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Spatial and temporal patterns of habitat use of Heaviside's dolphins in Namibia

By

Sara Golaski

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Declaration:

I, Sara Golaski, declare that the dissertation, which I hereby submit for the degree MSc (Zoology) at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

Signature: Sara Golaski

Date: 01 July 2016

Sara Golaski

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Title: Spatial and temporal patterns of habitat use of Heaviside's dolphins in Namibia

Student: Miss S. Golaski

Supervisor: Dr. S.H. Elwen

Degree: MSc (Zoology)

Department: Zoology and Entomology, University of Pretoria

Manuscripts:

Chapters 2 and 3 of this dissertation have been prepared as separate manuscripts to ease preparation for publication. There is some repetition between chapters for this reason, though this was minimised where possible.

Summary:

This thesis reports the findings of a fine-scale habitat selection study of Heaviside's dolphins (*Cephalorhynchus heavisidii*) at two sites in Namibia; Walvis Bay and Lüderitz. Walvis Bay and Lüderitz are the two largest embayments along the Namibian Coast, and therefore the two industrial ports in Namibia are located there. These bays are also inhabited year-round by Heaviside's dolphins, and, at Walvis Bay, a resident population of common bottlenose dolphins (*Tursiops truncatus)*. Heaviside's dolphins are endemic to the western coast of southern Africa ranging within the Benguela current ecosystem from Table Bay, South Africa, to southern Angola. They are not well-studied in the northern half of their range to date, and little is known about geographical variation in the ecology of this species. Furthermore, their coastal distribution and year-round residency near developing industrial ports could potentially put them at risk from human impacts, as industrial use of these areas increases. This study was conducted in order to obtain baseline information on fine-scale spatial and temporal patterns of

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distribution and important habitat parameters for this species in the northern half of its range in order to inform future management of commercial and industrial activities in these areas.

Two complementary methods were used to obtain data on dolphin presence: visual surveys from a small boat were conducted at both study sites over multiple years, and continuous acoustic monitoring was done at Lüderitz over a short period concurrent with one year's surveys. Visual surveys provided the flexibility to cover a wider area and to obtain presence and absence data, including positons of groups, while acoustic monitoring allowed for a continuous observational presence even during nighttime hours, allowing for the ability to detect diel patterns in area use.

The Namibian Dolphin Project has been conducting small boat surveys for cetaceans in Walvis Bay since 2008 and in Lüderitz since 2010, with a focus on Heaviside's dolphins and common bottlenose dolphins. Surveys were conducted in a non-systematic way, with the aim of covering the entire study area while maximizing opportunities for data collection from groups of animals, and was thus rather more focused on high-density areas for these two species. Effort-corrected encounter data from these surveys were mapped and linked spatially to habitat parameters using ArcGIS in order to identify areas of frequent dolphin presence for both species. Generalized Additive Models (GAMs) were used to discover the parameters relevant to habitat selection at each site for Heaviside's dolphins and at Walvis Bay for bottlenose dolphins. Habitat selection at Lüderitz was not examined for bottlenose dolphins, because there were too few encounters there.

Acoustic monitoring for dolphins at Lüderitz was conducted continuously over a two-month period in 2014 using five click-logging instruments called C-PODS moored at different sites from the harbour mouth westward across a series of small bays towards the open ocean, which make up the core study area for visual surveys at this study site. The data obtained give information on relative presence, both spatially between the deployment sites, and also temporally. Another aspect of the acoustic data which was examined was the prevalence of very rapid series of echolocation clicks used when an echolocating animal acoustically investigates a specific target, oftentimes a potential prey item. Spatial and temporal variation in the prevalence of these rapid click trains, hereafter referred to as potential 'feeding buzzes,' has implications regarding patterns of foraging.

Strong habitat preferences over a fine scale were found at both study sites, with areas of near-constant presence close to areas with very little presence. There are similarities between the most frequented areas at each study site: Pelican Point, in Walvis Bay, and Diaz Point, in Lüderitz. Animals in Lüderitz, however, made use of sheltered inshore waters, and were found much closer to the coastline, and in shallower waters, than animals in Walvis Bay. This may be due to the presence to bottlenose dolphins close inshore in Walvis Bay as the two species showed remarkably little overlap in distributions given the small scale of the study site.

Patterns of acoustic detections between C-POD deployment locations closely matched encounter rates from the small boat surveys around those locations, though with lower detections at night on all C-PODS, implying a diel movement offshore. Highest detections overall were at midday, except at Guano Bay (the most westerly site) where early morning detections were highest. Analysis of inter-click intervals showed a similar diurnal pattern in the proportion of potential 'feeding buzzes' to overall acoustic activity.

The continuous presence close to shore and strong habitat preferences of dolphins within both of these industrial ports put them at risk from anthropogenic activities that occur there. Continued monitoring of these populations in the future will help to identify and mitigate these risks. Identification of areas with the most frequent occurrence of dolphins at each study site should be used to inform management decisions in the future.

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Chapter 1

Introduction to the Heaviside's dolphin (*Cephalorhynchus heavisidii*) and to the study area along the Namibian Coast

1.1 General introduction:

Cetaceans are a diverse order of mammals which inhabit a wide range of habitats across the world's oceans, and some rivers (Jefferson *et al.* 1993, Reeves 2003). Although directed hunting of whales and dolphins has been greatly reduced since the International Whaling Commission (IWC) passed a moratorium on commercial whaling in 1982 (Knauss 1997), cetaceans worldwide still face many anthropogenic threats and many species are listed as endangered (IUCN 2015). Threats from human activities include chemical and sound pollution, habitat loss, disturbance or injury from vessels, and fisheries interactions such as entanglement in gear, incidental catch and resource competition (see Whitehead *et al.* (2000) for review). These threats often lead to injury or mortality but sometimes have more subtle effects such as energetic costs, or partial or complete abandonment of impacted habitats, which can still have disastrous effects on a population (Whitehead *et al.* 2000, Whitehead and Reeves 2005, Williams *et al.* 2006, Lusseau and Bejder 2007). Many of these threats, such as chemical pollution and high densities of fishing gear or boat traffic, are more prevalent in coastal areas leaving populations that inhabit coastal waters more vulnerable (Thompson *et al.* 2000). Particularly susceptible are those populations with limited distributions and small home ranges because even small-scale habitat loss or degradation can harm entire portions of a population directly or exclude animals from critical habitat. Of particular concern are species restricted to cold upwelling centres surrounded by warmer waters as temperature shifts caused by climate change could potentially reduce the suitable habitat within some species ranges to the point of causing species extinction (MacLeod 2009).

The marine habitat of cetaceans can make them extremely difficult to study. They spend much of the time out of sight underwater, leading to few data points for overall observation time (Zimmer 2011, Marques *et al.* 2013). Furthermore, opportunities for observation and data collection at sea can be expensive and are highly dependent on workable weather conditions. Because of this, certain basic aspects of the ecology of many cetacean populations remain unknown and many species are listed as data deficient (IUCN 2015). In many such populations, the effects of anthropogenic threats are not known (Taylor *et al.* 2000). It is important, particularly when dealing with coastal species, to have an understanding of small-scale habitat selection because management plans enacted at the wrong scale may serve to protect one portion of a population well while leaving another completely vulnerable or serve to protect from one threat while overlooking others (Thompson *et al.* 2000). Notwithstanding the challenges involved in studying them, cetaceans tend to be good indicator species of ecosystem changes because they are top predators and are sensitive to shifts in prey abundance, occurrence of toxins and other ecological factors (Hooker and Gerber 2004).

For this study, I investigated habitat selection of Heaviside's dolphins (*Cephalorhynchus heavisidii*) using two study sites in Namibia; Walvis Bay and Lüderitz. The Heaviside's dolphin is endemic to the Benguela ecosystem on the west coast of South Africa and Namibia. The species as a whole is not well-studied though their conservation status in South Africa is currently being updated from Data Deficient to Least concern based on new research (Elwen *et al.* 2006, Elwen *et al.* 2009a, Elwen *et al.* 2010, Gopal *et al.* 2012, Davis *et al.* 2014). The Heaviside's dolphin is a small, primarily coastal delphinid with a small home-range (~50-80 km alongshore along the western coast of South Africa where they have been previously studied) (Elwen *et al.* 2006, Davis *et al.* 2014). I used encounter data from small-boat surveys to examine fine-scale habitat selection at each study area, and acoustic monitoring at Lüderitz to investigate relative presence throughout the day and night. Leeney *et al.* (2011) conducted similar monitoring at Walvis Bay. Human impacts in both study sites are currently increasing greatly mainly through large-scale port-expansion projects (see Namport website for plans and EIA's etc.

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www.namport.com.na). Construction of an expanded harbour and container terminal are underway in Walvis Bay, while in Lüderitz, harbour expansion and a marine phosphate processing plant have been proposed (OLRAC 2009). The results of this study provide insight into the ecology of Heaviside's dolphins in the northern half of their range and will aid in the understanding the potential impacts of anthropogenic activities along the Namibian coast.

1.2 Aims and objectives:

The three broad aims of this study are as follows:

1.) Generate baseline information regarding the fine-scale habitat selection of a unique and endemic species in two high-density areas in a poorly studied part of their range.

2.) Provide information necessary for informed management of human activities in areas of overlap between high dolphin presence and human use.

3.) Test the effectiveness of using a combination of visual and acoustic methods to examine fine-scale habitat selection both spatially and temporally for this species in this area.

The specific objectives therein include:

1.) Identify areas within the study sites with the highest frequency of dolphin occurrence.

2.) Identify times of peak dolphin presence and acoustic behaviour.

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3.) Test the usefulness of using an array of multiple C-POD echolocation click loggers for Heaviside's dolphins by comparing and contrasting results with the visual component of the study.

1.3 Background to the study:

Study areas at Walvis Bay and Lüderitz:

Walvis Bay (23° 00'S, 14° 30'E) is the largest embayment along the Namibian coastline; roughly 10 x 10 km in extent, and falls within the region of the Benguela characterized by muddy, sulphurous sediment (Weeks *et al.* 2004). Walvis Bay is home to populations of Heaviside's dolphins and bottlenose dolphins (*Tursiops truncatus*) as well as a large (>12 000 in 2011) population of Cape fur seals (*Arctocephalus pusillus pusillus*) (Elwen *et al.* 2011a, Elwen *et al.* 2012). Dusky dolphins (*Lagenorhynchus obscurus*) are present offshore but rarely enter the bay. Larger cetaceans including migrating humpback whales (*Megaptera novaeangliae*) and southern right whales (*Eubalaena australis*) frequent this area during the austral winter and spring and many other cetacean species have been seen or have stranded in the Walvis Bay area including dwarf (*Kogia sima*) and pygmy (*Kogia breviceps*) sperm whales (Elwen *et al.* 2013), pygmy right whales (*Caperea marginata*) (Leeney *et al.* 2013), killer whales (*Orcinus orca*) (Elwen *et al.* 2011a) and the first grey whale (*Eschrichtius robustus)* reported in the southern hemisphere (Elwen and Gridley 2013).

Current human activities in Walvis Bay which impact the marine environment include commercial shipping, oyster and mussel aquaculture, seaward port construction and boat-based marine tourism (approximately 27 vessels from 8 companies plus 3 companies running kayak tours as of 2010) (Leeney 2014). There has been concern that the boat-based tourism industry may be having negative impacts on Walvis Bay wildlife (Elwen *et al.* 2011a, Leeney 2014), and the industrial construction may be causing noise pollution, and the associated dredging may be responsible for chemical pollution from the disturbed sediment (OLRAC 2009). Examination of bioaccumulation of heavy metals in Heaviside's dolphins shows particularly high levels of arsenic, cadmium and selenium in Walvis Bay (Serot 2013). Land-based sources of pollution occur (e.g. rubbish blowing into the sea or harbour), but the lack of perennial rivers along the Namibian coast other than at the country's northern and southern borders mean that river-borne chemical pollution in this area is low (De Kock *et al.* 1994).

Lüderitz (26° 38'S, 15° 9'E) also has populations of Heaviside's and dusky dolphins, as well as Cape fur seal populations about 20 km south in Wolf Bay and Atlas Bays. Humpback and southern right whales occur in winter and spring months and bottlenose dolphins from the Walvis Bay population have been encountered occasionally at Lüderitz (NDP unpublished data). There are also sporadic sightings of many other cetacean species offshore of Lüderitz though effort-corrected acoustic and visual surveys of this area have only been implemented since 2012 in order to determine cetacean presence in and around the recently established Namibian Islands' Marine Protected Area (NIMPA) (NDP unpublished data). The small bays of Lüderitz are surrounded by mostly rocky coastline and the waters are affected by the strong upwelling offshore at the Lüderitz upwelling cell, the strongest within the Benguela Ecosystem. Human activities in and around Lüderitz include marine mining for diamonds, recreational and commercial fishing, shipping and aquaculture of oysters as well as small-scale boat-based marine tourism from two vessels as of 2013 (Leeney 2014). Most of these activities occur away from the coast and outside the small bays of Lüderitz, and also on a much smaller scale than in Walvis Bay, so it is likely that the direct influence of anthropogenic activities, especially marine tourism, on dolphin populations is lower in Lüderitz than in Walvis Bay. Examination of bioaccumulation of heavy metals in Heaviside's dolphins showed particularly high levels of cadmium in Lüderitz (Serot 2013). Comparison of these two sites may provide insight into potential impacts of human activities on Heaviside's dolphins in Namibia.

Genus Cephalorhynchus:

Heaviside's dolphins are endemic to the coastal waters of southwestern Africa within the Benguela ecosystem. The other members of the genus *Cephalorhynchus* (a morphologically distinctive genus within the family *Delphinidae*) are endemic to coastal waters around the Southern Hemisphere with the subtropical convergence potentially acting as a barrier to more northerly distributions (Pichler *et al.* 2001). The genus also includes Hector's dolphins (*C. hectori*), endemic to the waters of New Zealand, Commerson's dolphins (*C. Commersonii*) and Chilean dolphins (*C. Eutropia*), both endemic to the waters of South America, except for a small population of Commerson's dolphins at the Kerguelen Islands in the southern Indian Ocean (Pichler *et al.* 2001). Two species within the paraphyletic genus *Lagenorhynchus*, *L. australis* and *L. cruciger*, could possibly be most closely related to *Cephalorhynchus*, and may even belong within the *Cephalorhynchu* genus (May-Collado and Agnarsson 2006). The four species currently within the genus are small (< 2 m total length), robust and porpoise-like in appearance (Best 2007). They show a preference for shallow waters over the continental shelves and have relatively small home ranges (Lescrauwaet *et al.* 2000, Bejder and Dawson 2001, Elwen *et al.* 2006, Ribeiro *et al.* 2007).

Other than the Commerson's dolphin and Chilean dolphin, the species of the genus *Cephalorynchus* are widely separated from each other geographically, due to their preference for coastal habitat and high site fidelity. All *Cephalorhynchus* are, however, sympatric with other members of the subfamily *Lissodelphininae (Heinrich et al. 2010).* This allopatric distribution within the genus indicates either convergent evolution or speciation through founder events after long migrations (Pichler *et al.* 2001). Analysis of mitochondrial DNA (Pichler *et al.* 2001) has shown that founder events are the more likely explanation and that the genus probably originated off the coast of southern Africa, then spread to New Zealand, and then on to South America, where the effects of glaciation (e.g. on sea level and temperatures) kept the now partially sympatric Chilean dolphin and Commerson's dolphin separate. This direction of radiation was probably constrained by the sub-Antarctic current, as proposed by Robineau (1989). Later, a population of Commerson's dolphins was founded at the Kerguelen Islands and the North and South Island populations of Hector's dolphins were separated by the Cook Strait. The North Island population is now considered a separate subspecies, the Maui's dolphin (*C. hectori maui*) (Baker *et al.* 2002).

Hector's dolphins have particularly small home ranges and high site fidelity (Bejder and Dawson 2001). Their population structure is comprised of very high and very low density areas with no evidence of alongshore movement beyond a few tens of kilometres and little overlap in range along the coastline (Bräger and Schneider 1998). This interrupted dispersion leads to small, discrete populations, leaving little habitat available for each population, as well as less genetic mixing and the inherent conservation concerns associated with this. Thus, even quite localised human impacts can have major effects on the species. For example, the Maui's dolphin had an estimated population size of 48-69 adults in 2012 after facing mortality as bycatch from gillnet fishing (Slooten *et al.* 2006a, Hamner *et al.* 2012). The small population size of this subspecies, resulting from its complete separation from the South Island populations, is a major conservation concern, especially as Hector's dolphins are listed as Endangered despite the creation of the Banks Island marine protected area (Slooten *et al.* 2006b, Reeves *et al.* 2013). The reasons for the discrete populations of Hector's dolphins in general are not fully understood though small home ranges and strong philopatry are likely important factors (Ferreira and Roberts 2003). Bräger *et al.* (2002) stress the importance of scaling management areas correctly especially for species with this type of discontinuous distribution pattern.

Like Hector's dolphins, Chilean dolphins also occur in pockets of high density with low-density areas in-between and are susceptible to pollution, boat activity associated with aquaculture and exclusion from critical habitat from this and other commercial and industrial activity (Ribeiro *et al.* 2005). Unlike other members of the genus, Chilean dolphins show strong avoidance of boats in the southern part of their range, possibly a function of group size or an acquired response to being hunted for bait (Pérez-Álvarez *et al.* 2007). Chilean dolphins are listed as near threatened (Reeves *et al.* 2013).

Commerson’s dolphins show high genetic heterogeneity and population structure (Cipriano *et al.* 2011). They have also been subject to anthropogenic mortality, particularly through fisheries bycatch (Iñíguez *et al.* 2003). The combination of high occurrence of incidental catch in gill nets along with high genetic heterogeneity has potentially left individual populations immediately vulnerable (see Cipriano *et al.* (2011) for review). Despite these conservation concerns, Commerson’s dolphins are still listed as data deficient (Reeves *et al.* 2013).

Current knowledge of Heaviside’s dolphins:

Heaviside’s dolphins are small and robust with a maximum body length of 1.75 m (there is little sexual dimorphism in size) and a maximum girth just before the flippers of about 62.5% of the length (Best and Abernethy 1994). They have conical heads and no pronounced beak, though there is demarcation between the melon and rostrum (Best and Abernethy 1994). They have fairly triangular dorsal fins which are about 9% of body length in height and short, blunt flippers (Best and Abernethy 1994). Their flukes span about 26.8% of body length and appear crescent shaped (Best and Abernethy 1994). They are dark grey in colour with lighter grey coloration forward on the body, and the light grey forms a cape pattern which runs from rostrum to blowhole dorsally but extends nearly the distance to the genital slit on either side, ending in flank blazes (Figure 1). There are four distinct white patches on the ventral side, one of which is diamond-shaped spanning between and wrapping around the front of the flippers, one oval-shaped behind each flipper and one trident-shaped extending posteriorly from between these to cover the genital slit and up each side to the light grey flank blaze (Best and Abernethy 1994). There is distinct sexual dimorphism in the shape of the white coloration covering the genital slit; in males, this ends in a point, but in females widens out to cover the mammary slits, ending more abruptly (Best and Abernethy 1994, Elwen *et al.* 2011a).

Many Heaviside’s dolphins gain individually distinctive markings in the form of notches or scarring on their dorsal fins, flukes and flippers and scarring on their bodies. This often occurs because of energetic social behaviour, or through interactions with predators or boats. Dorsal fin notches on dolphins are considered permanent and are used for photo-identification of many species because they are the most easily photographed feature of a dolphin as they are exposed on every breath. Due to the rapid healing rate of Heaviside's dolphins and other cetacean species, body scarring is most likely not distinctive over more than a few months (Elwen and Leeney 2010).

Heaviside's dolphins are endemic to the Benguela current ecosystem along the west coast of South Africa, Namibia and southern Angola with an apparent continuous distribution within this range (Findlay *et al.* 1992). Jansen van Vuuren *et al.* (2002) reported genetic homogeneity within the species across their range and high genetic diversity, which is good from a conservation point of view as highly fragmented populations with low diversity are much more susceptible to extinction. More recent work by Gopal (2014), using a larger sample size, examined both mitochondrial and microsatellite DNA from Heaviside's dolphins across five study sites in South Africa and two in Namibia (Lüderitz and Walvis Bay), and found high population connectivity and differing degrees of relatedness between sites, indicating some spatial structuring in the species. The results were contrasting, with Mitochondrial DNA indicating six populations among the seven study sites with low genetic diversities between them, and microsatellite data indicating only two populations with a high level of admixture between them (Gopal 2014). Differences in heavy metal bioaccumulation in populations of Heaviside's dolphins from the same seven study sites also indicated strong site fidelity with limited movements between sites (Serot 2013). Heaviside's dolphins are partially sympatric with bottlenose dolphins and are sympatric with dusky dolphins throughout their range and mixed groups are not uncommon (Elwen *et al.* 2010, Heinrich *et al.* 2010).

