucnredlist.org).

Heaviside's dolphin

The Heaviside's dolphin (*Cephalorhynchus heavisidii*) is one of the smallest dolphin species globally (reaching a maximum body length of 1.75 m) with an unmistakable blue-black and grey colour pattern. Heaviside's dolphins are endemic to the Benguela ecosystem of the west coast of South Africa, Namibia and southern Angola (Best 2007) with a near continuous distribution in the inshore environment along the coast (Elwen et al. 2010). The southernmost limit of their distribution range is thought to be Cape Point, however, there have been two sightings reported to the east of False Bay (Best 2007, Vinding et al. 2015), although these are considered vagrants due to their rarity. Heaviside's dolphins inhabit coastal waters from the breaker line up to 100m of depth (Findlay et al. 1992) and when close to shore, can often be seen at the exposed end of bays characterised by larger swell presence (Elwen et al. 2010). They feed on a variety of prey, including goby (*Sufflogobius bibartus*) and mackerel (*Trachurus trachurus*), with shallow water hake (*Merluccius capensis*) comprising approximately 50% of their diet (Sekiguchi et al. 1992). Heaviside's dolphins have been observed to show clear patterns of inshore-offshore movements related to feeding on juvenile shallow water hake that rise to closer the water surface at night (Elwen 2008). These findings suggest that there

is a clear link between the distribution pattern of the dolphins and that of their prey. It is possible that the offshore feeding preference of Heaviside's dolphins, allows for the co-occurrence in nearshore waters between Heaviside's and dusky dolphins (Heinrich et al. 2010). They generally appear in small groups, comprising an average of three individuals, but can be seen in groups of up to 10 individuals (Best 2007). Locally Heaviside's dolphins are currently listed as 'Least concern' (Gopal et al. 2016).

Short-beaked common dolphin

Common dolphins (two morphotypes: short- and long-beaked; Cunha et al. 2015) have distinctive golden-yellow and light grey colour markings in the shape of an hour glass on the thorax and flanks. Sexual dimorphism is distinguishable through size, with adult males reaching maximum body lengths of 2.54 m and adult females 2.22 m (Best 2007). Short-beaked common dolphins (*Delphinus delphis*; Cunha et al. 2015), from here onwards referred to as common dolphins, is a pelagic dolphin species (Saayman et al. 1972) but can be found inshore along the southern African south coast from St Helena Bay in the west to Richards Bay in the east (Findlay et al. 1992). They take a variety of prey which include mackerel and squid, and the long-beaked morphotype (*Delphinus capensis*) predominantly feeding on pilchard shoals (Best 2007; Cockcroft and Peddemors 1990). These dolphins are often seen in large feeding aggregations with other marine mammals during the 'sardine run' – a natural event which occurs annually on the South African south-east coast when large schools of sardine migrate south to east along the coast during austral winter (Best 2007, van der Lingen et al. 2010). Common dolphins are often seen in large groups of up to 10 000, with an average of ~600 animals per group and are generally highly vocal (Best 2007). Regionally common dolphins are listed as a species of 'Least Concern' (Plön and Cockcroft 2016).

Indian-Ocean humpback dolphin

In South Africa, the most westerly published record of occurrence of Indian-Ocean humpback dolphins (*Sousa plumbea*) is from a skull found in Muizenberg, False Bay, and it is suggested that the further extension of their range is limited by the cooler waters of the Benguela

current (Findlay et al. 1992, Best 2007). Previous sightings data suggest that Agulhas is the western limit to the humpback dolphin range (Findlay et al. 1992). However, Best (2007) proposes an extension of their range due to several encounters recorded from Danger Point. It is unclear whether this expansion is a result of poor observer effort in the past, or an increase to the western limit of their current distribution range. Humpback dolphins have an unmistakable fleshy hump on their back from where the dorsal fin protrudes (Best 2007). They are a large dolphin species with males and females reaching body lengths of up to 2.7 m and 2.49 m respectively. The group size of humpback dolphins seems to be quite variable, ranging from frequent observations of solitary individuals to groups comprising of up to 25 animals (Best 2007). Humpback dolphins frequently occupy the shallow inshore waters of the coast and are often subject to boat disturbance (Karczmarski et al. 1997). They tend to avoid boats by taking long dives or changing direction away from the boats (Karczmarski et al. 1997), as seen in Algoa Bay where humpback dolphins are subject to increased anthropogenic activities (Koper et al. 2015). Indian-Ocean humpback dolphins appear in relatively low densities throughout their range, with a discontinuous distribution (Best 2007). Their current global and regional Red List status is listed as 'Endangered' (Braulik et al. 2017, Plön et al. 2016). The humpback dolphin population off the Cape south coast is estimated less than 300 individuals (Vermeulen et al. 2017) and populations off the south coast are suggested to be strongly isolated from those found farther east (James et al. 2015; Vermeulen et al. 2017).

Indo-Pacific bottlenose dolphin

Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) are distinguishable from common bottlenose dolphins by their longer beaks and light grey blaze running from the side of the head along the length of the body (Best 2007). Body length can reach up to ~2.5 m, with little sexual dimorphism between males and females. Their range is sympatric to that of the Indian Ocean humpback dolphin along the southeast coast (Reisinger and Karczmarski 2009). Several genetically distinct subpopulations can be found from False Bay right up the east coast to southern Mozambique (Best 2007), with seasonal peaks in some areas of the south coast during summer and spring (Vinding et al. 2015). They can be seen in variable group sizes, with a mean estimate of 20 to 50 individuals (Best 2007) often within 2 km of the coast (Vinding et

al. 2015). Low re-sighting rates from a mark-recapture study performed in Algoa Bay (Reisinger and Karczmarski 2009) suggests an “open” population of bottlenose dolphins, with individuals frequently leaving and entering the bay, suggesting that they are part of the much larger population inhabiting an extensive proportion of the South African coastline. Bottlenose dolphins are subject to bycatch in anti-shark nets (Cockcroft et al. 1990) and direct and indirect takes by fisheries (Razafindrakoto et al. 2004). They are currently listed as ‘Vulnerable’ in South African waters (www.iucnredlist.org).

Southern right whale

Southern right whales (*Eubalaena australis*) are easily distinguishable from other large whale species by the distinct wart-like callosities on their heads and the lack of a dorsal fin (Best 2007). Their characteristic V-shaped blows can often be identified at sea when the animals rest on the water surface, which is common behaviour for this species (Best 2007). Southern right whales predominantly occur on the south coast of South Africa, usually in higher abundances between Walker Bay and St Sebastian Bay (Best 2000; 2007), with a peak between June – January (Vinding et al. 2015). In the study area, right whales can be encountered regularly, although usually in lower abundances. During austral winter and spring, southern right whales migrate from their southern feeding grounds to the South African coast, with the purpose to breed and calve within shallow, inshore habitats along the coast (Best 2000). Right whales are believed to predominantly feed on krill and copepods (Best 2007). Although it is suggested that animals do not feed in the coastal waters during their breeding season (Best and Schell 1996), southern right whales are increasingly observed feeding on the west coast during early summer months and it is proposed that the high productivity in this region is becoming a seasonal feeding ground for migrating southern right whales (Findlay et al. 2017). Other than large aggregations of feeding individuals, southern right whales are generally encountered in small groups of 1-10 animals, and mother-calf pairs can frequently be observed during their breeding season on the South African coast (Best 2000; 2007; Vinding et al. 2015). In the southern hemisphere, southern right whales were the first species targeted by commercial whaling, which inevitably led to a sharp decline in their population size (Best 2007). International protection for this species was implemented around

1935, which allowed the onset for recovery. Southern right whales are currently listed as 'Least Concern' in Southern Africa (Peters and Barendse 2016).

Humpback whale

Humpback whales (*Megaptera novaeangliae*) are recognised by their distinct dorsal fins, long pectoral fins and 'knob-like' bulges on their rostrum. The most characteristic feature of humpback whales are their tail flukes, which differ from all other whale species; the trailing edge of their flukes are extensively scalloped compared to the more gentle curve of other species (Best 2007). Humpback whales follow the same migratory pattern during the austral winter season when they migrate from higher summer feeding latitudes to the lower winter breeding latitudes. Their distribution along the South African coast during winter ranges from the west to east coast, with their proposed breeding destinations being Angola on the west coast, and Mozambique off the east coast (Best 2007). Humpback whales are known to feed off Cape Columbine (Best 2007), and it is suggested that the high productivity of the southern Benguela attracts large aggregations of feeding groups into the area (Findlay et al. 2017). Apart from the large feeding aggregations, humpback whales are generally encountered in groups between 1-5 individuals, however, on their breeding grounds, groups can consist of up to 15 animals, some of which are often male escorts accompanying mother-calf pairs (Best 2007). Humpback whales were the main target species during whaling in the early 1900's, when a significant number of whales were taken from Congo to Mozambique, which led to the collapse of stocks on both sides of the African coast (Best 2007). International protection of the species resulted in an increase in population size; humpback whales are currently listed 'Least Concern' regionally (Barendse and Carvalho 2008).

Bryde's whale

Bryde's whales (*Balaenoptera brydei*) can be identified by the distinctive ridge running along either sides of the animal's rostrum (Best 2007). Three separate populations of Bryde's whales are believed to occur in the subregion, one of which is resident to the Agulhas Bank (Best 2007). Unlike migratory whale species, Bryde's whales do not migrate to summer feeding

grounds in higher latitudes, and instead only make smaller seasonal movements up the coast, following their prey. They are year-round opportunistic feeders (Best 1977) which take a variety of prey, but predominantly feed on pelagic fish (Best 2007). Findings from whaling operations suggest that feeding on the west coast predominantly occurs during spring and summer months (Best 2007). On the east coast a peak in encounters are generally recorded in winter when animals follow the movement of fish during the winter sardine run (Best 2001; Penry 2010). These findings are supported by Vinding et al. (2015) which show a seasonal peak in Bryde's whale encounters on the south coast during autumn, immediately followed by a drop in numbers during winter. Bryde's whales are most often encountered in groups consisting of 1-2 animals, and individuals partaking in feeding groups are generally more spread out (Best 2007) compared to the tightly associated groups which are frequently observed in species such as humpback whales. The South African inshore population of Bryde's whales is currently listed as 'Vulnerable' (Penry et al. 2016).

CHAPTER 2: SPATIAL DISTRIBUTION OF CETACEANS AROUND THE SOUTHERN PENINSULA

ABSTRACT

Knowledge on species distribution plays a key role in the identification of areas of biological significance and conservation importance. Certain species are able to change their current distribution in response to biotic and abiotic changes. Global climate change can affect cetaceans through bringing about shifts in their distribution ranges as they respond to changing oceanographic conditions such as increases in water temperature. The waters off South Africa are home to a number of whale and dolphin species, several of which have their distributional ranges end around the Cape Peninsula. The aim of the present study was to determine the distribution of eight cetacean species frequently encountered in the southwestern Cape. Dedicated boat-based surveys resulted in detections of five dolphin species; dusky dolphins (*Lagenorhynchus obscurus*), Heaviside's dolphins (*Cephalorhynchus heavisidii*), common dolphins (*Delphinus delphis*), Indian Ocean humpback dolphins (*Sousa plumbea*) and bottlenose dolphins (*Tursiops aduncus*); and three whale species; southern right whales (*Eubalaena australis*), humpback whales (*Megaptera novaeangliae*) and Bryde's whales (*Balaenoptera brydei*). Dusky dolphins and Heaviside's dolphins were frequently and exclusively encountered west of Cape Point. Humpback dolphins were encountered off sandy beaches in False Bay, and despite being known to occur in the area, bottlenose dolphins were only seen twice. Bryde's whales were predominantly seen in False Bay, whereas the migratory humpback whales and southern right whales were encountered throughout the study area. The high encounter probability of Bryde's whales in False Bay indicates the importance of the area as a suitable habitat for this non-migratory species. Based on the present findings, the southern range limit of Heaviside's dolphins around Hout Bay is confirmed, suggesting a combination of water temperature and food availability as the limiting feature. Furthermore, the present study shows a clear westward extension of humpback dolphins into False Bay, likely as a result of increasing water temperatures providing suitable habitats. The likely effects of changing temperatures on species' distribution ranges are discussed, especially for those species whose distribution is limited by water temperature.

INTRODUCTION

Increases in water temperature as a result of global climate change are predicted to continue throughout most of the world's oceans (Learmonth et al. 2006; Levitus et al. 2000). A linear warming trend in ocean temperatures is apparent at most latitudes, with the exception of the equatorial region and the southern hemisphere tropics which are experiencing subsurface cooling. Changes in the oceans heat content have predominantly occurred within the upper 700 m of the world's ocean (Levitus et al. 2005). These changes fall well within the preferred depth range of many marine species, including cetaceans. The most likely direct effect global climate change will have on marine mammals is the shifting of their distribution ranges to track optimal habitats (Learmonth et al. 2006). Species which strongly respond to changes in their immediate environment are likely to adapt by changing their distribution to retain the desirable conditions within their fundamental niche (Wiens and Graham 2005). Species which are geographically restricted by physical barriers (e.g. land masses) or degrading habitats are of highest concern as such barriers inhibit them from adapting their behaviour and shifting their distribution ranges (MacLeod 2009; Simmonds and Isaac 2007). A group of special concern are those species which occur in temperate eastern boundary currents, as they are surrounded by bodies of water which are warmer than that of their current range. The Benguela Ecosystem off the west coast of South Africa is one such example. Cetaceans in this range are surrounded by a barrier of warmer waters and are subject to a reduction in their range as water temperatures increase as a result of climate change (MacLeod 2009; Thomas et al. 2004). Heaviside's dolphins (*Cephalorhynchus heavisidii*) are endemic to the Benguela Ecosystem and may face the risk of extinction if their preferred climatic range shrinks. In contrast, species which prefer more tropical waters along the South African east coast are expected to expand their ranges southward in response to rising temperatures (Griffiths et al. 2010).

The Benguela Current Large Marine Ecosystem is characterised as an eastern boundary upwelling system primarily driven by longshore winds (Armstrong et al. 1987). The Benguela is considered a unique upwelling system as it is bounded by warm water currents on both the equatorward and poleward sides, the Angolan Current and Agulhas Current respectively (Shannon et al. 1992).

The present study was conducted at the southern tip of the Benguela Current where the cooler, nutrient rich waters of the South African west coast meet and mix with warmer, nutrient poor waters of the Agulhas Current. Water temperatures between these two currents differ markedly (Figure 2). Temperatures close to shore in upwelling regions of the west coast range from approximately 10°C to 18°C in spring and summer (Shannon et al. 1992), whereas the more tropical water temperatures of the Agulhas Current fluctuate between 20°C to 28°C (Lutjeharms 1998). Anticyclonic eddies at the retroflection point of the Agulhas Current occasionally transports waters from the Indian Ocean into the cooler Benguela system (Shannon 1985), resulting in a thermal gradient (Armstrong et al. 1987). Some of the strongest thermal gradients in the southern Benguela can be found at the Cape Peninsula (Dufois and Rouault 2012; Hutchings et al. 1984; Figure 2). The current study area lies within the stretch of waters between the Cape Peninsula and Cape Agulhas, which is the transition area between the two oceanographic regimes (Figure 1 a,b).

With the exception of southern right whales, there have been no long term scientific studies investigating the distribution of cetaceans known to occur in the vicinity of the Cape Peninsula, from Table Bay in the North to False Bay and Cape Hangklip in the south-east (Best and Scott 1993; Elwen et al. 2011). Findlay et al. (1992) describes the geographical range and overlap of small odontocete cetaceans found between St Helena Bay and Cape Agulhas, using scientific surveys, opportunistic sightings and strandings data. Best (2007) gives a more recent, detailed description of the known distribution ranges, although at a very broad scale. The distribution and movement patterns of dusky dolphins and Heaviside's dolphins were described from a three-year study for the west coast North of Table Bay (Elwen et al. 2009), and southern right whale presence along the south coast were recorded from False Bay extending eastwards (Elwen and Best 2004). The most recent and relevant study describing cetacean distribution in an area near the current study site is by Vinding et al. (2015), approximately 150 km east of the current study area. Their study used opportunistic collected data over a ten-year period to assess the spatial and seasonal occurrence of cetaceans encountered between Danger Point and Quoin Point. It is clear that very little research has been focussed around the Peninsula, and that little survey data have been collected on the cetaceans that occupy these waters.

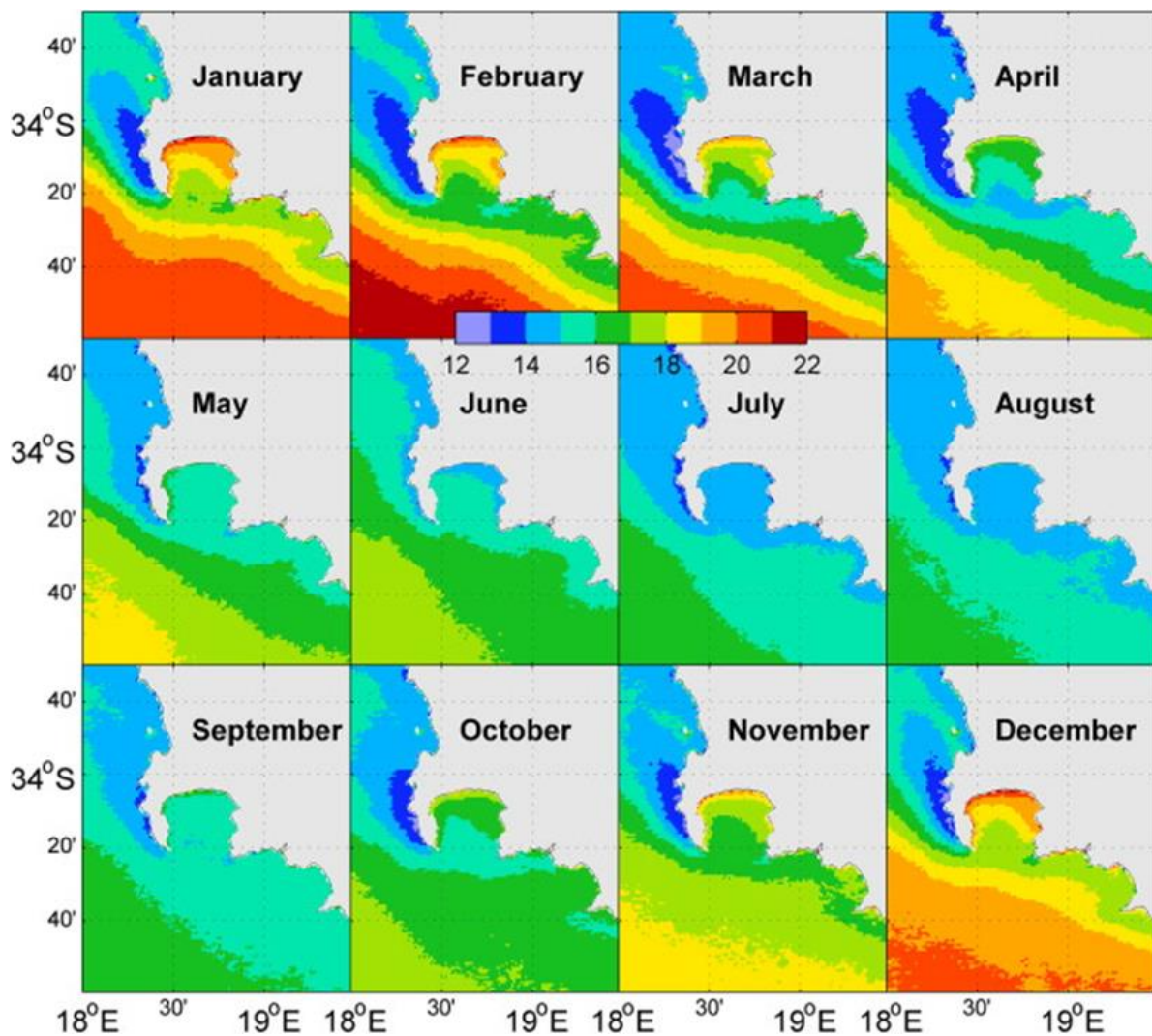


Figure 2. Monthly sea surface temperature (°C) around the southern Peninsula and False Bay in the south-western Cape of South Africa (Dufois and Rouault 2012).

In the face of a changing environment it is vital to be familiar with the current distribution of a species. Knowledge of species distribution is key for identifying areas of conservation importance and potential establishment of marine protected areas (Cañadas and Hammond 2008), and to assess and predict whether ranges are likely to decline or expand in response to global climate change (MacLeod 2009). The aim of this study was to determine the current distribution of several cetacean species known to occur around the Cape Peninsula, by means

of dedicated boat-based surveys. Dedicated boat-based surveying is a useful method for observing the spatial and temporal trends of a species current distribution (Mann 1999) and serves as a valuable platform for species abundance estimates and photo-identification studies (Aragones and Marsh 1997). Dedicated surveys allow for stratified search effort to be conducted within an area, and gaining regional information on the distribution, abundance and habitat utilisation of species (Aragones and Marsh 1997; Dawson et al. 2008).

This chapter primarily concentrates on the spatial distribution of cetaceans found within the study area. It also provides a brief overview of certain environmental factors which often influence the probabilities of observing marine mammals at sea. Survey effort is calculated as measures of time and distance, and the intensity of effort throughout the area is illustrated. The behavioural component of this research is included, as well as effort corrected species-specific sighting rates.

METHODS

Data collection

Data were collected from dedicated and occasional opportunistic surveys. Scientific surveys follow predetermined track lines and strict protocols for collecting data to minimize any bias. Surveys were carried out during daylight hours with a minimum of three experienced observers on board. Each survey generally lasted approximately six hours and covered an average distance of 60 kilometres (km) a day. The tracks were designed to search as much of the study area as possible and typically included coverage of inshore (<2 km from shore) and farther offshore waters (up to 12 km from shore). The tracks were continuous (in contrast to transect lines) and started and ended at the same harbour. Predetermined scientific surveys can often be time consuming and trained staff and expensive equipment is necessary (Dawson et al. 2008). An alternative method is using platforms of opportunity for similar data collection. These data can be collected from multiple platforms including commercial fishing and shipping vessels, cruise ships or tour operators such as whale watching boats. Although data collected opportunistically can allow for larger sample sizes or more frequent collection of data, such vessels do not follow predetermined track lines but rather random courses or

repeatedly visit areas where animals are known to occur frequently. In the present study, data were collected mainly from dedicated small boat surveys conducted in the waters off the Cape Peninsula, with the primary focus on False Bay and Table Bay area, with a few opportunistic trips from a whale watching vessel operating in False Bay.

