Occurrence and group dynamics of Heaviside's dolphins (*Cephalorhynchus heavisidii*) in Table Bay, Western Cape, South Africa

by

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Abstract

Heaviside's dolphins, *Cephalorhynchus heavisidii,* are among the least known cetaceans. They are endemic to the coastal waters along the west coast of southern Africa. The occurrence, behaviour and group dynamics were investigated for these dolphins in Table Bay, South Africa during the summer of 2008 and 2009. Mark-recapture photographic identification techniques, modelling techniques and Geographical Information System (GIS) were used to analyse the data.

The dolphins were observed primarily in a well-defined 7 km^2 area on the south side of Table Bay along a 3 km east-west stretch of coast known as Granger Bay, and within 2 km from shore. They used this area heterogeneously; for the array of behaviours observed, all core areas (50 % kernels) were located in Granger Bay with very little overlap of areas used for milling, socialising, resting and travelling. Milling and socialising were exhibited more often than travelling and resting. Foraging was never observed in areas close to shore, which supports earlier studies suggesting that these dolphins forage primarily offshore.

Of the 95 identified individuals, 24.2 % of the individuals were seen only once and 73.7 % of the individuals were sighted less than five times while two individuals were seen 11 times. Groups varied in size from one to 26 animals with a median of five animals. Many of the potential dyads were never seen and those observed had generally weak measure of association. The group structure appears highly dynamic, with great lability in group sizes and membership, suggesting a fluid social system with mostly weak inter-individual bonds. Individuals in Table Bay display low site fidelity, at least in the short-term.

The observed pattern of area use and behavioural preferences indicate that coastal management strategies should consider the ecological and behavioural needs of Heaviside's dolphins to appropriately safeguard this species as a valuable component of South African natural treasures and legally protected taxa. Further continuing research is needed to build on this initial study to better understand the processes that shape the population structure and group dynamics of Heaviside's dolphins, and to provide further detail on habitat preferences and areas used, both in Table Bay and environs.

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DECLARATION OF ORIGINALITY

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Declaration

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2. I declare that this dissertation is my own original work. Where other people's work has been used (either from a printed source, Internet or any other source), this has been properly acknowledged and referenced in accordance with departmental requirements.

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Chapter 1
Introduction to Heaviside's dolphins

The Genus: *Cephalorhynchus*

Heaviside's dolphins (*Cephalorhynchus heavisidii,* Gray 1828) are one of four species of dolphins that belong to the genus *Cephalorhynchus* (Delphinidae, Cetacea). Members of *Cephalorhynchus* are typically small dolphins each with a limited distribution and are endemic to respective regions of cool temperate coastal waters in the Southern Hemisphere (Dawson and Slooten 1988). Hector's dolphins (*Cephalorhynchus hectori,* van Beneden 1881) inhabit the waters around New Zealand (Dawson and Slooten 1988) and Maui's dolphins (*Cephalorhynchus hectori maui*), a subspecies of Hector's dolphin are found along the west coast of the North Island of New Zealand (Baker et al. 2002). Chilean dolphins (*Cephalorhynchus eutropia,* Gray 1846) are found along the Chilean coast from 33°S to Cape Horn (55°S), (Goodall et al. 1988a). Commerson's dolphins (*Cephalorhynchus commersonii,* Lacépède 1804) are separated by 8500 km and 130° of longitude into two distinct populations (Goodall 1994) although extra-limital sightings have been recorded (e.g. de Bruyn et al. 2006). The larger population is found in the south-western South Atlantic along the coast of Argentina from 41°S, including the Falkland Islands, the Drake Passage and extends as far south as the South Shetland Islands (62°S). This population's range overlaps with the Chilean dolphin along the west coast of Tierra Del Fuego, Chile/Argentina. A smaller population of Commerson's dolphins are found in the waters surrounding the Kerguelen Islands in the southern Indian Ocean (49°S, 69°E) (Robineau 1984, Goodall 1994). Heaviside's dolphins inhabit the waters along the west coast of southern Africa (Findlay et al. 1992). Figure 1.1 illustrates the global distribution of the genus *Cephalorhynchus*.

The Species: *Cephalorhynchus heavisidii*

Taxonomy

The Heaviside's dolphin should have been named after Captain Haviside, captain of an East Indiaman who sold the skull to the Royal College of Surgeons in 1828. However, it was named after Captain Heaviside, a surgeon who sold a collection of non-cetacean anatomical specimens (Fraser 1966). Watson (1981) suggested the

common name be changed to Benguela dolphin after the ocean current in which it is found, the Benguela Current. However despite the confusion in the spelling of the name and the suggestion of Benguela dolphin, the common name of Heaviside's dolphin prevails (Best 2007).
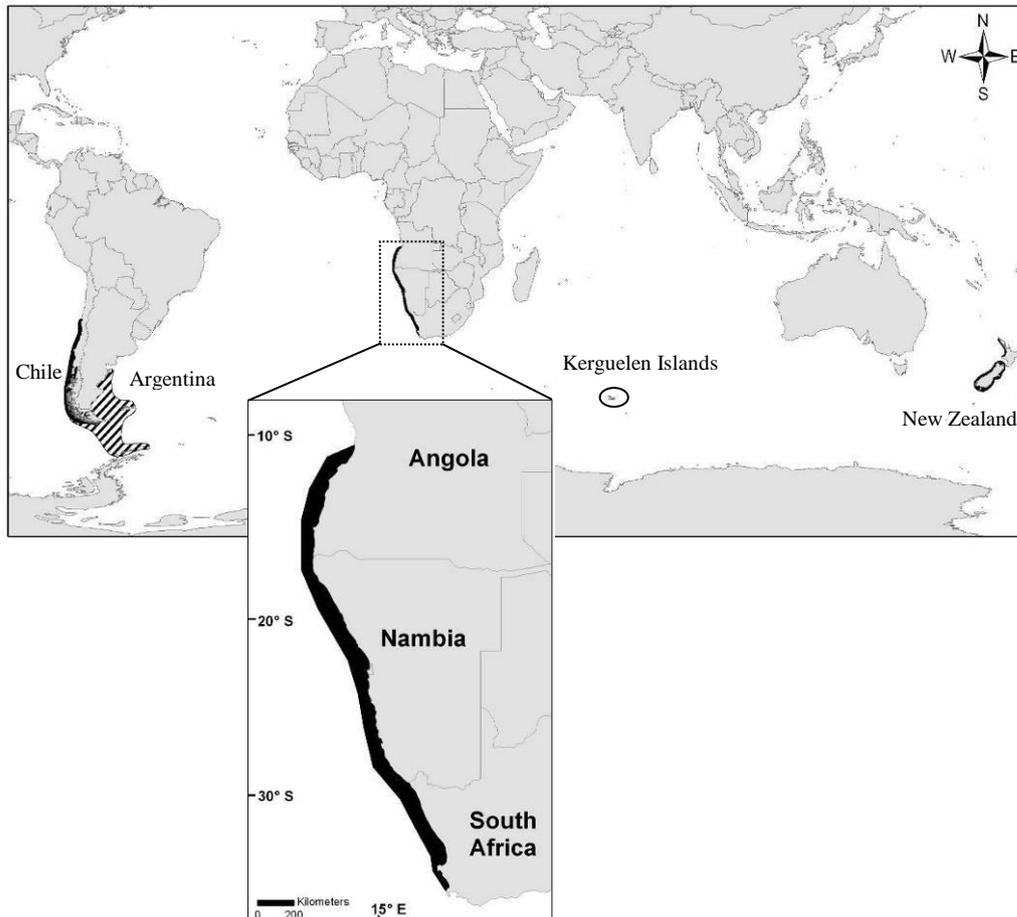
Figure 1.1: The genus *Cephalorhynchus* consists of four species of dolphins each with a limited distribution and each being endemic to different regions of cool temperate waters in the Southern Hemisphere. Hector's dolphins are found around New Zealand (solid black area); Commerson's dolphins occur along the coast of Argentina (hatched area) and around the Kerguelen Islands (highlighted by the black circle); and Chilean dolphin along the coast of Chile (solid black area). The insert shows Heaviside's dolphins distribution along the west coast of Southern Africa (redrawn from Reeves et al. 2008a, 2008b, 2008c, 2008d)

Appearance

Heaviside's dolphins are small, robust dolphins that weigh about 75 kg and reach between 1.65 – 1.71 m in length at maturity, with no obvious sexual dimorphism in size. The largest specimen measured was a male with a body length of 1.75 m (Best 1988). It looks similar in shape to a porpoise (family Phocoenidae) with a conical

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head and no pronounced beak, although there is enough differentiation between the rostrum and the melon that anything anterior of the melon may be interpreted as a small "beak" (Best 1988, 2007). The dorsal fin is low and almost triangular in shape, which helps to distinguish Heaviside's dolphin from other delphinids occurring in the same area. The leading edge is slightly convex in shape and longer than the trailing edge which is slightly concave (Best 1988).