Heaviside's dolphins are listed as data deficient internationally (Reeves *et al.* 2013) and the majority of data on the species to date arises from research in South Africa (Elwen *et al.* 2011b). Group sizes typically range from 1-30 with a mean of 3.15 (± SD 3.07) (Findlay *et al.* 1992). (Elwen *et al.* 2009b) reported an estimated abundance of 3,573 – 11,267 individuals for 390 km of coastline from just south of

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Cape Town to north of Lambert's Bay and 272–1,020 for a more intensively surveyed section of approximately 20 km long which is comparable to the areas studied here. Inshore presence of Heaviside's dolphins in South African waters appears to be strongly tied to light conditions. There, Heaviside's dolphins move offshore in late afternoon from around 15h00 to 05h00, but generally stay closer to shore between 06h00 and 12h00 (Elwen *et al.* 2006, Elwen *et al.* 2009a). Inshore presence is also positively correlated with brighter phases of the moon (Elwen *et al.* 2010). The offshore movement during times of lower light conditions is thought to be tied to higher prey availability, resulting from vertical migration of fish towards the surface during darker periods when visual predators (such as seals and many predatory fish) are less effective. Sekiguchi *et al.* (1992) reported that Heaviside's dolphins feed mostly on shallow-water juvenile hake (*Merluccius capensis*) and kingklip (*Genypterus capensis*), but also on goby (*Sufflogobius bibarbatus*) and horse mackerel (*Trachurus trachurus capensis*) as well as other fish and some cephalopod species. Prey distribution patterns indicate that they likely feed from nearshore out to the upper continental slope (Sekiguchi 1994). Hake are also targeted by fisheries in this region, but there is unlikely to be direct competition as the fishery targets larger fish further from shore than Heaviside's dolphins (Elwen *et al.* 2010). The stomachs of Heaviside's dolphins were fuller in the morning, implying that they feed at night offshore and dolphins were rarely seen feeding during the day but instead move inshore to rest, socialise and avoid predators (Sekiguchi *et al.* 1992, Elwen *et al.* 2006, Elwen *et al.* 2009a, Elwen *et al.* 2010).

Heaviside's dolphins in Walvis Bay, Namibia also show a diurnal variation in their behaviour, but it differs from that observed in South Africa. Continuous acoustic monitoring using a moored device in a high-density area at Pelican Point Walvis Bay revealed more frequent acoustic detections of Heaviside's dolphins in the inshore environment at night than during the day (Leeney *et al.* 2011), which is inverse to the pattern observed in South Africa where animals move offshore to feed at night (Elwen *et al.* 2009a). This may be in part due to differences in the type and availability of prey in Namibian waters. Shallow-water hake is abundant along certain areas of the Namibian coast, particularly the shelf area which lies between the two study areas, but is not very abundant at the upwelling cells themselves, and density at the Lüderitz and Walvis Bay study sites is relatively low (Payne *et al.* 1989, Burmeister 2001). The different pattern of diurnal movement observed at Walvis Bay (Leeney *et al.* 2011) and the low density of hake near either study area suggest that Heaviside's dolphins at the two study areas may be focusing on other prey and subsequently follow a different foraging pattern to the strong diurnal movement observed in South Africa (Elwen *et al.* 2006, Elwen *et al.* 2009a).

Elwen *et al.* (2010) examined the fine-scale habitat selection of Heaviside's dolphins in nearshore waters along the South African coast and reported that high-density areas were strongly correlated between years, suggesting long-term habitat preference or site fidelity. Heaviside's dolphins were most often encountered in areas with higher swell and where juvenile shallow-water hake density was higher over the long-term (Elwen *et al.* 2010). Fine-scale habitat selection in areas where feeding does not occur may be due to predator avoidance or to factors conducive to resting or socialising, but may also be influenced by competition with sympatric species (Elwen *et al.* 2010, Heinrich *et al.* 2010). In South Africa, Heaviside's dolphins occupy shallower, cooler water than dusky dolphins and although Heaviside's and dusky dolphins are regularly encountered near each other, they appeared to behave indifferently to each other with no obvious aggressive interactions or avoidance. Also, where there is overlap in prey species taken, Heaviside's dolphins tend to take larger prey, even though they are physically smaller than dusky dolphins, possibly suggesting some form of competition-mediated prey specialisation (Elwen *et al.* 2010, Heinrich *et al.* 2010).

The Benguela Current and the Namibian coast:

Namibia's coast is among the most energetic in the world, with sediment transport causing the shape of the coastline to change continually (Robertson 2012). Most of the Namibian coastline is sandy, but there are large areas of rocky coastline rich with kelp beds. These provide shelter for a variety of marine life and act as a nursery ground for some pelagic fishes such as horse mackerel (Hutchings *et al.* 2002).

Strong winds, driven by the South Atlantic Anticyclone, affect the coast during most of the year and the southern coast of Namibia, including Lüderitz, has the highest wind speeds in all of southern Africa (Robertson 2012). These strong winds are reinforced by land-sea breezes caused by the pressure gradient between cool coastal air and warm inland air. Wind speeds usually peak in the early afternoon, and at the central coast, including Walvis Bay, the winds often remain strong until evening.

The entire Namibian coastline falls within the Benguela current ecosystem. The Benguela is typical of eastern boundary upwelling systems and is characterized by extremely high productivity and relatively low species diversity. It is formed by a wide, shallow current driven by the South Atlantic Subtropical Gyre. The strong winds from the South Atlantic Anticyclone, also contribute to the northward water flow (Hutchings *et al.* 2009). The Benguela current runs along the southwest coast of Africa, beginning around Cape Town at a width of about 200 km and widening to about 750 km in the north, where it ends off the coast of southern Angola. It is characterized by a coastal branch with a mean flow of 10-30 cm/s and offshore oceanic flow which is more transient and is affected by large eddies shed from the retroflection of the Agulhas Current (Ansorge *et al.* 2007). There is also a deep poleward undercurrent running counter to the main surface flow (Veitch *et al.* 2010).

The Benguela is the only eastern-boundary subtropical current bounded by warm-water currents at both its northern and southern boundaries (Veitch *et al.* 2009). North of the Benguela and off the coast of Angola, the Angolan subtropical zone has a strong seasonal thermocline with warm waters overlaying cool productive waters from December to March. This is separated from the northern Benguela by the Angola-Benguela front, an area of strong thermal gradients. These fronts move seasonally but tropical hypoxic waters also advect further into the northern Benguela from the north. This phenomenon occurs about every decade and is termed the Benguela Niño. The warm waters of Benguela Niños can travel as far south as Walvis Bay (Gammelsrød *et al.* 1998).

An important characteristic of the Benguela current ecosystem is the extensive, coastal, wind-driven upwelling cells. Ekman transport, caused by the southerly winds from the South Atlantic Anticyclone, pushes the upper water layers seaward, resulting in the upward movement of deeper waters towards the surface. The Benguela upwelling is cold (sub-thermocline), nutrient-rich and extremely productive, with longshore fronts occurring at the seaward boundary of upwelled water. It extends from 14-37˚S and is the weakest from Möwe Bay to Walvis Bay where the coastline is concave, and is the most intense near Lüderitz and Cape Frio where the continental shelf is narrower, the coastline more northerly and the winds are strongest. The strength of the upwelling cells, and the winds that cause them, cause powerful waves along the coast and make the Benguela current one of the most productive marine areas in the world. The high productivity produced by the Lüderitz upwelling cell is actually distributed further north towards the Lüderitz study site by the flow of the Benguela current and because weather conditions prevent dense plankton concentrations. Upwelling there occurs year-round and it is the strongest year-round upwelling cell in the world, though wind stress is nearly four times higher in the austral summer than in the austral winter, with an associated decrease of water temperature during strong winds (Bakun 1996, Peard 2007). This area has the strongest winds and lowest sea surface temperatures in the Benguela, marking a division between the northern and southern Benguela (Hutchings *et al.* 2009). Topographically, this division is marked by a narrowing of the continental shelf at 28˚S (Veitch *et al.* 2009).

There is more continuous upwelling in the northern Benguela, which has lower oxygen concentrations and higher salinity than the southern Benguela. The northern Benguela and southern Benguela are seasonally out of phase and the northern Benguela is much more productive (Hutchings *et al.* 2009). The northern Benguela shelf has high plankton biomass and moderate to high fish biomass though pelagic fish abundance is currently depleted (Roux *et al.* 2013). Also, offshore transport of surface waters prevents large aggregations of planktivores, so fish biomass does not always match primary productivity (Weeks *et al.* 2004).

The northern Benguela also experiences low-oxygen-water (LOW) events, resulting from remotely advected hypoxic waters from the north and from more localized processes set in place by the strong upwelling and the extremely high productivity that results (see Monteiro *et al.* (2006) for review). The strong winds drive offshore transport of the surface layer, preventing build-up of herbivorous plankton colonies and causing large plankton cells to sink unconsumed to the sea floor where sulphide-oxidizing bacteria subsist on them (Weeks *et al.* 2004). The bacterial environment of the sediment thus contributes to build-up of poisonous hydrogen sulphide and methane gases, which erupt seasonally on the shelf area offshore of Walvis Bay, bringing hypoxic and anoxic waters up from the bottom as well (Emeis *et al.* 2004, Weeks *et al.* 2004). LOW events, and the frequently coinciding sulphur eruptions can have disastrous effects on marine life, resulting in major fish die-offs, sometimes with many animals coming out of the water onto the beaches, or other effects such as large-scale displacements or reduced gonad development (Gammelsrød *et al.* 1998). For example, in 1992-93 a catastrophic loss of Cape hake (*M. capensis*) occurred due to an anoxic outbreak (Weeks *et al.* 2002, Weeks *et al.* 2004).

The southern Benguela is influenced by offshore eddies shed from the warm Agulhas current, and this incursion of warm, Indian Ocean waters may be responsible for die-offs of fish larvae in the southern Benguela. Seasonal effects on the upwelling regime are stronger in the southern Benguela than the northern Benguela with maximum upwelling intensities occurring during the austral spring and summer (Veitch *et al.* 2009).

1.4 Motivation for the study:

Heaviside's dolphins have a relatively small global distribution, being endemic to the cold water Benguela ecosystem. This small geographic extent and apparently narrow range of preferred environmental parameters makes them inherently vulnerable to conservation threats. The species has not been well-studied in the past, and most research to date has taken place in the southern Benguela

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ecosystem off the coast of South Africa. Preliminary results from work in Namibia have already highlighted differences in their occurrence patterns and behaviour in the northern half of their range, which may be related to the differences in the oceanography and biological environment in the northern Benguela ecosystem. As other members of the genus *Cephalorhynchus* face many conservation concerns resulting from their use of coastal habitat and high site fidelity which can result in fragmented populations, understanding the ecology of Heaviside's dolphins across their entire range is crucial to the management of anthropogenic activities within their habitat. This study will provide important baseline information on Heaviside's dolphin habitat selection within Namibia and comparisons with the better-studied population in the southern Benguela should aid in a better understanding of the overall ecology and ecological plasticity of this coastal species. Habitat modelling may provide insight into interactions with other species as well as the abiotic features that influence occurrence of this species. By examining these elements, I hope to provide necessary information for ecologically relevant management of Heaviside's dolphins in the northern half of their range along the still-developing Namibian coast.

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1.6 Figures:

Figure 1: Heaviside's dolphins socializing in Guano Bay, Lüderitz, 2013. Sara Golaski.

Chapter 2

Spatial habitat selection of Heaviside's dolphins (*Cephalorhynchus heavisidii*) in Walvis Bay and Lüderitz, Namibia, with comparisons to bottlenose dolphins (*Tursiops truncatus*)

2.1 Abstract:

This study investigates spatial habitat selection of Heaviside's dolphins (*Cephalorhynchus heavisidii*), an endemic species to the west coast of Southern Africa at two areas of known high-density along the Namibian coast: Walvis Bay and Lüderitz. Comparisons are made at the Walvis Bay study site to common bottlenose dolphins (*Tursiops truncatus*), but this was not possible at Lüderitz as bottlenose dolphins are rarely encountered there. Information on animal locations was collected during a series of small-boat surveys conducted in Walvis Bay from 2008-2013 and in Lüderitz from 2010 to 2014. Encounters were mapped in ArcGIS 10.2 and spatially correlated with depth data and other spatial habitat variables for comparisons between study sites. Effort-corrected encounter rates were averaged over 1x1 km grids, which were also correlated with the same habitat variables. Highly frequented areas for both species were determined with this method, and the relationship of the habitat variables to effort-corrected encounter rates was examined with generalized additive models (GAMs). In Walvis Bay, distributions of the two species showed very little overlap except for an area with frequent encounters around Pelican Point, a long, sandy peninsula marking the western boundary of the bay. Bottlenose dolphins were most often encountered at shallow depths (all encounters were at depths under 30 m, and 58.29% were at less than 10 m) in the sheltered waters of the bay, whereas Heaviside's dolphins were mostly found outside of the bay or in deeper waters (84.09% of encounters were at depths greater than 15 m) at the Walvis Bay study site. This differed drastically from Lüderitz, where Heaviside's dolphins were often found close inshore in sheltered, shallow waters (90% of encounters were at depths under 20 m). This suggests a distributional response of Heaviside's dolphins in Walvis Bay to the presence of the much larger

bottlenose dolphins. Identification of the areas most frequented by dolphins at each site should serve to inform management decisions in these two areas, which are subject to industrial development and human activity in the marine sector.

2.2 Introduction:

Heaviside's dolphins (*Cephalorhynchus heavisidii*) are a robust, small-bodied species endemic to the coastal waters of southwestern Africa within the Benguela ecosystem. Most research to date on this understudied species has taken place in the southern Benguela, off the west coast of South Africa (Elwen *et al.* 2011b). The lack of information on Heaviside's dolphins from the northern half of their range limits the ability to manage threats to the population that may result from increasing human use of the Namibian coast. Here, we investigate coastal habitat selection of Heaviside's dolphins in the northern Benguela at two study sites in Namibia, Walvis Bay and Lüderitz, with the goal of describing habitat characteristics in high-use areas along this rapidly developing coastline. Habitat selection of resident common bottlenose dolphins (*Tursiops truncatus*) was investigated at the Walvis Bay study site but not for Lüderitz, as bottlenose dolphins are only seen infrequently in that area. The information gained from this study should prove useful in forming the basis of future spatial management initiatives in these two quite different locations.

Understanding a species' preferred habitat is vital for effective conservation and management because it allows for the mitigation of anthropogenic effects resulting from overlapping use of an area (Hyrenbach *et al.* 2000, Tyne *et al.* 2014). Because they are able to cover large distances quickly, many cetaceans respond rapidly to changes in the extremely fluid marine environment with changes in distribution patterns (Forney 2000). When human activities cause a lasting or repeated change in distribution from otherwise suitable habitat, it can have energetic costs for a population such as increased energy use (Williams *et al.* 2006), lost foraging or resting opportunities (Lusseau 2004, Bejder *et al.* 2006a,b) or increased predation (Heithaus and Dill 2002), particularly when equally suitable habitat is not available nearby, or is unknown to the population. This is especially problematic for species with a coastal distribution and small home ranges, as a much larger proportion of these species' habitat can overlap with areas of detrimental human activity. It is therefore important to recognize suitable habitat for these species within their range in order to predict and mitigate threats caused by human activities in and around the environments they utilize. As there can be population differences in habitat selection of a species, determining suitable habitat at different high-density sites is important and also provides information on the behavioral flexibility of the species.

Studying habitat selection of marine species comes with a unique set of challenges however. The marine environment is dynamic, and it can vary considerably over a small scale. Often, there is a spatial or temporal lag between physical processes and the resulting effects on species distributions, especially for top predators, such as cetaceans (Redfern *et al.* 2006). Also, data collection carries the challenges of being interrupted by weather conditions, as well as the difficulty of detecting animals that spend most of their lives out of sight underwater. For these reasons, visual observations of cetaceans often result in a small number of data points per effort, and thus modelling these encounter data with relevant habitat information can be difficult. See Redfern *et al.* (2006) for a detailed review of different habitat modelling methods and the considerations involved.

For this study, fine-scale spatial habitat selection was examined using ArcGIS 10.2 to link dolphin survey data with environmental parameters, and then investigate the relationship between them, for both environmental factors singly and using more comprehensive Generalized Additive Models (GAMs). The environmental parameters used in this analysis therefore vary spatially rather than temporally (i.e. depth and distance data rather than data on weather patterns, temperature, or chlorophyll concentrations). Temporal patterns of habitat selection are examined in Chapter 3. This information is effective for advising spatial management of anthropogenic activities within a population's home range. Spatial overlap of area use between Heaviside's dolphins and bottlenose dolphins in Walvis Bay is also examined.

Habitat selection of the genus Cephalorhynchus:

In general, *Cephalorhynchus* prefer coastal habitat and have relatively small home-ranges (Lescrauwaet *et al.* 2000, Bejder and Dawson 2001, Elwen *et al.* 2006, Ribeiro *et al.* 2007). Satellite tagging of Heaviside's dolphins in South Africa revealed home ranges of approximately 50-80 km along-shore (Elwen *et al.* 2006, Elwen 2008), but extending out to the 100m depth contour (up to 30 km from shore in that study). In the Southern Benguela, Heaviside's dolphins live on shallower parts of the continental shelf, out to approximately 100m depth (Findlay *et al.* 1992, Elwen *et al.* 2006) and prefer areas more exposed to swells, with sandy shores and offshore presence of juvenile hake, their dominant prey (Sekiguchi *et al.* 1992, Elwen *et al.* 2010). Elwen *et al.* (2009b) estimated that 1,721 to 6,828 dolphins utilise 150 km of coastline around St. Helena Bay, South Africa. A strong diurnal movement pattern with animals close to shore in the mornings but moving offshore in the afternoons to forage has been shown in South Africa (Elwen *et al.* 2006, Elwen *et al.* 2009a). However, acoustic monitoring in Walvis Bay, Namibia revealed a reversal of this diurnal pattern with detections highest inshore at night (Leeney *et al.* 2011). Diel patterns in acoustic presence in Lüderitz differ from both of these, but more closely resemble the pattern of offshore movement found in South Africa, with inshore detections highest around midday and another smaller peak in acoustic detections around dawn (see Chapter 3). These temporal differences in use of the inshore environment likely reflect different patterns of foraging in these three sites, related to different prey type and availability, and may also be influenced by the presence of other top predators. For example, dusky dolphins in Kaikoura, New Zealand, have a very strong diel pattern of offshore movement at night during the summer months, when killer whales are frequently sighted in the area, prioritizing foraging during times when prey is most available and seeking shelter otherwise (Srinivasan and Markowitz 2010). Bottlenose dolphins in Shark Bay, Australia, have also been shown to avoid shallow habitat where predation is more likely during times of higher shark presence (Heithaus and Dill 2002).

Bottlenose dolphin habitat selection:

Unlike the endemic Heaviside's dolphins, common bottlenose dolphins have a cosmopolitan distribution, though populations are often geographically, behaviourally and morphologically distinct (see Wells and Scott (1999) for review). The population genetic structuring of the species does not always match distributions, and some geographically separate populations show strong genetic similarity while conversely, there are sometimes strong genetic differences between parapatric populations with inshore and offshore populations differing genetically, morphologically and in prey preferences (Hoelzel *et al.* 1998, Wells and Scott 1999, Rosel *et al.* 2009).

It is therefore likely that the small coastal population of bottlenose dolphins using Walvis Bay is distinct despite the presence of *T. truncatus* offshore (Best 2007). Though their appearance is generally similar to that of other bottlenose dolphin populations, body size is larger (up to 3.6 m in length) than in many other populations (Best 2007). The entire range of this inshore population is unknown, though Findlay *et al.* (1992) report a range of just south of Walvis Bay to Cape Cross, with no sightings in South Africa from this population. In recent years, there have been sightings from just south of Lüderitz to just south of Möwe Bay (NDP unpublished data).