The project goal was to search as much of the focus study area as possible to ensure maximum spatial coverage. However, as a result of unpredicted weather, limited fuel on board, and dedicated launch sites, survey effort was higher close to the harbours, and within the bays. Data were collected from multiple boats, the most frequently used vessels being ~ 6 m rigid inflatables with outboard motors. Survey tracks were recorded using a Garmin eTrex GPS, which recorded the position of the boat once every minute. The average searching speed was around 7 knots, alternated with multiple point-search stops, to maximise encounter probability. Upon detection of animals, data on species identification, GPS location and group size were noted immediately. Group composition was assessed several times during an encounter, noting any individuals and subgroups leaving and/or joining the focal group, which resulted in estimates of minimum, best and maximum group size. Data collection also included photographic-identification (quality photographs of dorsal fins), general behaviour of the focal group and the presence of calves and juveniles. During behavioural observations, the activity of animals was recorded every three minutes, or when sudden changes in behaviour were noted. General patterns of behaviour were categorised as surface feeding, socialising, milling, resting or travelling based on the behaviour of the majority of the group at the time of assessment. This information was collected to explore how the waters off the Cape Peninsula are utilised by each species, to potentially identify biologically significant areas within the study region. Acoustic recordings were also collected during encounters but are not included in this study.

Environmental conditions, such as swell and sea state, can influence the probability of an observer to spot animals. Strong winds resulting in choppy water or large swell can easily disguise a whale blow or surfacing of a dolphin. Weather conditions on survey days were recorded at the start of the survey and updated at the beginning and end of every encounter, or when any sudden changes in conditions were noted. Environmental parameters collected during surveys included cloud cover, measured as a value out of 8, ranging from clear (0) to fully overcast (8), Beaufort sea state, swell (in meters), wind speed (in knots) and wind

direction. The logged data were used to quantify the probability of an observer spotting a whale or dolphin, defined as 'sightability', ranging from very limited visibility (1) to perfect spotting conditions with flat seas and clear skies (5). These data were then compared to encounter frequency to assess the influence of local weather conditions on the success of spotting cetaceans.

Calculating search effort and sighting rates

The study area was divided into square kilometre (1 km²) grid cells, to quantify search effort throughout the study period (Cañadas and Hammond 2008; Melly et al. 2018). Firstly, the search track, consisting of a series of points recorded every minute, was converted to a line using the 'Points to Line' tool in ArcGIS (ESRI Corporation, ArcMap 10.4) and the effort grid was generated using the 'Create Fishnet' tool in the Data Management Toolbox. The converted tracks were then 'intersected' to the grid to calculate the sum of track lengths within each one square kilometre cell. Two methods of measurement were used to represent the effort per grid cell; the total distance (kilometres surveyed per cell) and total time (minutes surveyed within each cell) were calculated for all 'on effort' and 'search effort' tracks. The latter includes search only tracks; search effort was paused as soon as animals were spotted and continued after completing an encounter (either when data collection was considered to be complete or the animals were lost). On the other hand, 'on effort' tracks include the time spent searching for cetaceans, all animals encountered during surveys (including non-target species like sharks), and the time spent with animals. Separate groups of animals were frequently observed while working with a group already. For example, it was especially common to see a whale in the distance while doing stationary acoustic work on a focal group. The intensity of effort was therefore calculated for both 'on effort' and 'search' tracks.

Sighting rates (as a measure of distance) and frequency (as a measure of time) were used to calculate the number of encounters recorded per square km grid cell, corrected for effort intensity, to describe the distribution patterns. Sighting rates were calculated for each species, and each grid, across the entire survey area and study period, to illustrate areas with highest effort and sightings/km². To determine areas with the highest number of overall detections,

all cetacean encounters were overlaid with the generated grid, to calculate the number of sightings recorded for each square km throughout the study area.

RESULTS

Overview of environmental factors

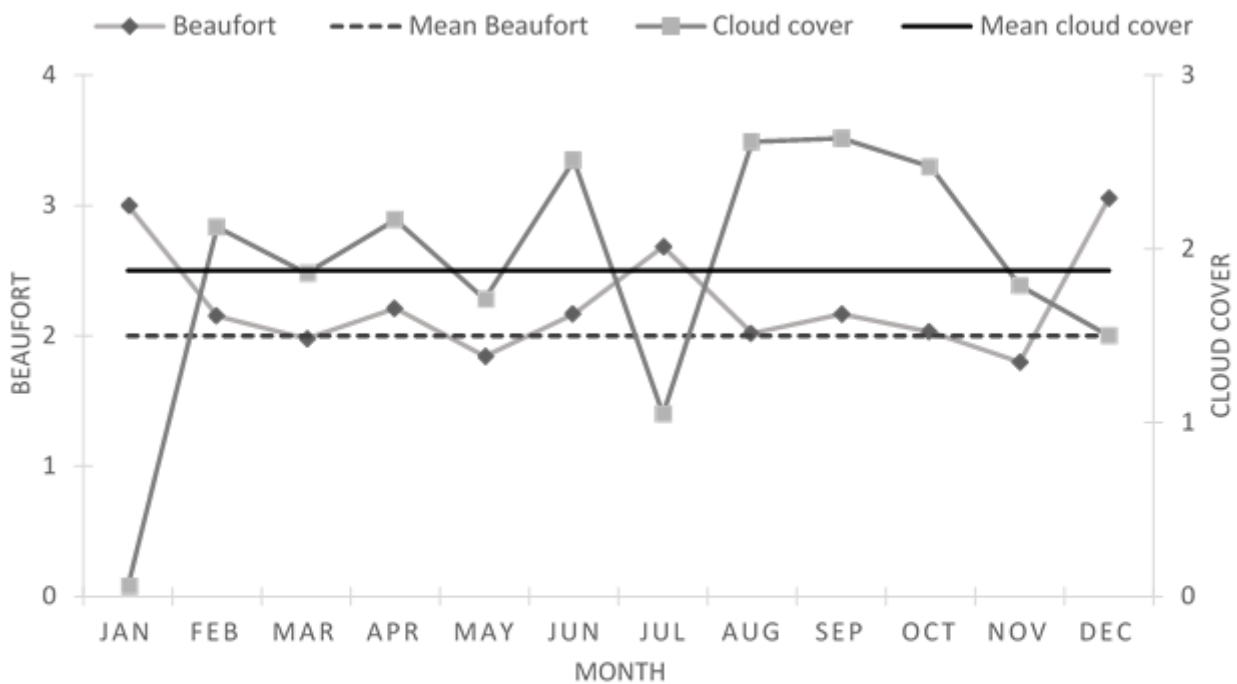


Figure 2.1. Average monthly Beaufort sea state and cloud cover recorded throughout the duration of the study period. Dashed lines represent the overall mean sea state (Beaufort 2) and cloud cover (2/8).

A mean sea state of Beaufort two was recorded throughout the study period, with a higher average sea state during summer (December and January; Figure 2.1). The mean cloud cover throughout the study period was 2/8 (very few clouds present; Figure 2.1).

Encounter probability was positively correlated to ‘Sightability’ (Figure 2.2a). Encounter probability was negatively correlated to Beaufort levels (Figure 2.2b), with sightings severely decreasing from sea state three and above

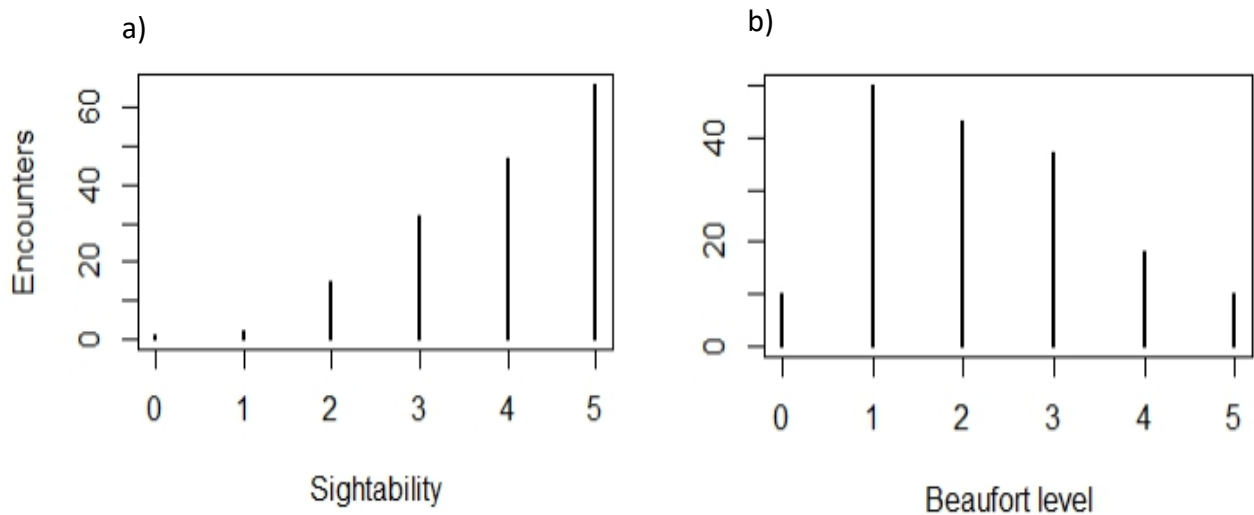


Figure 2.2. Animal sightings compared to (a) sightability and (b) Beaufort sea state. Good sighting conditions is equal to a value of 5. Beaufort 0 represents glossy surface conditions.

Search Effort

Between February 2015 and April 2017, a total of 61 dedicated boat-based survey trips were conducted in False Bay and Table Bay (Figure 2.3), spending 283 hours at sea and conducting just over 3 432 km in track. Of this, a total of 267 hours was spent “On effort”, covering 3 187 km. “Search only” effort totalled to 179 hours and 3 123 km of searching for cetaceans.

Highest search effort occurred in the western and northern part of False Bay, between Cape Point and Strandfontein; and centred around Hout Bay on the West coast (Figure 2.4). Launch sites would typically be from Simon’s Town harbour (34° 11’ S, 18° 26’ E) and Hout Bay harbour (33° 55’ S, 18° 25’ E). High survey effort was therefore concentrated around these areas, and closer to the coastline (Figure 2.4).

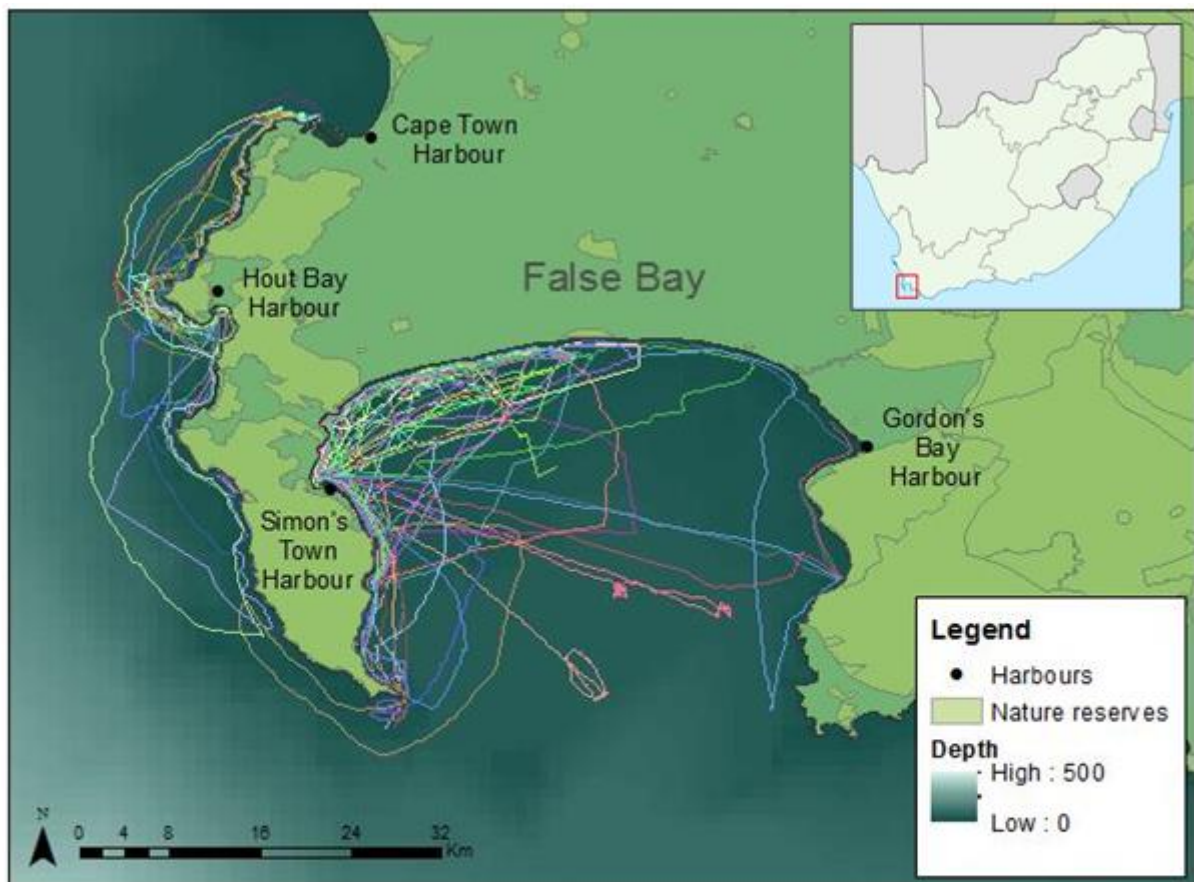


Figure 2.3. Map of study area, showing all search tracks completed in False Bay and Table Bay during the study period. Launch sites were from Simon's Town harbour and Hout Bay harbour. Colour lines represent the individual boat survey tracks.

The intensity of effort throughout the study area is illustrated as a measure of time (Figure 2.4) and distance (Figure 2.5). Maximum time spent in one 1 km² area totalled to 284 minutes (>four hours, Figure 2.4a), with effort being the highest around launch sites. The maximum distance covered within one grid block was 40 km of search track (Figure 2.5b). Both methods used for presenting the measure of effort (time spent surveying and distance covered) presented similar patterns of concentrated effort centred around the harbours.

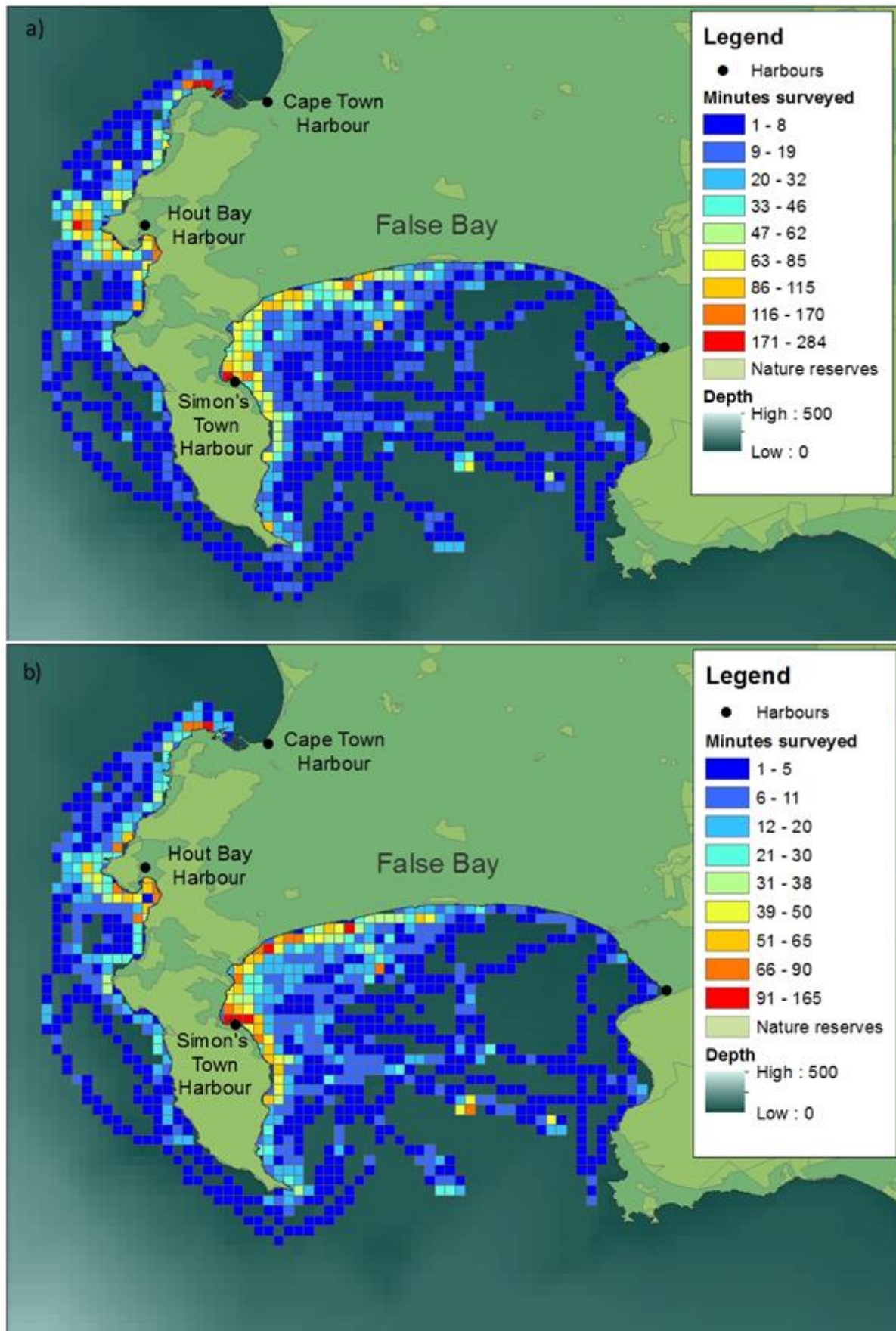


Figure 2.4. Intensity of effort as a measure of time, calculated as the total number of minutes spent per one square kilometre grid, for all (a) “On effort” and (b) “Search” track lines. The colour scale ramps from blue (low effort) to warm colours, orange to red (highest effort).

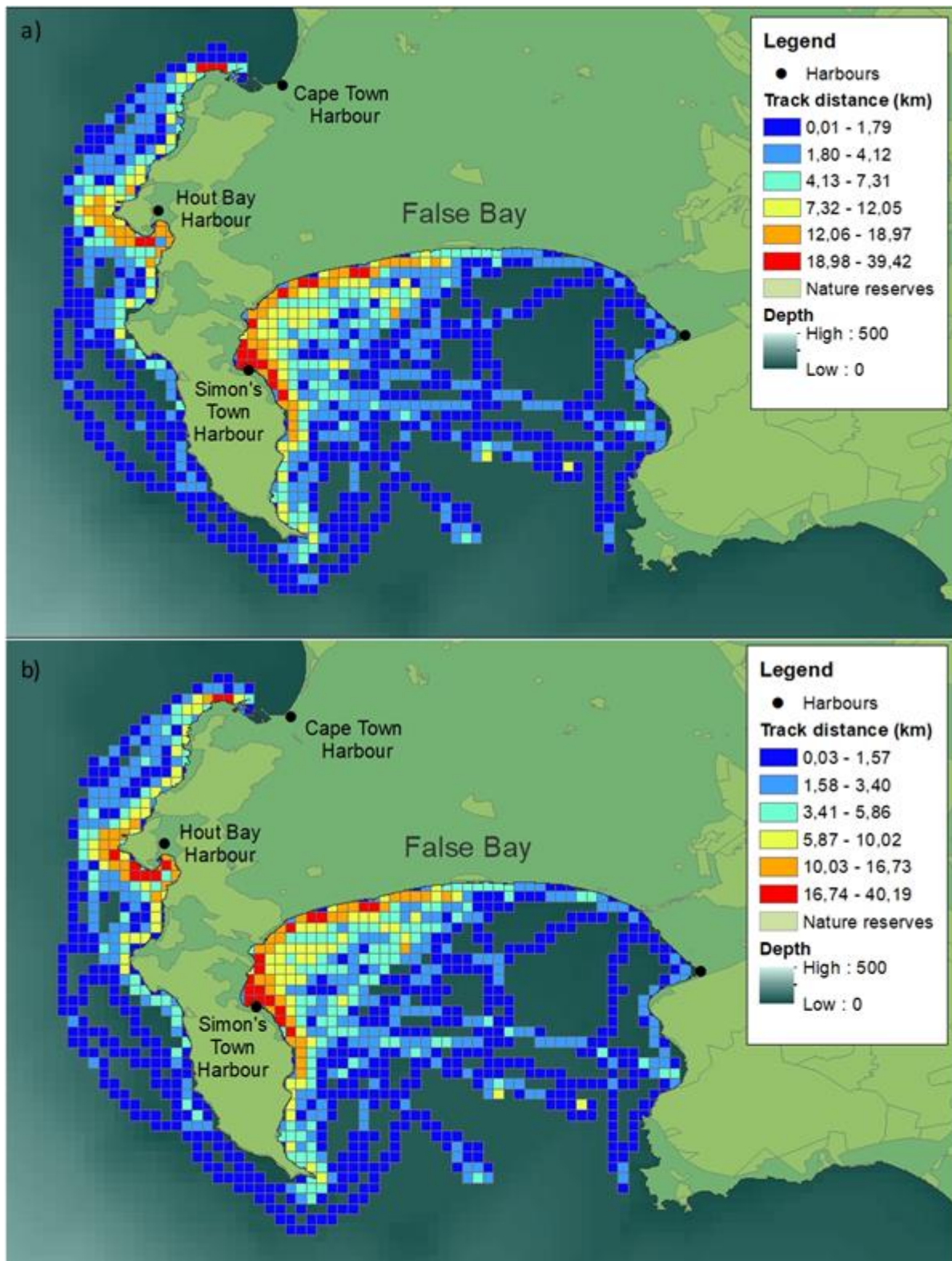


Figure 2.5. Intensity of effort as a measure of distance, calculated as the sum total of kilometres travelled per square kilometre grid, for all (a) "On effort" and (b) "Search" track lines. The colour scale ramps from blue (low effort) to red (highest effort).

Overview of cetacean sightings

Five dolphin species and three whale species were seen over 179 hours of search effort, totalling to 162 confirmed sightings (Table 2.1). An additional six sightings of whales were recorded as unidentified. Heaviside's dolphins had the highest number of encounters of all odontocete species; common dolphins were the second-most commonly encountered, while the longest duration of time spent with animals during encounters was with dusky dolphins (Table 2.1). Despite being known to occur in the area, bottlenose dolphins were only sighted twice throughout the study period, one of which was a single individual encountered off Gordon's Bay (Figure 2.1).

Table 2.1. Sightings summary for the eight cetacean species encountered throughout False Bay and Table Bay.