Figure 1.2: Lateral and ventral view of the colouration of the Heaviside's dolphin (Photos taken by C. Behrmann, Mammal Research Institute, University of Pretoria).

Heaviside's dolphins have a distinctive colour pattern (Best 1988, 2007, see Figure 1.2). Typically the dorsal surface of the body is dark blue-black in colour with a light grey cape over the head and thoracic region. There is a light grey dorso-lateral flank blaze and four well-defined ventral white areas. The light grey cape is separated mid-dorsally by a narrow isthmus of dark pigment which starts at the blowhole and widens about one third of the way down the body, completely displacing the light grey cape roughly at the level of the posterior insertion of the dorsal fin. There is an irregular oval of dark pigment around the eyes. The four ventral white areas consist of an approximately diamond-shaped chest patch that wraps around the front of the pectoral fins, small ovoid patches in the axillary region and a large trident-shaped mark which extends mid-ventrally from about the level of the posterior insertion of the pectoral

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fins to the anus, with a separate tongue extending up each side onto the flank. Between individuals there is variation in the shapes of these white marks, in particular the beginning of the trident marking and the chest patch. There appears to be some sexual dimorphism displayed in the way the trident mark terminates. In females the mark widens to include the mammary slits and terminates straight after the anus whereas in males it tends to taper to a point after the anus (Best 2007). This colour pattern seems to be present from birth (Best 1988). There have been sightings of at least four Heaviside's dolphins that are almost completely white in colour. Three of the sightings were in the Cape Town area (Rice and Saayman 1984, Best 1988) and one in the Luderitz area of the Namibian coast (Cole 2000 as cited in Fertl et al. 2004).

Distribution

Heaviside's dolphins are endemic to the west coast of southern Africa, and are distributed along the west coast of South Africa, Namibia and southern Angola (see Figure 1.1; Findlay et al. 1992). Cape Point on the Cape Peninsula seems to be the southern limit of its distribution although there has been an unpublished sighting of one animal in Plettenberg Bay, South Africa (Centre for Dolphin Studies unpublished reports). The northern limit of the Heaviside's distribution in Angola is not accurately defined but sightings have recorded up to 17˚S (Reeves et al. 2008b). This species is a coastal species with all published sightings in water shallower than 200 m, although the potential for observer bias is acknowledged in this regard. The highest sighting densities are inshore of the 100 m isobath (Findlay et al. 1992).

Shore observations and satellite tracking from the Western Cape show Heaviside's dolphins to have a diurnal pattern of movement, being close inshore in the mornings and further offshore in the afternoon and at night (Elwen et al. 2006, Elwen 2007). It is believed that these late afternoon and nocturnal migrations offshore may be related to the diurnal movements of the dolphin's main prey item, juvenile shallow water Cape Hake, *Merluccius capensis* (Elwen et al. 2006, Elwen 2007). In the morning the dolphins move inshore to rest and socialise (Best 2007).

Satellite tracking of five female Heaviside's dolphins indicate home range estimates of between 875 and 2000 km^2 (Elwen et al. 2006), indicating relatively limited

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dispersal. It is however expected that males will have a larger home range (Elwen et al. 2006).

Food

Heaviside's dolphins' diet consists of fish (73.7%) and cephalopods (26.3 %) (Best 2007). More than half of this total mass of prey consumed was made up of shallow water hake (*Merluccius capensis*), other *Merluccius* sp. (39.1 %) and kingklip (*Genypterus capensis,* 15.5 %). *Octopus* sp. (17.9 %) and *Loligo reynaudi* (8.4 %) contribute the cephalopod component (Best and Abernethy 1994, Best 2007). Most of the hake consumed were juveniles ranging in length from 5 to 28 cm ($\bar{x}$ = 19.5 cm; Sekiguchi et al. 1992).

Reproduction and growth

It is suggested that both sexes reach sexually maturity at about 1.56 – 1.59 m in length (Best and Abernethy 1994). Calves are approximately 87 cm in length at birth (Best 2007). Most evidence proposes a summer (December/January) birthing season however this season could be more prolonged (Best 2007). Of the 10 stranded females examined, the only two pregnant females were examined six months apart (October and April) but had very similar-sized foetuses (22.2 cm and 28.8 cm respectively) (Best and Abernethy 1994, Best 2007). Calves may start to wean from a body length of 110 – 118 cm (Best 2007). Both the length of gestation and the duration of lactation remain unknown (Best 2007).

Conservation status

Heaviside's dolphins are listed as Data Deficient (DD) on the IUCN Red List and are included on Appendix II of CITES (Reeves et al. 2008b). The South African Marine Living Resources Act (Act No. 18 of 1998) protects cetaceans from harassment, capture and intentional killing by vessels and humans. However, there are no restrictions on how close vessels can approach dolphins provided that the vessel does not deliberately move through a school of dolphins.

Coastal species of dolphins are more susceptible to inshore boat traffic, noise, shore developments, entanglement, pollution and heavy metals (Hale 1997). Along the west coast of South Africa, fishing nets are set inshore for mullet, sharks and other fish.

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Heaviside's dolphins' use of inshore areas makes them susceptible to death through entanglement in these nets (Best 2007). Only a small number of fishermen along the West Coast have permits for setting nets, despite this being a legal requirement. Due to the legal ban on the capture and killing of dolphins fishermen are less likely to report catches of Heaviside's dolphins thus complicating the attainment of a reliable estimate of the number of Heaviside's dolphins caught as by-catch (Best 2007, Elwen et al. 2010). By comparison, both Hector's and Commerson's dolphins are reported to be accidentally caught in gill nets (Dawson 1991, Iñíguez et al. 2003).

Although Heaviside's dolphins eat juvenile cape hake which is below the modal length of the commercially caught hake (Sekiguchi et al. 1992) there is still a potential that these dolphins will have indirect interactions with some fisheries (Best 2007). In 1990 one Heaviside's dolphin was caught in a mid-water trawl targeting juvenile hake but this was a research trawl and possibly an isolated incident (Best and Abernethy 1994)

Globally, inshore cetacean species have been found to have high concentrations of pollutants such as heavy metals and pesticide residues in their tissue (e.g. Indo-Pacific humpback dolphins *Sousa chinensis*– Minh et al. 1999, Hector's and Maui's dolphin – Stockin et al. 2010). High levels of Dichlorodiphenyltrichloroethane (DDT) have been found in Hector's and Maui's dolphin tissue (Stockin et al. 2010) and Commerson's dolphins around Kerguelen Islands (Abarnou et al. 1986). DDT is known to interfere with reproduction in the Hector's and Maui's dolphins (Stockin et al. 2010). Conversely, Heaviside's dolphins have been reported to have low concentrations of DDT and Polychlorinated biphenyls (PCB) in their tissues (de Kock et al. 1994). Twelve stranded Heaviside's dolphins examined by Henry and Best (1999) where found to have low concentrations of heavy metals .