Home ranges and habitat preferences for bottlenose dolphins vary extensively between populations and Ingram and Rogan (2002) stress the importance of determining important habitat for each population because of this. For example, the home range of the well-studied population at Sarasota Bay, Gulf of Mexico, is 100 km^2 (Wells 1991) and Ballance (1992) described re-sighting individuals at locations 25-65 km apart, and a habitat preference for shallow, turbid, sandy-bottomed estuarine areas for a population in the Gulf of California. Bottlenose dolphins studied on the west coast of Ireland also showed a strong preference for estuarine waters, but also for a sea bed with a greater slope, likely an aid to foraging

(Ingram and Rogan 2002). A population in Golfo San José, Argentina, show a strong preference for waters less than 10 m deep (Würsig and Würsig 1979). Studies of the population of bottlenose dolphins in NE Scotland by Hastie *et al.* (2004) showed that fine-scale habitat selection is directly related to prevalence of foraging behaviour and Heithaus and Dill (2002) showed that both food availability, and the presence of predators strongly affect dolphin distributions in Shark Bay, Australia.

2.3 Methods:

Study sites:

Walvis Bay (22˚55’ S 14˚30’E) is a large (roughly 10 x10 km), north-facing embayment which is bounded on the west side by a long sandy peninsula called Pelican Point, which acts as a breakwater sheltering the bay from the predominantly south-westerly weather. The bay is characterised by shallow water (7.3 m depth ± SD 4.6) and a flat, sandy sea bed. Walvis Bay is also characterized by high levels of anthropogenic activity, including marine tourism (11 companies running approximately 27 vessels in 2010), aquaculture of oysters and mussels, and increasing heavy industrial ship traffic (Leeney 2014). Seaward construction of an expanded port container terminal is underway, as well as construction of a new harbour area and a gas-offloading facility north of the harbour (OLRAC 2009, EnviroDynamics 2015). These projects involve dredging, and construction at sea, as well as a long-term increase in ship traffic.

In contrast to the sandy shoreline of Walvis Bay, Lüderitz (26˚36’S 15˚8’E) is dominated by a rocky coastline and is made up of several smaller, north-facing bays. Lüderitz experiences considerably lower levels of anthropogenic impacts than Walvis Bay as all of human activities take place on a much smaller scale. These include fishing, shipping, aquaculture of oysters (see Griffiths *et al.* (2005) for review), and two marine tourism companies operating a single vessel each in 2010 (Leeney 2014). There are also current plans for a phosphate processing plant and expansion of the industrial harbour. Bycatch is not a likely threat in either of these areas, although there is an unknown level of bycatch in South Africa from midwater trawls (Elwen *et al.* 2006). The day-to-day weather patterns at both sites are similar, with strong south-westerly winds picking up in the late morning or early afternoon on most days at both sites.

Data collection:

Boat-based surveys for cetaceans have been conducted by the Namibian Dolphin Project in Walvis Bay since 2008 and Lüderitz since 2010 with the primary goal of collecting photo-identification data. Photo-identification is the process of photographing individual animals to enable identification of unique natural marks used within a mark-recapture framework to provide information on a range of measures including abundance estimation and monitoring population trends. The main study area at Walvis Bay includes the entire bay, with survey effort concentrated around Pelican Point to the west (Figure 1). The main study area at Lüderitz includes several small bays to the west of the harbour where survey effort is concentrated (Figure 1). At both sites, the core study area is roughly 10x10 km, but there were surveys further afield, up to about 60 km along the coast, which have been included in analysis. Surveys were often ended in the early afternoon due to strong winds affecting sighting conditions.

Survey effort involved multiple observers scanning by eye, with the boat surveying at approximately 12-15 knots, but also includes 10-minute binocular searches for animals with the boat stationary. Boat position was recorded at 1-minute intervals by a Garmin GPS. Surveying was discontinued when sighting conditions deteriorated (Beaufort Sea states > 3), and any ‘off-effort’ sightings in these conditions were not considered in this analysis. Survey effort was designed to cover each study area entirely, but was non-systematic, and rather focused on known high-density areas in order to maximise encounters for photo-identification. During surveys, all encountered cetaceans were recorded and the same basic data were collected on group size, number of juveniles and calves, water depth and sea-surface temperature at the start and end of encounters. Encounters were defined from the first moment of close approach to the animals for photographs (less than 30 m) until data collection was completed or the group was lost.

Within high-density areas of Heaviside's dolphins, it was often difficult to distinguish between and maintain exclusive contact with a single group of animals due to the density of subgroups, long dive times and frequent changes in group composition and direction of the animals. In these situations, an encounter was begun when the first group of dolphins was approached, or approached the research boat, but photography was extended to include all subgroups within a radius of approximately 200 m. Animals within these encounters were in multiple groups of 1 - 8 animals, which would be approached for photography where possible. Each encounter, especially in high-density areas may therefore include multiple subgroups of animals worked over a small area. This was necessary because subgroups often approached the boat when it was slowed to collect photo-identification data, and distinguishing between subgroups was not always possible. Defining encounters in this way leads to fewer encounter start locations, but should lessen the issue of spatial autocorrelation within the dataset.

Data layers:

GPS tracks of dolphin surveys were recorded as a series of point samples one minute apart. These tracks were mapped using ArcMap 10.2 using the projection WGS 1984 UTM 33S and grid squares (1x1 km) were created using Repeating Shapes for ArcGIS (Jenness 2012). Survey effort within each grid square was calculated as the number of minutes surveyed within each grid square, defined as 'search minutes'. This is more representative than using distance covered, or simply 'number of times surveyed' in each grid square as it accounts for different search speeds and any time when the boat was stationary. Encounters per survey minute were calculated for each grid square for both Heaviside's dolphins (Lüderitz and Walvis Bay) and bottlenose dolphins (Walvis Bay only) using encounter start positions. This encounter rate was then adjusted by grid area to account for the area along the coastline. Depth soundings, depth contours and coast lines provided by the South African Naval Hydrographic Office were interpolated using the Spatial Analyst tool 'Topo to Raster' in ArcGIS at 10 m resolution to create a raster representing the bathymetry for each site. Depth data were extracted from these at each encounter start location and were also averaged over each grid square using the Spatial Analyst tool 'Zonal Statistics'.

The depth measurements extracted from the rasters at encounter start locations were then compared to data collected *in situ* to confirm the reliability of the data layers used. *In situ* measurements were on average 2.64 m deeper than raster values in Walvis Bay and 1.50 m deeper in Lüderitz. Some difference between the two is expected as *in situ* measurements are affected by tidal variation, and the depth soundings used in the raster reflect chart datum, or the depth at the lowest astronomical tide. The aspect and slope of the seafloor was similarly averaged over each grid square using the same bathymetry rasters. Distances from each encounter location and the centre of each grid square to the coastline, the 50 m isobath and the 100 m isobaths were measured using the 'near' tool in ArcGIS. These data layers were used to represent proximity to deeper waters for foraging and may be a consideration in habitat choice of near-shore waters, mainly used for resting and socializing. A data layer depicting coast type, the type of terrain along the coast, was provided by the Benguela Current Commission (De Cauwer 2007) and a data layer extracted from this was associated with all grid squares within 2 km of the coast. Coast type can reasonably be assumed to be representative of nearshore substrate following Elwen and Best (2004). Data from each encounter start location and each grid square were exported and all grid squares with at least 5 minutes' survey effort were further analysed in R version 2.15.1.

Habitat modelling – Direct comparisons:

Differences in habitat selection of Heaviside's dolphins between sites were examined with direct comparisons of single habitat measures (depth, distance from shore, distance from the 50 m isobath, distance from the 100 m isobath) extracted from data layers at encounter start locations. Depth and distance measures were included to examine the relative use of inshore vs. offshore areas, in order to elucidate patterns in foraging and predator avoidance. Comparisons were made using Welch's t-tests, as this is more robust to differences in sample size (the number of encounters at each site) and variance than Student's t-test (Ruxton 2006). Coast type was not considered in the models because only grid squares within 2 km of shore contained information, neither was it examined in a direct comparison between sites as the sites differ drastically in the predominant coast type. Instead, preferred coast type within the available range of coast types at each study site was examined using Chi-squared tests.

Habitat modelling – Generalised additive models:

To determine which of the measured variables may be important for habitat selection at each site, habitat selection of Heaviside's dolphins was further examined in R, using a series of backwards stepwise generalized additive models (GAMs), a model selection method which involves removing non-significant parameters one-by-one until model fit is no longer improved (see Redfern *et al.* 2006 for review of this method). This was done using data associated with each grid square. These modelled the effort-corrected encounter rates against the smoothed variables: depth, distance from shore, angle from shore, distance from the 50 m isobath, distance from the 100 m isobath, aspect of the sea floor, slope of the sea floor, and number of bottlenose dolphin encounters per grid square, as well as interaction terms between slope and aspect, and between the three distance measurements. Model selection was based on AIC values. Habitat selection of bottlenose dolphins in Walvis Bay was examined using the same process. Bottlenose dolphin habitat selection in Lüderitz was not analysed as they were only encountered three times there.

2.4 Results:

The results summarised here for Walvis Bay include 816 encounters (269 h 28 min of encounter time) with Heaviside's dolphins and 199 encounters (242 h 3 min of encounter time) with bottlenose dolphins over 499 h survey effort, and, for Lüderitz, 457 encounters (181 h 58 min of encounter time) with Heaviside's dolphins over 124 h survey effort. Although survey effort was considerably greater in Walvis Bay, the encounter rates per minute of survey effort for Heaviside's dolphins were higher in Lüderitz (3.69 encounter per hour) than Walvis Bay (1.64 encounters per hour). In contrast, there were only 3 'on effort' sightings of bottlenose dolphins in Lüderitz, precluding further bottlenose dolphin analysis for that study site, which is thought to be at the very southern limit of this population's range. At both study sites, survey effort was focused within the bays.

Heaviside's dolphins – Direct comparisons:

Although considerable survey effort took place within the sheltered waters of Walvis Bay, Heaviside's dolphins were rarely encountered there, with only 1 encounter far into the bay and none ever encountered near the harbour at the south eastern corner of the bay. The vast majority of encounters (708 of 817) with Heaviside's dolphins in Walvis Bay occurred within the relatively deep waters surrounding Pelican Point (Figure 2). This area is characterised by a rapid drop off from the point to 20 – 30 m depth and mixing of water currents as water circulates out of the bay. Nine encounters occurred at or beyond the 50 m depth contour; however, there was relatively little survey effort offshore. The remaining encounters were along the exposed coastline to the north and south of Walvis Bay.

The general distribution of Heaviside's dolphins in Lüderitz was similar to Walvis Bay in that the vast majority of sightings occurred in the area around Diaz Point, at the western side of the Lüderitz Bay area, and the two relatively sheltered bays to either side (Guano and Shearwater Bays, 227 of 457 encounters respectively) (Figure 2). In general, Heaviside's dolphins were considerably closer to shore and in shallower water than the Heaviside's dolphins in Walvis Bay (see below) and were occasionally encountered (n = 19) within the eastern most bay housing the commercial harbour.

Distance of Heaviside's dolphin encounters from shore was greater in Walvis Bay (875 ± 892 m) than in Lüderitz (414 ± 471 m), as was the water depth at the start of encounters (26.7 ± 9.5 m in Walvis Bay, with 84.09% greater than 15 m, and 12.2 ± 7.9 m in Lüderitz, with 90% under 20 m) (Table 1, Figures 2 and 3). Distance of encounters from the 100 m depth contour was also greater in Walvis Bay (20,790 ± 2,710 m) than in Lüderitz (10,910 ± 2,270 m); however, mean distance from the 50 m depth contour was greater in Lüderitz (5,090 ± 1,460 m) than in Walvis Bay (4,450 ± 1.840 m) (Table 1). The coastline in Walvis Bay is primarily sandy, while Lüderitz is primarily rocky. Even with survey effort accounted for,

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a significantly higher proportion of encounters were in the predominant coast type at each study site than would be expected from chance alone, with 635 of 684 inshore encounters in Walvis Bay adjacent to sandy coastline (Figure 4) ($\chi 2 = 181.26$, Df = 7, $p < 0.05$) and 390 of 428 inshore encounters in Lüderitz adjacent to rocky coastline (Figure 4) ($\chi 2 = 51.92$, Df = 4, $p < 0.05$).

Heaviside's dolphins – Generalised additive models:

Generalized additive models revealed that in Walvis Bay, factors significantly correlated with habitat selection of Heaviside's dolphins included depth and slope of the sea floor and distance from the 100 m isobath, with the aspect of the sea floor, although not significant, included in the best-fitting model (Table 2). Dolphins preferred habitat of 20 m depth, a slope of 0.7°, areas further from the 100m isobath and a generally westward facing slope.

In Lüderitz, significant factors correlated with habitat selection of Heaviside's dolphins include distance from the 100 m isobath, distance from shore and distance from the 50 m isobath, with angle of the coast, although not significant, included in the best-fitting model (Table 3). Although number of bottlenose dolphins was not included in the best-fitting models, this may be because an effort-corrected measure was not used as using the same method of effort-correction could cause the response and explanatory variables to be too similar. Dolphins preferred areas further inshore from the 100 m and 50 m isobaths approximately 1 km from shore, and a west-southwest-facing slope. They also preferred to occupy areas north-northwest of the nearest coastline.

Bottlenose dolphins – Direct comparisons

Bottlenose dolphins in Walvis Bay showed a nearly opposite distribution pattern to Heaviside's dolphins, except for an area of overlap at Pelican Point (Figure 5). Of the 199 bottlenose dolphin encounters, 71 were clustered around the point, with nearly all of the rest within the sheltered waters of the bay, usually quite close to the coast or in less than 15 m of water (Figure 2). Bottlenose dolphin encounters were at a mean depth of 12.82 ± 7.84 m, and all encounters were in waters less than 30 m deep. A total of 5 encounters occurred to the north or south of the bay, all very close to shore. Bottlenose dolphins are also frequently seen in the shallow lagoon area of Walvis Bay (NDP unpublished data), which is not included in this study as it is not possible to survey the lagoon by boat. Interestingly, sightings of bottlenose dolphins have been reported in the Lüderitz lagoon area as well (pers. comm.), which has a very low sighting rate for Heaviside's dolphins.

Bottlenose dolphins – Generalised additive models

Models suggest that the significant factors correlated with habitat selection of bottlenose dolphins include depth and distance from the 100 m isobath. The non-significant variables included in the best-fitting model include distance from shore, and the aspect and slope of the sea floor (Table 4). Bottlenose dolphins preferred habitat with a mean of 7 m depth, areas further inshore from the 100m isobaths and areas within 1.5 km from shore and with a west-southwest-facing slope of 0.4°.

2.5 Discussion:

Heaviside's dolphins in Walvis Bay were in deeper waters, further from shore, than those in Lüderitz. However, at both sites, high encounter rates were found in the waters surrounding north-facing peninsulas (Diaz Point and Pelican Point) exposed to prevailing wind and swell and close to the open ocean. Animals were encountered closer to the 50 m contour than the 100 m contour at both study sites. Distance to the 50m contour was similar at each study site, and though distance to the 100 m contour was greater in Walvis Bay, this is likely a result of the shape of the shelf at each study site (Figure 1). Heaviside's dolphins were effectively never seen in the protected parts of Walvis Bay and were rarely close to shore (except in the deep waters surrounding Pelican Point) or in the surf zone, while in Lüderitz, dolphins made extensive use of the nearshore waters in the bays either side of Diaz Point and also right into the most protected waters near the harbour. More encounters than would expected from chance were adjacent to sandy coastline in Walvis Bay, and rocky coastline in Lüderitz. This is due to the predominant coast type of each site's high-occurrence areas.

Differences in habitat selection between these study sites and previous studies of Heaviside's dolphins in the Southern Benguela indicate plasticity in the behavioural patterns underlying habitat selection. Some of these differences between Walvis Bay and Lüderitz may simply be due to the difference in available habitat between these quite different sites (e.g. coast type). However, these differences in habitat selection are also likely affected by the availability and distributions of prey species and also by presence and distributions of other top predators, both of which could be contributing to what appear to be two very different patterns in foraging behaviour between the two areas. Acoustic detections of Heaviside's dolphins in Walvis Bay are more frequent at night (Leeney *et al.* 2011), implying high nocturnal activity in the area with a high encounter rate at Pelican Point, most likely due to feeding. While in Luderitz, dolphins were most frequently detected during the first half of daylight hours in Guano Bay and at Diaz Point (Chapter 3). The kelp beds of the rocky southern coast of Namibia act as a nursery ground for potential prey species (Hutchings *et al.* 2002). Our results show that in Lüderitz, Heaviside's dolphins are found more often close to shore, including right next to and even within kelp beds, where they are frequently observed patrolling the reefs in foraging bouts (authors' personal observation). As the sandy coastline of Walvis Bay does not lend itself to kelp beds, this particular foraging opportunity is not likely as available at the Walvis Bay study site.

The main similarity between the sites is the very high encounter rates in the waters surrounding Pelican Point in Walvis Bay and Diaz Point in Lüderitz. Both are exposed to the prevailing swell and wind conditions and are areas where offshore waters and more sheltered waters mix. The preference for areas near the exposed corners of larger bays at the mixing point of sheltered and unsheltered waters seems to be a characteristic of the species, as this was also found by Elwen *et al.* (2009a) in the Southern Benguela. The use of inshore areas by cetaceans is often a means of predator avoidance (e.g. dusky dolphins (Srinivasan and Markowitz 2010)) and the pattern of habitat selection observed for this species may be a

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trade-off between predator avoidance close to shore and proximity to offshore foraging areas (Elwen *et al.* 2009a).

The use of deeper waters and the avoidance of the shallower, protected parts of Walvis Bay likely result from the presence of common bottlenose dolphins close inshore, as there was relatively little overlap of the areas used by the two species. Widespread (and sometimes fatal) attacks (as determined by necropsies and a few direct observations of aggressive behaviour) on harbour porpoises (*Phocoena phocoena*) by bottlenose dolphins have been reported from the Moray Firth, (Ross and Wilson 1996) and Cardigan Bay, United Kingdom, (Jepson and Baker 1998), as well as the coastal waters of California, United States (Cotter *et al.* 2012). The reasons for these attacks are unknown, and Cotter *et al.* (2012) suggest that causes likely differ between areas. Patterson *et al.* (1998) suggest that this behaviour, which may account for an estimated 63% of porpoises found dead in the Moray Firth (Jepson and Baker 1998), is practice for infanticide, which they report for that population. Spitz *et al.* (2006) examined diet overlap between bottlenose dolphins and harbour porpoises in the Bay of Biscay, NE Atlantic, and determined that interference competition is a likely explanation for the attacks, with even some overlap in prey species, because of the size of prey patches and foraging behaviours.

Though no aggression towards Heaviside’s dolphins by bottlenose dolphins has been observed, the similarity, particularly in body size, of Heaviside’s dolphins to harbour porpoises, and the propensity of occasional aggressive behaviour by bottlenose dolphins towards various other small cetaceans (see (Cotter *et al.* 2012) for a review) indicates the possibility of aggression or area avoidance occurring where both species are present. Differences in preferred prey or habitat preference may also act to mediate competition between sympatric species, and has been shown in many areas where dolphin populations broadly overlap (see Bearzi (2005) for review). Though niche separation in prey type and foraging behaviour for Heaviside’s and Dusky dolphins has been shown (Heinrich *et al.* 2010), this species is unlikely to be effecting site differences in habitat selection in Namibia, as dusky dolphins are present offshore at both study sites. Further comprehensive studies on prey availability and selection at these study sites would be needed to clarify any potential diet overlap and shed light on possibility of competition or niche partitioning driving foraging patterns or habitat use.

Management implications:

The use of deeper waters by Heaviside's dolphins in Walvis Bay does not exclude them from exposure to the high level of anthropogenic activity, namely constant ship noise compared to Lüderitz where there are relatively very few human impacts within the dolphins' habitat. Boat presence has been shown to affect the behaviour of cetacean species, and this can include area avoidance (Lusseau 2005). Other sources of anthropogenic noise may be present close to the much more developed Walvis Bay harbour, particularly with the recently begun construction of the port expansion (OLRAC 2009). Other activities, such as dredging drastically affect turbidity, which like noise, can influence dolphin distributions. For example, Bräger *et al.* (2003) studied habitat selection of Hector's dolphins and found a strong preference for very turbid waters.