Species	Total sightings	Sightings per survey	Sighting frequency (S.hr ⁻¹)	Total time (hours)
Heaviside's dolphin	18	0.30	0.10	7.75
Common dolphin	16	0.26	0.09	8.8
Dusky dolphin	15	0.25	0.08	9.62
Humpback dolphin	10	0.16	0.06	7.45
Bottlenose dolphin	2	0.03	0.01	1.02
Humpback whale	36	0.59	0.20	27.25
Southern right whale	26	0.43	0.15	6.46
Bryde's whale	39	0.64	0.22	14.5
Total (mean)	162	2.69 (0.34)	0.94 (0.12)	82.85

Bryde’s whales were the most frequently encountered whale species, observed throughout False Bay, and with only one out of the 39 encounters recorded off Hout Bay (Figure 2.6). With a sighting frequency of 0.22, and a highest encounter probability (0.64), Bryde’s whales were the most frequently spotted of all cetaceans in False Bay (Table 2.1). Approximately 27 hours were spent on humpback whale encounters (for which more research effort was focused) observed 36 times; nearly double the time spent on encounters with the more elusive Bryde’s whales (where only photo-ID was the main focus) (Table 2.1).

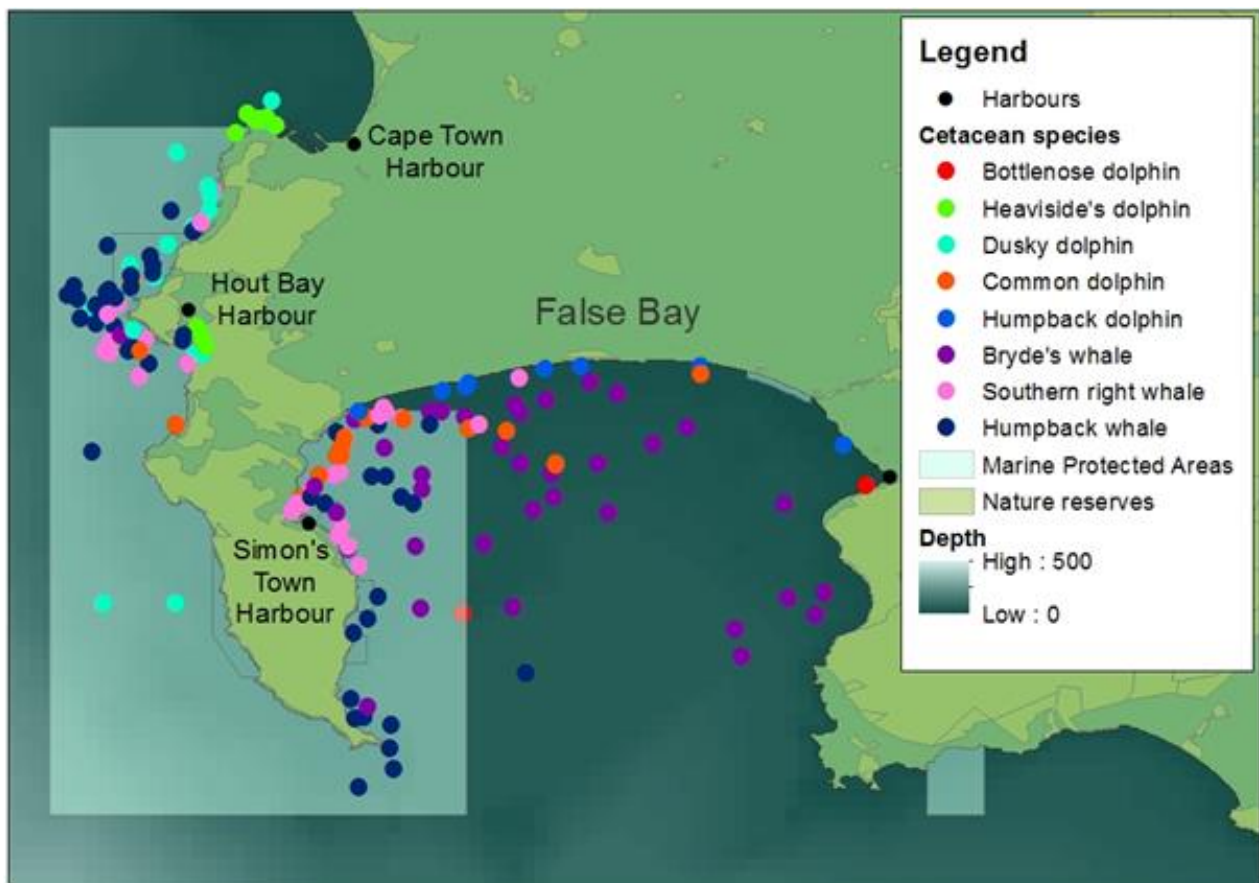


Figure 2.6. The spatial distribution of all cetacean encounters collected during dedicated boat based surveys conducted in the waters around the Cape Peninsula, between Table Bay and Cape Hangklip, between February 2015 and April 2017.

The spatial distribution of all cetacean sightings (Figure 2.6) was overlaid with a 1 km² grid to identify areas with the highest encounter frequency (Figure 2.7). The majority of sightings were recorded in shallow, inshore waters along the coastline in False Bay, and centred around Hout Bay. Areas with high sightings count (five encounters within one square kilometre grid) include the sheltered bay off Hout Bay harbour where sightings of Heaviside’s dolphins and dusky dolphins were common, as well as Sea Point (near Cape Town harbour) where groups of Heaviside’s dolphins were frequently seen (Figure 2.7).

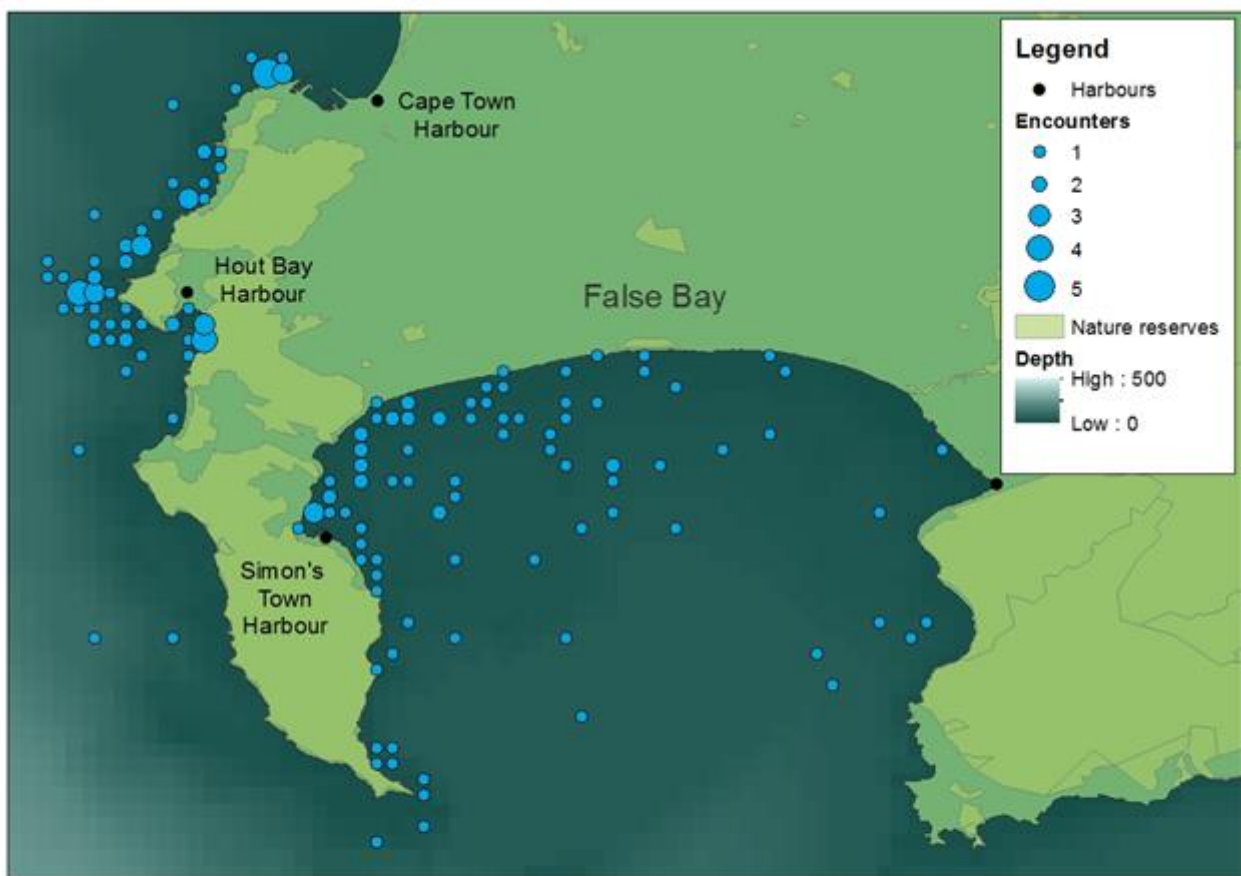


Figure 2.7. Graduated symbol counts illustrating the number of encounters per 1 km² grid, for all cetaceans encountered during dedicated boat surveys conducted in the waters between Table Bay and Cape Hangklip. Each symbol represents the total sightings within one square kilometre grid. Circle size indicates the number of sightings.

Encounters relative to distance from shore

Cetacean sightings were predominantly recorded within the shallow, inshore waters of the coast where effort was highest. This is especially true for dolphin encounters, the majority of which fell within 2 km from the coastline (Figure 2.8). Heaviside's dolphins and humpback dolphins were often found in waters less than 15 meters deep; Heaviside's dolphins were found exclusively in the shallow bay and kelp forests (mean = 0.26, range = 0.06 to 0.90 km from shore), and humpback dolphins were found within the surf or just behind the break line off the beach (mean = 0.39, range = 0.18 to 0.61 km from shore).

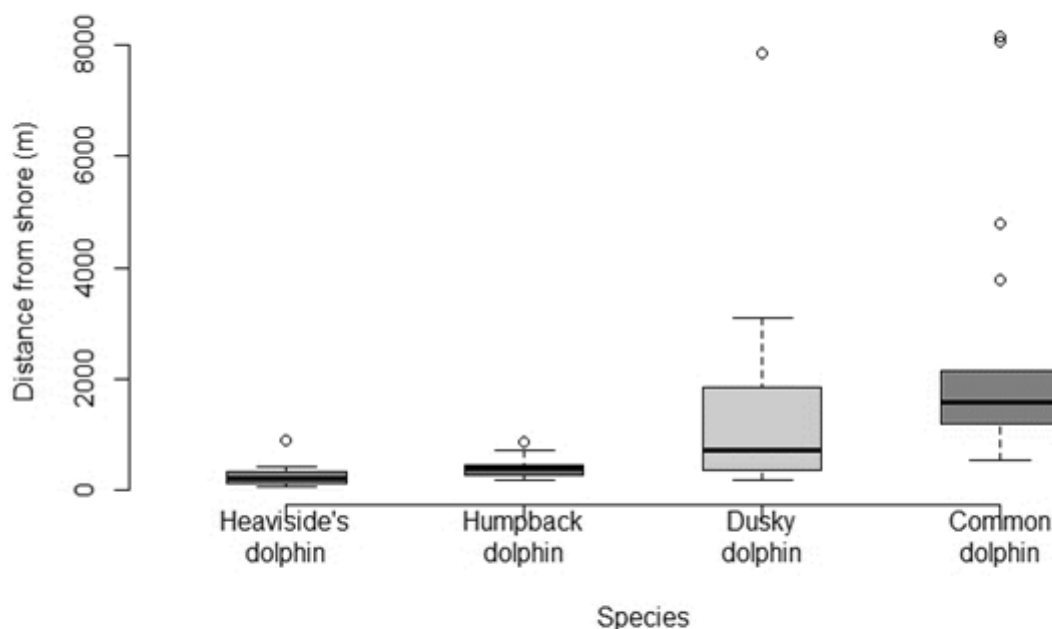


Figure 2.8. Box-plots illustrating the distance from shore (in meters) at which dolphin species were encountered, between Table Bay and Cape Hangklip, during dedicated boat surveys conducted between February 2015 and April 2017. Open circles represent outliers.

Dusky dolphins (mean = 1.40, range = 0.16 to 7.85 km) and common dolphins (mean = 2.50, range = 0.52 to 8.15 km) were found in deeper waters as far out as we surveyed (Figure 2.8), approximately 13 km from shore.

Whales were generally observed further offshore (Figure 2.9) than the dolphins (Figure 2.8). Bryde's whales were encountered the furthest distance from the shore with a maximum of

12 km from the coastline (mean = 4.74, range = 0.80 to 12.37 km) and in deeper waters of False Bay. Southern right whale sightings were in shallower, coastal areas and predominantly within 2 km from land (mean = 1.35, range = 0.23 to 3.55 km) resulting in southern right whales displaying the closest inshore mean distribution of all three whale species encountered throughout the study area (Figure 2.9). Humpback whales generally showed a near-shore distribution (mean = 2.24, range = 0.04 to 11.10 km) with the exception of a single encounter towards the middle of False Bay (Figure 2.9). They were also the only species encountered in the deeper waters off the tip of Cape Point (Figure 2.6).

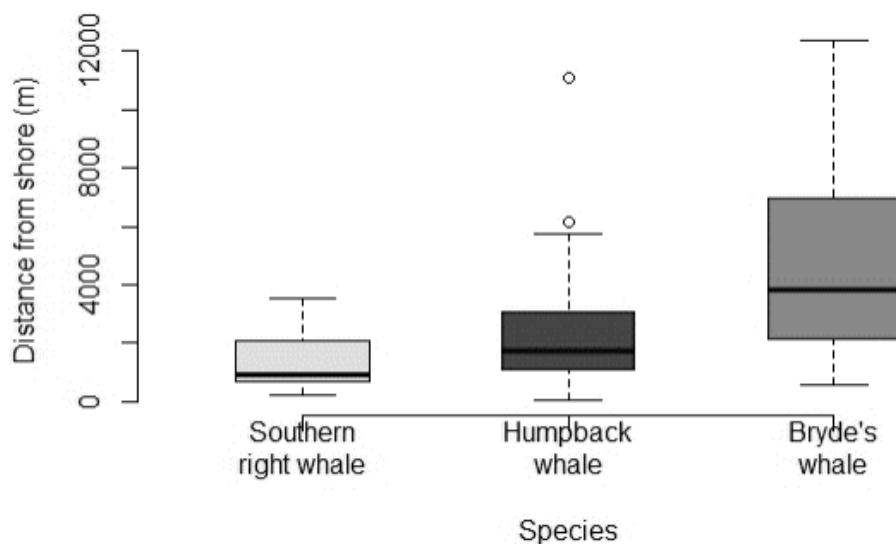


Figure 2.9. Box-plots illustrating the distance from shore (in meters) at which whale species were encountered between Table Bay and Cape Hangklip, during dedicated boat surveys conducted between February 2015 and April 2017. Open circles represent outliers. Boxes represent the mean distance from shore.

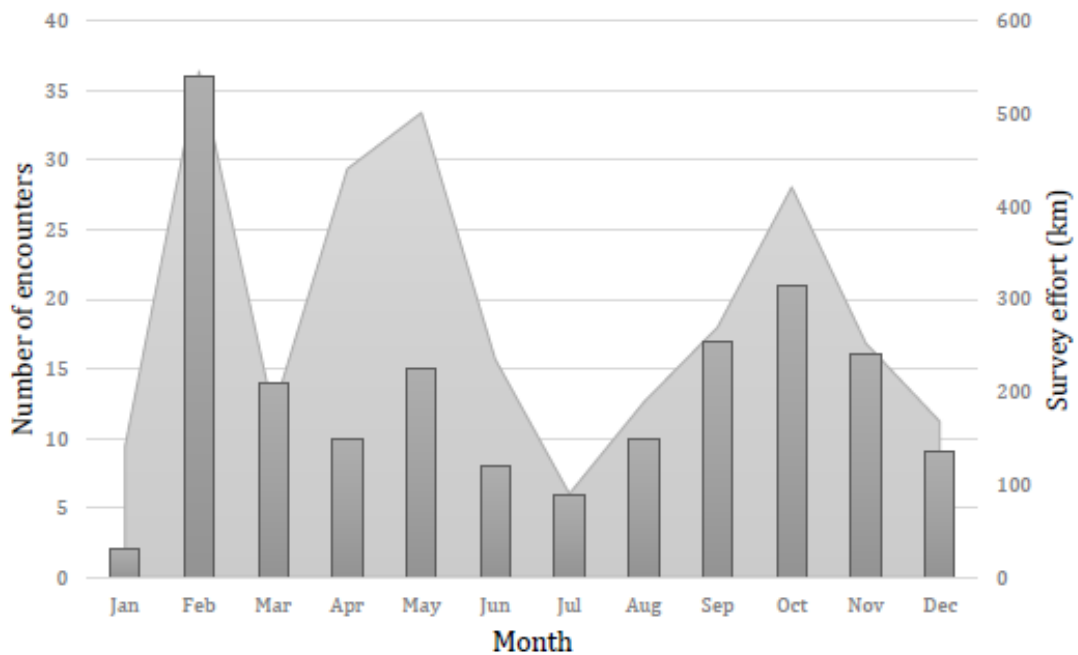


Figure 2.10. Total kilometres surveyed and the number of encounters recorded per month during dedicated boat-based surveys conducted between February 2015 and April 2017. An average of 286 km survey effort and 14 encounters were recorded per month. Vertical bars represent the total number of encounters; light grey shaded area represents the total kilometres of survey effort.

Survey effort and sightings

Due to restricted weather conditions, boat and crew availability, the number of surveys conducted per month and across years varied (Figure 2.10). There was a clear drop in survey effort during winter months (June to August), predominantly due to unfavourable weather conditions. Field days generally peaked around spring (September to November), and were especially high during February (Figure 2.10). A monthly average of 286 kilometres of survey effort was conducted throughout the study period, with a maximum of 546 km and 36 sightings recorded in February. The total kilometres surveyed each month was calculated and compared to the number of detections per month, to provide an indication of survey effort invested relative to encounter success (Figure 2.10). The number of encounters recorded was

proportional to the intensity of effort, except during April and May, when the number of encounters were low compared to high survey effort.

Spatial distribution and encounter rates

The spatial distribution of encounters for each species was corrected for the intensity of effort, to quantify the number of encounters recorded per one square kilometre (encounters/km²). The overall encounter rates calculated for all cetacean species was highest in the western half of False Bay and closer inshore (Figure 2.11a).

Dusky dolphins were commonly seen off the west coast (Figure 2.11b). Encounters were spread continuously from Mouille Point to Hout Bay, with the most frequent sightings off Camps Bay following the coastline of the Oudekraal Nature Reserve, and within the sheltered bay off Hout Bay harbour. Two observations were recorded further south and offshore of the Cape Peninsula, near Kommetjie. The encounter rate for dusky dolphins was higher off the Peninsula compared to Hout Bay where survey effort was higher (Figure 2.11b).

Heaviside's dolphins, endemic to the Benguela Current Large Marine Ecosystem, were exclusively found within the sheltered bay of Hout Bay, and between 3 Anchor Bay and Mouille Point near Cape Town harbour (Figure 2.11c). Groups were found in shallow inshore waters, hugging the coastline and staying within the same occupied area, with little distance travelled during focal follows. As a result of the restricted areas which Heaviside's dolphins occupy within the larger study area, effort corrected sighting rates were very low despite the high survey effort within and around said areas (Figure 2.11c).

Common dolphins were found throughout the study area (Figure 2.11d). The majority of sightings were in the western half of False Bay, with one sighting further East of the bay towards Gordon's Bay. A further three sightings were recorded on the West coast - off Hout Bay and Kommetjie. One sighting also included a group feeding alongside two Bryde's whales. The majority of common dolphin sightings (75%) fell within the larger Table Mountain National Park Marine Protected Area (MPA) Common dolphins had overall low calculated

encounter rates, apart from two high sightings/km² cells, located south of Hout Bay and North-East in False Bay, where effort was considerably lower (Figure 2.11d).

The first humpback dolphin encounter was recorded in 2016, during the second year of the study period, when a small group was found off Strandfontein towards the middle of False Bay (Figure 2.11e). They were generally in small groups, staying within close proximity of one another. One encounter was of a single, sub-adult individual. The western-most observation of humpback dolphins was recorded off Muizenberg beach. Humpback dolphins showed increasing encounter rates following the coast from west to east in False Bay (Figure 2.11e).

Southern right whales were observed throughout the study area (Figure 2.11f). Right whale encounters were predominantly in the shallow, inshore waters along the coast. In False Bay, all sightings were recorded in the western half of the bay, with most of the sightings centred around Simon's Town. Multiple sightings were also recorded off Hout Bay. These encounters were largely collected during the annual whale season (July to November), when right whales migrate to the South African coastline to breed (Best and Scott 1993). Southern right whales were mainly encountered (92% of sightings) within the Table Mountain National Park Marine Protected Area. The highest count of southern right whales detected per 1 km² was recorded off Hout Bay, in comparison to False Bay, where right whales were observed more frequently, and effort intensity was greater (Figure 2.11f).

Humpback whales were predominantly sighted during the winter migration period (July – November) when the whales migrate north past the South African coastline to breed (Best et al. 1998). Sightings were recorded off the west coast, predominantly centred around Hout Bay; and the western half of False Bay, from Muizenberg beach spread south towards Cape Point (Figure 2.11g). The majority (97%) of all humpback whale sightings fell within the Table Mountain National Park Marine Protected Area. High encounter rates of humpback whales were off Hout Bay (Figure 2.11).

Bryde's whale encounters were spread over the entirety of False Bay, with 97% of sightings recorded in False Bay and a single sighting in Hout Bay (Figure 2.11h). Bryde's whales, unlike southern right whales and humpback whales, are non-migratory species and were frequently encountered throughout the study period. The two migratory species showed clear occurrence patterns in the inshore waters around the Hout Bay and the western half of False Bay, whereas Bryde's whales showed no clear distribution patterns other than a seemingly high preference for False Bay (Figure 2.11h).