This research project

Background

Along the southern African coastline there are 18 different species of dolphins (Family Delphinidae) but only the Heaviside's dolphin (*Cephalorhynchus heavisidii*) is endemic (Findlay et al. 1992). These dolphins are among the least known cetaceans with almost all aspects of its population dynamics and behavioural ecology remaining

unknown. Prior to Elwen (2007) there were only few studies on the external appearance (Best 1988, Griffin and Loutit 1988), diet (Sekiguchi et al. 1992, Best and Abernethy 1994, Best 2007) and distribution (Findlay et al. 1992) of the species. Elwen (2007) described the distribution, movements and abundance of Heaviside's dolphins between 32°S and 34°S although the main focus area was St Helena Bay (32°S). This study provided some new insights into diurnal movements, home range estimates, site fidelity, distribution and population estimate.

Elwen et al. (2006, 2009a) showed that Heaviside's dolphins have a limited home range with onshore-offshore movements and suggested a limited dispersal. There is an increase in the numbers of dolphins near-shore in the mornings before noon and during periods of full moon (Elwen et al. 2009a). The distribution of these dolphin sightings were higher in areas exposed to more swells and areas with greater long-term availability of their main prey, juvenile Cape hake (*Merluccius capensis*) (Elwen et al. 2010). Mark-recapture efforts proposed an initial population estimate of 6 300 dolphins distributed between 32°S and 34°S, however, as suggested by Elwen et al. (2009b) this might be an underestimate due to a small sample size and low proportion of individually recognized animals.

Heaviside's dolphins in Table Bay are poorly studied with the last published study focusing on sightings of these dolphins in Table Bay from 1979 to 1984 (Rice and Saayman 1984). Subsequent studies (Elwen et al. 2006, Elwen 2007, Elwen et al. 2009a, 2009b, 2010, Elwen and Leeney 2010) did a limited number of surveys in Table Bay and Namibia, which leaves a gap in the understanding of the population in the area.

Objectives of this study
Without reliable population and behavioural information, robust management and conservation plans cannot exist. At best authorities can only implement the precautionary principle until research can provide better understanding of this species. To better understand a species one needs to understand the population and its structure; in order to develop a comprehensive conservation and management strategies, information based on several population throughout the species' range should be reviewed (Rayment et al. 2011).

The overall objective of this study was to investigate three elements of the population structure, namely the spatial distribution, behaviour patterns and the short term group dynamics of Heaviside's dolphin in Table Bay, South Africa, the southern limit of their distribution.

Specifically, these objectives were addressed in two chapters of this thesis. In Chapter 4 I describe the distribution and spatial behaviour patterns of Heaviside's dolphins in Table Bay. Using a variety of analytical techniques, I investigated if there were different areas of Table Bay that the dolphins were using, and if there were any core areas that displayed prominent behavioural groupings.

The second component of this thesis investigates the group dynamics of Heaviside's dolphins in Table Bay (Chapter 5). Using mark-recapture photographic identification techniques, I calculated the group size of Heaviside's dolphins in Table Bay and constructed basic models of individual association pattern and site fidelity.

This project is an initial, exploratory phase of a larger-scale multifaceted research (L. Karczmarski, University of Pretoria and University of Hong Kong; study in progress) which, among other, includes the recently completed acoustics component (Morisaka et al. 2011), on-going genetic component (K. Gopal, PhD candidate at University of Pretoria), further mark-recapture and spatial modelling, socio-behavioural and conservation ecology research.

Chapter 2

Application of geographical information systems and photographic identification techniques in studies of cetaceans

Geographical Information Systems (GIS)

Geographical information systems (GIS) have developed into a valuable research and analysis tool for the investigation of relationships between a variety of spatial and temporal variables. It is a computer-based system used for the capture, storage, manipulation, analysis, and display of spatially referenced data (Durr and Gatrell 2004). Although originally designed for the terrestrial environment, GIS is quickly developing and increasing in applicability to the marine environment, especially with the "development" of Marine Protected Areas (MPA - Hoyt 2005).

As with previous studies using GIS, the basic application of GIS is looking at the area use and distribution of an animal by plotting the animals' locations (latitude and longitude) in GIS. This can be done on either a population level (e.g. Wedekin et al. 2007) or, when combined with photo-identification, an individual level (e.g. Hooker et al. 2002). Within their home range, animals tend to have areas of concentrated use (known as core areas) and areas used less often (Samuel et al. 1985; Karczmarski et al. 2000). The identification of these cores areas is important for understanding the ecological factors that determine the use of an area (Samuel et al. 1985). Kernel density estimates (KDE) can be used to help determine these core areas (e.g. Samuel et al. 1985, Gubbins 2002, Nelson et al. 2008, Rayment et al. 2009).

In order to better understand core areas and spatial ecology of organisms, one needs to understand the interaction between organisms and environmental factors (e.g. sea surface temperature, winds, chlorophyll concentrations, ocean depths, El Niño events etc.). Complex interrelationships between organisms and their environment are ideally suited for GIS technology, as animal migration patterns, individual identification, habitat use and environmental factors may be georeferenced as separate layers in GIS. By combining these various layers, researchers can investigate how habitat utilisation is affected by environmental factors (e.g. Whitehead and Rendell 2004, MacLeod and Zuur 2005).

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With the advancement of GIS researchers are able to use GIS to develop predictive models which can be used for the development of conservation and management plans such as MPAs. For cetaceans these models have been use to predict resource and habitat use, migration, foraging patterns and potential conflicts with vessel traffic or fisheries (e.g. Whitehead and Rendell 2004, Kaschner et al. 2006, Rayment et al. 2010, Garaffo et al. 2011).

Photographic Identification techniques

Individual animal recognition has been a necessary part of research since early studies of behaviour and ecology (Lorenz 1937). Photographic identification (photo-ID) is a method by which photographs are taken of identifying marks in order to identify individual animals. In the 1950s and 1960s it was thought that individuals needed to be artificially tagged but with the increasing number of long-term studies being conducted on wild animals, researchers have found natural markings (e.g. stripes on a zebra or notches on the dorsal fins of dolphins and sharks) that can be used for individual identification (Würsig and Jefferson 1990). Würsig and Würsig (1977) pioneered photo-id and the practice is very common in the field of marine mammalogy.

Photo-ID has been used in a large number of field studies on both terrestrial and marine mammals and has been proven as a useful tool in the estimation of a variety of population parameters (Hammond et al. 1990). A broad range of terrestrial mammals species have been individually recognised for example, Terrestrial: zebras (*Equus burchelli* – Peterson 1972), giraffes (*Giraffa camelopardalis* – Foster 1966), African elephant (*Loxodonta africana* – Douglas-Hamilton 1973), chimpanzees (*Pan troglodytes* – Goodall 1986), wild dogs (*Lycaon pictus* – Frame et al. 1979), cheetah (*Acinonyx jubatus* - Caro 1994), lions (*Panthera leo* – Schaller 1972). In similar context the photo identification approach has also a well-established protocol for whales, such as the southern right whale (*Eubalaena australis* - Best and Underhill 1990), humpback whales (*Megaptera novaeangliae* - Mizroch et al. 1990), sperm whale (*Physeter macrocephalus* - Whitehead 1990).

For dolphins and porpoises, the shape of the trailing edge of the dorsal fin is the most identifying feature (Würsig and Jefferson 1990). It abrades and tatters easily,

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resulting in clear notches. The notch pattern varies between individuals as a result of incidental events and has been used by many researchers for identification of free-ranging small cetaceans. Photo-identification has been used in long term and published research on killer whale (*Ornicus orca* - Bigg 1982), bottlenose dolphin (*Tursiops truncatus* - Würsig and Würsig 1977), Hector's dolphin (*Cephalorhynchus hectorii* – Dawson and Slooten 1987), Heaviside's dolphin (*Cephalorhynchus heavisidii* – Rice and Saayman 1984, Elwen 2007), spinner dolphins (*Stenella longirostis* - Norris and Dohl 1980), short-finned pilot whale (*Globicephala macrorhynchus* - Miyashita et al. 1990), harbour porpoise (*Phocoena phocoena* - Watson and Gaskin 1983), Dall's porpoise (*Phoceoenoides dalli* - Miller 1990) and baiji (*Lipotes vexillifer* - Yuanyu et al. 1990).