It is clear from the comparatively high rate of encounters inside vs. outside of the bays surveyed that both Walvis Bay and Lüderitz are important habitat for Heaviside's and bottlenose dolphins. Both of these populations must continue to be carefully monitored in order to detect and mitigate potential human impacts. For Heaviside's dolphins, this is especially true of Lüderitz, where they utilize areas close inshore, including the harbour. In Walvis Bay, the high use by bottlenose dolphins of areas close inshore make them particularly susceptible to impacts from increased industrial activity. Also, the area around Pelican Point is a high-use area for both species examined, and indeed the only area where both species have much overlap. Though not yet under development, that area is subject to a high level of boat activity, especially marine wildlife tours, and use of this area should be closely monitored in the future.

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2.7 Tables and Figures:

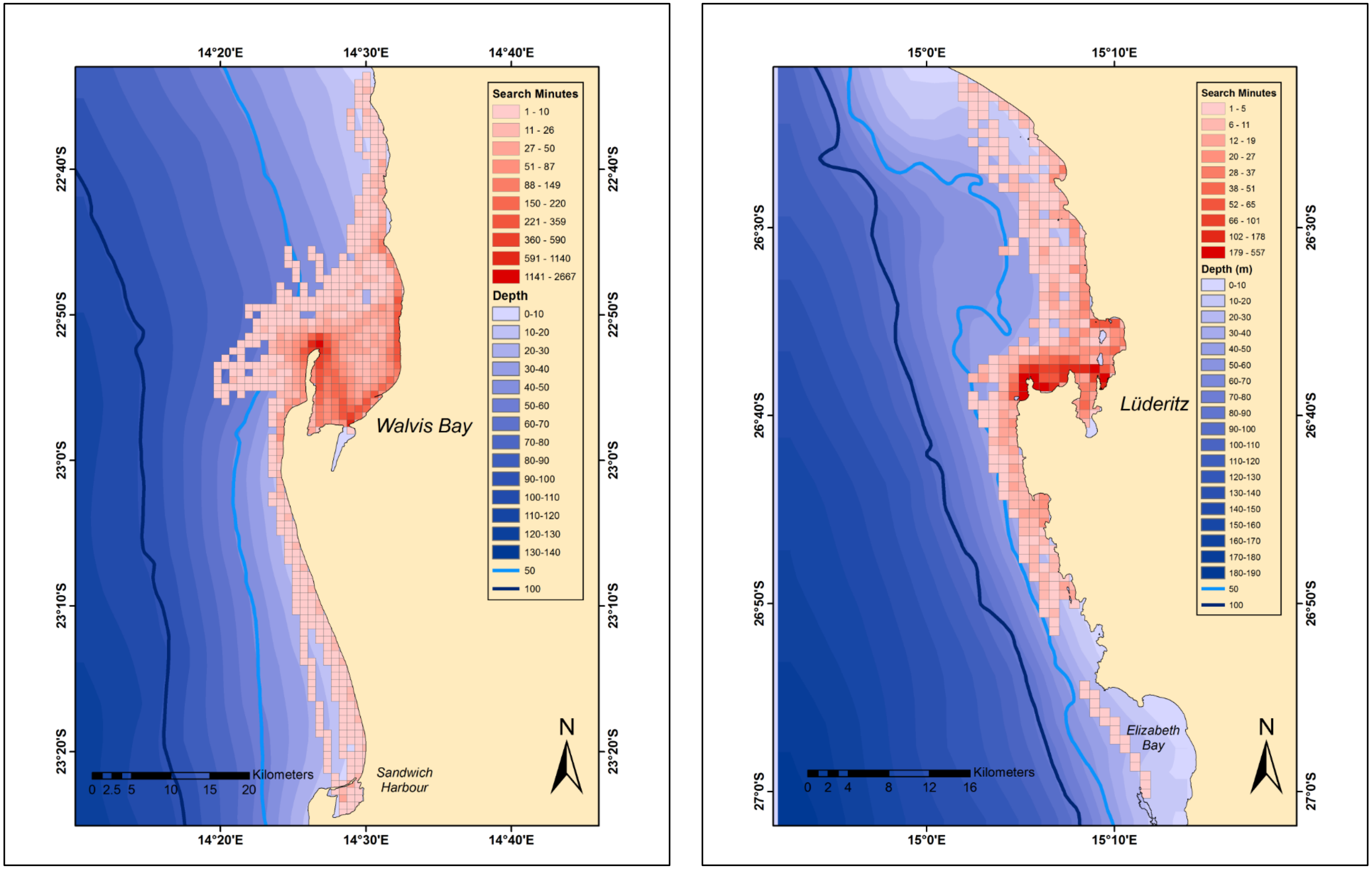

Figure 1: Map of the study areas at Walvis Bay (left) and Lüderitz (right), showing grid squares (1x1 km) of survey effort coloured by number of minutes searched. Note different scales.

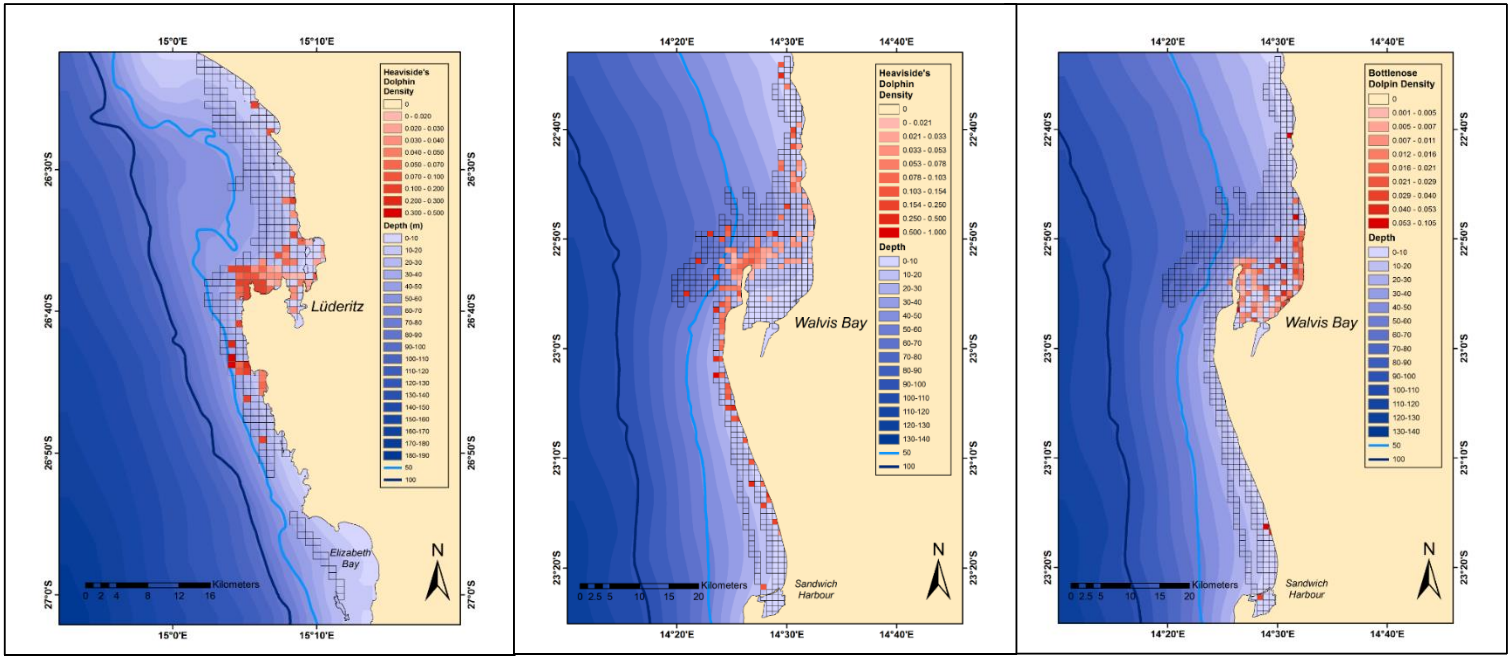

Figure 2: Map showing the frequency of encounters (encounters per minutes searched, for each 1x1 km grid cell) for Heaviside's dolphins in Lüderitz (left) from data collected during 88 surveys conducted between 29 Jan, 2010 and 31 May, 2014, and Walvis Bay (centre) from data collected during 264 surveys conducted between 01 Jun, 2008 and 16 Oct, 2013, and for bottlenose dolphins in Walvis Bay (right). Some of the grid squares which appear to be high-use areas simply have a low search effort, affecting the ratio displayed. This was accounted for during analysis by excluding each grid with fewer than 5 minutes' search effort.

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Table 1: Data from Walvis Bay and Lüderitz, Namibia, for environmental parameters recorded at the start locations of Heaviside's dolphin encounters. Comparisons were made using Welch's t-test, which is more reliable when comparing samples with unequal variance**s.**

	Walvis Bay	**Lüderitz**	
	Mean (SD) (metres)	**Mean (SD) (metres)**	**p-value**
Distance from shore	875 (892)	414 (471)	$p < 0.05$
Water depth	26.7 (9.5)	12.2 (7.9)	$p < 0.05$
Distance from 50 m contour	4 450 (1 840)	5 090 (1 460)	$p < 0.05$
Distance from 100 m contour	20 790 (2 710)	10 910 (2 270)	$p < 0.05$
Sample size	816	457	

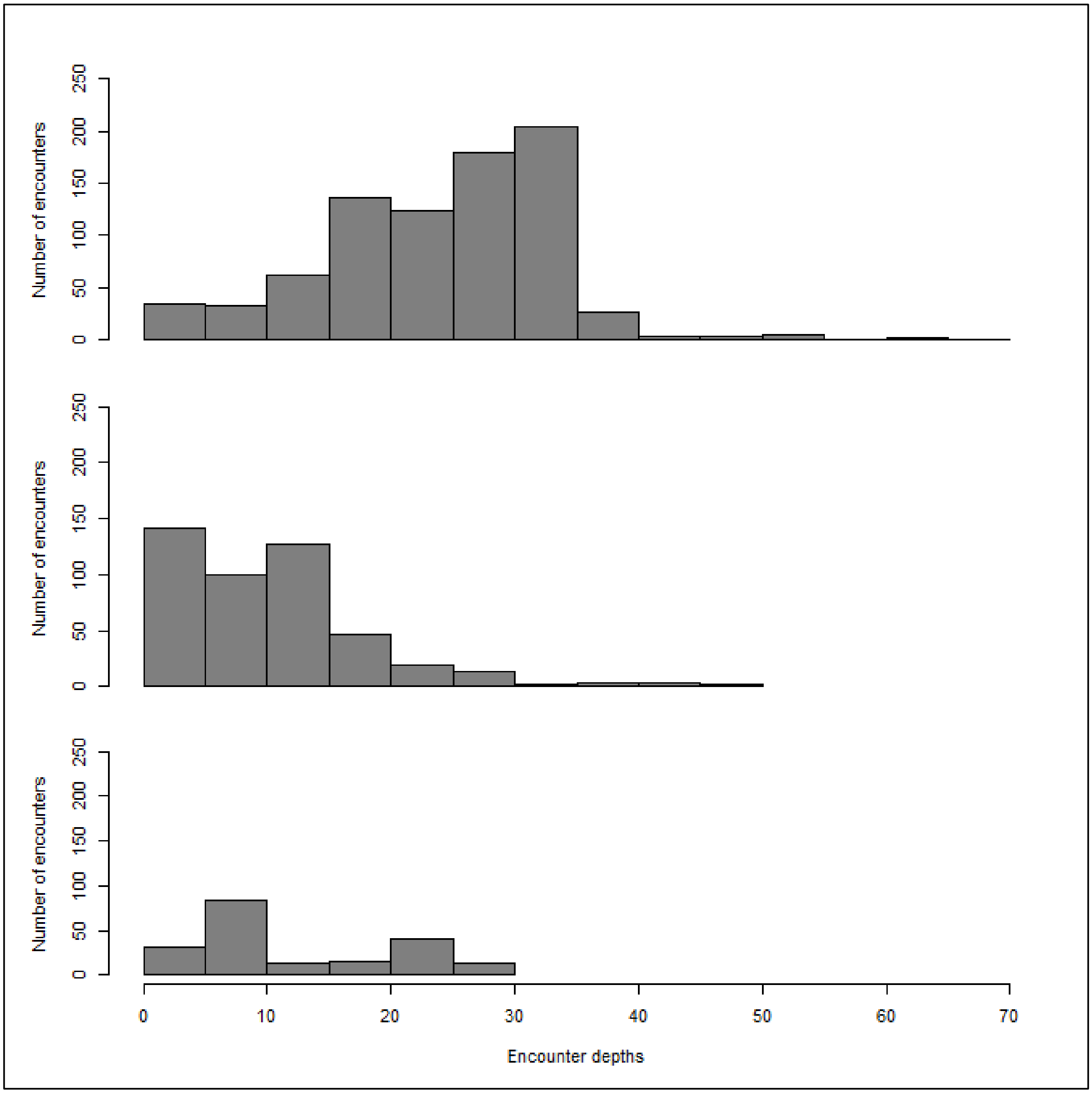

Figure 3: Histograms showing depth distribution for Heaviside's dolphin encounters in Walvis Bay (top) and Lüderitz (middle) and for bottlenose dolphins in Walvis Bay (bottom).

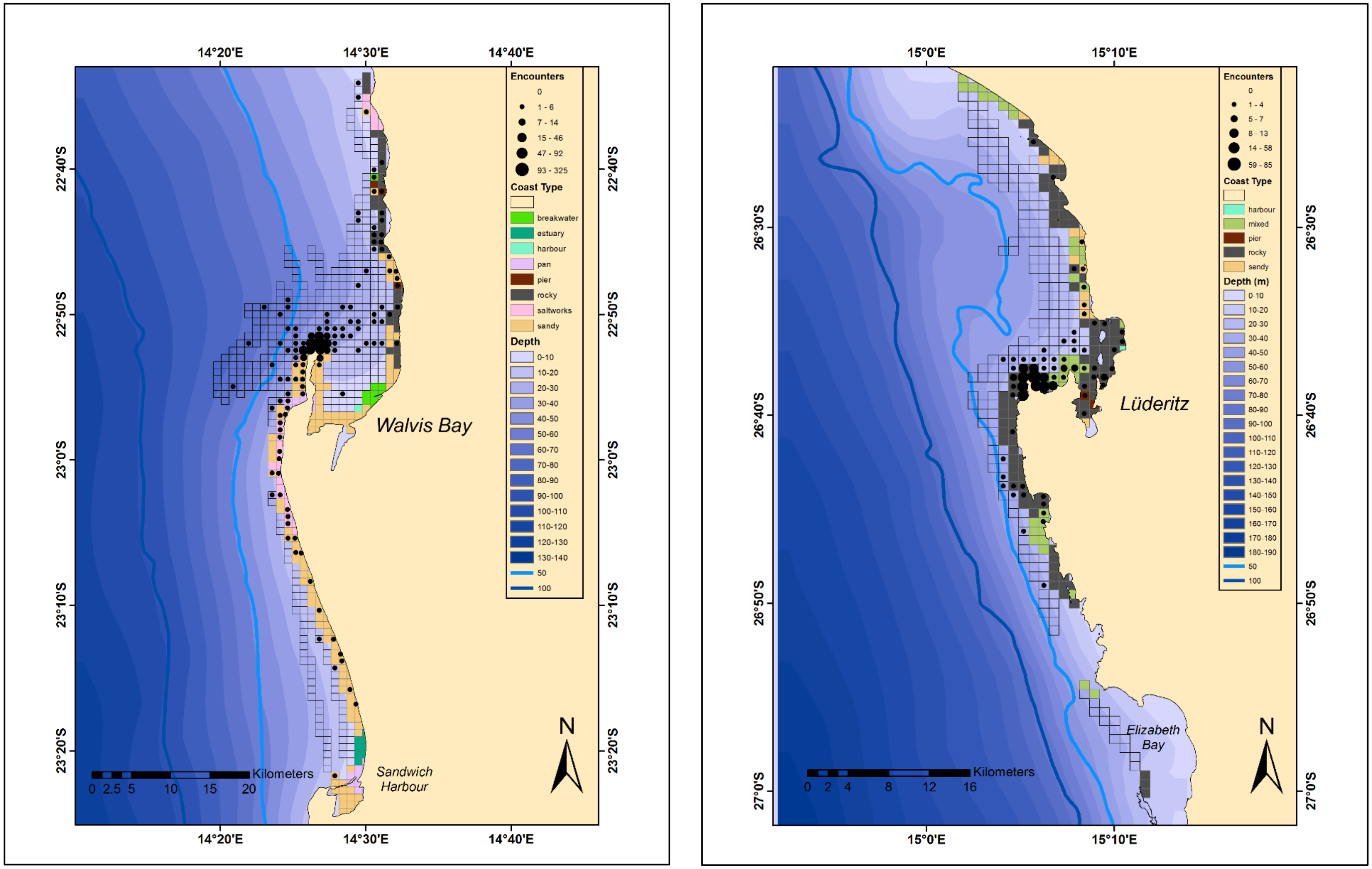

Figure 4: Map of Heaviside's dolphin encounter rates by coast type in Walvis Bay (left) and Lüderitz (right), Namibia. Grid squares (1x1 km) within 2 km of the coast type. The points at grid square centres are scaled by the total number of encounters for that grid square.

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Table 2: Results of stepwise backwards Generalized Additive Models selecting habitat variables relevant to Heaviside's dolphin encounters in Walvis Bay. The models compare values for the effort-corrected encounter rate and smoothed habitat variables for each grid square (n = 413) with at least 5 minutes' survey effort. The selected model is in bold. Variables include the effort-corrected encounter rate for Heaviside's dolphins (CHSPUE), depth, distance from shore (DFS), distance from the 100 m isobath (DF100), the number of bottlenose dolphin encounters (TTEnc) and aspect and slope of the sea bed.

Model	**df**	**AIC**	**AICc**	**% Dev**	**R^2 (adj.)**
CHSPUE ~ s(Depth) + s(DFS) + s(DF100) + s(TTEnc) + s(Aspect) + s(Slope) + Aspect * Slope	15	-1635.41	-1634.21	18.2	0.156
CHSPUE ~ s(Depth) + s(DFS) + s(DF100) + s(Aspect) + s(Slope) + Aspect * Slope	14	-1636.15	-1635.1	18	0.155
CHSPUE ~ s(Depth) + s(DF100) + s(Aspect) + s(Slope) + Aspect * Slope	13	-1636.82	-1635.95	17.6	0.154
CHSPUE ~ s(Depth) + s(DF100) + s(Aspect) + s(Slope)	**12**	**-1638.12**	**-1637.39**	**17.4**	**0.155**
CHSPUE ~ s(Depth) + s(DF100) + s(Slope)	10	-1636.58	-1636.05	16.4	0.148

Table 3: Results of stepwise backwards Generalized Additive Models selecting habitat variables relevant to Heaviside's dolphin encounters in Lüderitz. The models compare values for the effort-corrected encounter rate and smoothed habitat variables for each grid square (n = 210) with at least 5 minutes' survey effort. The selected model is in bold. Variables include the effort-corrected encounter rate for Heaviside's dolphins (CHSPUE), depth, distance from shore (DFS), distance from the 100 m isobath (DF100), distance from the 50 m isobath (DF50) and slope and angle of the sea bed.