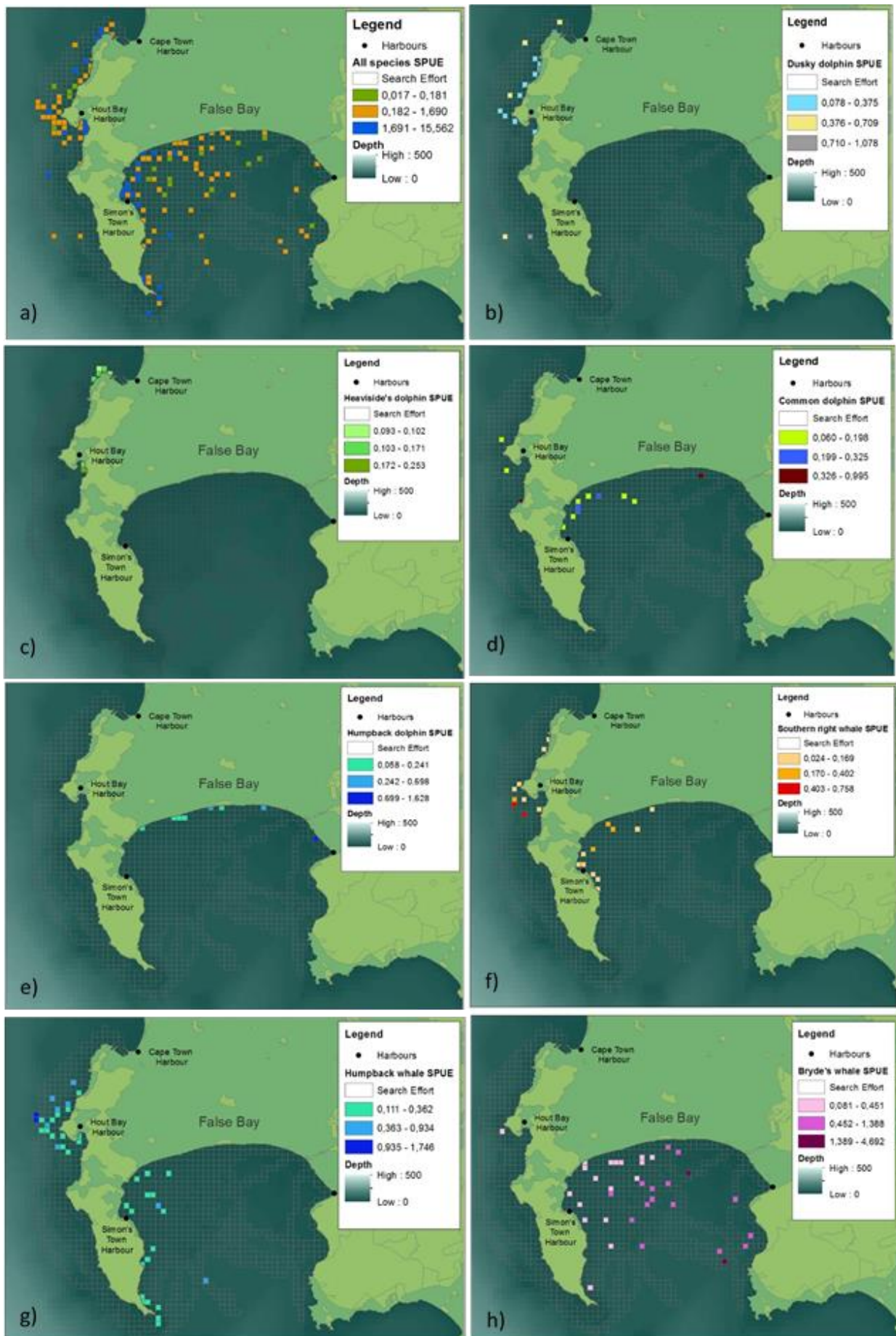


Figure 2.11. Effort corrected encounters per 1 km² for (a) all cetacean encounters, (b) dusky dolphins, (c) Heaviside's dolphins, (d) common dolphins, (e) humpback dolphins, (f) southern right whales, (g) humpback whales, and (h) Bryde's whales recorded during boat surveys conducted between Table Bay and Cape Hangklip, between February 2015 and April 2017. Empty cells represent the areas which were surveyed with no detections recorded.

Behavioural observations

General behaviour of animals was documented during cetacean encounters to provide a more meaningful idea on how species utilise the waters off our coastline. Behavioural observations were recorded only on 34 occasions throughout the study period, as data collection was often more focused on photo-identification during group encounters. Common dolphins (8 observations), dusky dolphins (5 observations), humpback dolphins (6 observations) and humpback whales (5 observations) were seen foraging (Figure 2.12), which could suggest potential key habitats for cetaceans in waters around the Cape Peninsula. Humpback whales were also seen travelling, resting and milling, while southern right whales were exclusively seen travelling during a single recording of their behaviour, and Bryde’s whales (6 observations) were either seen milling or travelling (Figure 2.12). Heaviside’s dolphins (3 observations) were predominantly seen milling, with very little travelling done, and different groups of dusky dolphins were either observed traveling, socialising or milling. Note that mating behaviour was categorised as socialising.

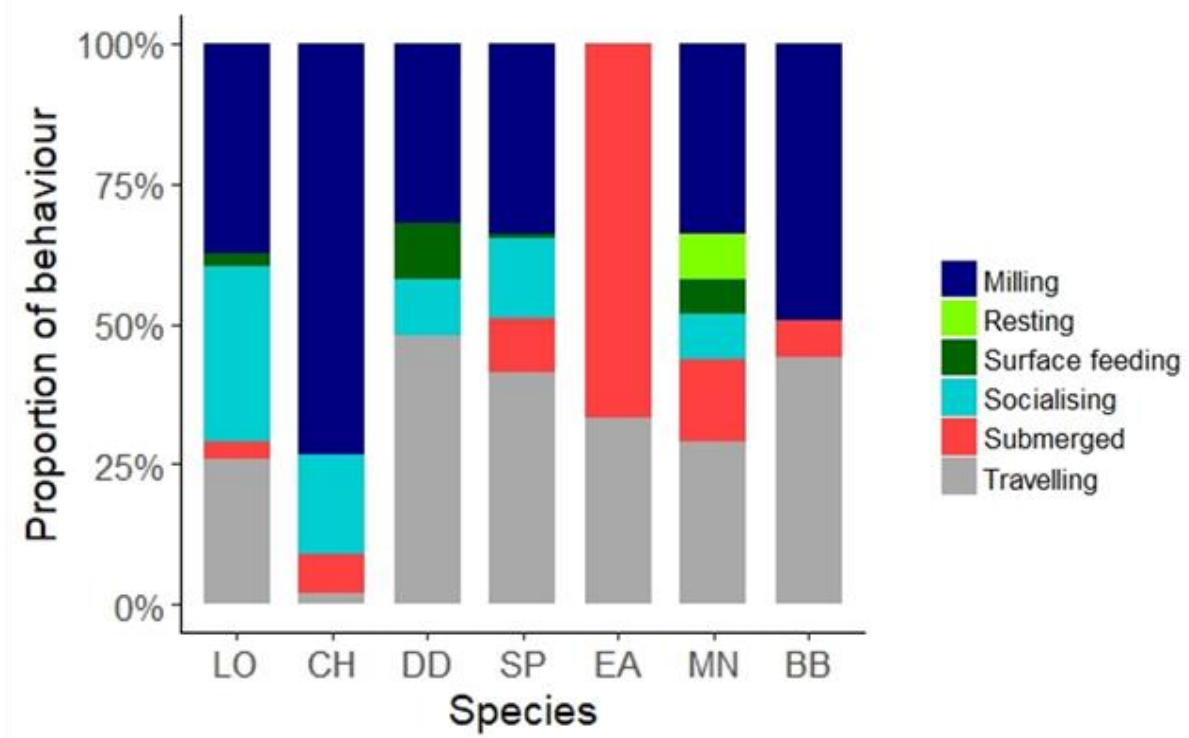


Figure 2.12. Behavioural observations recorded during cetacean encounters collected from dedicated boat surveys conducted in the waters around the Cape Peninsula, between February 2015 and April 2017. Species code: LO (dusky dolphin), CH (Heaviside’s dolphin), DD (common dolphin), SP (humpback dolphin), EA (southern right whale, single recording), MN (humpback whale), BB (Bryde’s whale).

DISCUSSION

The waters off the south-western Cape consist of two unique oceanographic regimes which are affected by global climate change. Increasing temperature of the water bodies surrounding the Benguela Ecosystem can cause a reduction of suitable habitat for cool water limited species like dusky dolphins and Heaviside's dolphins.

The aim of the current chapter was to explore the distribution ranges of several cetaceans occupying the waters around the Southern Peninsula by means of scientific surveys. The goal was to relate these findings to current knowledge in order to detect any possible changes.

All of the recorded encounters fell within the currently described ranges of each species (Best 2007), however, the present study provides insights into their current distribution at a substantially finer scale than was previously available. The findings of all eight encountered species are discussed below. Since our research was centered around exploring distributional changes, more focus is placed on dolphins which have their ranges end within the study region while a less detailed discussion is provided for whale species.

Dusky dolphins

The distribution of dusky dolphins along the west coast ranges from the surf zone to deeper waters (at least 500 m deep) several kilometres offshore (Elwen et al. 2009; Findlay et al. 1992). In the present study dusky dolphins were frequently encountered within a distance of 2km from land, although surveys were conducted as far as 13 km from shore. Behaviours like socialising, feeding and milling were observed during encounters with dusky dolphins. To date, there has been very limited research done on the abundance and population status of dusky dolphins found on the South African continental shelf (Elwen et al. 2011). The southern limit of their range is proposed to be at Cape Point (Best 2007). The southernmost encounter during the present study was off Kommetjie, on the southern Peninsula, however, survey effort was low south of Kommetjie. Dusky dolphins off the west coast of South African can be considered a cool water limited species (MacLeod 2009) which means that their distribution is likely restricted only by surrounding warmer waters. As a result of increasing temperatures, the ranges of such species are expected to shrink as their preferred habitat becomes less

suitable (MacLeod 2009). The continued increase in temperature of the waters surrounding the Benguela could result in the reduction of suitable habitat for dusky dolphins. Some studies suggest that warming of the Agulhas Current intensifies from east to west, so that the warming effect is strongest and most important in the western retroflection area (Rouault et al. 2009). Such a thermal gradient will act as a strong boundary to the eastward expansion of dusky dolphins. Incidental sightings collected as part of the broader project indicate regular sightings of dusky dolphins are made in the south-western side of False Bay, suggesting these animals do come around Cape Point into the bay. However, our data do not reflect it. This particular corner of False Bay has a temperature range similar to that of Cape Point with a mean annual temperature of 12-14°C (Smit et al. 2013). These similar water temperatures could explain the incidental sightings of dusky dolphins around the Peninsula. However, the warmer temperatures present in the rest of the bay, reaching an annual mean of 16°C, and during summer an abrupt rise over 18°C in Muizenberg (Smit et al. 2013), it is likely that this south-west corner of False Bay could be the effective range limit of dusky dolphins with water temperature acting as the main cue or limiting factor preventing regular movement east of this.

Heaviside's dolphins

Heaviside's dolphins are endemic to the Benguela ecosystem, with a distribution range between southern Angola and Cape Point (Best 2007; Findlay et al. 1992). Cape Point is the proposed southernmost range end of Heaviside's dolphins (Best 2007), with only vagrant sightings documented east of this (Best 2007; Vinding et al. 2015). Some research has been done on the resident population occupying the inshore waters of the west coast, although this is mainly focussed within the core of their range north of Table Bay (Elwen et al. 2006; 2009; 2010). High sightings rates of Heaviside's dolphins have been recorded along the open coasts north of Table Bay (Elwen et al. 2010) and previous studies focusing on the population in Table Bay indicates the preference and importance of this area for the species (Behrman 2011). Few encounters have been recorded south of the Granger Bay area in Table Bay (Behrman 2011) although this could be due to low observer effort.

In the present study, Heaviside's dolphins were exclusively spotted in Sea Point and Hout Bay. Our results therefore largely confirm this pattern of high density at Table Bay and limited sightings south of that. However, we also recorded regular encounters in Table Bay. The lack of observations even coastally between these two areas – which is contradictory to the high encounter rates along the open coast north of this region (Elwen et al. 2010) – may be habitat related. Heaviside's dolphins generally prefer areas consisting of sandy beaches (Elwen et al. 2010) whereas the coastal stretch between Granger Bay and Hout Bay is predominantly rocky shores which could explain the lack of encounters along this part of the coastline. The further lack of sightings south of Hout Bay can possibly be linked to strong upwelling cells. There is a large upwelling cell just off the southern Peninsula (Shannon and Nelson 1996) which could limit the movement of animals along this cooler stretch of waters along the western side of the Peninsula. Elwen et al. (2010) notes lower densities of Heaviside's dolphins in upwelling zones and much higher abundances north of upwelling areas. This resembles the observed distribution of Heaviside's dolphins in the current study area where animals were absent within the proposed upwelling region along the southern Peninsula but encountered regularly in Hout Bay, just north of this region.

Based on temperature estimates only, Heaviside's dolphins should theoretically occupy the waters off the Peninsula to Cape Point, the proposed range by Best (2007), as sea water temperature is optimal. Furthermore, the cool temperate waters of the Benguela extend around the Peninsula as annual mean temperatures stay below 15°C in the bottom south-western corner of False Bay (Smit et al. 2013), which further supports previous range estimates of the species (Best 2007). However, from the present study, and the findings by Behrman (2011), it is clear that Heaviside's dolphins do not occupy these areas and that other factors should be considered when describing the possible limiting factors to their range.

The movement patterns of Heaviside's dolphins have been linked to prey density as dolphins were found to reflect the distribution of shallow-water hake (Elwen et al. 2009) and animals were shown to occur in higher abundances in areas where prey availability was greatest and north of upwelling zones (Elwen et al. 2010). These findings could apply to the current study area where the extensive coastal upwelling system off the Peninsula drives the cold, nutrient rich waters of the west coast and subsequently results in high productivity (Shannon and Nelson 1996), supporting our observations of high encounter rates north of an upwelling zone

and complete lack of sightings within the zone. We therefore propose that the combination of temperature and food availability, rather than Cape Point itself, is a main factor describing the southern range limits of Heaviside's dolphins. Considering the previously mentioned barriers as described by MacLeod (2009), the distribution of Heaviside's dolphins can be described more clearly by considering ecological barriers, like prey distribution, in addition to oceanographic barriers (i.e. water temperature). Similar to dusky dolphins, Heaviside's are a cool water limited species (MacLeod 2009) and their range is expected to decrease as a result of increasing water temperatures. This means that Heaviside's dolphins are likely to face severe negative impacts of increased ocean temperatures as a result of global climate change as suitable habitats shrink and their endemism to the Benguela bioregion could result in a risk of future species extinction (Thomas et al. 2004).

Common dolphins

Common dolphins were encountered throughout the study area, predominantly seen in False Bay while only three sightings were recorded off the West coast. Common dolphins were observed further from the shore than the other dolphin species. Behavioural observations included feeding, which may indicate the importance of the bay as an important foraging habitat for this species. They are considered to be pelagic species which opportunistically enter inshore bays in search of prey (Best 2007). One encounter included a large group of dolphins foraging alongside two Bryde's whales with many diving birds associated. Similar encounters seem to be a frequent observation along the south African coast (Best et al. 1984; Melly et al. 2018; O'Donoghue et al. 2010; Saayman et al. 1972). Common dolphins are known to follow the annual sardine run (van der Lingen et al. 2010) following the movement of fish up the east coast, with a peak in observations on the Natal coast during winter (Cockcroft and Peddemors 1990). Findings from a number of studies, including the present one, seem to suggest that common dolphins aren't constrained by one particular environmental variable, but rather follow the distribution of their prey and occur in many offshore areas along the coast, often on the continental slope, between 100 and 200 meters deep (Cañadas and Hammond 2008; Cockcroft and Peddemors 1990; Findlay et al. 1992; Melly et al. 2018; Peddemors 1999).

Humpback dolphins

Humpback dolphins are found in the Agulhas bioregion off the south coast and along the east coast of Africa (Best 2007). Humpback dolphins have a tendency to prefer highly coastal, shallow waters (Atkins et al. 2004; Karczmarski et al. 2000; Melly et al. 2018; Ross et al. 1994; Saayman et al. 1972; Saayman and Tayler 1979; Vinding et al. 2015). Along the South African shore, humpback dolphins generally occur near sandy beaches such as Franskraal (Vinding et al. 2015), and rocky reefs in Algoa Bay (Karczmarski et al. 2000; Saayman and Tayler 1979) and it is suggested that these dolphins prefer to feed on reef dwelling fish and disperse to coastal, rocky areas to do so (Atkins et al. 2004; Karczmarski et al. 2000; Melly et al. 2018; Saayman et al. 1972). They are known to utilise the shallow, sheltered waters of bays on the south-east coast for resting and social interactions (James et al. 2015; Melly et al. 2018; Saayman et al. 1972). In the present study humpback dolphins were encountered several times off sandy beaches in False Bay, as far west as Muizenberg in the north-western corner of the bay. Previous studies defined the range end to be off Agulhas (Findlay et al. 1992) which was later suggested to expand further west towards Danger Point (Best 2007).

The present study not only supports the westward expansion suggested by Best (2007) but shows a clear extension of humpback dolphins into the north-western corner of False Bay. This westward range expansion is thought to be constrained by the cooler waters of the Benguela Current (Best 2007, Findlay et al. 1992). Muizenberg, where the westernmost sighting was recorded in the current study, is largely protected from nearshore upwelling and temperatures in this region have been found to reach 18+°C during summer months, corresponding to the annual mean temperatures east of Cape Agulhas of around 17-18°C (Smit et al. 2013). The sheltered and seasonal warm temperate waters in this corner of the bay imitate the preferred tropical habitat of the species and could explain the westward expansion of humpback dolphins into the region. However, annual mean temperatures around Cape Point measure about 12-14°C (Smit et al. 2013). This drop in temperature, starting south of Simon's Town and continuing around the Peninsula, possibly limits the farther westward extension of humpback dolphins. Furthermore, the steep rocky shores of the Peninsula and reduction of estuarine habitats along the south-west coast, the preferred habitat for this species (Melly et al. 2017, Saayman et al. 1972, Saayman and Tayler 1979, Vinding et al. 2015) could also act as dispersal barriers. We propose that the south-western

corner of False Bay is most likely the real western boundary limit to the humpback dolphin's distribution range.

Although global climate change is predicted to result in regional coastal cooling of certain areas because of increased upwelling intensity (e.g. the Port Alfred upwelling cell in the Agulhas Current; Rouault et al. 2009; 2010), an apparent warming in the retroflection zone on the south coast has recently been recorded (Rouault et al. 2009). This warming trend as a result of climatic change could further facilitate the range expansion of humpback dolphins as they track suitable habitats.

Southern right whales

Past studies defined southern right whale distribution to be primarily on the south coast of southern Africa, with higher abundances between Walker Bay and Plettenberg Bay (Best 2000; Elwen and Best 2004). From recent literature (Barendse and Best 2014; Melly et al. 2018; Peters et al. 2011), however, southern right whales are increasingly being observed further along the coastline. The west coast, particularly Saldanha Bay, is increasingly used as feeding grounds for southern right whales (Barendse and Best 2014, Peters et al. 2011), and a recent study conducted in Algoa Bay showed an increase in sightings in the area over the last few years (Melly et al. 2018). These findings indicate possible range expansion of southern right whales in both directions along the coast, which is likely a result of a recovering population. In the present study, right whale encounters peaked during their wintering season, June to November (Best and Scott 1993), when individuals were recorded in the shallow, inshore waters of the coast. Migrating southern right whales prefer sandy bottom type habitats in shallow, protected bays along the South African coast which they utilise for the rearing of their young (Best et al. 2001; Elwen and Best 2004). The frequent encounters of southern right whales around Hout Bay in the present study, support the findings that the west coast is progressively being utilised by right whales (Barendse and Best 2014) possibly for feeding towards the end of their wintering season.

Humpback whales

Humpback whales were mainly encountered during winter months, coinciding with their wintering breeding seasons (Best 2007), with sightings recorded predominantly off Hout Bay and in the western half of False Bay. Humpback whales were the only animals encountered off and around the tip of Cape Point, where strong local winds drive the upwelling system of the southern Peninsula. Humpback whales are known to utilise the coastal waters of the South African shore as a passage from their feeding grounds, in Antarctica, to tropical breeding grounds in the lower latitudes (Best 2007; Findlay et al. 1994). Contradictory to this, feeding behaviour was observed during encounters in the present study. Recent studies show that South African west coast is now becoming an important feeding ground for humpback whales (Findlay et al. 2017) and they are increasingly observed feeding in the southern Benguela (Barendse et al. 2010). It is unclear to which populations whales between Cape Point and Cape Agulhas belong, but based on seasonality (Vinding et al. 2015), it is possible that the individuals encountered in the present study are part of the breeding stock population which feeds off the west coast towards the end of their breeding season (Barendse et al. 2010, 2011; Vinding et al. 2015).

Bryde's whales

In the present study Bryde's whales were the most frequently sighted cetacean throughout the study period which is contradictory to other studies conducted on the South African south coast where Bryde's whales were encountered notably less frequently than humpback- and southern right whales (Melly et al. 2018). Findings from the present study may thus indicate the importance of False Bay as a key habitat for this species. Observations of Bryde's whales were spread throughout the bay and recorded the furthest distance from shore in waters as far out as surveys were conducted, which is comparable to findings in other parts of the coastline (Melly et al. 2018, Vinding et al. 2015). There are at least three known stocks of Bryde's whales present around southern Africa from Gabon to Madagascar (Best 2001) and the inshore population is thought to be relatively small (Best et al. 1984). Unlike southern right and humpback whales, Bryde's whales are non-migratory (Best 2001), engaging only in small-scale movements along the coast following seasonal trends in prey distribution,

specifically the 'sardine run' on the east coast (Best 2001; Best et al. 1984; O'Callaghan and Baker 2002; Penry 2010) which can explain the year-round observations of Bryde's whales during the study period compared to the migratory whale species.

Conclusion

Findings from the present study define the southern range limit of Heaviside's dolphins at Hout Bay with an absence along the southern Peninsula and Cape Point. We also propose that Heaviside's dolphins are likely restricted by a combination of cool waters and prey availability, rather than by Cape Point itself. For humpback dolphins, our findings confirm a clear westward expansion of their current distribution range which was previously thought to end around Danger Point (Best 2007). This extension is likely facilitated by an increase in mean water temperature along the south coast and a strong seasonal increase in temperature off Muizenberg (Smit et al. 2013) where the most westerly sighting for humpback dolphins were recorded. Migratory whale species, that is southern right whales and humpback whales, were predominantly encountered during their winter breeding season, with both species suggested to be part of the populations which utilise the west coast as seasonal feeding grounds. Although only a small sample size of behavioural observation data was collected during the present study, noted observations suggest the importance of key foraging and resting habitats for cetaceans in the inshore waters along the southern Peninsula of the Western Cape, between Table Bay and Cape Hangklip. The findings of this chapter can be use as the foundation for building species distribution models, which is discussed and analysed in the following chapter.