Benefits of technology

Photo-ID has benefited from the advancement of technology. Early studies used manual focus, film, 35 mm single-lens reflex camera with a variable focal length (zoom) lens (e.g. 80 – 200 mm) as the primary tool. Manual focus film cameras limited the quality and the quantity of the photographs as film was expensive to develop. The development of auto-focus cameras improved the quality of the photos but the digital camera has greatly improved the quality and quantity of identification photographs. Digital cameras allow researchers to take large numbers of photographs in rapid section with most advanced digital cameras being able to take 6-8 photographs in under 10 seconds. The digital zooms (100 – 400 mm) coupled with the speed of the digital camera allows even amateur photographers to take good photos thus reducing the amount of training time.

The advancement of technology has also helped to shorten the time taken for photo analysis. Early studies had limited methods for analysing the photos however the main method was to produce slides from the film which could then be projected onto the wall using a slide projector with a zoom lens. Using the best quality photo for each individual, the dorsal fins where traced on to sheets of paper. These tracings were used to create the catalogue of the individuals (Würsig and Jefferson 1990).

This process was time consuming and expensive. Computers have helped to reduce the expense and time taken to analyse photos. Instead of waiting days or weeks for

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the slides to be produced, digital photos can be uploaded onto the computer when the researcher returns to the lab, making them immediately available for analysis. Photographic software programmes (e.g. Cannon Digital Photo Professional) are used for analysis, allowing researchers to zoom even further into the photographs to see smaller details. And lastly, even though digital photos can be quite large in file size (e.g. 4 or 5 MB each) the storage of the digital photos is still far easier and less space consuming than printed photos.

Computer assisted programs

The digital camera has allowed researchers the freedom to take many photos in an encounter. However manually processing large amounts of photographs can be time consuming and can be prone to error. Computer-aided programs help to limit the amount of photos that need to be visually confirmed as the same individual by the researcher (Kelly 2001). No computer-aided program is fully automated and the final decision of whether two individuals are a match is done by the researcher (Whitehead 1990). These programs still require a high quality photograph with none or small parallax to make a successful match as subtle differences between two individuals are not detected by the programme (Kelly 2001). Computer-aided programs have been developed for a range of animals. For example: cheetahs (Kelly 2001), zebras (Foster et al. 2007), marbled salamander (*Ambystoma opacum* - Gamble et al. 2008), whale sharks (*Rhincodon typus* - Arzoumanian et al. 2005), spotted raggedtooth shark (*Carcharias taurus* - van Tienhoven et al. 2007), grey seal (*Halichoerus grypus* - Hiby and Lovell 1990), polar bear (*Ursus maritimus* - Anderson et al. 2010), humpback whales (Mizroch et al. 1990), sperm whale (Whitehead 1990), and various marine animals (Hillman et al. 2003).

Methodology assumptions

For photo-ID to provide realistic estimates the following assumptions need to be met: natural marks should be a) recognisable over time, b) be unique to the individual and c) have an approximately equal probability of being sighted and resighted (Würsig and Jefferson 1990). The heterogeneity of the data collection can be difficult to establish as some individuals are more distinctive than others and some individuals are more boat shy than others (Würsig and Jefferson 1990). Individuals with markings that are not distinctive enough to ensure future recognition should not be

used for population size analysis but can be used for movement and range information (Hammond 1986).

General methods

Photo-ID can be conducted from shore, boats or airplanes. Each method has advantages and disadvantages but for the purpose of this study only boat based observations will be described.

Boat based observations are the most practical approach to studying small cetaceans (Würsig and Jefferson 1990). A boat allows researchers to find and follow dolphins and manoeuvre near the group for the best possible view. As boats can potentially disrupt the natural behaviour of the dolphins the boat operators need to learn to approach the dolphins slowly, parallel to the group and not herd the animals with the boat. A small, manoeuvrable vessel (< 10 m in length) allows for close approach (within 5 – 10 m of individuals) and low angle photography. Fast speeds that encourage dolphins to bow-ride are not advised as this disrupts the normal behaviour and the spray thrown up by the animals can obscure the dorsal fin and back making individual identification difficult. Photographs are to be taken as perpendicular to the body axis as possible. The dorsal fin and back should appear large enough in the frame so that 1cm nick is visible (Würsig and Jefferson 1990).

Applications

The recognition of individual animals allows researchers to look at the group composition and "fidelity' of certain individuals to the group to determine group structure (e.g. Würsig 1978). Individual animals photographed in more than one locality can help determine area distribution, short-term movement patterns and migrations (e.g. Wells et al. 1990). By following certain individuals researchers can obtain information on behaviour patterns such as resting, travelling, socialising and feeding (e.g. Tayler and Saayman 1972) as well as interactions and associations with other individuals.

Other techniques, such as mark-recapture and photogrammetry (Wester et al. 2010), can be applied to photo-ID to increase a researcher's knowledge of a species.

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Mark-recapture techniques is applied to photo-id to determine a species population size (e.g. Reisinger and Karczmarski 2010). Mark-recapture techniques estimate the population size by capturing and marking a sample of animals from a population and then determining the proportion of marked animals in subsequent recapture samples. It is assumed that the proportion of marked animals in the subsequent samples to be the same as that in the total population, allowing the estimation of the overall population size (Greenwood 1996).

Photogrammetry is the use of photos to measure objects. Although photogrammetry does not require the identification of individuals, measuring of individuals with known age and sex can help researchers establish growth rates and other life history information over time. Researchers can also obtain information on the age-sex composition of a group using a particular area (e.g. Cosens and Blouw 2003).

Long-term photo-ID studies, in conjunction with other studies, can enhance the descriptions of life history parameters such as age at sexual maturity, calving intervals, reproductive span and total life span (e.g. the bottlenose dolphins of Sarasota Bay, Florida - Wells and Scott 1990).

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Chapter 3

Study Area

This chapter gives an introduction into the physical oceanography and anthropogenic uses of the whole Table Bay area. The area of Table Bay studied and the details of the launch site and survey routes taken in this study are described in detail in the methods section of Chapters 4 and 5.

Physical features

The study area is located in Table Bay (33.9˚S 18.4˚E) situated to the west of Cape Town harbour, South Africa. The bay covers an area of approximately 100 km^2 (Quick and Roberts 1993) and is flanked by Robben Island and the Atlantic Ocean to the west and the city of Cape Town to the east (Figure 3.1; van Ieperen 1971). The shape of Table Bay is planimetric, and resembles a negative log-spiral curve (Werz and Martin 1994).

Bathymetry and geology

The bathymetry is uneven with a maximum depth of 35 m between Robben Island and Green Point (Werz and Martin 1994). The harbour entrance has been dredged to a depth of 15.9 m to allow large cargo vessels to gain access to the harbour (Transnet National Ports Authority 2010). The geology is mainly Malmesbury bedrock (characterised by shales, slates and minor sandstone) with most of the bay covered with fine to course sediment (Woodborne 1983, McLachlan 1991). The eastern shore of the bay consists mainly of sandy beaches whereas the southern coastline is characterised by harbour works and the south-western section, near Granger Bay and Mouille Point, has rocky outcrops (Woodborne 1982).

Hydrology

Table Bay faces northwest and is partly open to the deep-sea swells of the Atlantic Ocean. The swell entering the bay is refracted by geomorphological features such as the Cape Peninsula to the south and Robben Island to the west (Werz and Martin 1994). Approximately half of the total wave energy that enters Table Bay originates from a south-westerly direction with a quarter each from the west and north-west

direction. A negligible amount of wave energy comes from a southerly direction (Werz and Martin 1994). The weak northward flowing Benguela current and the southward flowing inner current have little influence on the currents within Table Bay (van Ieperen 1971, Neshyba et al. 1989). The majority of these Table Bay currents are wind-driven. The surface currents are 20 - 30 cm/s and the bottom currents are on average < 5 cm/s (van Ieperen 1971). The overall movement of water in Table Bay is in a northward direction with water entering the bay between Green Point and Robben Island and leaving between Robben Island and Bloubergstrand (van Ieperen 1971, Werz and Martin 1994). The northward movement of currents and water is more pronounced in summer as the south-south-easterly winds dominate in summer while in winter there is no predominant wind direction (van Ieperen 1971).