Model	df	AIC	AICc	% Dev	R^2 (adj.)
CHSPUE ~ s(Depth) + s(DFS) + s(DF100) + s(DF50) + s(Angle) + s(Slope) + DFS * DF50	18	-741.775	-738.077	31.6	0.258
CHSPUE ~ s(DFS) + s(DF100) + s(DF50) + s(Angle) + s(Slope) + DFS * DF50	17	-743.199	-739.877	31.4	0.26
CHSPUE ~ s(DFS) + s(DF100) + s(DF50) + s(Angle) + DFS * DF50	**12**	**-742.277**	**-740.603**	**27.8**	**0.24**
CHSPUE ~ s(DFS) + s(DF100) + s(DF50) + DFS * DF50	11	-741.655	-740.229	26.9	0.235
CHSPUE ~ s(DFS) + s(DF100) + s(DF50)	12	-737.233	-735.728	25.6	0.219

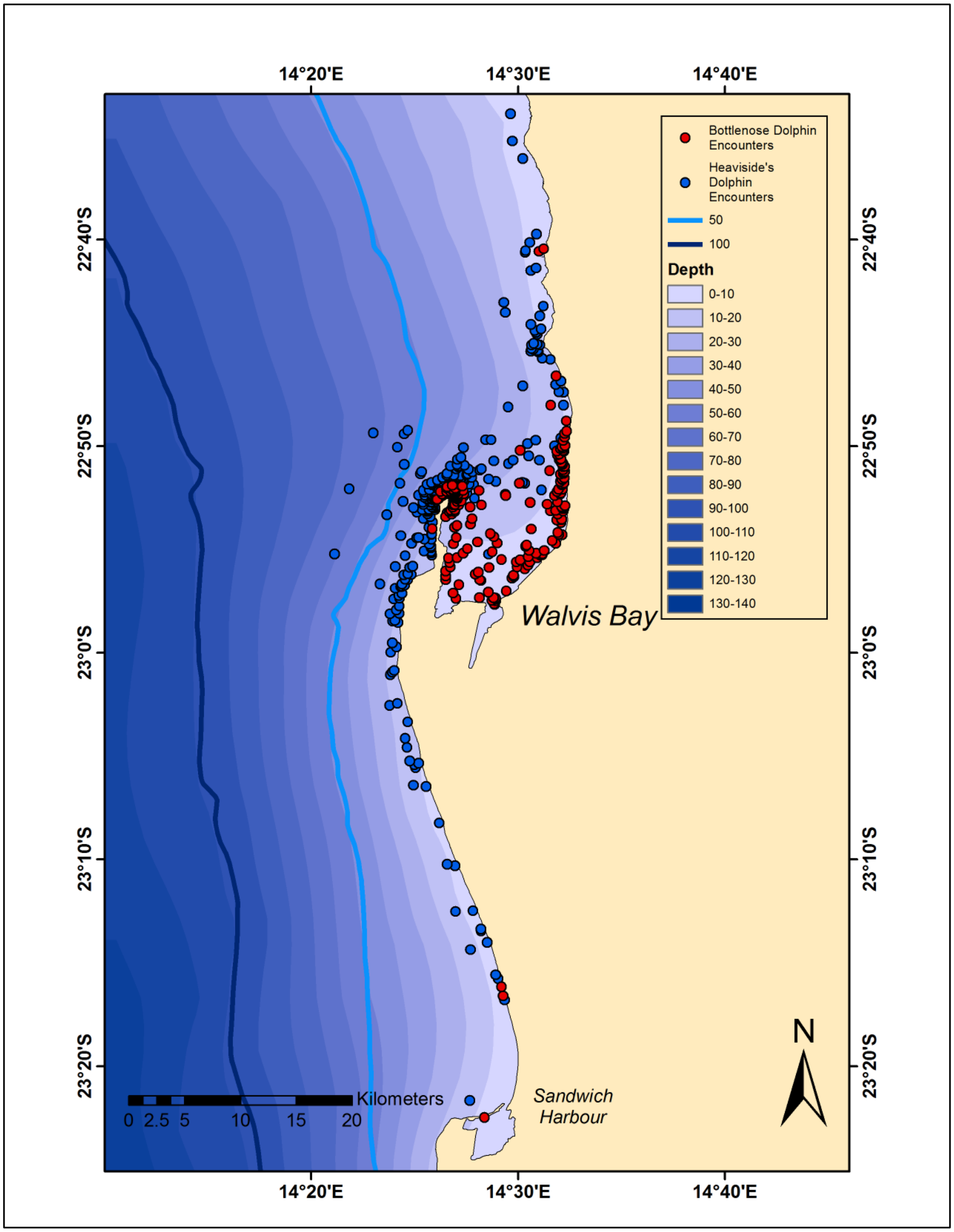

Figure 5: Map of all encounter locations for both Heaviside's dolphins and bottlenose dolphins.

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Table 4: Results of stepwise backwards Generalized Additive Models selecting habitat variables relevant to bottlenose dolphin encounters in Walvis Bay. The models compare values for the effort-corrected encounter rate and smoothed habitat variables for each grid square (n = 413) with at least 5 minutes' survey effort. The selected model is in bold. Variables include the effort-corrected encounter rate for bottlenose dolphins (TTSPUE), depth, distance from shore (DFS), distance from the 100 m isobath (DF100), distance from the 50 m isobath (DF50) and aspect and slope of the sea bed.

Model	df	AIC	AICc	% Dev	R^2 (adj.)
TTSPUE ~ s(Depth) + s(DFS) + s(DF100) + s(DF50) + s(Aspect) + s(Slope) + Aspect * Slope	15	-1685.52	-1684.27	18.8	0.161
TTSPUE ~ s(Depth) + s(DFS) + s(DF100) + s(Aspect) + s(Slope) + Aspect * Slope	18	-1687.03	-1685.23	20.3	0.17
TTSPUE ~ s(Depth) + s(DFS) + s(DF100) + s(Aspect) + s(Slope)	**17**	**-1688.18**	**-1686.6**	**20.1**	**0.17**
TTSPUE ~ s(Depth) + s(DFS) + s(DF100) + s(Slope)	11	-1685.89	-1685.19	17.3	0.154

Chapter 3

Foraging ecology and acoustic behaviour of Heaviside's dolphins (*Cephalorhynchus heavisidii*) in Namibia – Insights from passive acoustic monitoring

3.1 Abstract:

This study was designed to investigate diel patterns in acoustic activity of Heaviside's dolphins to provide insight into their foraging ecology and movement patterns in a high-density area at Lüderitz, Namibia. Heaviside's dolphins range along the west coast of South Africa and Namibia and are endemic to the cool Benguela current ecosystem. The acoustic repertoire of the species consists of Narrow-Band-High-Frequency (NBHF) echolocation clicks centred around 125 kHz and they are the only species using the study area that are known to produce NBHF clicks. Acoustic monitoring was conducted using C-POD click loggers at five deployment sites around Lüderitz, spaced roughly 2 km apart in a line from east to west. This study was conducted concurrently to a series of small boat surveys for cetaceans at the same location, the results of which serve to visually confirm the findings of this study (Chapter 2). There were differences between sites in the rate of acoustic detections, with some sites showing a near-constant presence, and others showing very few detections, implying strong habitat selection within the study area. There was also a strong diurnal pattern of presence at all sites, with peak detections at midday, except at the most western site, which had peak detections around dawn, implying a movement offshore in the later part of the day and overnight. The findings on spatial and temporal variation in detections of Heaviside's dolphins can serve to form the basis of dynamic management initiatives, such as shutting down noisy industrial activities during hours of peak dolphin presence to avoid disturbance to animals in the areas in which they are most frequently present.

3.2 Introduction:

Heaviside's dolphins (*Cephalorhynchus heavisidii*) are a small-bodied, porpoise-like species endemic to the Benguela current along the west coast of southern Africa, ranging from Table Bay, South Africa, to southern Angola. The species is not well-studied off the Namibian coast, although it is known to have a nearshore distribution (Findlay *et al.* 1992) and makes use of the two large bays housing industrial ports along the Namibian coast, Walvis Bay and Lüderitz. Although the Namibian coastline is largely unpopulated, these areas of human commercial and industrial activity are also high-density areas for Heaviside's dolphins, prompting further investigation (Findlay *et al.* 1992, Elwen *et al.* 2011a).

The species is known to show strong diurnal patterns of movement in both South Africa, where inshore presence is positively correlated with daylight hours and brighter phases of the moon (Elwen *et al.* 2009a). Leeney *et al.* (2011) used acoustic monitoring to examine dolphin presence in Walvis Bay, and found that inshore presence of Heaviside's dolphins is greater at night. Diel patterns in acoustic presence of cetacean species are often related to environmental factors, such as tidal state or light levels and this relation usually reflects diel patterns in their prey species, driven by vertical migration of organisms at lower trophic levels (e.g. Baumgartner and Fratantoni 2008), which is essentially related to avoidance of predators, especially those which hunt visually. Diurnal patterns in movement of Heaviside's dolphins in South Africa are driven by a nocturnal movement offshore to hunt their primary prey species there, Cape hake (*Merluccius capensis*), which rise in the water column during hours of darkness and become more readily accessible to the dolphins, with a subsequent return to more protected coastal waters when prey availability is low (Gordoa and Macpherson 1991, Sekiguchi *et al.* 1992, Elwen *et al.* 2009a). This study was designed to investigate diel patterns of Heaviside's dolphins in Lüderitz to examine habitat selection and foraging patterns. This chapter examines diel patterns in acoustic presence as well as acoustic indicators of foraging, and how these temporal patterns vary over a small spatial scale. Similar monitoring has been done in Walvis Bay, the larger of the bays, by Leeney *et al.* (2011). These two sites not only have differing levels of human impacts, but are also quite different ecologically (see Chapter 2). Other dolphins present at Lüderitz are dusky dolphins (*Lagenorhynchus obscurus*), which are observed in the area fairly regularly and bottlenose dolphins (*Tursiops truncatus*), which have been observed in the study area only occasionally. Since both these species use broadband echolocation clicks (Au 1993, Au 2004), they are easily differentiated acoustically from Heaviside's dolphins.

Acoustic monitoring of echolocation activity of Heaviside's dolphins was done using C-PODs, which are self-contained underwater acoustic data loggers that detect and record information on tonal clicks including echolocation clicks from odontocete cetaceans (see below). C-PODs were deployed concurrently to a study of fine-scale habitat selection taking place in the same study area, which involved a series of small boat surveys for dolphins (see Chapter 2). This study was designed to examine fine-scale spatial and temporal patterns in habitat selection of Heaviside's dolphins in a previously unstudied high-density area.

Passive acoustic monitoring:

Sound travels over 4 times faster in water than air, and travels the furthest of any form of radiation in the marine environment, making sound a very powerful means of communicating in and sensing the marine environment (Au and Hastings 2008). Cetaceans have evolved to take advantage of this sensory modality and they rely strongly on the acoustic medium for communication, orientation and feeding (Tyack and Clark 2000, Berta *et al.* 2005). Passive acoustic monitoring (PAM) of cetaceans involves detecting cetaceans through their natural vocalizations using either towed or moored hydrophones, either singly or in an array (Mellinger *et al.* 2007). PAM methods have been increasingly used as a supplement or alternative to visually searching for marine mammals (Zimmer 2011). This is due in part to the relative ease and sometimes lower cost of acoustic techniques when compared to using solely visual observations for certain studies. Visual surveys often incur high running-costs and are easily interrupted by bad weather or sighting conditions. Acoustic monitoring is currently the only feasible means of monitoring for cetaceans continuously over a potentially large area for long periods of time. Because cetacean behaviour

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can vary diurnally, observing cetaceans with both acoustic and visual surveys can lead to a more thorough understanding of the ecology of species of interest. Static systems like the C-PODs used in this study reduce the potential disturbance to the study animals in comparison to studies conducted from a vessel. PAM allows for a better understanding of cetacean species, as it allows for observation overnight, and provides the ability to detect rarely-sighted species, because of the potential for more constant coverage, especially of remote or offshore regions or areas with poor weather conditions.

Some caveats to PAM are that only vocalizing animals can be detected, and it is difficult to tell the number of individuals vocalizing at once (Mellinger *et al.* 2007). For many species, PAM is therefore better suited to give a minimum or relative estimate of animal occurrence, rather than an estimate of absolute abundance (Mellinger *et al.* 2007). Many calls are undocumented and there is similarity between some species' calls, which can lead to many unknowns within an acoustic dataset (Caillat *et al.* 2013). It is therefore important to ground-truth acoustic data with some form of visual confirmation (Castellote *et al.* 2013), particularly when using call types that can be attributed to more than one species. Most of these limitations can be mitigated, however, with enough prior information. For example, animal density can be estimated using PAM if the call rate is known along with an accurate estimation of detection probability for the recording equipment and acoustic environment (Marques *et al.* 2013). It is also important to understand variation in call rate, which can act as a cue for the number of animals present and of group behaviour (Whitehead and Weilgart 1990) and also the rate of false positive detections compared to true detections (Marques *et al.* 2009). PAM also requires very specialized equipment. Localization of individuals using acoustic signals requires syncing an array of multiple recording units in close proximity, which we were unable to do for this study. PAM sometimes creates massive datasets, especially when dealing with high frequency sounds, which then require large storage volumes and time-consuming analysis. Thus automated detectors for specific call types can be an extremely useful aid for data analysis though manually checking a proportion of any data run through automated detectors is important.

Odontocete vocalizations:

The calls produced by odontocete cetaceans fall into three broad categories: tonal whistles, burst-pulses and clicks (Janik 2009, Richardson *et al.* 2013). Dolphin whistles are longer-duration signals (100 ms to around 4 s) (Buckstaff 2004) used for communication between conspecifics and have fundamental frequencies between 800 Hz (Schultz and Corkeron 1994) and 28.5 kHz (May-Collado and Wartzok 2008), though this varies with both species and population (Janik 2009). Whistles vary in complexity of frequency modulation and contain a varying number of harmonics (see Janik (2009) for review). Burst pulses are very rapid series of clicks, which fall somewhat between whistles and trains of distinct clicks, though there is no single quantitative definition to separate these from the other two types of calls (Janik 2009). Click trains are also used for communication, though the extent of this is unknown, as the primary function of clicks for most species seems to be for echolocation (Janik 2009). Clicks are produced much more frequently than whistles, but do not tend to travel as far making them less useful for detection of rare species (Oswald *et al.* 2007, Janik 2009). Species identification from acoustic cues only is still a new and rapidly developing field (Oswald *et al.* 2003), with most effort focussing on whistles (Oswald *et al.* 2007), though echolocation clicks have been used (e.g. Soldevilla *et al.* 2008).

There are two major categories of clicks produced by odontocetes: narrow-band high frequency (NBHF) clicks and short-duration broadband clicks (Morisaka 2012). All odontocete species which produce whistles also produce these broadband clicks (Morisaka and Connor 2007). NBHF clicks have a peak frequency over 100 kHz, and a waveform with increasing amplitude over the first 5 cycles before it decays exponentially. The main pulse of broadband clicks usually contains one or two cycles with the first cycle having the maximum amplitude (Au 1997). NBHF clicks have a longer duration (>125 µs) and are less intense (by approximately >20 dB) than broadband clicks, which are usually <50 µs in duration and often >200 dB re 1 µPa (Nakamura and Akamatsu 2004). Broadband clicks often have a -3dB bandwidth of > 10 kHz, whereas NBHF clicks have a -3 dB bandwidth of <10 kHz (Au 1997, Morisaka *et al.* 2011, Morisaka 2012).

NBHF echolocation clicks have been reported in all *Cephalorhynchus* species (Kamminga and Wiersma 1982, Dawson 1988, Götz *et al.* 2010, Morisaka *et al.* 2011), all porpoises, pygmy sperm whales (*Kogia breviceps*) (Madsen *et al.* 2005) and also for two *Lagenorhynchus* species: hourglass dolphins (*L. cruciger*) (Tougaard and Kyhn 2010) and Peale's dolphins (*L. australis*) (Kyhn *et al.* 2010). NBHF clicks are also likely produced by *Pontoporia blainvillei* (Von Fersen *et al.* 2000, Morisaka and Connor 2007) and given similarity of vocal structures between the two kogiid species, dwarf sperm whales (*K. sima*) (Clarke 2003, Morisaka and Connor 2007, Thornton *et al.* 2015). Morisaka and Connor (2007) propose that NBHF clicks, as well as whistle loss, may have evolved convergently in this paraphyletic set of species as a means of anti-predator acoustic crypsis to avoid detection by *Orcinus orca*. NBHF detections in Lüderitz and Walvis Bay can be confidently attributed to Heaviside's dolphins as they are the only NBHF click producing species that frequents the inshore waters of Namibia.

Heaviside's dolphin vocalisations:

The acoustic repertoire of Heaviside's dolphins was first investigated by Watkins *et al.* (1977), when four animals were caught and temporarily held in a small cement pool. However, the recordings procured were limited in bandwidth as the frequency response of the system was 60 Hz to 10 kHz ±2 dB and thus do not reflect the true nature of the calls. In the Watkins *et al.* (1977) study, sounds were produced throughout the recording period, often with 1-10 seconds in between vocalisations. There were only 6 cases of overlapping vocalisation and one silent period of 4 minutes 45 seconds during the entire recording period. Unfortunately, the vocalisation rate for unrestrained Heaviside's dolphins remains unknown.

The characteristics of the echolocation clicks of Heaviside's dolphins were described more fully by Morisaka *et al.* (2011) who used a T-shaped hydrophone array (sensitivity 70-160 kHz ± 3 dB). They determined that Heaviside's dolphins produce four types of NBHF clicks, classified by differences between the second peak and highest spectral peak. The NBHF clicks produced by Heaviside's dolphins have a mean apparent source level of 173 dB re 1 µPa, an average duration of 74 µs, inter-click intervals

(ICIs) that range from 2-113 ms (mean 58) and centroid frequencies that range from 121-130 kHz (mean 125) (Morisaka *et al.* 2011). The -3 dB bandwidth ranges from 6-21 kHz (mean 15 kHz) (Morisaka *et al.* 2011). ICIs were positively correlated with click duration and negatively correlated with bandwidth and Morisaka *et al.* (2011) propose that Heaviside's dolphins may adjust their click duration and bandwidth based on detection range. The peak frequencies in Heaviside's dolphin echolocation clicks show a bimodal distribution, and individual clicks showed either one peak or bimodal peaks in frequency at around 122 and 130 kHz, which Morisaka *et al.* (2011) suggest indicate an asymmetry in the vocal production structures, the monkey lips/dorsal bursae (MLDB) complex following Cranford *et al.* (1996), who noted that the bimodal peak frequency in the pulsed signals of false killer whales (*Pseudorca crassidens*) (Thomas *et al.* 1988, Au *et al.* 1995) could be connected to dorsal bursae length.

Vocalisations of dusky dolphins and bottlenose dolphins:

The vocalizations of the dusky dolphin population along the Namibian coast have not been described in detail, and these could differ either in use, or in certain acoustic properties between populations. For example, Vaughn-Hirshorn *et al.* (2012) compared clicks and burst-pulses from dusky dolphins in Argentina and New Zealand, noting differences in ICIs between the two populations. The New Zealand dusky dolphins produce echolocation clicks with bimodal peaks in frequency around 40-50 kHz and 80-110 kHz with the lower-frequency peak dominant in low-source-level signals and the higher-frequency peak dominant in signals with higher source levels. Peak-to-peak source levels for this species can be as high as 210 dB re 1 µPa (Au and Würsig 2004).

The vocal repertoire of the bottlenose dolphin population which visits Lüderitz includes whistles, echolocation clicks, burst pulses, low-frequency narrow-band ('LFN') sounds, 'brays' and 'chirps' (Gridley *et al.* 2015). The echolocation clicks of this particular population have not been fully described, but bottlenose dolphin clicks typically have peak frequencies up to 120-130 kHz, a duration of 40-70 µs and peak-to-peak source levels between 210 and 227 dB re 1 µPa (Au 1993). Houser *et al.* (1999)

distinguished different types of calls based on bandwidth and peak frequency parameters, identifying a 'Wideband call' with a -3db bandwidth of < 85 kHz. The C-PODs used in this study do not differentiate between bottlenose dolphin and dusky dolphin click trains. Due to the rare occurrence of bottlenose dolphins at Lüderitz, broadband click detections are likely dusky dolphins, except when bottlenose dolphins have been visually confirmed near the C-PODs.

Potential 'feeding buzzes':

In echolocating species, as the range to a target decreases, the ICI of echolocation clicks decreases, sometimes linearly (e.g. Verfuß *et al.* 2005), although there is often a more sudden rapid burst of clicks as a target is approached (Schevill *et al.* 1969). For example, Miller *et al.* (2004) used D-Tags on sperm whales (*Physeter macrocephalus*) to verify that the rapid bursts of clicks termed 'creaks' emitted in-between their regular, slower-interval clicks were likely emitted during prey capture based on changes in swim speed, orientation, and overall dive time associated with creak production. Verfuß *et al.* (2009) found that as harbour porpoises (*Phocoena phocoena*) approach a prey item, the ICI of their echolocation clicks drops from around 50 ms to under 10 ms, remaining constant at under 2 ms thereafter. Carlström (2005) chose the proportion of trains with ICIs below 10 ms as an indication of foraging or close investigation of objects based on the distribution of recorded ICIs. Although feeding success cannot be inferred from solely acoustic data, this relative proportion of 'buzzes' could indicate potential feeding activity in echolocating cetaceans (Todd *et al.* 2009).