CHAPTER 3: ENSEMBLE SPECIES DISTRIBUTION MODELLING: INVESTIGATING FACTORS DETERMINING HABITAT USE OF CETACEANS IN THE WESTERN CAPE, SOUTH AFRICA

ABSTRACT

Species distribution models are important for the identification of suitable habitats. In the present study, an ensemble model was applied to sightings data of eight cetacean species collected from dedicated boat surveys: dusky dolphins (*Lagenorhynchus obscurus*), Heaviside's dolphins (*Cephalorhynchus heavisidii*), common dolphins (*Delphinus delphis*), Indian Ocean humpback dolphins (*Sousa plumbea*), bottlenose dolphins (*Tursiops aduncus*), southern right whales (*Eubalaena australis*), humpback whales (*Megaptera novaeangliae*), and Bryde's whales (*Balaenoptera brydei*). The ensemble model consisted of a combination of five independent species distribution models: generalised linear model (GLMs), generalised additive model (GAMs), generalised boosting model (GBM), random forest (RF) and maximum entropy (MaxEnt). Four environmental variables (water depth, bathymetric slope, sea surface temperature (SST) and chlorophyll *a* concentration (Chl *a*)) were used to generate predicted occurrences for each species. Overall, RF and GAMs were the highest performing models; GAMs consistently outperformed GLMs, and MaxEnt generated the lowest predicted accuracies. SST and Chl *a* were the most important predictor variables for dusky dolphin and Heaviside's dolphin occurrence; SST was the most influential variable for common dolphins; and depth and SST were most important for humpback dolphin and bottlenose dolphin distribution, respectively. Southern right and Bryde's whale distribution were mainly influenced by SST, whereas depth was suggested as the most influential variable for humpback whales. The influence of the oceanographic variables was mainly attributed to their direct effects on primary productivity and prey availability, which influence the distribution of cetaceans. The predicted distributions identify areas of suitable habitat and indicate the importance of the western Cape as a key area utilised by cetaceans.

INTRODUCTION

Understanding the relationship between species and their environment is essential for the identification of biologically significant areas and managing conservation efforts (Elith and Leathwick 2009; Guisan and Thuiller 2005). Species distribution models (SDMs) correlate environmental variables to the geographical distribution of a species (Miller 2010) and are increasingly being used as a method to predict cetacean distribution and habitat suitability (Ainley et al. 2012; Gregr 2011; Moura et al. 2012; Pitchford et al. 2016; Smith et al. 2012; Zanardo et al. 2017). They can also be used for predicting presences in areas which have not previously been surveyed (Elith and Graham 2009; Guisan and Thuiller 2005; Segurado and Araújo 2004).

There are two groups under which all habitat models fall, and the chosen model is dependent on the data set and method used to record sightings data. The first group is presence-absence models, which requires presence data (sightings of target species) and information on search effort collected during planned surveys (Guisan and Zimmermann 2000; Tsoar et al. 2007). Presence-absence models, such as generalised additive models (GAM) and generalised linear models (GLM), fit practical relationships between sighting locations or rates and the local environmental conditions (Guisan and Zimmerman 2000) and estimating the probability of detecting a species and subsequently predicting habitat suitability (Brotons et al. 2004; Gormley et al. 2011). It is important to note that the number of absences (zeros) in such datasets can be large due to the restricted distribution range of a species, low species abundances, and poor detection, as well as low or biased search effort. It can also be challenging to differentiate between true and false absences, where true absences are when it can be said with certainty that the species is absent from the area at that particular time and place; and the latter when the species is present but poorly detected due to a lack of observer effort (Martin et al. 2005; Ridout et al. 1998).

The second group is known as presence-only models where effort data are not available, such as opportunistically collected data, or data from a range of sources where information on survey effort is not comparable (Hirzel et al. 2001; Zaniwski et al. 2002). Presence-only models such as Maximum Entropy Modelling (MaxEnt, Phillips et al. 2006) use the presence localities of a species, and the environmental conditions at that site, to make inferences about

the habitat preference of that species (Barry et al. 2006). Some models also make use of “pseudo-absence” data as species absence locations (Phillips et al. 2006, Zaniwski et al. 2002).

The performance and output of any single model varies across studies and is dependent on the type of study and species (Elith and Graham 2009; Guisan and Zimmermann 2000; Marmion et al. 2009; Segurado and Araújo 2004; Thuiller et al. 2009; Virgili et al. 2017). By combining single-model outputs, ensemble modelling can overcome the inconsistency of model outputs, resulting in higher and less biased predictions (Araújo and New 2007; Franklin 2010; Scales et al. 2015; Thuiller et al. 2009). Ensemble modelling, also known as ‘ensemble ecological niche modelling’ (Araújo and New 2007) creates a single predictive surface by combining the output of multiple algorithms. The combined model predictions of ensemble models often produce higher accuracies than that of separate single models (Marmion et al. 2009) resulting in stronger, less biased estimates of species distributions (Grenouillet et al. 2011; Marmion et al. 2009; Scales et al. 2015) and has been used to predict the habitat use patterns of a range of terrestrial (Diniz-Filho et al. 2009) and marine species (Gårdmark et al. 2013; Scales et al. 2015) including cetaceans (e.g. Zanardo et al. 2017).

In the present study, we modelled cetacean distribution by applying an ensemble model to presence-absence datasets, utilising five different modelling algorithms implemented within the BIOMOD2 package in R v.3.4.1 (Thuiller et al. 2009). The ensemble set of models involved a combination of regression type and machine learning methods, including generalised linear models (GLM, McCullagh and Nelder 1989), generalised additive models (GAM, Hastie and Tibshirani 1987), generalised boosted models (GBM, Ridgeway 1999), random forests (RF, Breiman 2001a) and maximum entropy (MaxEnt, Phillips et al. 2006). The goal was to generate the best estimate of predicted distribution ranges for eight cetacean species, by evaluating the performance accuracy of each individual model and to identify which environmental factors have the greatest influence on said ranges.

Generalised linear model (GLM)

Regression models can relate response variables to either a single (simple regression) or combination (multiple regression) set of environmental variables (i.e. the predictor variables). GLMs use a built-in link function to relate the combination of predictor variables to the response variable mean (Guisan and Zimmerman 2000, McCullagh and Nelder 1989). GLMs are parametric models which are frequently used to produce trends of species' presence-absence responses (Guisan and Zimmermann 2000; Praca et al. 2009). These models can be useful for evaluating the significance of the environmental variables used for describing gradients in species distribution modelling (Franklin 2010). They are suggested to perform better than some classification trees (Thuiller et al. 2003) and can produce better results when fitted to datasets with "overabundant" species (Hirzel et al. 2001; Segurado and Araújo 2004).

Generalised additive model (GAM)

Generalised additive models are an extension of GLMs and use the application of a smoothing function for the predictor variables rather than the linear function (Hastie and Tibshirani 1987). The ability of GAMs to fit non-linear relationships allows for greater flexibility in comprehending a wide variety of relationships between explanatory variables, and subsequently generating more complex response shapes (Hastie and Tibshirani 1987; Yee and Mitchell 1991). The biggest advantage of using GAMs in habitat modelling is that they aren't constrained to any specific a priori functional forms (Pearce and Ferrier 2000) which allows for capturing more accurate, non-parametric relationships between cetaceans and their habitat (Redfern et al. 2006). Furthermore, GAMs have been shown to generate models with strong predictive accuracy, often higher than that of other regression model types (Franklin 2010; Pearce and Ferrier 2000; Thuiller et al. 2003). GAMs have also been applied to studies modelling cetacean habitat suitability (Marmion et al. 2009; Redfern et al. 2006; Zanardo et al. 2017).

Generalised boosting model (GBM)

Generalised boosting models are non-parametric models which have recently been introduced in the field of ecology and are considered very efficient in data fitting (Marmion et

al. 2009; Ridgeway 1999). 'Boosting' is a technique where a new tree is added at each step which best minimizes the loss function (such as deviance). The residuals of a tree are then used to build the following step (Ridgeway 1999; Wisz et al. 2008). The origin of GBMs lie within machine learning and has been proposed as an advanced form of regression (Hastie and Tibshirani 1987; Ridgeway 1999). The main difference between regression models and boosting models is that models like GBM use the boosting technique to combine large numbers of regression trees to optimize the predictive performance, whereas regression models produce a single best performing model (Elith et al. 2006; Elith et al. 2008). The basic idea behind boosting is to merge the results generated by multiple algorithms, generally through techniques like bagging and stacking, rather than identifying one model with the highest predictive accuracy (Schapire 2003).

Random forest (RF)

Random forest is a machine learning algorithm which combines multiple classification trees (Breiman 2001a). RF produces hundreds of trees, randomly selecting environmental variables for each tree node (Elith et al. 2008). The model will cluster points with high similarity and run cross-validation to produce higher accuracies of variable importance (Cutler et al. 2007). RF is also able to perform multiple types of data analysis, such as regression, survival analysis and classification. The specific variables selected by the model as being the most important driver for species classification and distribution have also been observed to match expectations derived from literature (Cutler et al. 2007).

Maximum entropy (MaxEnt)

Maximum entropy, which also forms part of the various machine-learning methods available for species distribution modelling, uses a statistical approach to find the most uniform, or spread out, probability distribution generated from the data. It then converts the study area into pixels containing the presence records of the target species and the input environmental features (Phillips et al. 2006). MaxEnt is particularly suited for datasets with small sample sizes and habitat modelling of rare species (Hernandez et al. 2006; Wisz et al. 2008) and has been

applied in a range of cetacean studies (Ainley et al. 2012; Gregr 2011; McClellan et al. 2014; Moura et al. 2012; Pitchford et al. 2016; Smith et al. 2012; Thorne et al. 2012; Zanardo et al. 2017).

The goal was to apply ensemble modelling to presence-absence datasets of eight different cetacean species falling within the same geographical extent, and using the same set of explanatory environmental layers, to predict areas of high occurrence probability. These data were collected from dedicated boat surveys conducted in the waters off the southern Peninsula (as described in chapter two) as well as data collected from associated research focused slightly further east. The additional data were from research surveys with similar methods within the main study area and confident species identification. The modelling algorithm with the highest predictive power (i.e. best performance) was used to reflect on species distribution. The objective was to use the information produced by the ensemble model to explore which environmental factors likely determine the distribution of each species.

METHODS

Data collection

Sightings were collected during boat-based surveys conducted off the south-western coast of South Africa, within False Bay and the Table Bay region, as well as Walker Bay, Struisbaai and Saint Sebastian Bay, between February 2015 and June 2017. The dataset used in the present chapter was a combination of survey data collected during dedicated small boat surveys (the distribution data from chapter two) and data forming part of an extended project focusing more on humpback dolphins but also recording all cetacean species encountered. This resulted in a bigger dataset with increased sightings, compared to the previous chapter, covering a larger extent of the south coast.

Information collected during surveys included species identification; group size and composition, group behaviour, photo identification and the weather conditions of the day. Environmental data were not measured directly due to the data being collected from multiple

boats with different, non-calibrated instruments. For full data collection methods and study site description see previous chapter (chapter two).

Environmental data

Four environmental variables were used to model whale and dolphin distribution: water depth (meters), seabed slope (degrees), sea surface temperature (SST - degree Celsius) and chlorophyll *a* concentration (Chl *a* - mg.m⁻³). The geographical variables, water depth and bathymetric slope, were created from shapefiles in ArcGIS (ESRI Corporation, ArcMap 10.4). To calculate the depth of the study area, a triangular irregular network (TIN) raster was created from a fine scale bathymetry shapefile using the 'TIN' tool within the 3D Analyst toolbox. The original depth layer was also used to create the slope of the seabed, applying the 'Slope' tool within the Spatial Analyst extension. The final raster layers were converted to ascii (.asc) files which are suited for use by the models.

The oceanographic variables, SST and Chl *a*, were satellite derived data retrieved from the NASA Giovanni portal (Geospatial Interactive Online Visualization and Analysis Infrastructure; <http://gdata1.sci.gsfc.nasa.gov/>) on a monthly scale, at 4 km resolution. Direct measures of SST or Chl *a* were not possible due to non-calibrated or unavailable instruments, as a result of collecting sightings from various platforms. Although *in situ* data exist for certain coastal regions in South Africa, the majority of it is collected on archival instruments only downloaded a few times as year, which makes it challenging to access such data for real time projects such as the present study. Temperature data required for the present study was only partially available and inconsistently measured across years and locations, and thus not used for this study.

Monthly SST and Chl *a* layers were averaged into seasons: summer (December to February), autumn (March to May), winter (June to August) and spring (September to November). All predictor variables used for modelling need to have the same spatial extent and resolution. The layers were prepared in R software and ArcGIS and converted to ascii files.

Software

All statistical models were fitted in R (R Development Core Team) under version 3.4.1 using the BIOMOD2 package.

Analytical approach

The goal was to use the sightings locations and the associated environmental factors at that location to determine the predicted areas of suitable habitat for each species using species distribution modelling. The additional sightings data obtained from the combined dataset was used to increase the species presence dataset to reduce bias or weak predictions generated by the model. Absence data were generated from the presence localities of non-target species (i.e. when an area was surveyed, and the target species was not observed, the species was recorded as absent in that particular space and time). Presence points were recorded as the initial location (longitude and latitude) at the onset of an encounter, reflecting the position where the animal was first spotted. Before the ensemble model was applied, the input data were converted to a specific format in order for the analysis to run correctly. During the data formatting phase, the response variables (x-y coordinates of the sighting) and explanatory variables (corresponding environmental data) were defined, and data points without associated environmental data were automatically removed from the dataset and subsequently excluded from further analysis. The ensemble model was performed separately for each species, each consisting of its own presence-absence dataset, and predictions were generated only up to the 200 m contour line. The data were also grouped into seasons, however, due to irregular sampling throughout the year and the natural variation of species encounter rates between seasons, models were generated only for those seasons with sufficient sample sizes.

Model comparison

The predictive performance of a model is evaluated by its ability to deal with raw sightings data and comparing the outputs generated by multiple models (Pearce and Ferrier 2000). Quantifying model performance allows us to determine the suitability of a model (Barry and Elith 2006; Guisan et al. 2006), compare between modelling techniques (Pearson et al. 2006), and assess the accuracy of the prediction maps generated by each model (Segurado and Araújo 2004). One method which is often used is the Area Under the Curve (AUC) of the Receiving Operating Curve (ROC), which is a single threshold-independent measure of model performance (Brotons et al. 2004). However, the practical application of species distribution models (SDMs), such as species hotspot identification or conservation planning, require presence-absence maps to be transformed from ordinal scores into presence-absence predictions of distribution, to which ROC curves cannot be applied (Allouche et al. 2006; Berg et al. 2004; Loiselle et al. 2003). Another increasingly popular method measuring the accuracy of presence-absence predictions is Cohen's kappa (Berg et al. 2004; Loiselle et al. 2003; Pearson et al. 2004; Segurado and Araújo 2004). However, a study by McPherson et al. (2004) concluded kappa's sensitivity as unsuitable for model comparison between species or regions (detailed explanation in McPherson et al. (2004)). Allouche et al. (2006) quantified and compared the predictive accuracies of kappa, the true skill statistic (TSS) and calculated AUC statistics, and concluded that TSS should be the preferred method of quantifying predictive accuracy and serves as a suitable alternative to AUC where model predictions are expressed as presence-absence maps, and kappa as a threshold-dependant measure. It was therefore decided to use the true skill statistic (TSS) to measure the performance of the presence-absence models and predictive maps produced in the present study. The importance of each environmental variable was calculated as a value from 0 to 1, with 1 being the highest ranking and indicating the variable with the strongest influence on the model. Studies investigating the effects of sample size on the performance of SDMs have found that data had to consist of at least 30 samples ($n > 30$) to consistently generate good predictions (Wisz et al. 2008). Therefore, predictions were generated only for datasets where species had a collective presence-absence count of more than 30 sightings within a season.

RESULTS

Dedicated boat-based surveys conducted in the waters off the south-western Cape, between January 2015 and April 2017, as well as the added data collected from dedicated boat surveys conducted in Walker Bay, Struisbaai and St Sebastian Bay, resulted in 425 cetacean encounters (Figure 3.1).

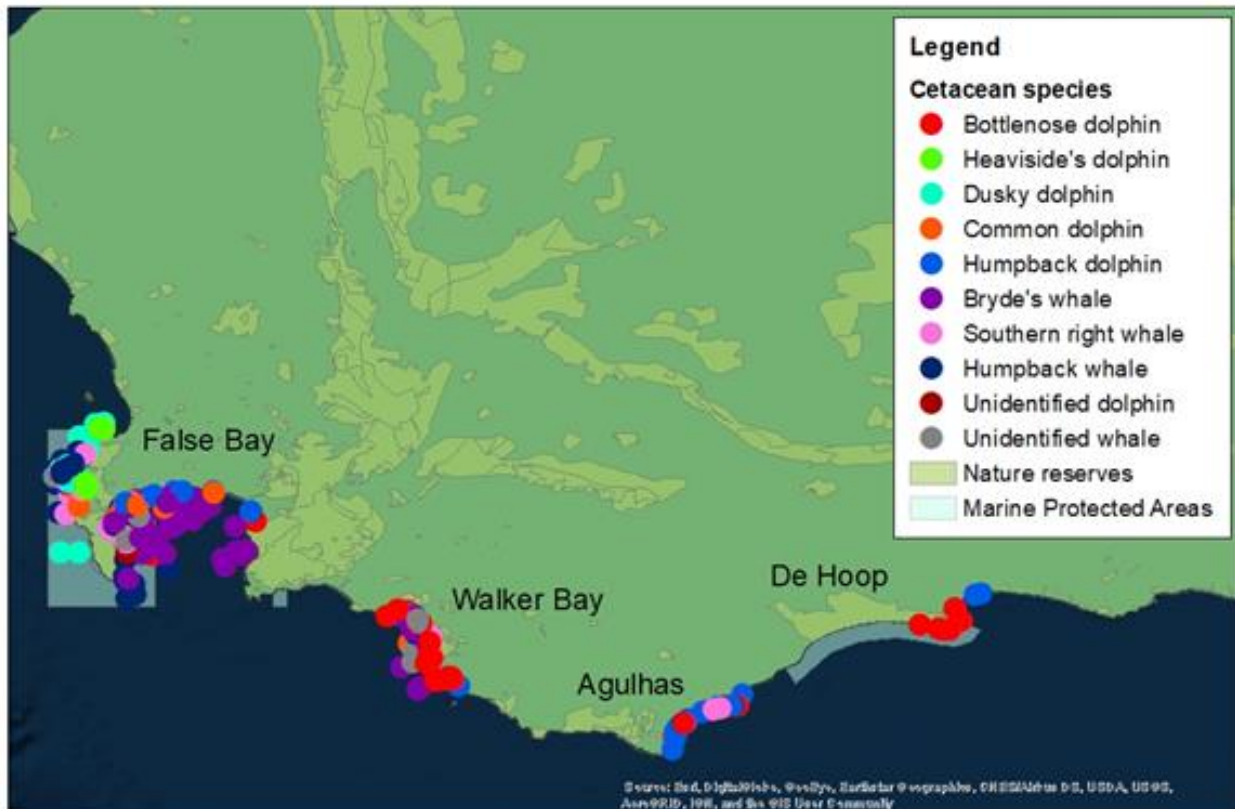


Figure 3.1. The spatial distribution of all cetacean encounters collected during dedicated boat based surveys between February 2015 and April 2017.

Survey effort varied across years and between seasons, mainly as a result of restricting whether conditions. A total of eight species were encountered during the study period; dusky dolphins (*Lagenorhynchus obscurus*), Heaviside's dolphins (*Cephalorhynchus heavisidii*), common dolphins (*Delphinus delphis*), humpback dolphins (*Sousa plumbea*), bottlenose dolphins (*Tursiops aduncus*), and three whale species; southern right whales (*Eubalaena australis*), humpback whales (*Megaptera novaeangliae*) and Bryde's whales (*Balaenoptera brydei*). Ensemble models and subsequent predictions were generated for all eight species.

Dusky dolphin

Dusky dolphins were encountered 28 times off the West coast, predominantly around Table Bay area, during spring and summer. The ensemble model was applied only to encounters collected during spring, as the sample size for summer was too small (presence=3). After data formatting (i.e. matching the sightings location to its associated environmental conditions), the presence-absence (PA) dataset for encounters recorded during spring comprised of 65 observations (presence=7, absence=58). RF and GBM performed equally well (TSS=0.77), generating similar projections of predicted distribution. GAM generated the second highest score (TSS=0.74), followed by GLM (TSS=0.67) and MaxEnt (TSS=0.53). The oceanographic variables, SST and Chl *a*, were the most influential variables for all five SDMs (Table 3.1). GLM and GBM indicated SST as the most important variable, and GAM, RF and MaxEnt suggested Chl *a* as the strongest predictor for dusky dolphin distribution in spring (Table 3.1). The ensemble model predicted a near-continuous distribution of dusky dolphins along the West coast, ranging from the central Cape Peninsula to St Helena Bay (Figure 3.2).

Table 3.1. TSS value outputs of ensemble modelling of dusky dolphins in spring. Models run include GLM (Generalised linear model), GBM (Generalised boosting model), GAM (Generalised additive model), RF (Random forest) and MAXENT (Maximum entropy). Environmental variables include chlorophyll *a* concentration (Chl *a*), sea surface temperature (SST), bathymetry (depth in meters), and slope. Values in bold indicate the variables of highest influence.

	GLM	GBM	GAM	RF	MAXENT
Chl <i>a</i>	0.328	0.196	0.614	0.386	0.744
SST	0.626	0.868	0.433	0.153	0.147
Bathymetry	0.000	0.045	0.004	0.010	0.069
Slope	0.000	0.046	0.109	0.008	0.001

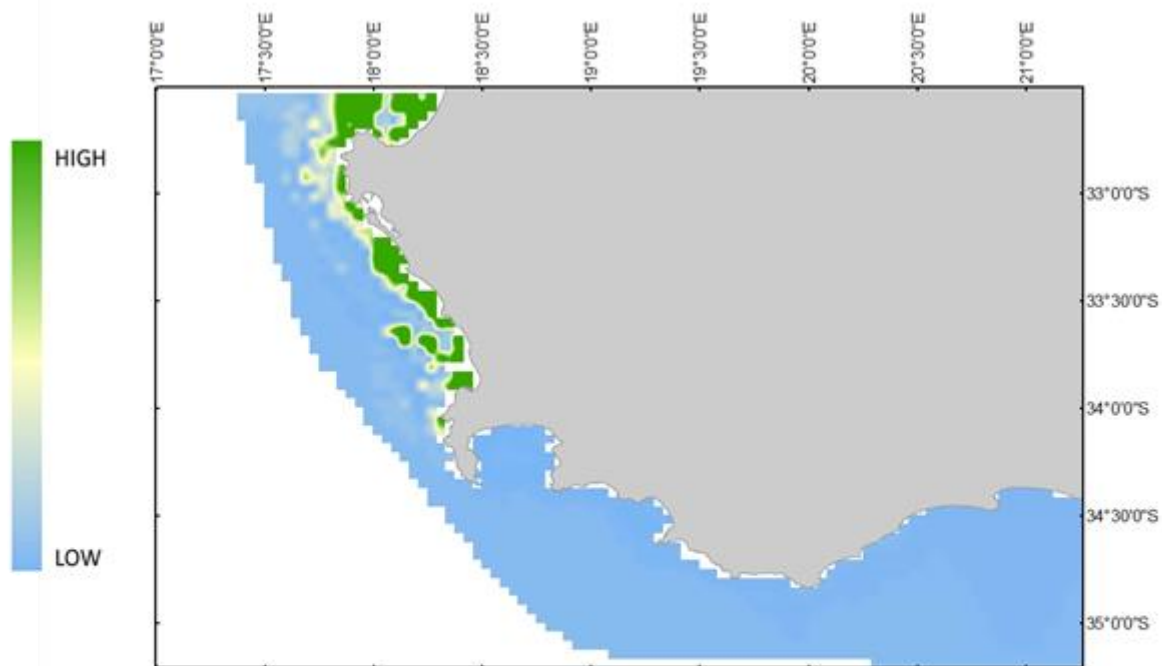


Figure 3.2. The predicted distribution from ensemble modelling of dusky dolphins in the south-western Cape, South Africa during spring. Green colours indicate a higher probability of occurrence. White coloured cells indicate areas where environmental data were not available.