Temperature, salinity and upwelling

Sea surface temperatures (SST) range from 10 to 15 °C (mean 13 °C) with the coldest waters found closest to shore (van Ieperen 1971). Although the SST's tend to be higher in winter (August - October) than in summer there is no significant difference found between winter and summer sea surface temperatures (van Ieperen 1971). Salinity ranges from 34.4 ‰ to 35.5 ‰.

Along the coast of south western Africa (including Table Bay), upwelling by South Atlantic Central Water (SACW) (Shannon 1966, van Ieperen 1971), provides large concentration of nutrients from upwelling and results in an excellent habitat for plankton and other marine life. This is one of the reasons why the west coast of Africa has fertile fishing grounds (van Ieperen 1971).

The most pronounced phases of upwelling along the Cape Peninsula occurs from September to March (Andrews and Hutchings 1980) with the peaks in November and March at Cape Point due to favourable winds (Shannon 1985).

Human activities

Table Bay has various uses such as being a harbour, recreational area, a rock lobster reserve and fishing area (Quick and Roberts 1993). Cape Town Harbour has been a meeting place for trading ships from different nations since the late 15th century (Werz and Martin 1994). It is positioned along one of the world's busiest trade routes

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and is one of South Africa's busiest harbours. It handles the largest amount of fresh fruit and is the second to Durban as the busiest container harbour (Ports & Ships 2010). For the period of 2003 to 2008, the annual average number of vessels arriving at the harbours is 3 239 vessels (Gross tonnage of 48 283 254 m^3) for Cape Town Harbour and 4 395 vessels (Gross tonnage of 95 364 033 m^3) for Durban Harbour. These vessels include ocean going vessels (e.g. cargo ships and car carriers), coastwise going vessels (e.g. cargo ships), South African trawlers, foreign fishing vessels and miscellaneous vessels (e.g. oil rigs, tugs, naval vessels etc.) (Transnet National Ports Authority 2010). Cape Town Harbour has a dry dock with repair and maintenance facilities that are used by several large fishing fleets and the West African oil industry. As there are many tourist attractions in Cape Town and its surrounding region, many cruise ships berth in the harbour (average for 2003 to 2008 is 34 passenger vessels arriving annually – Ports & Ships 2010, Transnet National Ports Authority 2010).

There are two rivers, the Diep and the Salt, three deep-ocean outfalls and numerous storm-water outfalls which discharge into Table Bay. The Green Point and Camps Bay outfalls discharge partially treated wastewater and the Caltex and Kynoch outfalls discharge industrial effluent (Quick and Roberts 1993). Treated wastewater from quarries is discharged into the Salt River Canal which in turn flows into Table Bay. Since the currents in the Bay are generally weak and the residency period for the water in Table Bay is on average approximately four days (van Ieperen 1971), the Bay should be highly polluted. However the various studies that have been conducted on the water-quality of the Table Bay area (for review see Quick and Roberts 1993) have shown that pollutants (mainly phosphorus, nitrogen, lead and zinc) discharged into Table Bay do not have a recorded negative impact on the studied facets of the environment (Quick and Roberts 1993).

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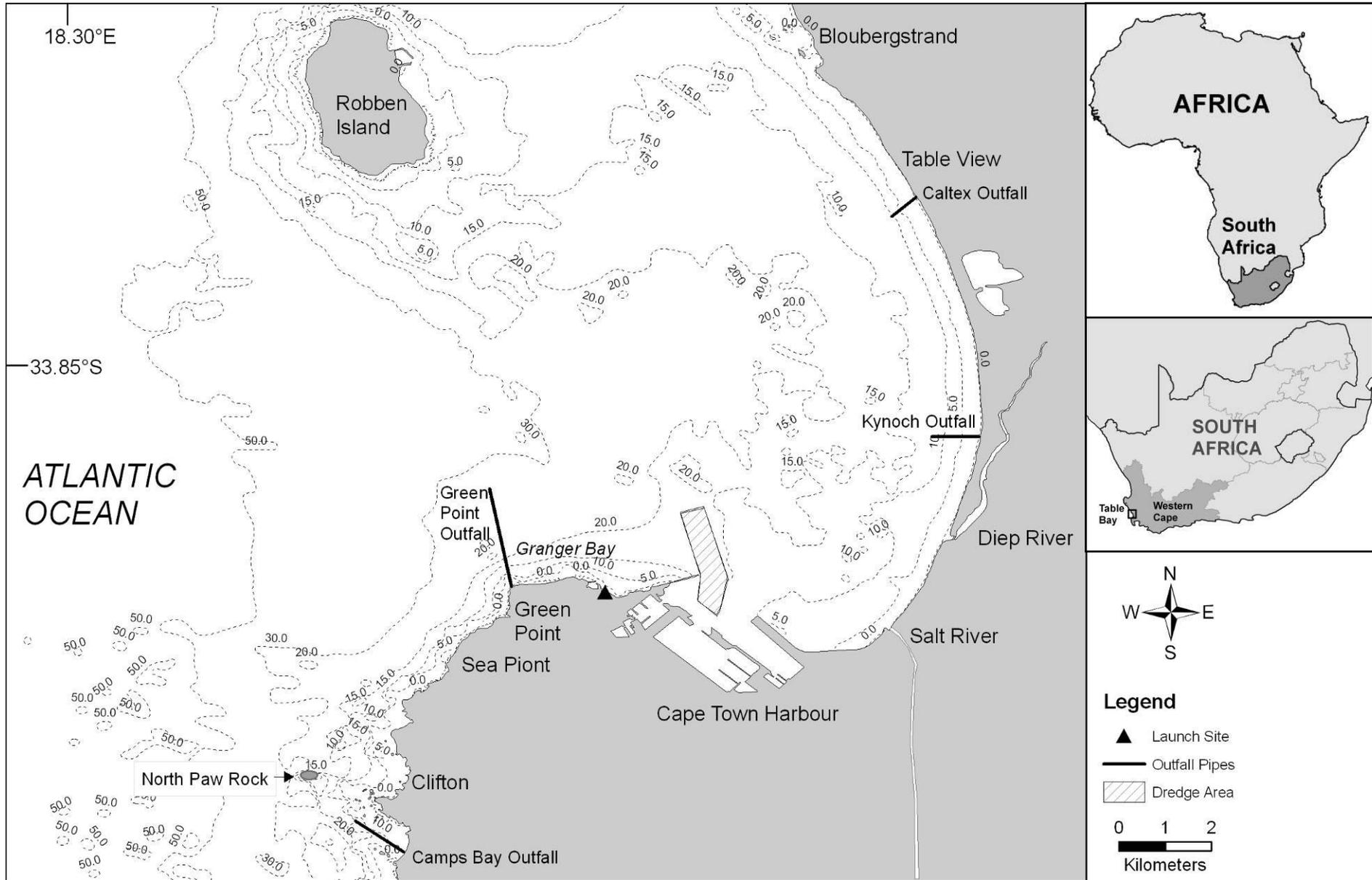
Figure 3.1: Map of the study area, Table Bay on the West Coast of South Africa showing bathymetry (depth in metres), launch site and outfalls.