C-POD Hydrophones:

C-PODs (Chelonia Ltd., Mousehole, U.K.) are underwater acoustic data loggers which record a range of information on all tonal clicks within a broad frequency range. Clicks may come from a range of sources including clicks made by dolphins, porpoises, snapping shrimp, water splashes and white noise from surf zones and sediment moving. Logged clicks are later classified using custom software (CPOD.exe) into those likely to be made by cetaceans, boat sonars and unknown sources. Cetacean clicks are further classified as either broadband clicks, or NBHF clicks. Using C-PODs for continuous acoustic monitoring, rather than recording sounds directly at the high sampling rate necessary for the high frequency range of NBHF species, greatly reduces the data volume recorded, increasing the possible duration of deployments. Only certain information is recorded, however, and there are currently limited automatic detection functions available, which can make species identification difficult. Classification of NBHF clicks tends to have a lower instance of both false positives and undetected calls than detection of broadband clicks, because clicks from 'noise' tend to be more broadband in nature and because broadband cetacean click trains are not easily recognised if the orientation of the vocalizing animal in relation to the receiver changes during train production (Castellote *et al.* 2013). C-PODs are therefore most useful for studies which require long periods of continuous monitoring and for which there is limited overlap of species with similar echolocation types. C-PODs, and their predecessor, the T-POD, have been used in several published studies (for a full list, see http://www.chelonia.co.uk/publications.htm), including studies on diel patterns in acoustic presence and in inter-click intervals (ICIs) or click rate in NBHF species (Carlström 2005, Todd *et al.* 2009, Leeney *et al.* 2011).

C-POD functioning:

C-PODs consist of an omnidirectional hydrophone at the top end, with an amplifier and electronic filter, 10 1.5V D-cell alkaline batteries, all contained in a water-tight polypropylene tube 67 cm long with a 9 cm diameter. With batteries, C-PODs weigh approximately 3.5 kg and have a positive buoyancy of approximately 0.7 kg in water. C-PODs only log data when in a vertical position, saving battery and memory between when they are set up and when they are deployed.

To detect clicks, C-PODs use digital time domain waveform analysis, examining times of zero-crossings and inflection point amplitudes for real-time signal processing (for more information, see http://www.chelonia.co.uk). The system gain is unique to each C-POD and is pre-set during the

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manufacturer's calibration process. The minimum detection threshold varies slightly between units, because the standardisation process prioritises that units give a uniform pressure reading when averaged radially, allowing for accurate logging of click sound pressure levels (SPL) (for more information on the standardisation process, see http://www.chelonia.co.uk/c-pod_standardisation.htm). Clicks with an SPL of 12 or above register on all C-POD units. Radial variation of units at 130 kHz is < ± 3 dB. Clicks with frequencies between 20 and 160 kHz are registered and the following information recorded: start time (5 μs resolution) and duration, based on the number of cycles at the dominant frequency, dominant frequency based on zero-crossing intervals of the first 10 cycles of the click sound wave, end frequency from the final zero-crossing interval, sound pressure level, bandwidth and envelope (see Au and Hastings (2008) for full definitions). C-PODs also record the unit's angle from vertical and surrounding water temperature once per minute. All information is stored on a 4GB SD card. To prevent the SD card becoming full or the battery running low in noisy environments, a limit can be set on the number of clicks for which information is recorded in any given minute, so that after that limit is reached, no more clicks are logged until the following minute. The detection range of C-PODs for Heaviside's dolphins is unknown, but Rayment *et al.* (2009) found that the effective detection range (the range within which all groups are reliably detected) of T-PODs for the closely related Hector's dolphins (*Cephalorhynchus hectori*) was 198-239 m, and no detections were made beyond 500 m. Tougaard *et al.* (2006) reported a similar detection distance of 250 m for harbour porpoises, so it is reasonable to assume a similar range for Heaviside's dolphins.

C-POD data processing:

In order to examine the data obtained from C-PODs, it must be opened in the CPOD.exe software (Chelonia Ltd.). Detection and classification of cetacean click trains is then done with the software's train detector called the KERNO classifier. This identifies click 'trains', which are series of regularly spaced clicks with similar attributes. Trains are classified as 'NBHF' (narrow-band high frequency clicks), 'other cet' for more broadband clicks from other odontocetes, as 'Sonar' for boat sonars or 'unidentified'. Click trains identified as NBHF, other cetaceans or sonar are then further categorised by confidence of correct identification, based on the probability of a train arising by chance from non-train sources, as ‘Hi’, ‘Mod’, ‘Low’, and ‘?’ for doubtful. For this study, only high and moderate certainty trains with a high certainty species classification were analysed further in order to minimise the chance of false positive detections.

The KERNO click train classifier works by comparing the data to a probability model of a train, which relates the probability of a click falling near the centre of the interval between the preceding and following click, the prevailing click rate and the interval size and the regularity of trains to determine the probability of the identified train occurring by chance. Factors such as the variability in the prevailing click rate lead to certain limitations in the train detector. Trains with slower, or irregular click rates are less likely to be recognised and the train detector is affected by noise clicks and by simultaneous cetacean trains. Trains of fewer than 5 clicks are not recognised. The physical properties used by the train classifier are modal frequency, number of clicks in the train, click rate, and mean SPL. Data on each click can be exported either before or after processing with the classifier; however, a train ID is present in KERNO-classified train data.

Finally, the train data are run through an encounter classifier, which identify times of multiple, higher-certainty detections of the same species classification. Encounter classifiers were designed to increase the number of true detections while minimising false positives within a data set, and to improve discrimination between species as there is sometimes misidentification between NBHF and broadband clicks with the KERNO classifier, often with broadband clicks being misclassified as NBHF clicks. If an encounter classifier is not selected, then the generic classifier, ‘GENENC’ is run automatically along with the KERNO classifier. When GENENC is used, click trains identified as NBHF, other cetaceans, or sonar are categorised into high or low certainty bins with regard to species classification rather than train quality being separate from species classification. Using the encounter classifier is optional as either the KERNO-classified data or the GENENC data are displayed and exported. Along with train quality and species classifications, data can be further filtered by the quality of the ICIs recorded and by the amount of noise in the minute the train occurs in. Exports useful for determining relative presence of a species are detection-positive minutes (DPM), detection-positive 10 minutes, and detection-positive hours (DPH). These can be exported for each C-POD hour or for each day.

3.3 Methods:

Study site:

The study area at Lüderitz surrounds a small port with a tidal range of approximately 1.2 m and includes several small, north-facing bays (Figure 1). The prevailing weather conditions along the Namibian coast are driven by the South Atlantic Anticyclone and consist of predominantly southerly wind and south-westerly swell (Robertson 2012). There are strong winds along the entire coast, but Lüderitz experiences some of the strongest winds, primarily in the afternoon. These winds drive the Lüderitz upwelling cell, offshore of the study site, which is one of the strongest year-round upwelling areas and contributes to the high productivity of the Benguela current (Robertson 2012). There are populations of Heaviside's dolphins, bottlenose dolphins (*Tursiops truncatus*) and dusky dolphins (*Lagenorhynchus obscurus*) in the inshore waters of the Namibian coast. At the Lüderitz study site, the Heaviside's dolphins are the only species with a near constant presence, with only occasional incursions of dusky dolphins and rare sightings of bottlenose dolphins (see Chapter 2).

Data collection:

Echolocation activity of Heaviside's dolphins was monitored in the core study area at Lüderitz using C-PODs. Five C-PODs were deployed over a two-month period in April and May 2014, with a battery change and download mid-deployment (see Table 1). The deployment sites were chosen to provide temporal habitat selection data in areas with a high amount of visual search effort from the small boat surveys (see Figure 1). This is particularly useful as there were very few boat surveys that lasted late into the day and diel patterns cannot be examined using the boat-based survey data. The Guano Bay deployment site was the most exposed to swell, so C-POD 577 was placed further South than other C-PODs to protect it from the prevailing south-westerly swell, which would likely move or destroy a mooring in shallow water. C-PODs were deployed roughly 2 m from the bottom using custom-made moorings with surface markers, except C-POD 577 in Guano Bay, which was deployed at the bottom in a lobster trap to hold it upright.

Each C-POD was set to log click data continuously while deployed, except when oriented at an angle > 82˚ from vertical or if 4,096 clicks had already been logged within a minute. Only clicks with a minimum duration of 5 μs and a minimum SPL of 3 were logged, in accordance with the standard settings and limitations of the C-PODs.

C-POD data processing:

The data from each deployment at Lüderitz were downloaded and examined in CPOD.exe version 2.044 (www.chelonia.uk), and the KERNO classifier and encounter classifier 'GENENC' run to detect NBHF and broadband click trains. The encounter classifier output was not used for NBHF species detection in this study as the study site is a high-density area for Heaviside's dolphins, there are no other NBHF species known to be present at the study site, and there are few enough sightings of broadband clicking species within the core study area that misclassification is not an issue for Heaviside's detections. This was verified by visual observations of the harbour mouth where C-POD 701 was placed, by two experienced observers scanning by eye and with binoculars from a high cliff. During visual observations, the number of animals present in the area was recorded every minute. Two hours with no visual sightings were compared to C-POD data from the same time period and no NBHF detections were made during this time. Moreover, Lüderitz is also a relatively quiet environment with little anthropogenic or other noise and false NBHF detections are rare, even in studies that take place in noisy environments. The encounter classifier GENENC was used for detection of cetacean species with broadband vocalisations, as these are more easily misclassified, and there are few enough sightings of species that produce broadband clicks within the core study area that false positives could drastically skew results.

NBHF trains:

Only high and moderate quality click trains with a high certainty species classification from the KERNO classifier were used for analysis. Only trains with high quality ICIs were used for ICI analysis and minutes with continuous noise were excluded. In order to compare dolphin detections between sites, NBHF detection-positive minutes per hour (DPM/h) were exported for each deployment location. To examine diel patterns in NBHF calls, the DPM/h were then averaged over the entire running time for each hour of the day to obtain DPM per hour running time for each hour of the day at each site. To further analyse how light conditions affect diel patterns in NBHF detections, each hour of the day was grouped into one of four categories based on the time and duration of the changing light conditions around sunrise (6:25) and sunset (17:27) determined at the middle of the study period (3 May, 2014) (times were calculated using http://www.suncalc.net). The categories assigned are ‘dawn’, ‘day’, ‘dusk’ and ‘night’. Ten hours of each 24-hour period were assigned to each day and night, whereas only two hours were assigned to the dawn and dusk categories.

Information on each click train was exported, and the mean ICI of each train calculated following Leeney *et al.* (2011). The mean ICI of each train was averaged per hour and the percentage of trains in each hour of the day with mean ICIs under 10 ms, considered potential ‘feeding buzzes’, were averaged over the entire study duration for all deployment sites combined to examine diel patterns in ICI. These ‘feeding buzz’ percentage data were further subdivided by site to examine difference in ICI and ‘feeding buzz’ diel patterns by site.

Other cetacean trains:

In order to examine inshore presence of dusky dolphins (or possibly bottlenose dolphins), the ‘other cet’ trains identified by the encounter classifier ‘GENENC’ were investigated and DPM/h exported for each deployment. The encounter classifier was used for detection of these broadband-clicking species, but not the NBHF click-producing Heaviside's dolphins, because of the comparatively higher risk of false positives and missed calls for broadband clicking species. DPM/h were then averaged over the entire study period for each site, as with the NBHF trains.

3.4 Results:

The first C-POD deployment was on the 6th of April 2014, and the final retrievals were on the 31st of May 2014 for a total study duration of 5,932 recording hours over 5 deployment locations during this period. There was relatively little noise interfering with detections, and only 1.939 recording minutes were filled with continuous noise. Boat sonar presence differed by site, but was relatively low in occurrence overall (Table 2). The two sites with highest sonar detections (Angra East and Diaz Point) did not experience consistent sonar presence, but rather periods of continuous sonar lasting up to a few days in a row and low sonar presence otherwise, likely caused by boats anchoring nearby for extended periods. Visual observations around the harbour C-POD 701 and close examination of portions of the data confirmed that noise and sonars, though present, were not likely to be interfering with detection of dolphins.

Boat surveys:

Small boat surveys were conducted on 19 days around Lüderitz during the time the C-PODs were deployed (Chapter 2). Heaviside’s dolphins were observed during every survey. Dusky dolphins were observed during 5 surveys, but never within the core study area where C-PODs were deployed (Figure 1). There was one sighting of bottlenose dolphins from land during visual observations around C-POD 701. There were no sightings of bottlenose dolphins or of other odontocete species during small boat surveys.

Site differences in acoustic presence of Heaviside’s dolphins:

There were 1,626 hours containing NBHF detections of the 5,932 recorded C-POD hours. Acoustic detections of Heaviside’s dolphins varied considerably between the five sites (Table 3). Most detections were at Diaz Point and the fewest at the east side of Angra Point. This is consistent with the findings from the small boat surveys in these areas, both during the study and in previous years (Chapter 2).

Diel patterns in acoustic presence of Heaviside's dolphins:

As there were 4,318 hours with zero detections, the data were not normally distributed, and so were further examined using non-parametric tests. There was a significant difference in detection-positive minutes per hour between the four light conditions with all study sites grouped (Kruskal-Wallis test; $\chi^2 = 307.03$, $p < 0.01$). Dunn's test of multiple comparisons with Bonferroni correction revealed no significant difference in detections between dawn and day light conditions, which were significantly higher than detections at dusk and night (Figure 2, Table 4). When examined individually, each deployment site showed significant differences in detection positive minutes between light condition category (Table 5), although multiple comparisons of each light category for each site differed somewhat (Table 6, Figures 3 and 4). Notably, for the three deployment sites with the most detections (Lüderitz Harbour, Diaz Point and Guano Bay), there is a significant difference between acoustic presence of Heaviside's between dawn and daylight hours, with higher detections during daylight hours at Diaz Point and Lüderitz Harbour, and higher detections at dawn in Guano Bay. There was no difference between night and dusk in acoustic presence for any of the deployment sites. Closer examination of detections for each hour of the day (Figures 5 and 6) show a clear eastward (inshore) movement early in the day, though with far fewer detections to the East of Angra Point, with detections peaking around 0600h in Guano Bay, and around midday at both Diaz Point and Lüderitz Harbour, with very few detections at dusk and night further inshore (Figures 5 and 6).

Diel Patterns in click train ICIs:

Heaviside's dolphin click trains had a mean inter-click interval of 28.33 ± 19.43 ms, though trains with much higher ICI's were detected (Figure 7). There were significant differences in the mean ICI between hours (Kruskal-Wallis test; $\chi^2 = 367.55$, $p < 0.01$) (Figure 8), and significant differences between hours in the proportion of click trains with a mean ICI under 10 ms (Test of equal proportions; $\chi^2 = 906.45$, $p < 0.01$), which was considerably higher during the daytime (Figure 9). Further examination of the proportion of click trains under 10 ms for each hour, a possible indicator of feeding activity, showed that each site followed the same general pattern of a higher ratio of potential ‘feeding buzzes’ during the daylight hours (Figure 10). Data from the two deployments to the East and West of Angra Point were not examined further however, as there were too few detections at these deployment sites.

Other cetaceans:

Broadband cetacean click trains were detected on 22 days of the 54-day study, and on all of the C-PODs, but there were very few detections overall, with only 46 DPH of the 5,932 recorded hours (Table 7). This is consistent with the occasional presence of dusky dolphins inshore at the core study area observed during small boat surveys. Notably, detections on the morning of 21 April are of bottlenose dolphins as they were sighted swimming past the C-POD at that time, but for other detections, a species is not attributed. A portion of the detected trains was visually examined using CPOD.exe to ensure that they were consistent with broadband click trains produced by dolphins. There was not a high enough sample size for further analysis of broadband species presence.

3.5 Discussion:

Site differences in overall detections of Heaviside’s dolphins closely reflect the findings from the small boat surveys in regards to spatial distribution within the study area at Lüderitz. The similarity between daytime encounter data and 24-hour acoustic data provides evidence that the Heaviside’s dolphins at Lüderitz are rarely making use of the bays furthest from the open sea and their presence is highest around Diaz Point (C-POD 705) and into Guano Bay (C-POD 577). In contrast, the Heaviside’s dolphins using Walvis Bay are almost exclusively clustered around the sand spit forming the north-western tip of the bay and rarely use sheltered bay waters (see Chapter 2), while those in South Africa appear to prefer the surf zones along exposed sandy coastlines (Elwen *et al.* 2010), not entirely unlike the high-density areas around Pelican Point in Walvis Bay and Diaz Point in Lüderitz.

The high rate of detections of Heaviside's dolphins in Lüderitz during the morning and daylight hours is similar to the pattern of inshore presence in the Western Cape, South Africa, where inshore presence is highest before midday (Elwen *et al.* 2009a), but is nearly opposite to the findings of Leeney *et al.* (2011) in Walvis Bay, where the highest detections and lower mean inter-click intervals (faster click trains) occurred at night, though with no apparent diel pattern in feeding buzz ratio, leading to uncertainty about how exactly the diel pattern in acoustic activity relates to foraging behaviour. Any further investigation into diel patterns of presence for this species should focus on use of offshore areas.

Differences in patterns in nearshore and offshore presence between populations are likely driven by prey type and availability and the associated differences in foraging patterns. Heaviside's dolphins in Lüderitz have been observed in feeding aggregations near Diaz Point of 10s of animals co-occurring with seals and seabirds, as well as patrolling reef areas close inshore where they are thought to be feeding (authors' personal observation). The high proportion of feeding buzzes during the daytime in Lüderitz supports the observations of inshore feeding at Lüderitz, and of differing foraging patterns between these three areas. Differences in patterns of presence may also be mediated by sympatry with other top predators i.e. bottlenose dolphins close inshore in Walvis Bay and dusky dolphins offshore in Lüderitz in an example of spatial niche separation.

Management implications:

The near-constant presence of Heaviside's dolphins, particularly at Diaz Point and Guano Bay, is of interest to potential management initiatives, as they are clearly important areas of use, particularly in light of the lack of detections around Angra Point nearby, which implies strong habitat selection on a very fine scale. Avoiding disturbance to these areas in general would be ideal, but for impacts with only an immediate effect (such as noise pollution, which only affects animals which are present while the noise is occurring), negative impacts could be reduced by halting activities during regular times of peak presence i.e. early morning in Guano Bay and midday near Diaz Point and at the harbour mouth. As acoustic monitoring has proven effective for identifying high-use areas, and temporal patterns in presence of Heaviside’s dolphins, acoustic monitoring at potential impact sites should be implemented to ensure the least disturbance.

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3.7 Tables and Figures:

Table 1: Deployment locations and dates for C-POD hydrophones used to monitor acoustic activity of Heaviside's dolphins at Lüderitz, Namibia. C-PODs are listed by location from East to West. All C-PODs were deployed approximately 2 m above the seabed except for C-POD 577, which was deployed at full depth.