Heaviside's dolphin

Heaviside's dolphins were exclusively encountered off Hout Bay and Mouille Point. A total of 25 encounters were recorded during the study period, mostly during summer. After the data were formatted to fit the model, Heaviside's dolphins had the lowest count of presence-absence points (presence=13, absence=20). As a result of the small sample size, two models, GAM and GBM, failed during analysis. GLM, RF and MaxEnt performed equally well (TSS=0.70). Both GLM and RF suggest SST to be the most important predicting environmental factor, whereas MaxEnt suggested Chl *a* (Table 3.2). The predicted occurrence of Heaviside's dolphins was restricted to the inshore waters of Table Bay, Saldanha Bay and St Helena Bay on the West coast (Figure 3.3).

Table 3.2. TSS value outputs of ensemble modelling of Heaviside’s dolphins in summer. Models run include GLM (Generalised linear model), GBM (Generalised boosting model), GAM (Generalised additive model), RF (Random forest) and MAXENT (Maximum entropy). Due to a limited sample size, two of these models failed: GAM and GBM. Environmental variables include chlorophyll *a* concentration (Chl *a*), sea surface temperature (SST), bathymetry (depth in meters), and slope. Values in bold indicate the variables of highest influence.

	GLM	RF	MAXENT
Chl <i>a</i>	0.000	0.305	0.489
SST	0.894	0.351	0.431
Bathymetry	0.000	0.000	0.246
Slope	0.000	0.071	0.004

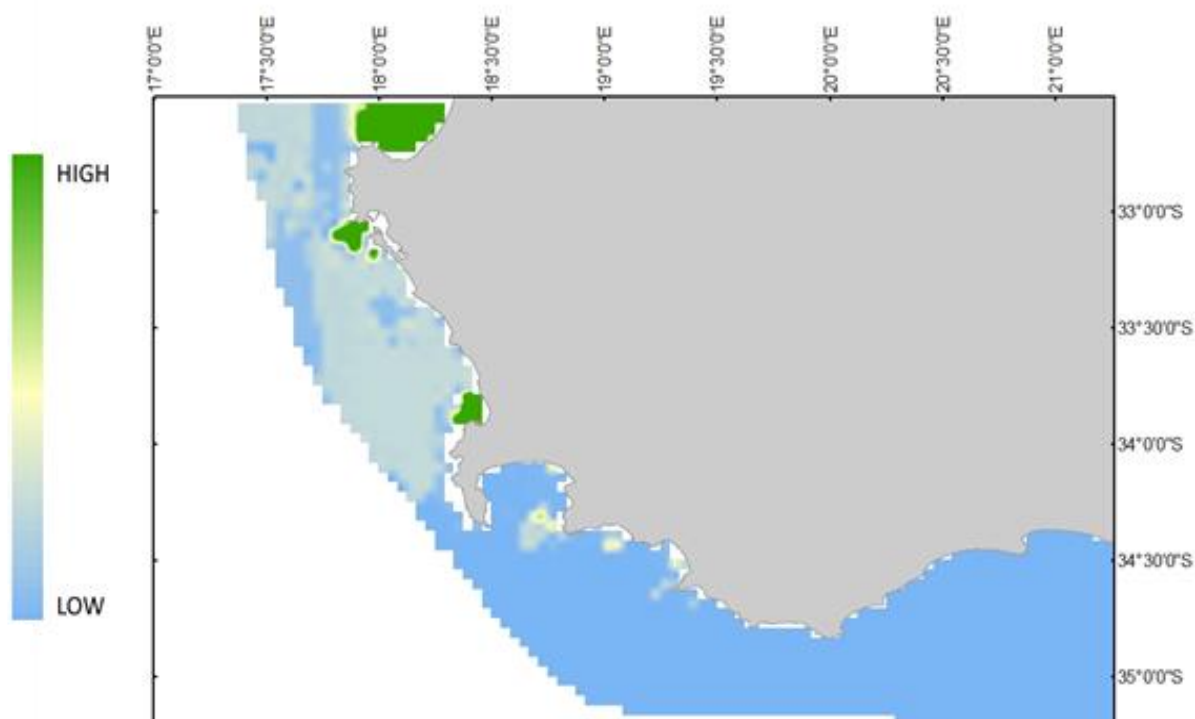


Figure 3.3. The predicted distribution of Heaviside’s dolphins in summer. Green colours indicate a higher probability of occurrence. White coloured cells indicate areas where environmental data were not available.

Common dolphin

Common dolphins were observed a total of 21 times during the study period. After data formatting, the ensemble model was performed for sightings during autumn (presence=9, absence=60), when most encounters were recorded. GLM, GAM, and RF were the three highest performing models, generating very high predictive accuracies (TSS =0.96). All three best performing SDMs identified SST as the most influential variable determining common dolphin distribution (Table 3.3). GBM (TSS=0.61) identified Chl *a* as the most important predictor, and Maxent, which performed poorly (TSS=0.47), suggested bathymetric slope as a strong variable (Table 3.3). Common dolphins were predicted to occur in the offshore waters along the west- and south coast during autumn (Figure 3.4).

Table 3.3. TSS value outputs of ensemble modelling of common dolphins in autumn. Models run include GLM (Generalised linear model), GBM (Generalised boosting model), GAM (Generalised additive model), RF (Random forest) and MAXENT (Maximum entropy). Environmental variables include chlorophyll *a* concentration (Chl *a*), sea surface temperature (SST), bathymetry (depth in meters), and slope. Values in bold indicate the variables of highest influence.

	GLM	GBM	GAM	RF	MAXENT
Chl <i>a</i>	0.472	0.377	0.318	0.084	0.000
SST	0.932	0.114	0.919	0.134	0.115
Bathymetry	0.399	0.012	0.392	0.021	0.107
Slope	0.586	0.044	0.461	0.040	0.771

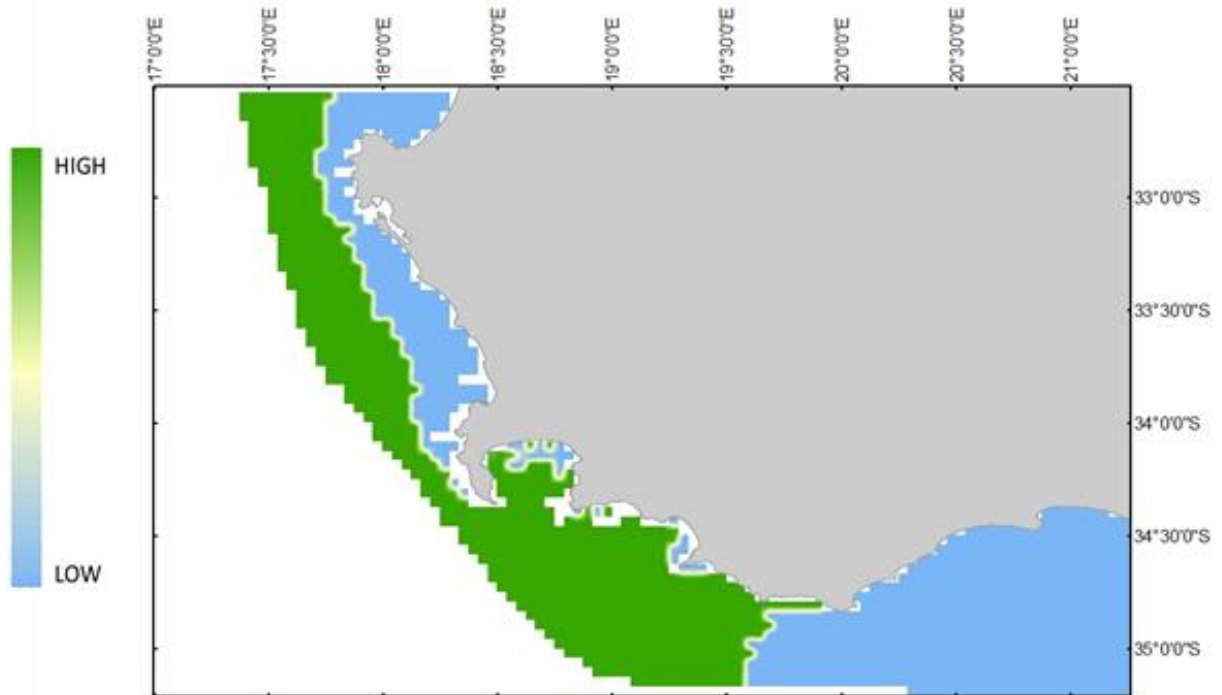


Figure 3.4. The predicted distribution of common dolphins in autumn. Green colours indicate a higher probability of occurrence. White coloured cells indicate areas where environmental data were not available.

Humpback dolphin

Humpback dolphins were all encountered very close to shore in waters east of Cape Point (see Chapter 2), leading to a total of 47 observations. The ensemble model was performed for encounters recorded during autumn (presence=13, absence=47). GLM, GAM, and RF generated equally high scores (TSS = 0.91), followed by GBM (TSS=0.85) and MaxEnt (TSS =0.80). All models indicated depth as the most influential variable determining humpback dolphin distribution (Table 3.4), and predicted occurrences were restricted to coastal habitats along the south-east coast (Figure 3.5).

Table 3.4. TSS value outputs of ensemble modelling of humpback dolphins in autumn. Models run include GLM (Generalised linear model), GBM (Generalised boosting model), GAM (Generalised additive model), RF (Random forest) and MAXENT (Maximum entropy). Environmental variables include chlorophyll *a* concentration (Chl *a*), sea surface temperature (SST), bathymetry (depth in meters), and slope. Values in bold indicate the variables of highest influence.

	GLM	GBM	GAM	RF	MAXENT
Chl <i>a</i>	0.499	0.001	0.309	0.007	0.039
SST	0.000	0.405	0.665	0.237	0.294
Bathymetry	0.722	0.678	0.693	0.366	0.930
Slope	0.000	0.000	0.514	0.017	0.015

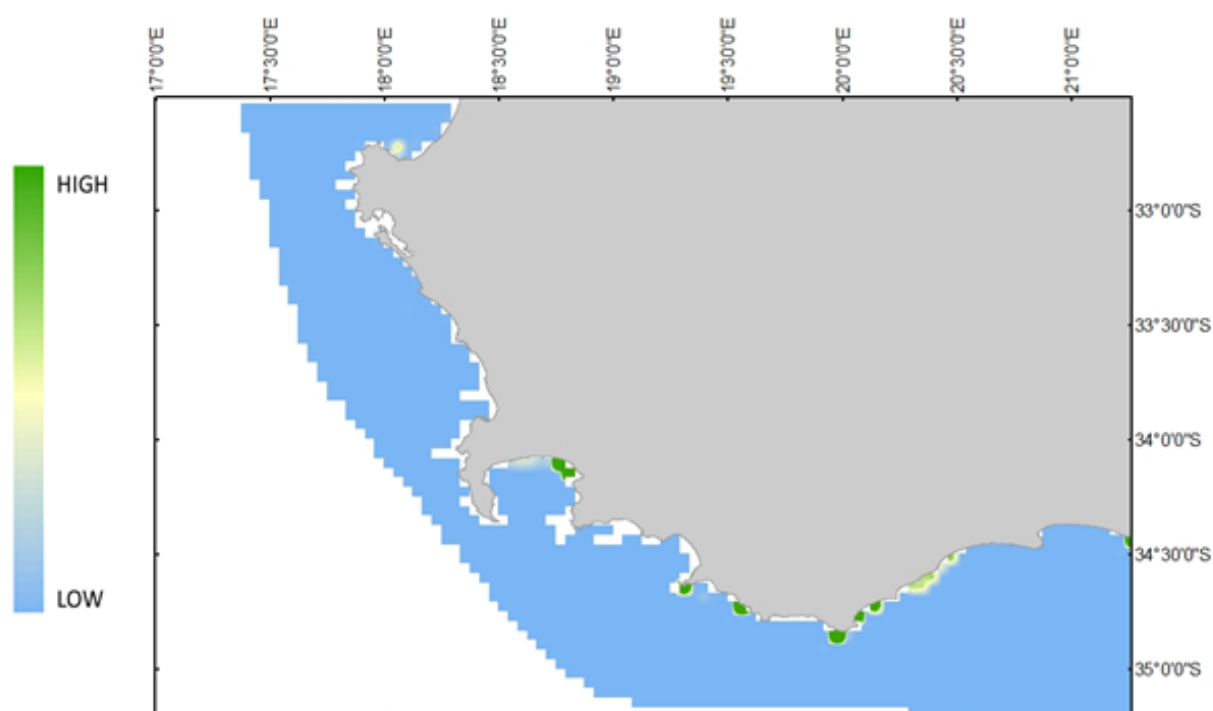


Figure 3.5. The predicted distribution of humpback dolphins in autumn. Green colours indicate a higher probability of occurrence. White coloured cells indicate areas where environmental data were not available.

Bottlenose dolphin

Bottlenose dolphins were recorded 44 times during the study period. The ensemble model was applied for encounters during autumn (presence=15, absence=53). GAM generated the highest predictive accuracy (TSS=0.62), followed by GBM (TSS=0.61), GLM (TSS=0.59), RF (TSS=0.57) and MaxEnt (TSS=0.48). SST was the most influential variable for the four highest performing single SDMs, with GLM generating a near perfect score (> 0.9) and GAM a perfect score of 1.0 (Table 3.5). MaxEnt identified Chl *a* as the strongest predictor (Table 3.5). The model predicted bottlenose dolphins to occur mainly in the offshore waters of the south-east coast (Figure 3.6).

Table 3.5. TSS value outputs of ensemble modelling of bottlenose dolphins in autumn. Models run include GLM (Generalised linear model), GBM (Generalised boosting model), GAM (Generalised additive model), RF (Random forest) and MAXENT (Maximum entropy). Environmental variables include chlorophyll *a* concentration (Chl *a*), sea surface temperature (SST), bathymetry (depth in meters), and slope. Values in bold indicate the variables of highest influence.

	GLM	GBM	GAM	RF	MAXENT
Chl <i>a</i>	0.487	0.052	0.441	0.018	0.614
SST	0.959	0.810	1.000	0.384	0.011
Bathymetry	0.290	0.206	0.810	0.137	0.593
Slope	0.000	0.039	0.532	0.036	0.456

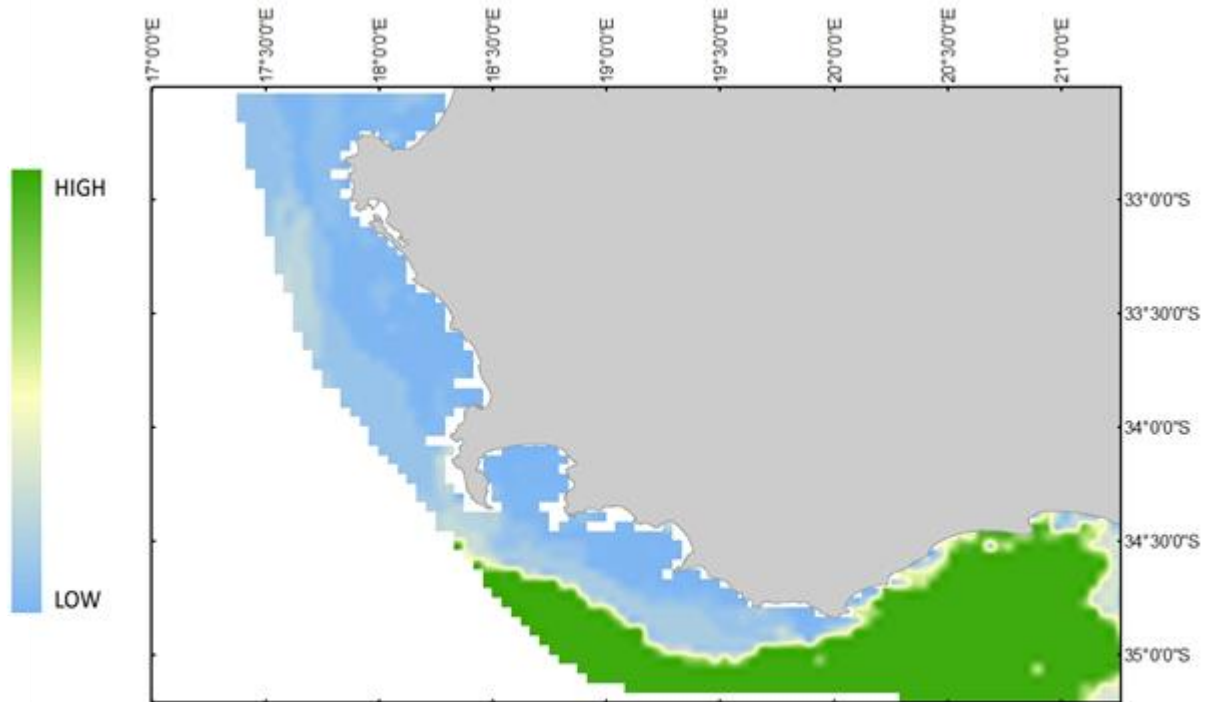


Figure 3.6. The predicted distribution of bottlenose dolphins in autumn. Green colours indicate a higher probability of occurrence. White coloured cells indicate areas where environmental data were not available.

Southern right whale

Southern right whale encounters were higher in winter (49 observations) than in spring (28 observations). The best performing models for encounters during winter (presence=21, absence=16), were GBM, GAM, and RF (TSS=0.82), followed by GLM (TSS=0.78) and MaxEnt (TSS=0.46). The oceanographic variables were identified as important predictors for southern right whale distribution in winter (Table 3.6). Chl *a* was the most important variable for GBM, RF and MaxEnt, and SST was the most important variable chosen by GLM and GAM (Table 3.6). The predicted occurrence for whales in winter were spread along the inshore waters of the coastline, with the highest occurrence predicted on the south coast (Figure 3.7a).

Model performance was similar to that of winter for encounters recorded during spring (presence=16, absence=30). GAM and RF were the highest performing models (TSS=0.86), followed by GBM (TSS=0.83), GLM (TSS=0.70) and MaxEnt (TSS=0.67). The importance of environmental variables varied from winter, and between each of the single SDMs; GLM, GBM and RF identified SST as the most important environmental predictor, GAM suggested depth and MaxEnt suggested slope as the important drivers (Table 3.6). Right whales were predicted further offshore and to the East of the region during spring (Figure 3.7b).

Table 3.6. TSS value outputs of ensemble modelling of southern right whales in winter and spring. Models run include GLM (Generalised linear model), GBM (Generalised boosting model), GAM (Generalised additive model), RF (Random forest) and MAXENT (Maximum entropy). Environmental variables include chlorophyll *a* concentration (Chl *a*), sea surface temperature (SST), bathymetry (depth in meters), and slope. Values in bold indicate the variables of highest influence.

	Winter					Spring				
	GLM	GBM	GAM	RF	MAXENT	GLM	GBM	GAM	RF	MAXENT
Chl <i>a</i>	0.559	0.547	0.351	0.429	0.732	0.000	0.022	0.619	0.015	0.091
SST	0.724	0.210	0.812	0.194	0.000	0.991	0.775	0.176	0.433	0.055
Bathymetry	0.000	0.014	0.538	0.015	0.150	0.000	0.02	0.779	0.049	0.57
Slope	0.242	0.139	0.306	0.095	0.175	0.167	0.081	0.567	0.121	0.509

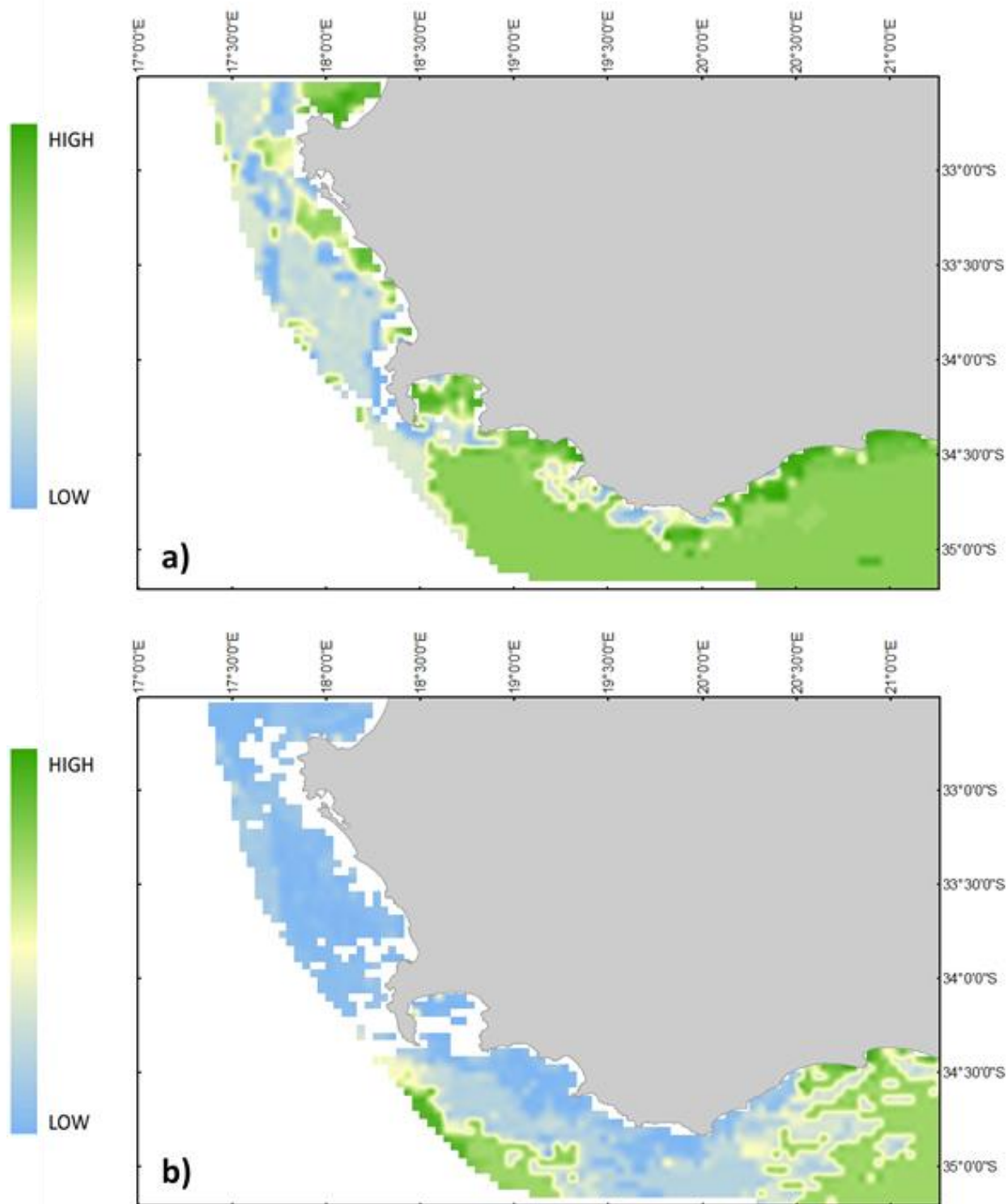


Figure 3.7. Predicted distribution of southern right whales during (a) winter and (b) spring. Green colours indicate a higher probability of occurrence. White coloured cells indicate areas where environmental data were not available.