Chapter 4

Pattern of occurrence and local distribution of Heaviside's dolphins (*Cephalorhynchus heavisidii*) in Table Bay

Abstract

Heaviside's dolphins are coastal dolphins endemic to the west coast of Southern Africa. Although opportunistic sightings of these dolphins in Table Bay have been published, no research has been conducted on their occurrence and use of Table Bay coastal waters. This study investigated the spatial and behaviour distribution of Heaviside's dolphin in Table Bay, South Africa during summer in 2008 and 2009 using GIS and general liner modelling. The dolphins did not use the area homogeneously and were observed in a well-defined 7 km^2 area on the south side of Table Bay along a 3 km east-west stretch of coast. The dolphins were seen within 2 km from shore. For the array of behaviours observed, the core density areas (50 % Kernel) were observed in the Granger Bay area and there was very little overlap (6 %) of core areas used for milling, socialising, resting and travelling. Foraging was never observed in areas close to shore, which supports earlier studies suggesting that these dolphins forage primarily offshore. The observed pattern of area use and preference provides indications for consideration in coastal management strategies, while further research is recommended to build up on this current preliminary work.

Introduction

Habitat use patterns are believed to be a function of the habitat heterogeneity and the biological requirements of a species, populations of a species and/or individuals from a population (Rosenzweig 1981). An animal's home range typically represents a heterogeneous environment with patches rich or poor in resources (Samuel et al. 1985, Karczmarski et al. 2000, Laca 2008). The size of theses patches are determined by the abundance, distribution and availability of the resources within the environment. The importance of the different patches in the animal's daily life is indicated by the varied use of the areas (McNab 1963, Samuel et al. 1985, Brown 1988). The home range of a wild animal is made up of minimum number of critical resources and is likely to be larger if the critical resources are smaller and more

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dispersed (Karczmarski et al. 2000). Critical habitats refer to parts of a species range that are essential for day-to-day survival, as well as for maintaining a healthy population growth rate (Hoyt 2005). Areas that are regularly used for feeding, breeding, raising calves and migration are all part of the critical habitats. The adequate identification of critical habitats within a population's home range is an important part to understanding the species ecology and is important for the conservation and management of the species/population on both local and regional scale (Karczmarski 2000, Karczmarski et al. 2000).

Among the *Cephalorhynchus* genus, Hector's (*C. hectorii*), Commerson's (*C. commersonii*) and Chilean dolphins (*C. eutropia*) have endemic and apparently patchy coastal distributions with high site fidelity (Goodall et al. 1988a, Bräger et al. 2002, Garaffo et al. 2011). Heaviside's dolphins have a continuous, coastal distribution along the west coast of southern Africa (Findlay et al. 1992, Elwen et al. 2010). No seasonal migrations of these dolphins have been found, but this could be due to the absence of winter surveys. Recent studies in St Helena Bay, South Africa, show that Heaviside's dolphins have limited small home ranges and daily migrations moving inshore during the mornings and moving further offshore in the evenings and at night (Elwen et al. 2006).

Although there have been some opportunistic sightings of Heaviside's dolphins in Table Bay (e.g. Rice and Saayman 1984 and Best and Abernethy 1994), research into their occurrence, daily behaviours and area use in Table Bay coastal waters has not yet been undertaken. This chapter describes first attempts to describe these patterns and set up a stage for further, more in-depth work that is currently on-going.

Materials and Methods

Data Collection

Boat-based photo-identification surveys were conducted in Table Bay, South Africa on a 6 m semi-rigid, outboard powered inflatable from January 2008 to May 2009. After launching at Granger Bay (Figure 3.1), the boat followed a circular route, travelling west along the coast until North Paw Rock, near Clifton and then travelling offshore (approximately 1.5 km from the coast) back to the launch site, until a dolphin group was encountered. At the start and end of each encounter, the geographical

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position, sea surface temperature (SST, °C), sea state and water depth (m) were recorded. During the encounters from November 2008 to May 2009 dominant group behaviour, water depth and geographical position were recorded at approximately 10 minute intervals or when a change in behaviour was observed. The geographical positions (dd.dddd, WGS 84) of the dolphins and a record of the boat track taken during the survey, with measurements every 30 minutes, were recorded using a Garmin Global Positioning System (GPS) map 72C (Olathe, Kansas USA), which is accurate to 5 m. The SST and water depth were recorded using a Garmin Fishfinder 120 (Olathe, Kansas USA). The surveys were terminated when rain, fog, or deteriorating sea state (exceeding four in a Beaufort scale) precluded further work. On the 17th February 2009 the weather conditions were favourable to conduct a transect to the west of Cape Town harbour along the coastline to Melkbos and then back across the bay.

Definitions

Each time the boat went out searching for dolphins is referred to as a survey. Only one survey was conducted per day. Each time a dolphin group or solitary animal was located is referred to as an encounter. An encounter lasted until 100 % coverage of the group was obtained or the animals were lost. A group is defined as a spatial aggregation of more than one dolphin, that are involved in similar (often the same) activity and interact over time scales sufficiently short that there are few changes in the group membership (Whitehead and Dufault 1999). Groups frequently consisted of several smaller units (referred to as subgroups), ranging in size between two to five individuals with the distance between individuals less than two body lengths; these subgroups were considered to be part of a group.

Daily activities of dolphins were classified into four categories of behaviour following a similar approach by Karczmarski and Cockcroft (1999); *travelling* consisted of persistent, directional movement, with synchronised diving and surfacing of all group members, *resting* consisted of a low level of activity with slow forward movement and synchronised diving and surfacing of all group members, *socialising:* consisted of various vigorous activities including leaping out of the water, riding the waves in the surf zone, high speed movement with frequent direction changes and prolonged body

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contact with other dolphins and *milling* consisted of moderate speed movement with frequent directional changes and minimal body contact with other dolphins.

The observed habitats were identified from the boat and are defined as s*andy*: areas covered with sand, *kelp*: areas where kelp, *Ecklonia maxima* were present, *rocky*: areas with dominant rock cover, and *offshore*: where the bottom type and bathymetry could not be identified due to researchers unable to see the ocean floor.

Data Analysis

Search Effort

As the primary objective of this research project was a mark-recapture photo-identification study, with a considerable amount of time spent following dolphin groups, the search effort needs to be taken into account to offset any potential analytical bias. A grid of 0.5 by 0.5 km squares (cells) was constructed for the whole Table Bay area to test for search effort. A minimum of two consecutive track points, from the GPS tracking record, needed to be present in the grid cell for that track/cell to be included. A Pearson's Chi square test was used to test if there is a difference between the expected (equal distribution) and observed search effort data.

Occurrence and behaviour

The full duration of this study was divided into lunar months; the start of a new moon was selected to indicate the start of a lunar month. An occurrence map was created by entering all the geographical positions (latitude-longitude, n = 436) into ArcMap version 9.3 (Environmental Systems Research Institute, Inc.) using a map of Table Bay supplied by the South African Navy Hydrological Office (SANHO). The spatial data was projected into the Universal Transverse Mercator (UTM) Zone 34S using the WGS 1984 datum.

Spatial patterns within the data were investigated using minimum convex polygons (MCP) and kernel destiny estimates (KDE) to estimate the area (km^2) of occurrence and observed behaviours. MCP are created by connecting the peripheral points in a group of points (Mohr 1947). Kernel analysis is a nonparametric statistical method for estimating probability densities from a set of points (Worton 1989). The MCP is appropriate for calculating area in territorial animals that demarcate their territories

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using marking behaviour. Whereas the KDE is more appropriate to use for animals that are likely to move beyond the outermost observation locations (Rachlow et al. 1999).

MCP were calculated using the Animal Movement option on the Hawth's Analysis Tools (Beyer 2004). KDE were calculated using the Home Range Tools ArcGIS 9 extension (HRT) (Rodgers et al. 2005). The HRT extension's adaptive kernel method with least-squares cross-validation technique and automatically generated smoothing parameter h based on the h-ref value was used to create 50 % (K_{50}) and 95 % (K_{95}) kernels. The smoothing parameter controls the amount of variation in each component of the estimate. Small h values reveal the fine details of the data while large h values obscure all but the most prominent features (Worton 1989). Whenever there was an overlap of the area estimates with land, the area of terrestrial habitat was subtracted from the final estimate using the clip function in ArcGIS 9. The MCP and 95 % kernel were used for the whole occurrence estimations and the 50 % kernel was used for the core area of occurrence estimation. The percentage of overlap of the areas used for all the behaviours was calculated using intersect tool in ArcGIS. The areas of KDEs was measured using XTools Pro 7.1 area calculation tool (Data East 2003).