Deployment Location:					**Deployment 1:**			**Deployment 2:**		
Location	**C-POD #**	**Latitude**	**Longitude**	**Depth**	**Start**	**End**	**Total Days**	**Start**	**End**	**Total Days**
Harbour	701	-26.6347	15.15527	6m	6-Apr 09:56	1-May 11:40	25	2-May 12:28	31-May 12:02	29
Angra East	704	-26.63147	15.13464	9.3m	10-Apr 13:54	1-May 12:24	21	2-May 07:31	31-May 10:51	29
Angra West	578	-26.6312	15.12188	11.2m	17-Apr 08:03	1-May 11:51	14	2-May 07:48	31-May 10:00	29
Diaz Point	705	-26.63277	15.09651	13m	10-Apr 15:58	1-May 11:40	21	2-May 08:02	31-May 09:32	29
Guano Bay	577	-26.64788	15.08412	9.2m	10-Apr 15:53	1-May 11:24	21	2-May 08:31	31-May 09:15	29

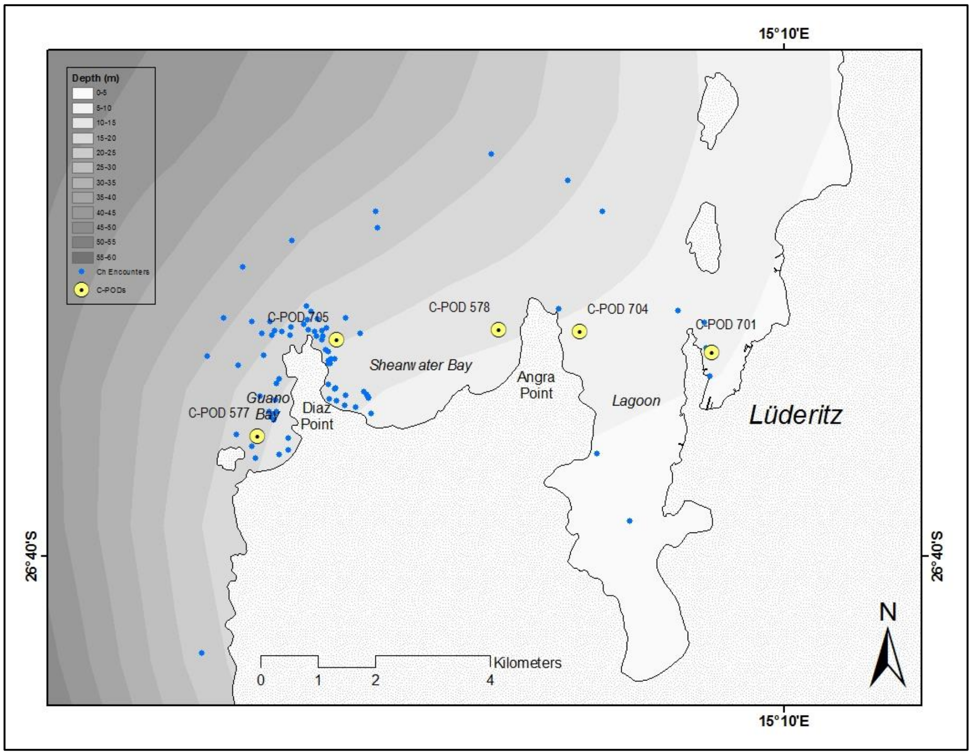

Figure 1: Map of C-POD deployment locations within the core study area at Lüderitz, Namibia and encounters (start locations) with Heaviside's dolphins made during concurrent boat surveys in the area. See Chapter 2 for effort-corrected maps showing density of Heaviside's dolphin encounters. There were no encounters with bottlenose dolphins or dusky dolphins within the core study area during C-POD deployment.

Table 2: Sonar detections from C-PODs deployed at Lüderitz, Namibia. Columns show the mean detection-positive minutes per hour (DPM/h), mean detection-positive-hours per day (DPH/d) and the total number of sonar trains detected by each C-POD for the study duration.

Site	Mean DPM/h	Mean DPH/d	No. 'sonar' trains
Harbour	1.01	**5.84**	9874
Angra East	1.84	**3.44**	20224
Angra West	0.28	**0.74**	1143
Diaz Point	2.81	**4.52**	21701
Guano Bay	0.09	**0.39**	1174

Table 3: Narrow-band-high-frequency detections from C-PODs deployed in Lüderitz, Namibia. Columns show the mean detection-positive minutes per hour (DPM/h), mean detection-positive-hours per day (DPH/d) and the total number of narrow-band-high-frequency (NBHF) click trains detected by each C-POD for the study duration.

Site	Mean DPM/h	Mean DPH/d	No. NBHF trains
Harbour	0.91	**3.75**	2794
Angra East	0.06	**0.78**	152
Angra West	0.69	**4.29**	1753
Diaz Point	5.92	**15.93**	16287
Guano Bay	1.92	**8.09**	4936

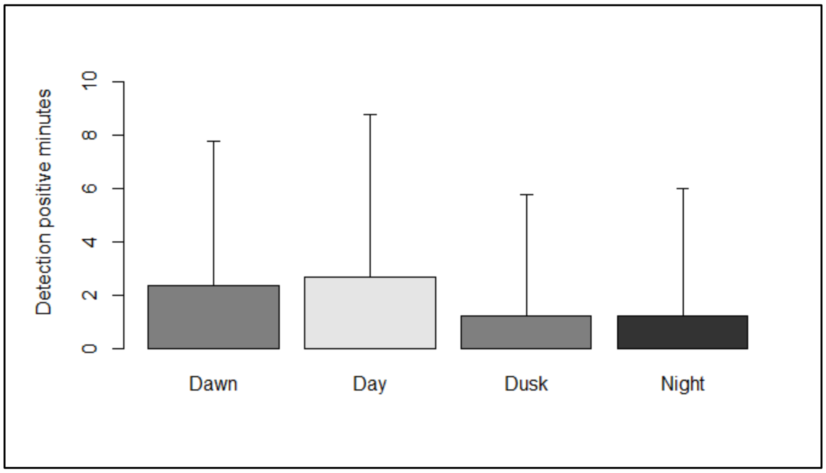

Figure 2: Mean detection positive minutes per hour of NBHF clicks for each of four light conditions from all C-POD deployment sites combined. The error bars show the standard deviation from the mean.

Table 4: Significance table for Bonferroni-corrected Dunn's test of multiple comparisons on detection-positive minutes per hour of NBHF clicks between the four light conditions for all C-POD deployment sites combined.

	dawn	**day**	**dusk**
day	0.58	-	-
dusk	***< 0.01***	***< 0.01***	-
night	***< 0.01***	***< 0.01***	1.00

Table 5: Results of Kruskal-Wallis tests of NBHF detection positive minutes per hour by light condition category for each C-POD deployment site.

Site	χ2	df	p-value
Harbour	174.17	3	***< 0.01***
Angra East	28.99	3	***< 0.01***
Angra West	34.52	3	***< 0.01***
Diaz Point	136.22	3	***< 0.01***
Guano Bay	100.62	3	***< 0.01***

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Table 6: Results of Bonferroni-corrected Dunn's test of multiple comparisons on detection-positive minutes per hour of NBHF clicks between the four light conditions for each C-POD deployment site individually. a.) Lüderitz Harbour C-POD 701 b.) Angra East C-POD 704 c.) Angra West C-POD 578 d). Diaz Point C-POD 705 e.) Guano Bay C-POD 577.

a.)	**dawn**	**day**	**dusk**
day	***< 0.01***	-	-
dusk	0.63	***< 0.01***	-
night	0.15	***< 0.01***	1.00

b).	**dawn**	**day**	**dusk**
day	0.79	-	-
dusk	0.68	***0.02***	-
night	0.18	***< 0.01***	1.00

c).	**dawn**	**day**	**dusk**
day	0.48	-	-
dusk	***< 0.01***	***< 0.01***	-
night	***< 0.01***	***< 0.01***	0.71

d.)	**dawn**	**day**	**dusk**
day	***0.01***	-	-
dusk	0.07	***< 0.01***	-
night	***< 0.01***	***< 0.01***	1.00

e.)	**dawn**	**day**	**dusk**
day	***0.01***	-	-
dusk	***< 0.01***	***< 0.01***	-
night	***< 0.01***	***< 0.01***	0.47

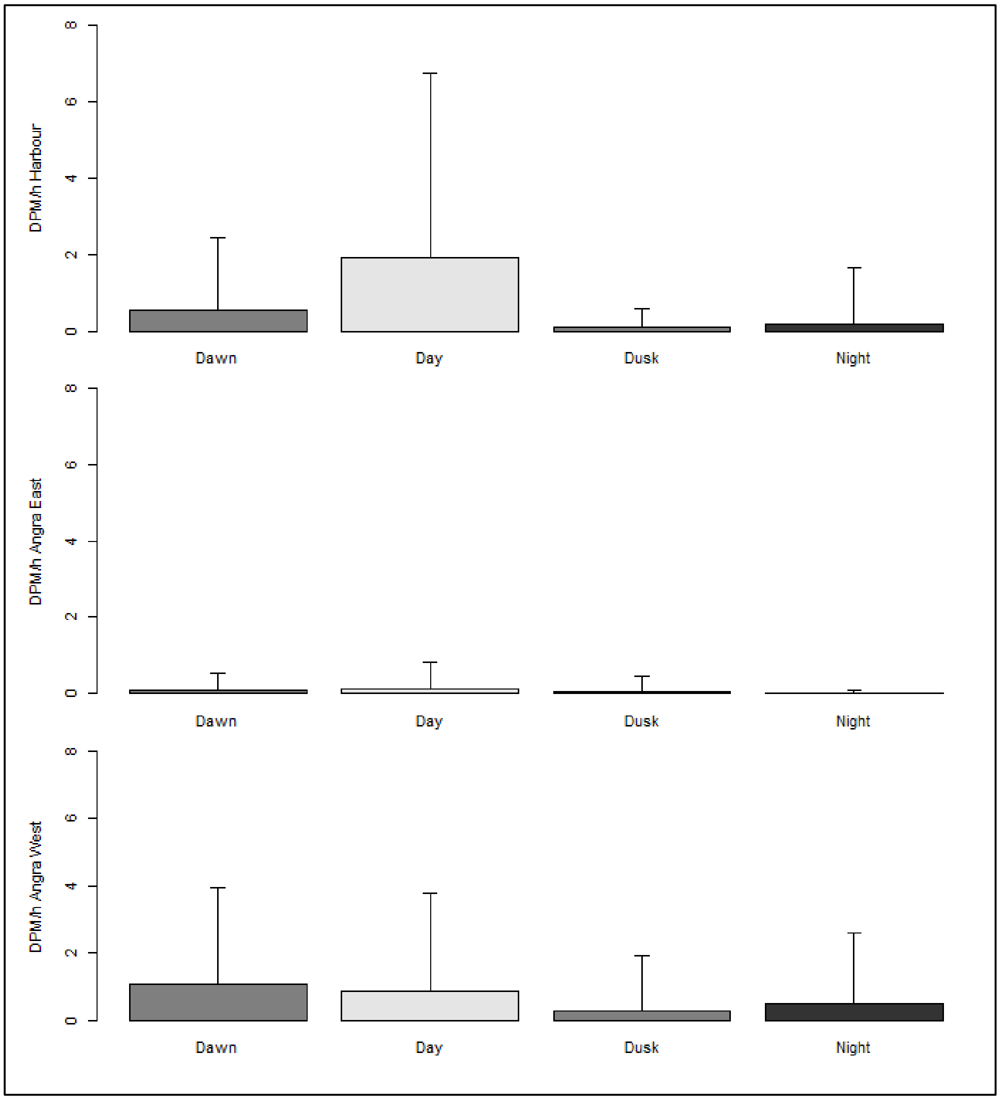

Figure 3: Detection positive minutes per hour (mean + SD) of NBHF clicks for each of four light conditions from the three Eastern-most C-PODS. Listed from East to West; Lüderitz Harbour (top), Angra Point East (middle) and Angra Point West (bottom). The error bars show the standard deviation from the mean.

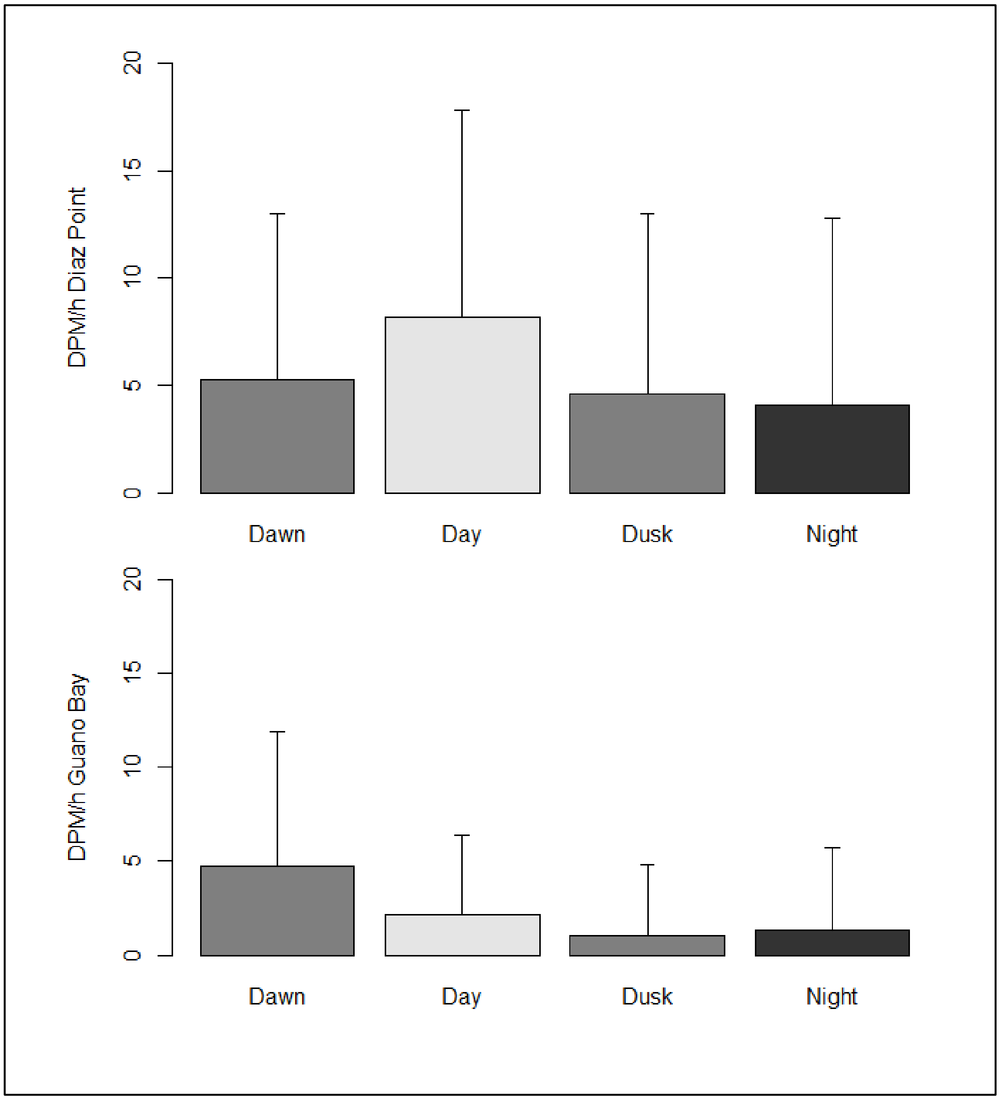

Figure 4: Detections of Heaviside's dolphins clicks for each of four light conditions from the two higher-density sites, Diaz Point (top) and Guano Bay (bottom) C-PODS (detection positive minutes per hour, mean + SD). Note the difference in scale from Figure 3. The error bars show the standard deviation from the mean.

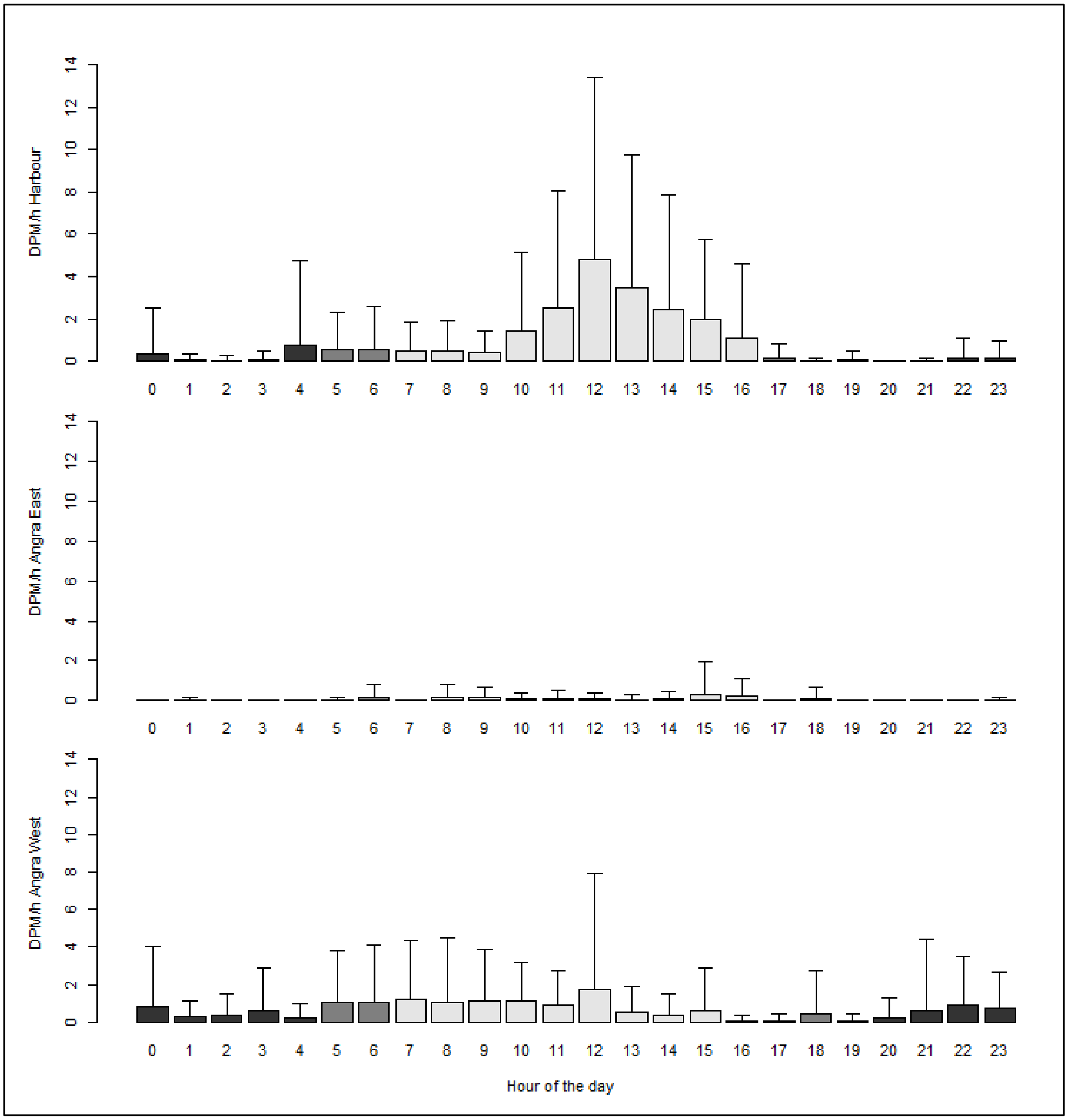

Figure 5: Mean detection-positive-minutes per hour from the three eastern-most C-PODS. Listed from East to West; Lüderitz Harbour (top), Angra Point East (middle) and Angra Point West (bottom). The error bars show the standard deviation from the mean.