Humpback whale

Humpback whale encounters were more frequent in spring (43 observations) than winter (17 observations). The performance of models for winter (presence=7, absence=32) were lower compared to spring. GAM generated the highest predictive accuracy (TSS=0.87) for winter, followed by RF (TSS=0.85), GBM (TSS=0.81), GLM (TSS=0.65) and MaxEnt (TSS=0.57). GLM, GAM and MaxEnt identified depth as the most important environmental predictor, whereas GBM and RF suggested slope as the most important predictor (Table 3.7). Humpback whales were predominantly predicted to occur off the West coast during winter (Figure 3.8a).

The highest performing models for humpback whale encounters in spring (presence=22, absence=45) were GBM, GAM, and RF (TSS=0.91), followed by GLM (TSS=0.72) and MaxEnt (TSS=0.68). All models identified depth as the most influential environmental factor, except for GLM, which suggested SST as the most important factor driving humpback whale distribution in spring (Table 3.7). The model predicted high occurrence of whales throughout the study region (Figure 3.8b).

Table 3.7. TSS value outputs of ensemble modelling of humpback whales in winter and spring. Models run include GLM (Generalised linear model), GBM (Generalised boosting model), GAM (Generalised additive model), RF (Random forest) and MAXENT (Maximum entropy). Environmental variables include chlorophyll *a* concentration (Chl *a*), sea surface temperature (SST), bathymetry (depth in meters), and slope. Values in bold indicate the variables of highest influence.

	Winter					Spring				
	GLM	GBM	GAM	RF	MAXENT	GLM	GBM	GAM	RF	MAXENT
Chl <i>a</i>	0.000	0.224	0.318	0.328	0.413	0.262	0.007	0.336	0.027	0.002
SST	0.000	0.025	0.376	0.037	0.001	0.800	0.093	0.472	0.135	0.012
Bathymetry	0.936	0.148	0.676	0.325	0.780	0.000	0.699	0.722	0.443	0.932
Slope	0.000	0.573	0.510	0.432	0.025	0.057	0.048	0.282	0.027	0.003

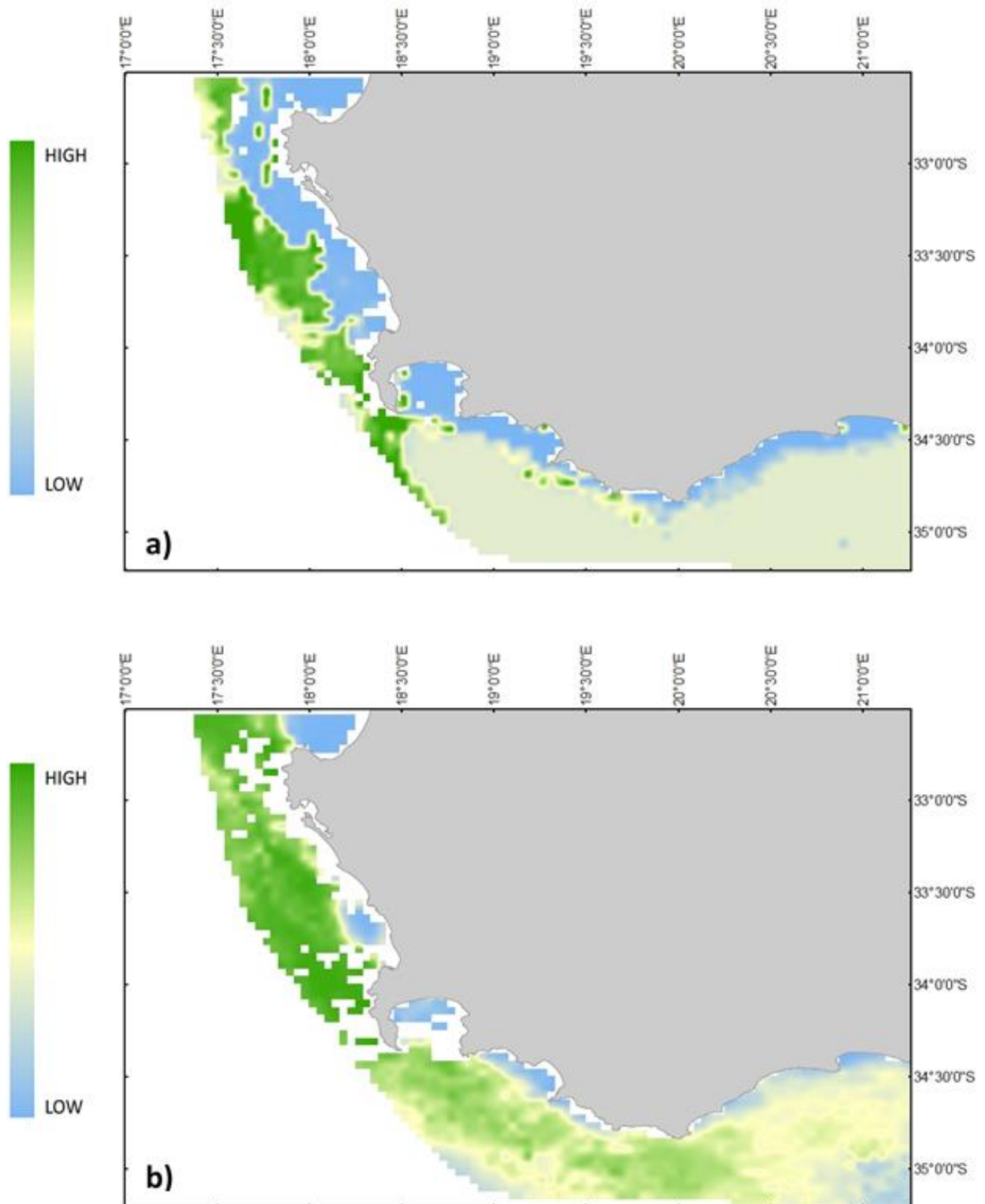


Figure 3.8. Predicted distribution of humpback whales during (a) winter and (b) spring. Green colours indicate a higher probability of occurrence. White coloured cells indicate areas where environmental data were not available.

Bryde's whale

Bryde's whales were the most frequently encountered cetacean species throughout the study period, with a total of 82 observations. The ensemble model was applied to encounters recorded during autumn (44 observations) and spring (27 observations). The highest performing model for autumn (presence=27, absence=36), was RF (TSS=0.68), followed by GAM (TSS=0.63), GBM and GLM (TSS=0.58) and MaxEnt (TSS=0.44). All models, except for MaxEnt, identified SST as the most important predictor, with GLM generating a near perfect score (> 0.9) and GAM a perfect score of 1 (Table 3.8). MaxEnt identified Chl *a* as the most important environmental driver (Table 3.8). The predicted range for Bryde's whale occurrence in autumn was spread throughout the study region (Figure 3.98a).

The highest performing models for spring (PA=75: presence=27, absence=48) was RF and GBM (TSS=0.76), followed by GAM (TSS=0.71), GLM (TSS=0.48) and MaxEnt (TSS=0.42). SST was the most important predictor for GBM, GAM, and RF, whereas depth was the most important variable for GLM and MaxEnt (Table 3.8). The predicted distribution for Bryde's whales in spring was restricted to the inshore waters between False Bay and Cape Agulhas (Figure 3.9b).

Table 3.8. TSS value outputs of ensemble modelling of Bryde's whales in autumn and spring. Models run include GLM (Generalised linear model), GBM (Generalised boosting model), GAM (Generalised additive model), RF (Random forest) and MAXENT (Maximum entropy). Environmental variables include chlorophyll *a* concentration (Chl *a*), sea surface temperature (SST), bathymetry (depth in meters), and slope. Values in bold indicate the variables of highest influence.

	Autumn					Spring				
	GLM	GBM	GAM	RF	MAXENT	GLM	GBM	GAM	RF	MAXENT
Chl <i>a</i>	0.319	0.108	0.376	0.133	0.852	0.000	0.033	0.248	0.041	0.217
SST	0.922	0.588	1.000	0.285	0.021	0.000	0.600	0.918	0.338	0.000
Bathymetry	0.000	0.069	0.044	0.077	0.103	0.780	0.039	0.068	0.038	0.534
Slope	0.288	0.044	0.146	0.065	0.064	0.342	0.133	0.009	0.137	0.373

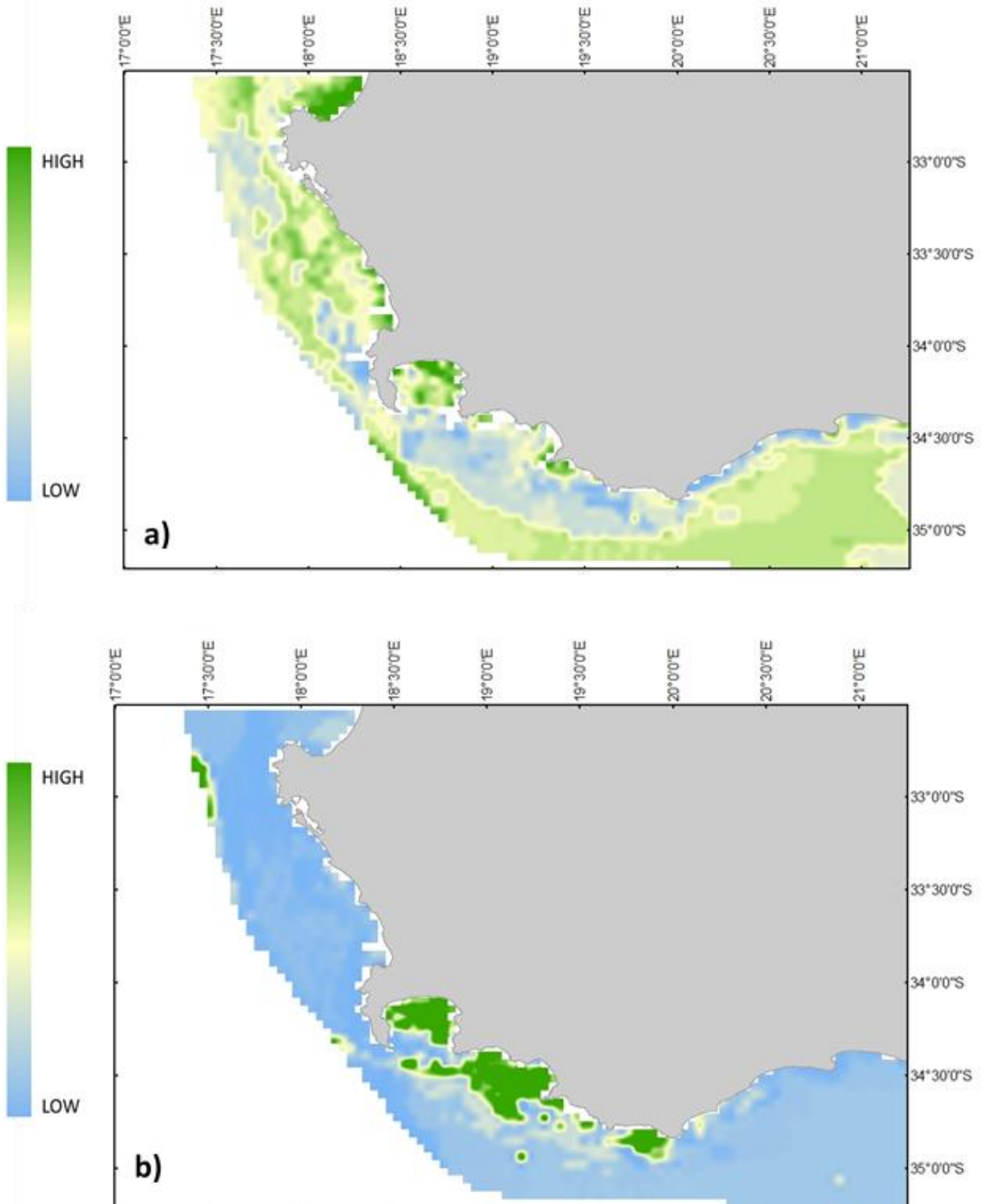


Figure 3.9. Predicted distribution of Bryde's whales during (a) autumn and (b) spring. Green colours indicate a higher probability of occurrence. White coloured cells indicate areas where environmental data were not available.

DISCUSSION

Species distribution models are frequently used by ecologists to explore relationships between species and their environment. These models are useful for identifying ideal environmental conditions, prioritizing the importance of explanatory variables, and predicting the occurrence of species in unknown areas (Elith et al. 2008). The outputs of species distribution models are influenced by the choice of environmental variables (Araújo and Guisan 2006) and are considered a crucial step in model selection (Guisan and Zimmermann 2000). In the marine environment, oceanographic features, like sea surface temperature (SST) and primary productivity (chlorophyll *a* concentration), are considered important drivers influencing variability in cetacean seasonality and habitats (Burtenshaw et al. 2004). Sea surface temperature can have direct or indirect effects on cetacean distribution. Firstly, it can act as a thermal barrier to movement; the “thermoneutral zone” of dolphins is the specific temperature range within which animals spend the least amount of energy to maintain their core temperature. Alternatively, sea surface temperatures can indirectly affect cetacean movement by affecting prey movements (Barco et al. 1999; Lusseau et al. 2004). Increases in water temperature result in the shift in distribution ranges of fish species (Perry et al. 2005). Plankton communities are also affected by sea surface temperatures, and productivity can be reduced as a result of unfavourable climatic conditions - such as increases in water temperature (Shannon et al. 1992). Geographical variables such as water depth and bathymetric slope are also considered to be important for determining cetacean distribution, although the effects are likely more direct in relation to the distribution of their prey (Cañadas et al. 2002).

Results from the present study indicated that SST was an important driver determining the distribution of Heaviside’s dolphins, common dolphins as well as bottlenose dolphins. Chlorophyll *a* concentration was suggested as the most important driver for dusky dolphin distribution, while depth was the most important factor determining the distribution of humpback dolphins.

The most important driver determining the distribution of southern right whales changed from Chl *a* in winter, to SST in spring. Depth was suggested as the driver for humpback whale

movements in both winter and spring, and SST the most important factor determining Bryde's whale distribution in autumn and spring.

Explanatory data and their implications

The oceanographic variables used in the present study were derived from satellite imagery. This was largely owing to the sightings data being collected from multiple platforms with different, non-calibrated instruments, or in some cases where the appropriate instruments were not available. Satellite-derived data, such as SST and Chl *a*, are often applied to studies modelling the distribution of cetaceans (e.g. Cañadas et al. 2005; Cañadas and Hammond 2008; Moura et al. 2012; O'Donoghue et al. 2010; Praca et al. 2009). However, Smit et al. (2013) describe the concerns around using satellite-derived data rather than direct measures of environmental data, especially when targeting coastal habits. During their study, sea surface temperatures derived from satellite images were compared to *in situ* measures taken within 400 m from the South African shore, showing large biases (sometimes up to +6°C) in satellite-derived data (Smit et al. 2013). Temperatures measured from satellite imagery were mainly warmer than those taken from direct measurements, however, colder estimates were also common on the south and west coast (Smit et al. 2013).

During the data formatting phase of species distribution modelling, sample sizes are reduced when any of the associated environmental data are missing as these points are removed from analysis. Generally, sighting localities without associated environmental data were automatically discarded by the model, leading to a reduction in the final number of presence points available for analysis. This is typical in studies using remotely-sensed satellite data, which often contain "no-data" cells due to limitations of satellite coverage or cloud presence. Areas with unavailable data are usually located close to shore, which is of obvious concern for studies targeting coastal species (Smit et al. 2013). Many encounters recorded in the present study were within two kilometres of the coastline, which resulted in several presence localities with no, or incomplete, associated environmental data. We therefore strongly suggest the use of *in situ* environmental data concurrent with sightings data, or at least complete environmental data coverage of the target region in the case where the use of satellite data cannot be avoided.

The performance of models

Statistical models typically have a set preference for specific types of response variables and their associated functions for generating distribution probabilities (Guisan & Zimmerman 2000). Machine learning methods are essentially a set of algorithms developed by computer scientists, to generate predictions without the initial assumption of an appropriate model (like regression methods), by first observing the relationship between the input and response variables before identifying the dominant patterns (Breiman 2001b). This could explain the higher performance accuracy of the machine learning methods applied in the present study, especially the random forest model, compared to some regression type models.

Generalised linear models (GLMs) are considered useful for testing the significance of environmental variables (Franklin 2010) and often perform better than other classification type models (Thuiller et al. 2003). In the present study, however, GLMs performed worse than generalised additive models (GAMs), generating lower predictive accuracies for all three whale models (consisting of data sets with larger sample sizes), and most of the dolphin models, with the exception of Heaviside's dolphins, when GAM failed to produce any predictions due to the small dataset. Apart from that, GAMs were one of the top performing models, generating high predictive accuracies and consistently being one of the top three best performing algorithms of all generated models.

MaxEnt has been suggested as a suitable model for datasets with small sample sizes and rarely encountered species (Hernandez et al. 2006; Pearson et al. 2006; Wisz et al. 2008). These findings, together with the increasing popularity of its use in species distribution modelling, motivated the decision to include MaxEnt in the present study, as some of our species did have notably small sample sizes, particularly humpback- and Heaviside's dolphins. Although Heaviside's dolphins were encountered more frequently than humpback dolphins, they had the smallest sample size across all species, followed by humpback dolphins. As expected, the predictive scores produced by MaxEnt for all species were the highest for these two dolphin species. However, the individual performance of the models was compared for each species independently, and not across species, as each dataset and its matching environmental data varied between seasons and species. Within species-specific groups, MaxEnt consistently

generated the lowest predictive accuracies, indicating weaker discrimination of suitable habitats by this model compared to the other models.

The predicted ranges of species

Dusky dolphins

The ensemble model predicted a near-continuous distribution of dusky dolphins along the west coast, ranging from the southern Peninsula to St Helena Bay. The distribution of cetaceans on South Africa's west coast is influenced by the cool waters and associated upwelling cells of the Benguela Current (Findlay et al. 1992). The Cape Columbine upwelling cell is situated off St Helena Bay (Shannon et al. 1992) creating areas of high productivity within the region, which could explain the high occurrence of cetaceans, including dusky dolphins, in and around the area (Elwen et al. 2009). The most influential variables for dusky dolphin distribution were SST and chlorophyll *a* concentration. The intrusion of unusually warm waters with low chlorophyll *a* concentration in cold water systems like the Benguela can negatively affect the spawning success of fish, subsequently reducing the abundance of available prey (Shannon et al. 1992). Chlorophyll concentrations can directly affect the productivity of plankton communities, which in turn impacts the abundance and availability of fish (Shannon et al. 1992), and subsequently the movement of cetaceans (Lusseau et al. 2004). Therefore, the predicted influence of sea surface temperature and chlorophyll *a* concentration on dusky dolphin distribution is likely indirect, acting through the distribution of their prey. Furthermore, the number of observed dusky dolphins in the inshore waters of St Helena Bay has been shown to decrease significantly when upwelling conditions were present further offshore (Elwen et al. 2009). In other parts of the world, dusky dolphins are also strongly associated with cool water temperatures, generally around 14°C to 15°C (Gaskin 1968).

Heaviside's dolphins

Heaviside's dolphins are endemic to the Benguela Ecosystem and commonly found in waters less than 100 m deep (Findlay et al. 1992). In the present study, restricted occurrences of Heaviside's dolphins were predicted at three sites along the west coast: Hout Bay, Saldanha Bay and St Helena Bay. Similar to the findings for dusky dolphins, SST and chlorophyll *a* were suggested as the variables most strongly influencing the distribution of this species. Strongly linked patterns between the movement of Heaviside's dolphins and their prey have been observed in their predicted range on the west coast (Elwen et al. 2006; 2009). Findings from Elwen et al. (2009) show that Heaviside's dolphins demonstrate clear movement patterns between the inshore and offshore waters in St Helena Bay, as they move offshore at night to feed, and utilise the sheltered inshore waters of the coast during the day to rest. The inshore-offshore movement pattern of Heaviside's dolphins is presumably driven by their prey (Elwen et al. 2009), predominantly consisting of hake (*Merluccius capensis*; Sekiguchi 1994), which are thought to migrate to the surface waters during the night (Pillar and Barange 1995). This could explain the strong suggested influence of the oceanographic variables on this species, although more indirectly, as chlorophyll concentrations and sea surface temperature directly influence the distribution of their prey (Moura et al. 2012; Perry et al. 2005; Shannon et al. 1992). As Heaviside's dolphins are resident to the cool waters of the Benguela Ecosystem, the identification of SST as a main predictor variable could indicate that variations in climatic conditions, especially increases in water temperature, may have direct impacts on the distribution of this species, possibly resulting in the reduction of their preferred range.

Common dolphins

Common dolphins were predicted to occur in the offshore waters of the west- and south coast during autumn, and sea surface temperature was identified as the most important environmental variable determining their distribution. The cool waters of the Benguela Ecosystem are associated with upwellings of high productivity which can influence the availability of prey species (Cañadas and Hammond 2008, Shannon et al. 1992). The high productivity and subsequent prey availability in this region can explain the high predictive occurrence of common dolphins in the south-western region of the study area. Similar

findings were described for common dolphins in the southwestern Mediterranean, where strong increases in common dolphin density were found in areas with higher chlorophyll concentrations, caused by upwellings of high productivity as a result of cool waters (Cañadas and Hammond 2008). Yet, Neumann (2001) strongly suggests that SST is not a primary factor influencing the distribution of common dolphins but rather has a more direct effect on the distribution of their prey, which in turn influences the seasonal movements of the dolphins. Common dolphins are also known to follow the annual winter migration of their prey along the South African east coast, during the sardine run, which is the result of cold water counter current formations by temporary cyclonic eddies (Roberts et al. 2010). The influx of sardines on the narrow continental shelf of the east coast and their accompanying predators (including several species of cetacean, sharks and birds) form a concentrated mass of marine life in the inshore waters (Caputo et al. 2017; van der Lingen et al. 2010; Roberts et al. 2010). Common dolphins are strongly associated with sardines and considered a main predictor of sardine presence (O'Donoghue et al. 2010).