While preference ratios lack statistical precision, they provide a crude but easily understood comparison of selection and avoidance for particular behaviours (Shannon et al. 2006). Preference ratios were therefore calculated for different behaviours as the proportion of locations in a particular behaviour as a ratio of the proportional area of that behaviour, that is: (number of occurrences of a specified behaviour / the total number of occurrences) / (the area of the specified behaviour / the total area).

The differences between monthly occurrence area sizes were tested using the Mann-Whitney U test (Zar 2009) in Statistica 9 software. Due to unequal sample sizes among behavioural area size, a Spearman correlation tests (r_S) (Sokal and Rohlf 1995) was used to test the influence of the sample size of the behaviours (N) on the range/area size of all behaviours together and separately.

Generalised Linear Model (GLM)

The behaviours defined during the dolphin encounters were treated as binomial variables (non-travelling=1, and travelling = 0). The non-travelling behaviour is a combination of milling, socialising and resting. Such data is therefore suitable for logistic regression analysis where a generalized linear model is fitted to the data by using maximum likelihood techniques (McCullagh and Nelder 1989). Thus, we applied mixed generalized linear models (GLMM) using restricted maximum likelihood techniques (family=binomial, logit link function, lmer() in R Ver. 2.10; R Development Core Team 2009), to account for temporal pseudoreplication.

Initially we modelled the probability of Non-Travelling (NT) by including the following continuous explanative variables into a global model: Latitude, Longitude, Depth, Month, Hour, and Habitat. To test whether latitude, longitude and depth, affected the feeding probability we also included the interaction terms between the three variables into the global model (Latitude:Longitude:Depth). To account for the dependency of behaviours within encounters we included (1|GROUPENC) as random factor. We then composed a set of ecologically relevant alternative simplifications of the global model (Burnham and Anderson 2002).

Model selection by use of the Akaike's Information Criteria (AIC)

To compare alternative nested models we applied the principle of Akaike's Information Criteria (*AIC*, Akaike 1973, Burnham and Anderson 1998). In particular we applied the *AIC*-weight criteria (*w*) which reflects the relative performance of models and can be interpreted as the probability that a given model is the best model, i.e. the model that minimizes the Kullback-Leibler discrepancy (Burnham and Anderson 2002, Wagenmakers and Farrell 2004). In the evaluation of alternative models we also made use of the evidence ratio expressed as a normalized probability as $w_m(AIC)/w_n(AIC)$, where model *m* is the best fitting model compared to model *n* (see Wagenmakers and Farrell 2004).

Because all models had the same structure and sample size, the respective AIC values from the different models were comparable (Burnham and Anderson 1998).

Correlation among explanative variables

In order to account for the problem of multicolinearity among explanative variables the intercorrelation among the explanative variables was tested by using a Spearman correlation tests (r_S).

Results

Photo-identification surveys were conducted from January 2008 to May 2009 (Table 4.1), and 222 hours (out of 447 hours of effort) were of direct observation of dolphin groups. The dolphins were observed on 67 of the 69 surveys which resulted in a total of 166 encounters. The mean direct observation time for the same group of dolphins during an encounter was 1.05 hours (range 0.02 to 4.62 hours). The majority of surveys ended in the early afternoon (before 14:00) due to the dolphins moving further offshore.

Table 4.1: The data was divided into months using the lunar cycle with the new moon indicating the beginning of a month. This table shows the lunar months with the corresponding Gregorian calendar dates, total number of surveys conducted, and total hours spent observing the dolphins and field effort.

Year	Lunar Month	Gregorian Calendar Dates	Number of Surveys	Direct Observation (hours)	Field Effort (hours)	Percentage of time spent with the dolphins (Observation/ effort*100)
2008	January	8 Jan – 6 Feb	12	34.57	62.80	55.05 %
	February	7 Feb – 6 Mar	6	22.87	61.30	37.31 %
	March	7 Mar – 5 Apr	5	13.10	22.13	59.20 %
	April	6 Apr – 4 May	5	18.17	27.63	65.76 %
	November	28 Oct – 26 Nov	2	1.68	6.28	26.75 %
	December	27 Nov – 26 Dec	5	4.58	14.95	30.64 %
2009	January	27 Dec – 25 Jan	9	20.65	30.88	66.87 %
	February	26 Jan – 24 Feb	9	56.03	92.55	60.54 %
	March	25 Feb – 25 Mar	10	41.00	74.78	54.83 %
	April	26 Mar – 24 Apr	4	5.35	47.17	11.34 %
	May	25 Apr – 23 May	2	4.68	7.00	66.86 %

The percentage of time spent actively searching for dolphins in Table Bay during January to April 2008 and November 2008 to May 2009 is shown in Figure 4.1. The requirement for two consecutive GPS track points within a cell was violated 149 times (out of 2958), resulting in that section of the track being excluded from the total

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search effort calculation. Cells with darker colours indicate more time spent actively searching for the dolphins. The cells with the highest percentage (≥ 4 %) of search effort were located closest to the coastline and in the Granger Bay area. The Pearson's Chi square test ($\chi^2 = 34574.72$, df = 293, p = 0.00) shows that the observed search effort is significantly different to an search effort with equal distribution.
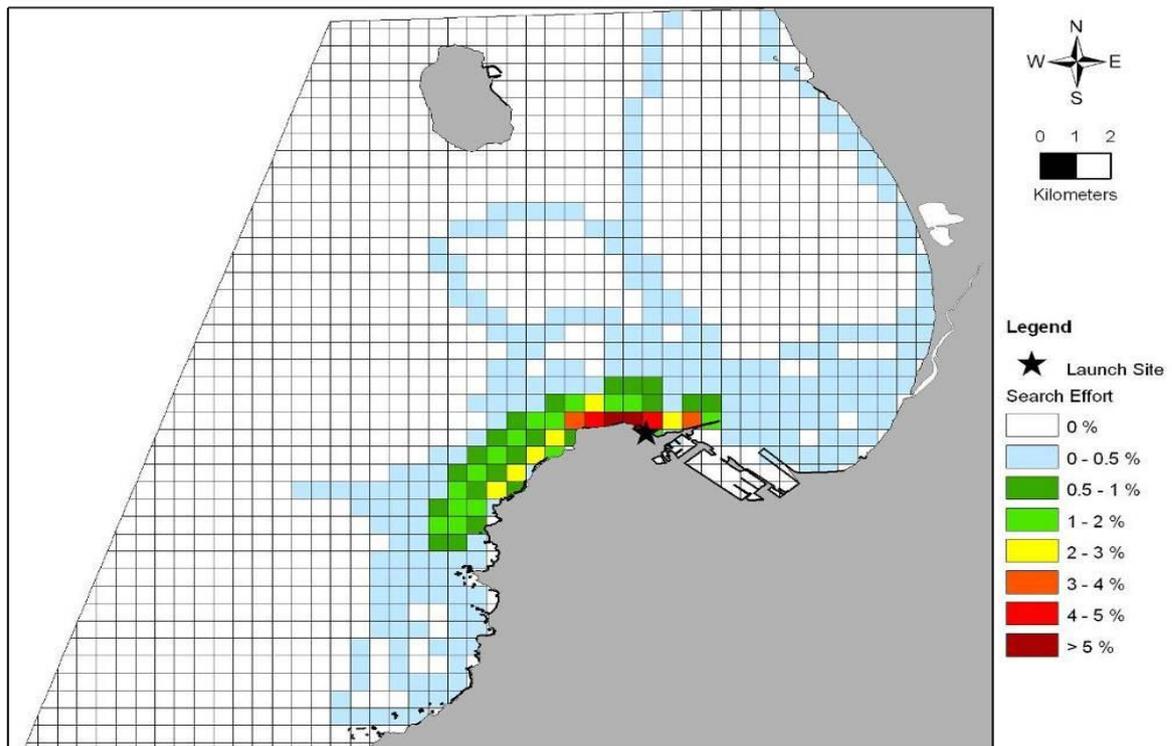
Figure 4.1: Percentage of total time spent actively searching for Heaviside's dolphins in Table Bay, South Africa during 2008 and 2009. Grid size is 0.5 km^2.