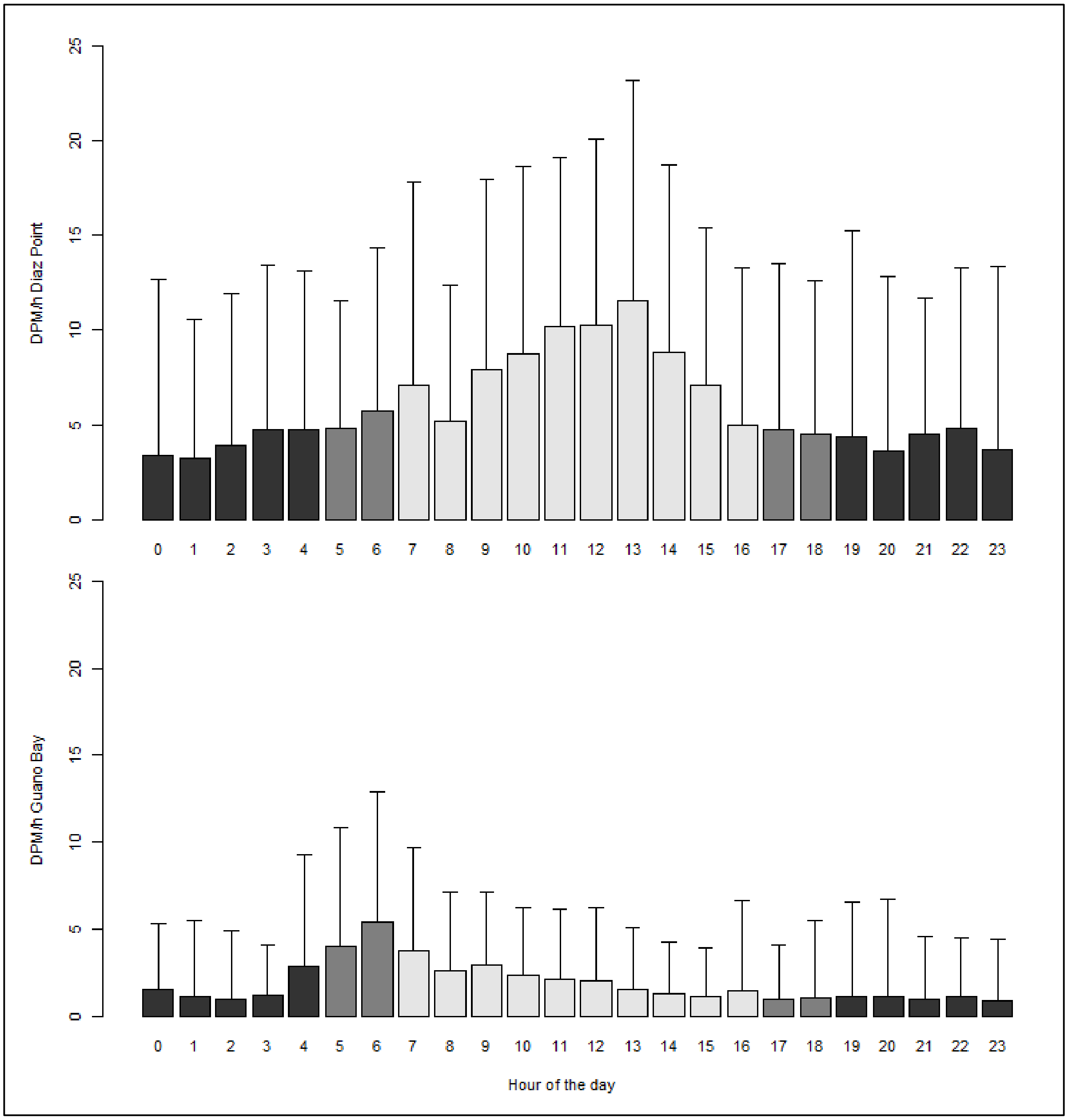

Figure 6: Mean detection-positive-minutes per hour from the Diaz Point (top) and Guano Bay (bottom) C-PODS. The error bars show the standard deviation from the mean. Note the difference in scale from Figure 5.

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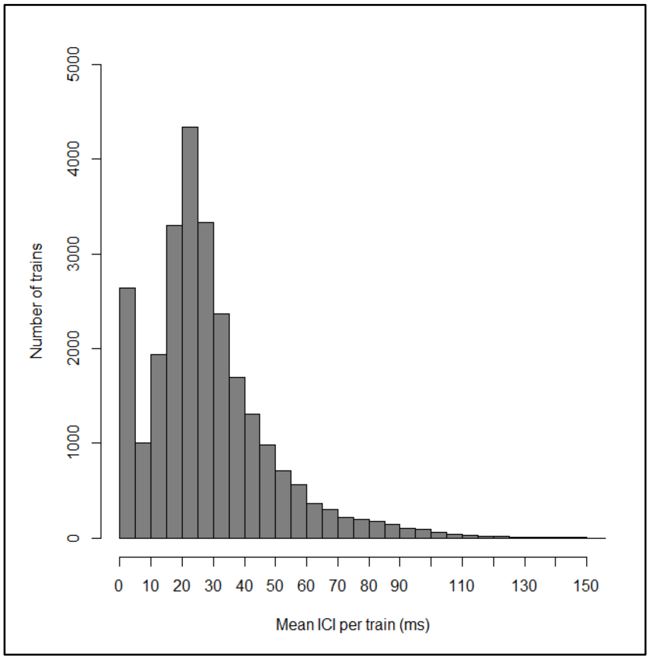

Figure 7: Histogram of mean ICIs from each click train. Click trains with a mean ICI of 10 ms or below are considered potential ‘feeding buzzes’.

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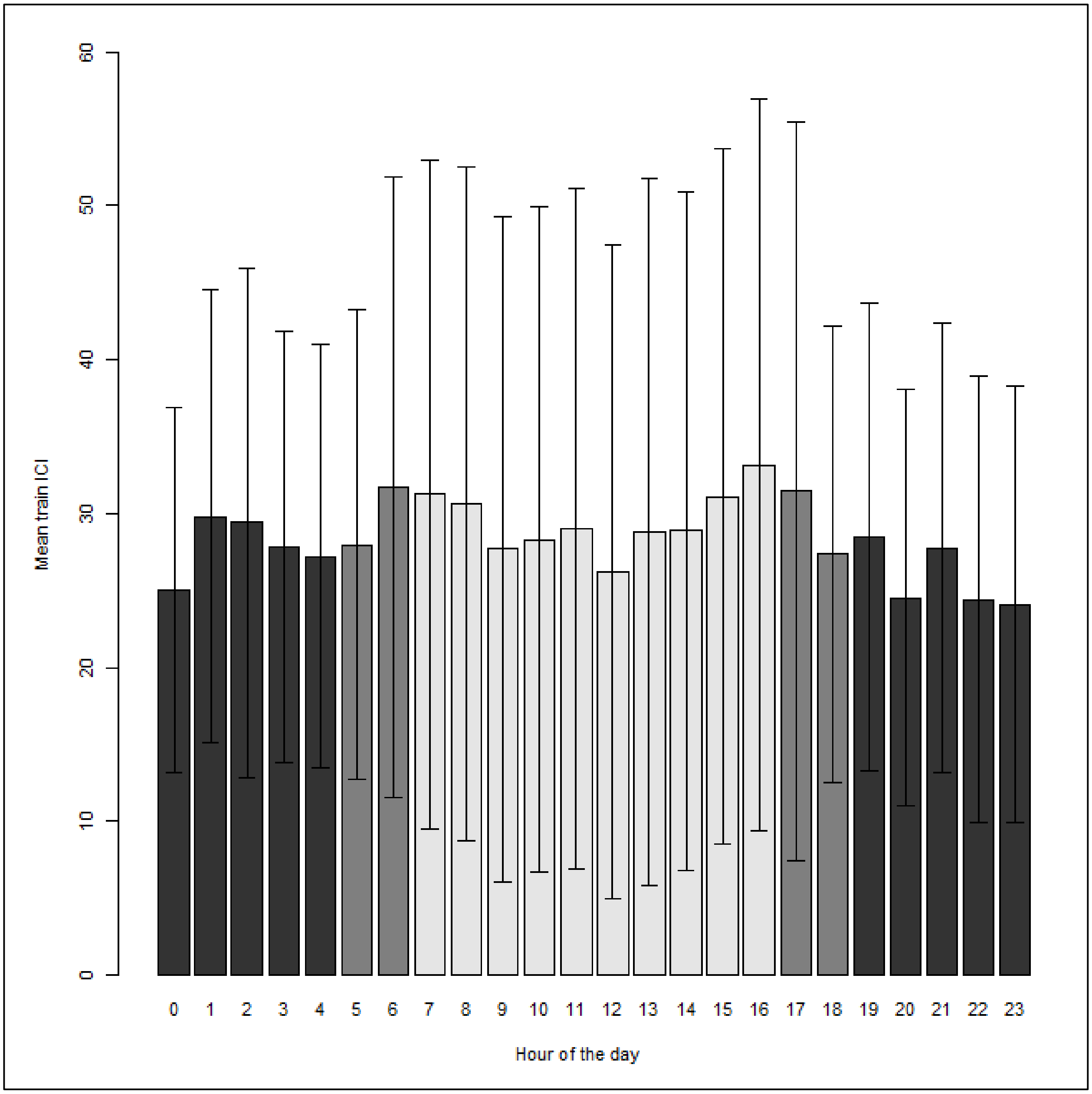

Figure 8: Mean train inter-click intervals averaged by hour of the day for all C-POD deployment sites combined. Error bars show the standard deviation from the mean.

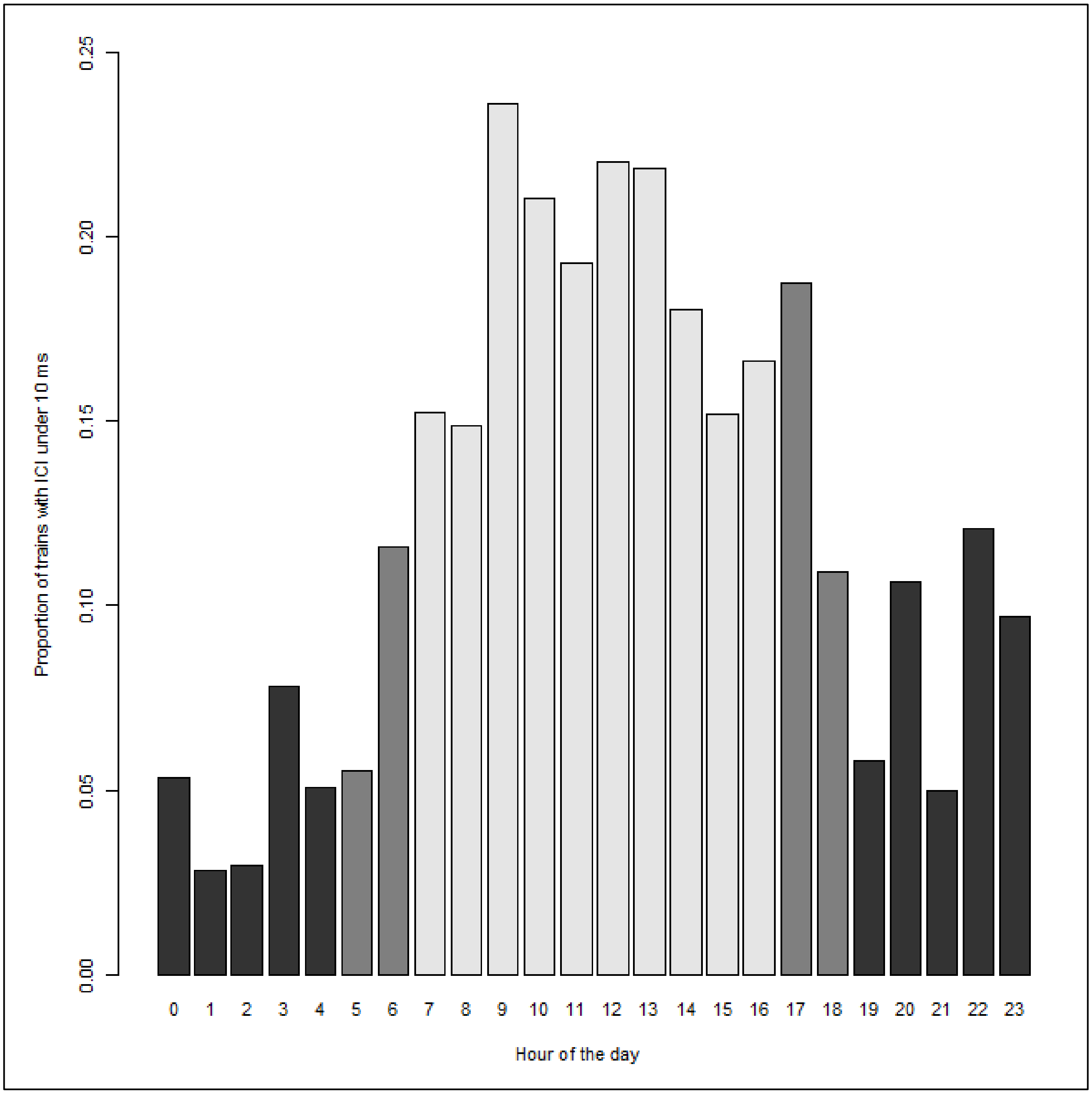

Figure 9: Proportion of click trains per hour with a mean inter-click interval under 10 ms duration (i.e. 'feeding buzzes') for all C-POD deployment sites combined.

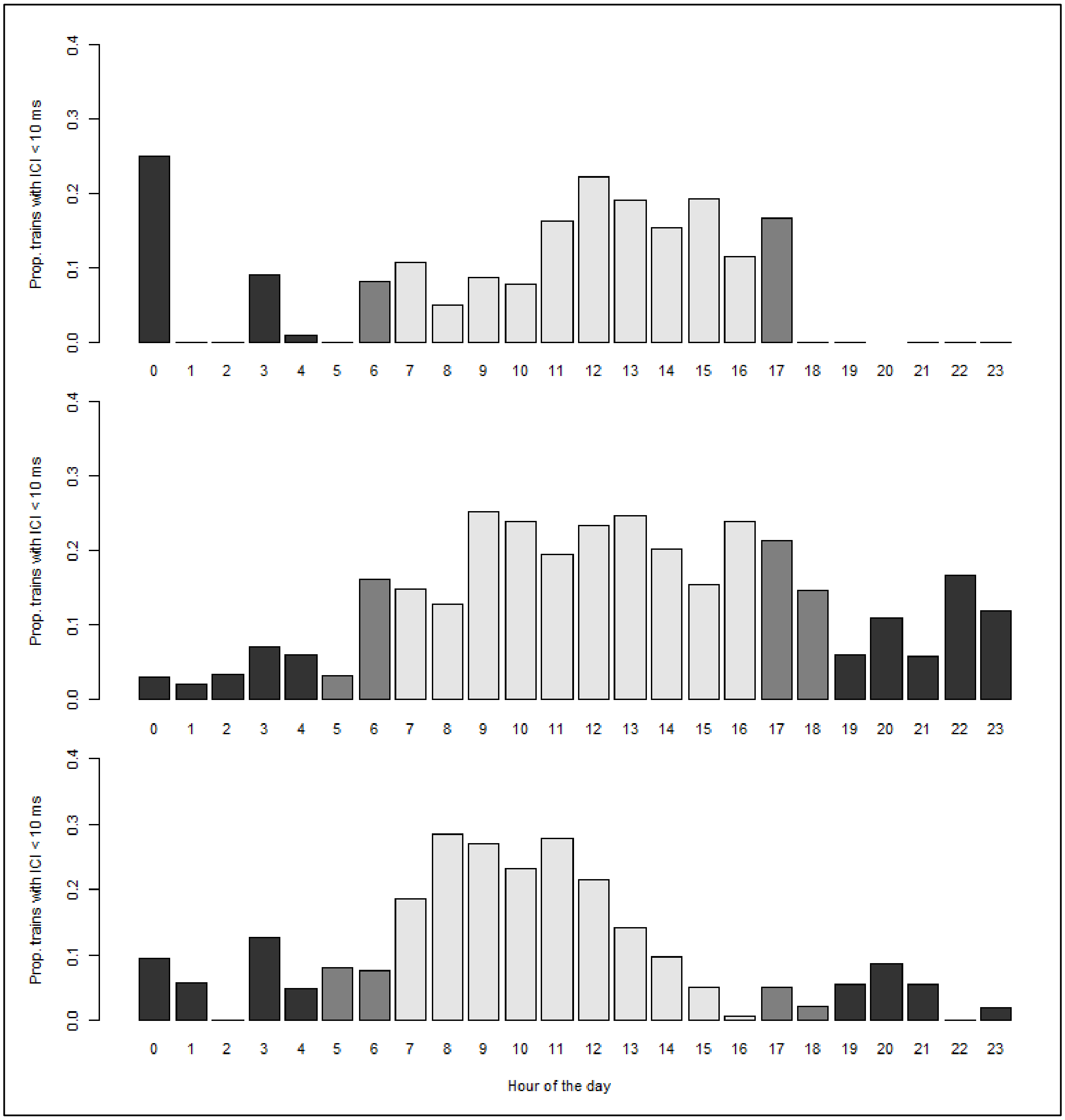

Figure 10: Proportion of click trains per hour with a mean ICI under 10 ms (i.e. 'feeding buzzes') for the three C-POD deployment sites with the highest detections. Listed from East to West; Lüderitz Harbour (Top), Diaz Point (middle) and Guano Bay (Bottom). The C-PODs deployed at either side of Angra Point were not included as there were too few click trains detected.

Table 7: Broadband click detections from C-PODs deployed in Lüderitz, Namibia. Columns show the mean detection-positive minutes per hour (DPM/h), mean detection-positive-hours per day (DPH/d) and the total number of broadband echolocation click trains detected by each C-POD for the duration of the study.

	Mean DPM/h	**Mean DPH/d**	**No. 'other cet' trains**
Harbour	0.04	**0.18**	337
Angra East	< 0.01	**0.02**	23
Angra West	0.05	**0.13**	561
Diaz Point	0.19	**0.37**	1787
Guano Bay	0.03	**0.19**	260

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Chapter 4 - Conclusions

4.1 Aims and findings of the study:

The principal aims of this study were as follows:

1.) Generate baseline information regarding the fine-scale habitat selection of a unique and endemic species in two high-density areas in a poorly studied part of their range.

2.) Provide information necessary for informed management of human activities in areas of overlap between high dolphin presence and human use.

3.) Test the effectiveness of using a combination of visual and acoustic methods to examine fine-scale habitat selection both spatially and temporally for this species in this area.

The specific objectives therein include:

1.) Identify areas within the study sites with the highest frequency of dolphin occurrence.

2.) Identify times of peak dolphin presence and acoustic behaviour.

3.) Test the usefulness of using an array of multiple C-POD echolocation click loggers for Heaviside’s dolphins by comparing and contrasting results with the visual component of the study.

Principal findings:

Heaviside's dolphins show strong habitat selection on a very fine spatial scale within both study sites, though the areas with the highest encounter rates at each site differ. Most similar between sites are the frequented areas at Pelican Point and Diaz Point, which are both exposed to swell and prevailing weather conditions. The most drastic difference between sites is the complete avoidance of sheltered waters in Walvis Bay vs. the use of areas close inshore in Lüderitz. One notable exception to this is the lack of encounters and acoustic detections to the Eastern side of Angra Point, where the lagoon lies. This may again be related to use of the Angra point lagoon by sharks, or because of a preference for proximity to open waters. Bottlenose dolphins are sighted occasionally by oyster farm workers in the lagoon (pers comm.) despite the low overall encounter rate for this species in Lüderitz. This is unsurprising as the bottlenose dolphins make frequent use of the shallow Walvis Bay lagoon, a physically similar area. The lack of overlap between Heaviside's and bottlenose dolphin encounters in Walvis Bay is another main finding and strongly supports spatial niche separation of the two species in shallow water.

Acoustic detections show an essentially constant presence of this species throughout the day at Diaz Point, and there is no regular period of time of no detections at any of the deployment sites, except perhaps to the East of Angra Point at night. Boat surveys support this finding of a constant presence in Lüderitz, whereas surveys in Walvis Bay do not always include sightings of Heaviside's dolphins, even when the area around Pelican Point is well-searched.

Effectiveness of methodology:

Visual surveys in Walvis Bay, and especially in Lüderitz provided a high encounter rate per survey effort, and were a very effective method for identifying the areas with the most frequent presence of this species. The main concern with using the survey data to make generalizations about such fine-scale habitat selection was that with few exceptions, surveys were only conducted during the first half of the day, creating the possibility of missing out on fine-scale temporal patterns. This possibility prompted the use of acoustic monitoring as a complementary method.

The use of continuously collected acoustic data in conjunction with visual surveys provided a robust method of understanding fine-scale area use for this coastally-distributed species. Even the relatively simple acoustic array used in this study provided information which could not be obtained solely from visual observations, and did so with relatively little time involvement in the field. Deployments and retrievals of C-PODS in the field were quick and corresponded nicely with the visual surveys already being conducted. More importantly, only two deployments were made for each C-POD because of the low data volume created in comparison with other acoustic monitoring devices.

The use of C-PODs to study the ecology of Heaviside's dolphins has proven useful in supplementing ongoing research on the species in Namibia and has provided information on inshore/offshore movement patterns and on potential feeding activity comparable to that of Elwen *et al.* (2006), Elwen *et al.* (2009) and Leeney *et al.* (2011). The use of C-POD recorders for bottlenose dolphins and dusky dolphins did not provide enough information on the short timescale of this study for the same level of analysis, but this information could be gleaned from a similar setup over a longer study duration.

4.2 Literature cited:

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