Humpback dolphins

The predicted occurrence of humpback dolphins was restricted to areas on the south and east coast. They are currently known to occur in shallow waters along the south and east coast of South Africa (Peddemors 1999; Plön et al. 2016; Vermeulen et al. 2017). All models identified depth as the most influential variable determining humpback dolphin distribution, a well-known characteristic of this species as the majority of the population is suggested to occur within 2 km of the coastline (Plön et al. 2016). Humpback dolphins were also predominantly observed in shallow habitats during other studies further along the coast in Plettenberg Bay (Saayman. et al. 1972), Algoa Bay (Karczmarski et al. 2000), and Richards Bay (Keith et al. 2013). A previous study which focused on the relationship between humpback dolphins and their surrounding environmental conditions in Plettenberg Bay, reported no seasonal variations in sighting rates and abundance in response to sea surface temperature (Saayman et al. 1972). Similar findings were noted in Richards Bay, where the spatial distribution of humpback dolphins was unrelated to a combination of environmental variables, including temperature (Atkins et al. 2004). However, the authors suggested that it could likely be due

to the measured variables falling within the ideal range of humpback dolphins (Atkins et al. 2004).

A recent study in Mossel Bay, about 500 km east of False Bay, shows a degree of overlap between humpback dolphins in Mossel Bay and Plettenberg Bay (James et al. 2015), suggesting long distance movement along the coast. James et al. (2015) suggests a seasonal movement from Mossel Bay to Algoa Bay during winter, and a westward movement from Algoa Bay at the end of summer. This could explain the lack of seasonal movement observed in Plettenberg Bay by Saayman et al. (1972), as this is a central area between seasonal movements along the south coast. Vermeulen et al. (2018) show regular movements of up to 200 km along the shore, with occasional movements up to 500 km.

In the present study humpback dolphins were encountered in False Bay on multiple occasions, exclusively in the shallow waters along the stretch of sandy beaches. As discussed previously, the western range limit has previously been defined as Cape Agulhas (Findlay et al. 1992), after which Best (2007) proposed a westward expansion of animals up to Danger Point based on more updated sightings. The present study indicates a clear range extension of humpback dolphins into False Bay, with the westernmost encounter recorded in Muizenberg. The cooler waters of the Benguela ecosystem have been suggested as the limiting factor restricting a westward expansion (Best 2007, Findlay et al. 1992). However, it is likely a combination of geographic and physical factors that is creating a boundary for this species.

Humpback dolphins are known to prefer estuaries (Atkins et al. 2004, Karczmarski et al. 2000, Vinding et al. 2015) which are less prevalent to the west of Muizenberg and Cape Point. They also prefer sandy beaches (Atkins et al. 2004, Saayman et al. 1972, Vinding et al. 2015) and the majority of the Cape Peninsula consists of steep rocky shores. It is likely that the rocky shore dominated Peninsula, vacant of large river mouths and the presence of cool temperate waters below 15°C (Smit et al. 2013) inhibits the further westward expansion of humpback dolphins. Furthermore, we suggest that the north-western corner of False Bay is the effective western range end of humpback dolphins. Moreover, the possible reduction of the transitional warm-temperate ecoregion on the south-east coast noted by Mead (2011) and Mead et al. (2013) as a result of increasing sea temperatures in the western edge of the Agulhas Current (Rouault et al. 2010) as well as the increased abundance of tropical fish in the region (Lloyd et al. 2012) due to a southward range expansion (James et al. 2008) could further

motivate and explain the observed westward expansion of humpback dolphins into this region. Given the different suite of environmental conditions present at this end of the species' range, it would be reasonable to expect a strong influence of oceanographic variables such as water temperature on their distribution. However, all models in the present study identified water depth as the most influential variable determining humpback dolphin distribution. The preference of shallow habitats is important for feeding behaviour (Atkins et al. 2004; Keith et al. 2013) which could support the strong suggested influence of shallow waters as the most suitable habitat.

Bottlenose dolphins

Indo-Pacific bottlenose dolphins were predicted in slightly deeper waters off the south-east coast of the study region. This prediction falls within the current known distribution range of bottlenose dolphins, ranging from Cape Agulhas, along the east coast and into the Indo-Pacific, with the most westerly observations recorded in False Bay (Best 2007). Our models predicted strong habitat use in the offshore region over the continental shelf. However, Indo-Pacific bottlenose dolphins typically occupy shallower inshore waters of the coast (Peddemors 1999; Reisinger and Karczmarski 2009; Ross et al. 1989; Vinding et al. 2015). In the present study, the most important environmental predictor describing bottlenose dolphin distribution was SST. The waters of the Agulhas Current on the east coast are warmer than those of the Benguela Current on the west coast (Findlay et al. 1992; Lutjeharms et al. 1989). Globally, Indo-Pacific bottlenose dolphins have also been found to prefer areas with higher water temperatures (Barco et al. 1999; Pitchford et al. 2016; Saayman. et al. 1972). These findings support the predicted occurrence of this species in the warmer waters of the east coast.

It has also been suggested that there is a strong link between bottlenose dolphin distribution and associated foraging opportunities (Hastie et al. 2004). They are considered generalist feeders (Cockcroft and Ross 1990) and are frequent predators in the annual sardine run off the KwaZulu Natal coast (Caputo et al. 2017; O'Donoghue et al. 2010), often being the most frequently sighted cetaceans during this event (O'Donoghue et al. 2010). Correspondingly, SST is suggested as the main predictor determining the sardines' eastward migration (Armstrong et al. 1991). The inshore waters of the east coast experience seasonal cooling

during winter, subsequently falling within the preferred temperature range of the sardines (Barange and Hampton 1997). The high occurrence of bottlenose dolphins during this event indicates a tolerance by this species for both warm and cooler temperatures. Similar findings were observed during a study in Mossel Bay, where high encounter rates were recorded at both ends of the temperature range (Levy 2017).

The inshore occurrence of bottlenose dolphins and the opposing offshore habitat suitability predicted by the models, suggest that there might be other factors driving the coastal distribution of bottlenose dolphins. Off the Natal coast, bottlenose dolphins have been found to actively avoid large shark species (Cockcroft et al. 1989). Shark attacks on Natal bottlenose dolphins are fairly common and as a result these dolphins have likely adapted their behaviour in response to the predation pressure of sharks (Cockcroft et al. 1989). It is likely that such predation pressures together with the distribution of prey species have a more direct influence on the movements and coastal distribution of bottlenose dolphins, rather than physical oceanographic conditions like sea surface temperature, as predicted by the models in the present study.

Southern right whales

Southern right whales are increasingly observed along the Southern African coastline (Barendse and Best 2014; Best 2007; Melly et al. 2018; Vinding et al. 2015) with a peak in encounters during their winter breeding season when the whales migrate from their feeding grounds in the Southern Ocean to lower latitudes where they breed and rear their young (Best and Scott 1993). Southern right whale distribution shows a preference for shallow, protected waters associated with sandy bottom types off the South African coast during winter and spring (Elwen and Best 2004). The calm, shallow waters of coastal areas aid in the protection of cow-calf pairs from potential predators (Thomas 1987), as well as a decrease in the energy expenditure of new born calves who are still weak swimmers (Thomas and Taber 1984). Calm water is considered a primary factor determining the habitat choices of right whales during their breeding season (Elwen and Best 2004). This preference for shallow, sandy beaches can explain the high predicted occurrence by our models in areas such as St Helena Bay, False Bay,

Walker Bay (also shown in Elwen and Best 2004), Struisbaai and De Hoop, which all consist of sandy beaches.

The predicted offshore movement of right whales in spring coincide with the migration period (June – December) (Best and Scott 1993) and can be interpreted as the whales' departure from the coastline during spring (the end of their breeding season) to return to their southern feeding grounds. It is suggested that right whales rarely feed in coastal waters during their breeding season (Best 2000; Best and Schell 1996). However, more recent patterns propose feeding of right whales in the southern Benguela (Barendse et al. 2010) and studies now show that the South African west coast is increasingly being used as a feeding ground for this species (Barendse and Best 2014; Peters et al. 2011). Correspondingly, our models indicated chlorophyll *a* concentration as a strong predictor affecting right whale distribution in winter. These findings suggest that the animals seen in the current study region form part of a feeding aggregation of individuals which are no longer within a breeding phase, but rather utilising the coast for migration and feeding at the end of the season.

Humpback whales

The winter migration of humpback whales from their southern feeding grounds to their northern breeding grounds has been described as a predictable and seasonal event (Best et al. 1998; Best et al. 1995) when humpback whale encounters peak along the South African coast (Vinding et al. 2015). The most important driver describing humpback whale distribution patterns is suggested to be suitable reproductive habitats, to the extent that individuals are likely to inhabit areas of less optimal water temperatures during their wintering season if those areas provide them with protected, shallow breeding habitats (Rasmussen et al. 2007). Although it has been noted that some whales utilise certain areas of the coast (currently unidentified) as breeding and calving grounds (Carvalho et al. 2014), migrating humpback whales are frequently observed feeding in the Southern Benguela (Barendse et al. 2010). Findlay et al. (2017) suggests that the west coast is becoming an important seasonal feeding ground for humpback whales, which attracts significant movements of this species into the area in late spring to early summer, and that animals are possibly suspending their migration in order to feed along the coast.

In the present study, humpback whales were predicted to occur predominantly on the west coast during winter and spread through the entirety of the study region in spring. Depth was indicated as the most influential environmental predictor determining the distribution of humpback whales along the South African coastline during winter and spring. The suggested importance of depth corresponds to other studies indicating water depth as the main driver for humpback whales during breeding season (Smith et al. 2012). This could be a result of the coastal occurrence of humpback whale encounters recorded in the present study area. The proposed breeding of some individuals along the coast (Carvalho et al. 2014) further supports the predicted importance of depth as an environmental driver.

The suspended migration and subsequent feeding behaviour (Best et al. 1995, Findlay et al. 2017) could explain the persisted occurrence of this species throughout spring, as indicated by my models. Humpback whales encountered at the beginning and end of the wintering season are likely those migrating to and from their breeding grounds in the north. It would therefore be reasonable to expect the ambiguity of predictors, since environmental predictors might not have a strong influence on animals just passing through our coastal waters. On the other hand, the suspended migration of those individuals gathering in large groups in the southern Benguela to feed (Best et al. 1995, Findlay et al. 2017), are more likely to be influenced by cool water temperatures and high productivity as these factors influence prey availability (Perry et al. 2005). However, my sample size prevented me from determining if this was the case in the present study.

Bryde's whales

Bryde's whales have a year-round occurrence in the shelf waters of South Africa (Best 2001) as they do not migrate to specific breeding or feeding grounds (Best 1977). Best (2001) proposes that it is likely that individuals of the inshore Bryde's whale population moves north along the west and east coast during autumn and winter and return to the Agulhas Bank in spring. These movements are related to the eastward migration of prey during the annual sardine run, where large shoals of fish aggregate off the Natal coast (Best 2001; O'Donoghue et al. 2010; Penry 2010; Penry et al. 2011; Wiseman and Nicky 2008). The seasonal patterns described by Best (2001) are supported by the findings of the present study where our models

predicted Bryde's whale occurrence spread throughout the south-western Cape region in autumn (when individuals move north along both coasts), and the restricted distribution between the False Bay and Cape Agulhas during spring (when individuals return to the Central Agulhas Bank). The most important predictor variable suggested by our models was sea surface temperature, corresponding to findings further along the south coast where encounter rates of Bryde's whales were positively related to SST (Perry et al. 2011). The effect of SST on this species is most likely indirect. Water temperature can affect productivity (Cañadas and Hammond 2008), and subsequently prey movement and availability (Perry et al. 2005), which in turn influences the distribution patterns of cetaceans (Barco et al. 1999; Lusseau et al. 2004; Wiseman and Nicky 2008).

In conclusion, sightings data collected by means of dedicated surveys provide valuable information on the current distribution of species and can be applied to presence-absence models to generate predictions on the distribution of species. However, the selection of explanatory variables should be carefully considered. In the present study, machine learning methods had a tendency to perform better than the other models. Random forest and generalised additive models were generally the two best performing models. Generalised additive models outperformed generalized linear models in most cases, and maximum entropy produced the lowest predictive accuracies for all models. Overall, the predicted distributions for species occurrence fell within the current known ranges.

Sea surface temperature was indicated as an important driver in determining the distribution of several cetacean species including dusky dolphins, Heaviside's dolphins, common dolphins, bottlenose dolphins, southern right whales and Bryde's whales. Heaviside's dolphins are of particularly high concern as they reside in the cool Benguela Ecosystem which is surrounded by bodies of warmer water (Shannon et al. 1992). Increasing water temperature as a result of climate change can cause a contraction in the distribution range of Heaviside's dolphins as their preferred habitat is degraded. The strong influence of SST on this species could mean that these dolphins may likely not be able to adapt to these changes and could subsequently face the risk of extinction (Thomas et al. 2004). Alternatively, increasing water temperatures can facilitate range expansion of some species. For example, humpback dolphins have experienced a westward expansion of their distribution range as a result of warmer waters present in False Bay (Smit et al. 2013).

Another important driver defining the distribution of cetaceans is chlorophyll *a* concentration, as indicated for dusky dolphins and southern right whales. Cetacean distribution ranges are strongly influenced by the abundance and movement patterns of their prey (Lusseau et al. 2004). Changes in water temperatures due to climate change can negatively affect primary productivity which in turn directly affects the abundance and distribution of fish (Perry et al. 2005). This underlines the concern of changing SST as a result of climate change as water temperature is considered to have the strongest influence on the distribution of cetaceans, either by limiting range expansion in order to adapt, or by directly affecting the distribution of their prey.

CHAPTER 4: CONCLUSIONS AND FUTURE RECOMMENDATIONS

The world's ocean has been experiencing net warming due to excess heat accumulation as a result of global climate change (Hansen et al. 1997; Levitus et al. 2000). The majority of this heat is being stored in the upper layers of the ocean (Bindoff et al. 2007), affecting ocean productivity (Behrenfeld et al. 2006), acidification (Bindoff et al. 2007; Hoegh-Guldberg and Bruno 2010) and currents (Bindoff et al. 2007). Such physical changes strongly impact the distribution and abundance of many temperature limited marine species. Amongst these, include distribution shifts of important fish stocks (Comte and Grenouillet 2013) which not only has severe impacts on commercial fisheries (Perry et al. 2005) but also on the breeding success of other marine species as prey becomes less available (Crawford et al. 2006).

The South African coast is characterised by the confluence of two major current systems with an overlapping region on the south coast (Griffiths et al. 2010; Lutjeharms et al. 2000; Shannon et al. 1992). Intense upwelling regions on the west coast support high productivity (Armstrong et al. 1987) and subsequent large fish populations (Shannon et al. 1992). Global climate change is impacting the intensity of upwelling (Rouault et al. 2010) and causing warming of surrounding waters (Rouault et al. 2009) along the South African shore. As a result of changing water temperature, the distribution range of some marine species has shifted (Bolton et al. 2012) and in some cases constricted (Lloyd et al. 2012; Mead 2011).

The most likely effect climate change will have on cetaceans is a shift in distribution range as they attempt to track preferred conditions (Harwood 2001, Learmonth et al. 2006). The three factors which primarily define the preferred ecological niche of cetaceans include water temperature, depth and those factors affecting the distribution and abundance of their prey (Learmonth et al. 2006; MacLeod 2009; Simmonds and Isaac 2007). Water temperature is considered to have the strongest influence on the geographic ranges of cetaceans (MacLeod 2009), which highlights the concern around changing water temperatures as a result of global climate change.

The current study was focused around the Cape Peninsula, where one of the strongest thermal gradients in the southern Benguela occurs (Armstrong et al. 1987). False Bay, which lies on the eastern side of the Peninsula and falls within the transition zone between the

Benguela Current and Agulhas Current, is considered the only bay along the South African shore that is deep enough to provide significant shelter from wave exposure (Griffiths et al. 2010) and has a high seasonal variety in mean sea surface temperature (Smith et al. 2013). The unique oceanographic features off the tip of southern Africa are home to a variety of cetacean species, of which eight (five dolphin species and three whale species) can regularly be seen in the waters around the Cape Peninsula in the south-western Cape (Best 2007, Findlay et al. 1992). Four dolphin species have their local or global distribution ranges end within this region, and two migratory whale species are also increasingly being encountered during their breeding seasons. The goal of the present study was to investigate the fine scale distribution of cetaceans frequently encountered off the southern Peninsula by means of small boat surveys, and subsequently identifying suitable habitats for each species.

Boat-based surveys are a valuable method to study and monitor the current distribution of cetaceans and can provide occurrence data on a finer scale. The main benefit of dedicated surveys is that they provide researchers with information on search effort, which can be used to calculate effort corrected sightings rates and allow for the recording of concurrent environmental and behavioural data.

Findings from the present study provided insight into the true or effective range ends of several dolphin species, which had been previously described based largely on strandings and the physical-geographical boundary of Cape Point. Dusky dolphins, which are not constrained to the very shallow belt of water near the beaches like the east coast species. They are likely limited by a combination of increases in water temperature in the north-western corner of False Bay and changes in their prey type and availability, rather than rocky shores around Cape Point itself. These dolphins are likely to move around the Peninsula following optimal conditions as they occur, and the effective range limit is thus the south-western corner of False Bay. Heaviside's dolphins were regularly encountered along the rocky shore on the east side of Hout Bay followed by an absence in sightings further south along the Peninsula. I propose that the southward expansion of Heaviside's dolphins is restricted by a combination of water temperature (caused by the presence of a large upwelling cell) and prey availability. My study defines the southern range end of Heaviside's dolphins as occurring in the area between Hout Bay and Kommetjie, rather than Cape Point as previously suggested by Best (2001). Common dolphins were encountered throughout the study area as expected from

earlier descriptions of their habitat use (Best 2007). The effective western limit of humpback dolphins' distribution range was previously described as around Danger Point (Best 2007), roughly 100 km east of Muizenberg. However, regular encounters were recorded in False Bay during this study, as far west as Muizenberg, where seasonal increases in mean water temperature (Smit et al. 2013) resembles that of their preferred range. A further westward expansion is likely limited by a combination of the sudden decline in water temperature in south-western corner of False Bay, south of Simon's Town and the presence of steep rocky shores and estuaries. Here I redefine the effective westward range end of humpback dolphins as Muizenberg in False Bay.

Findings from the present study support the regular use of our coast by right whales (Barendse and Best 2014). Humpback whales were predominantly encountered during their wintering season when individuals migrate along the South African coast to their equatorial breeding grounds (Best 2007, Findlay et al. 1994). Humpback whales are increasingly observed feeding off the west coast and it is suggested that the southern Benguela is becoming a key habitat area for migrating whales (Barendse et al. 2010, 2011; Findlay et al. 2017). In the present study, humpback whales were encountered primarily off Hout Bay and the eastern half of the Peninsula, and it is likely based on their timing, that these animals are part of the west coast breeding stock (see also Vinding et al. 2015). The Bryde's whales encountered during this study are part of the non-migratory inshore stock (Best 2001). Sightings occurred throughout the year, especially within False Bay, and generally in deeper water than the two migrating species. The high encounter probability of Bryde's whales indicate the importance of False Bay as a suitable habitat for the species.

The predicted ranges generated by the models fell within the current known distribution ranges of all eight cetacean species. The most influential variables predicted by the model determining dusky dolphin distribution were water temperature and chlorophyll concentration. These variables directly affect plankton productivity and subsequently fish availability (Shannon et al. 1992) and thus the distribution of top predator species like dolphins (Elwen et al. 2009). Changing conditions, and specifically increases in water temperature, will affect the movement patterns of prey and consequently result in distribution shifts of this species.

Heaviside's dolphins were predicted to occur predominantly at three sites along the west coast, each supported by recent literature as key habitats for the species (Behrmann 2011; Best 2007; Elwen et al. 2009). Similarly to dusky dolphins, SST and chlorophyll concentration were considered as the main factors driving the distribution of Heaviside's dolphins through the more direct effects on the spatial occurrence of their prey. These findings coincide with the strong associated patterns between the movement of Heaviside's dolphins and their prey (Elwen et al. 2006; 2009). The Benguela has a very narrow temperature range (Smit et al. 2013) which adds to the concern of range contraction as the surrounding bodies of warm water are increasing. This means that endemic species such as Heaviside's dolphins are at a very high risk of being negatively impacted by global climate change.

Common dolphins were predicted to occur off the west coast and south coast in waters slightly further offshore. SST was determined as the most influential variable driving their distribution. Common dolphins are known to follow the seasonal movements of their prey and are frequently seen foraging in large groups of bait shoals (O'Donoghue et al. 2010; Roberts et al. 2010). Common dolphins will likely be impacted by climate change through the predicted changes in ocean temperature which affects prey availability and subsequently the movement of dolphins.

Humpback dolphin occurrence was restricted to the inshore waters of the south and east coast and all models indicated bottom depth as the most important variable determining their distribution. The clear westward expansion of this species could be a result of increasing water temperatures specifically at the retroflexion point of the Agulhas Current (Rouault et al. 2009), facilitating the extension of humpback dolphins into False Bay. Any negative impacts as a result of climate change could threaten the conservation status of this already endangered species.

Bottlenose dolphin occurrence was predicted in offshore waters of the south-east coast. Although sea surface temperature was indicated as an important environmental driver, bottlenose dolphins have been shown to occur at both ends of the temperature range (Levy 2017). They are the most frequently observed predators during the Natal sardine run (Caputo et al. 2017; O'Donoghue et al. 2010), indicating the importance of prey availability. The most likely direct effect climate change will have on bottlenose dolphins will be through the distribution shift of their prey as a result of changing water temperature.

FUTURE RESEARCH

Given the implications of climatic changes and the possible effects on a species' distribution and conservation status, it is essential to be familiar with the geographical area a species occupies. It is therefore important for future studies to continue to investigate current distribution ranges to effectively compare it to past distributions to detect and monitor potential changes.

Species of high concern include the endemic Heaviside's dolphin as range reduction could have severe impacts on the population. Monitoring of this species should be focused at the southernmost range end with high effort to the south of Hout Bay to confirm the absence of Heaviside's dolphin further south along the coast and/or the observation of a further southerly range expansion. Monitoring of the dolphin species which have their ranges end within the south-western Cape could result in a better understanding of the effects of a changing climate as this region provides a unique study area for observing any possible range expansion or reductions in response to global climate change.

Similar research should consider directly measuring environmental data or have additional sources where *in situ* environmental data are readily available and corresponding to the time frame of the project. Passive acoustic monitoring may provide the ideal tool for looking at animal presence along the coast in conjunction with environmental variables. Long-term research should also ensure consistency in data collection within and between years, to investigate the seasonal occurrence of species on a fine scale and subsequently generate predicted habitat suitability for species across all seasons.

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