Heaviside's dolphins did not use the area homogeneously and were observed in a well-defined 7 km^2 area on the south side of Table Bay along a 3 km east-west stretch of coast, Granger Bay (Figure 4.2). The furthest occurrence point was recorded 2 km offshore. Majority of the sightings (69.72 %) were in waters < 15 m in depth with the average depth of sightings being 12 m (S.D = 6 m).

Overall the MCP yielded a relatively large area of occurrence, with 12.51 km^2 (Table 4.2). In contrast the K$_{95}$ area of occurrence for all point yielded an area of 4.59 km^2 with an overall K$_{50}$ core area use of 0.33 km^2. February and March 2009 were very successful months in terms of time spent with the dolphins hence the highest number of data points (N = 137 and 113 respectfully). Although February 2009 has the
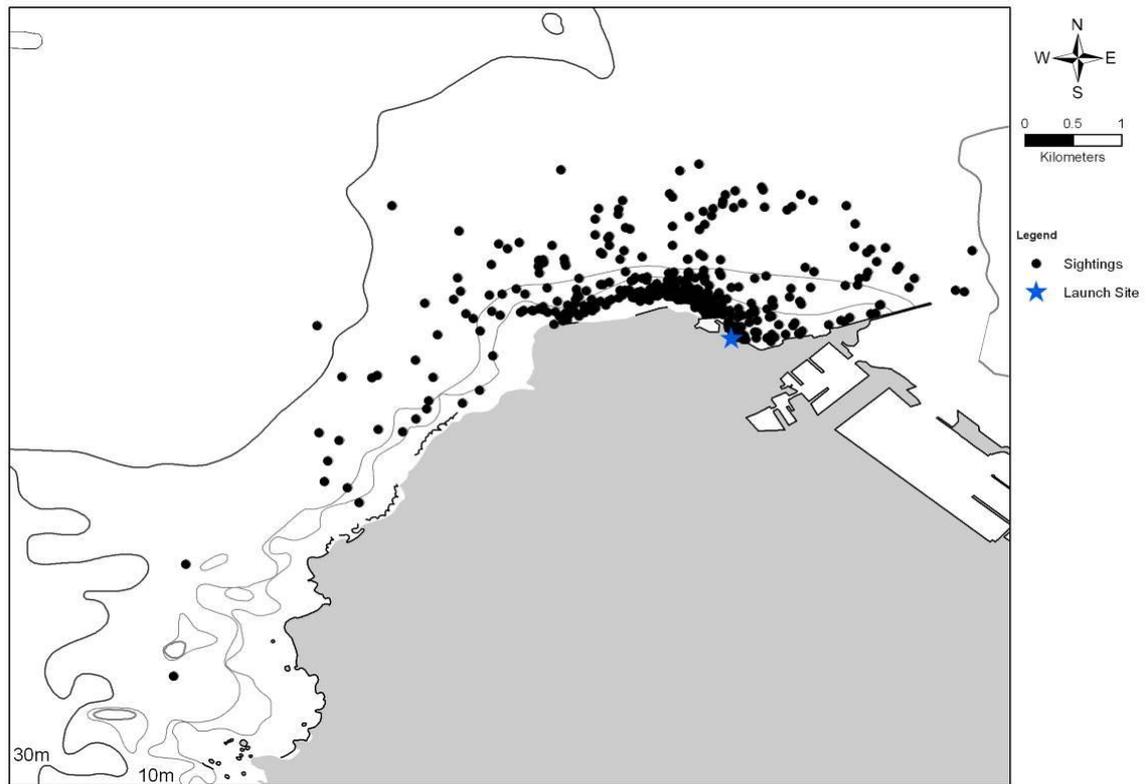
Figure 4.2: The distribution of Heaviside's dolphin sightings (black dots; 166 encounters) for 2008-2009 in Table Bay, South Africa. The launch site location is indicated by the blue star and the 10 m and 30 m isobaths are displayed.

Table 4.2: Monthly occurrence area sizes of Heaviside's dolphin using the minimum convex polygon (MCP) and K_{50} and K_{95} methods in Table Bay, with the Kernel Density Estimate constructed by using Home Range Tools ArcGIS 9 extension least-squares cross-validation technique and automatically generated smoothing parameter h which are based on the *h-ref* value.

Lunar Month	MCP (km^2)	K_{95} (km^2)	K_{50} (km^2)	h	*h-ref*	N points
January 2008	6.78	8.79	1.30	0.19	0.57	29
February 2008	3.76	3.93	0.68	0.21	0.64	14
March 2008	2.73	6.82	0.77	0.36	0.71	8
April 2008	3.33	16.61	2.36	0.59	0.68	10
November 2008	0.18	1.58	0.31	0.66	0.71	8
December 2008	0.80	2.53	0.52	0.62	0.64	15
January 2009	3.01	1.65	0.24	0.15	0.53	43
February 2009	6.36	1.51	0.12	0.08	0.44	137
March 2009	7.34	3.75	0.49	0.10	0.45	113
April 2009	1.45	0.79	0.12	0.17	0.56	32
May 2009	2.37	5.41	1.45	0.47	0.58	26

highest N value (N = 137), it has the second smallest K_{95} (1.51 km^2) and the smallest K_{50} (0.12 km^2). In general there was a similar pattern in MCP and K_{95} for the range estimates (Mann-Whitney U = 51, p = 0.55, N= 11). The K_{50} estimate was much smaller and concentrated (< 1.50 km^2).

A total of 348 behavioural records were available for analysis from January to May 2009. In Table Bay the dolphins were observed milling, resting, socialising and travelling. Foraging was never observed, while travelling was the pre-dominant behaviour of the sightings along the 'western side of the study area (Green Point to Camps Bay)' (Figure 4.3). Resting was infrequently seen (n = 19) with the highest h value (h = 0.59, h-ref = 0.62) compared to the other three behaviours; socialising (n = 110, h = 0.12, h-ref = 0.46), travelling (n = 40, h = 0.10, h-ref = 0.54) and milling (n = 179, h = 0.08, h-ref = 0.42), which resulted in a coarse representation of a home range estimate for resting behaviour. Travelling had the largest K_{95} (4.48 km^2) in comparison to resting (3.40 km^2), socialising (3.02 km^2) and milling (1.82 km^2). There is a clear concentration of points in the Granger Bay area with the K_{50} for all four behaviours (0.10 km^2) located close to the coastline in Granger Bay (Figure 4.4). However the percentage of overlap for the core area (K_{50}) used for all four behaviours is small (5.89 %). The two most exhibited behaviours were milling (51.44 % of total occurrence) and socialising (31.61 %) while travelling (11.49 %) and resting (5.46 %) are exhibited less often, at least within the study area.

There was no correlation between the direct observations of behaviours and the size of the area used for socialising: K_{50} (Spearman's R Correlation = -0.05, p = 0.94, N = 5) and K_{95} (Spearman's R Correlation = 0.36, p = 0.55, N = 5) and milling: K_{50} (Spearman's R Correlation = -0.75, p = 0.08, N = 6) and K_{95} (Spearman's R Correlation = -0.75, p = 0.08, N = 6). Since the sample sizes did not influence the size of the area of the behaviour, a comparison between the area size and group activity could be made.

KDE could not be calculated for the months where there were insufficient amount of data points (N < 5). For travelling there are only two months (February and March 2009) and for resting there is only one month (February 2009) that had sufficient number of points (N > 6) to calculate a KDE. Therefore a Spearman's R correlation could not be calculated for these two behaviours.
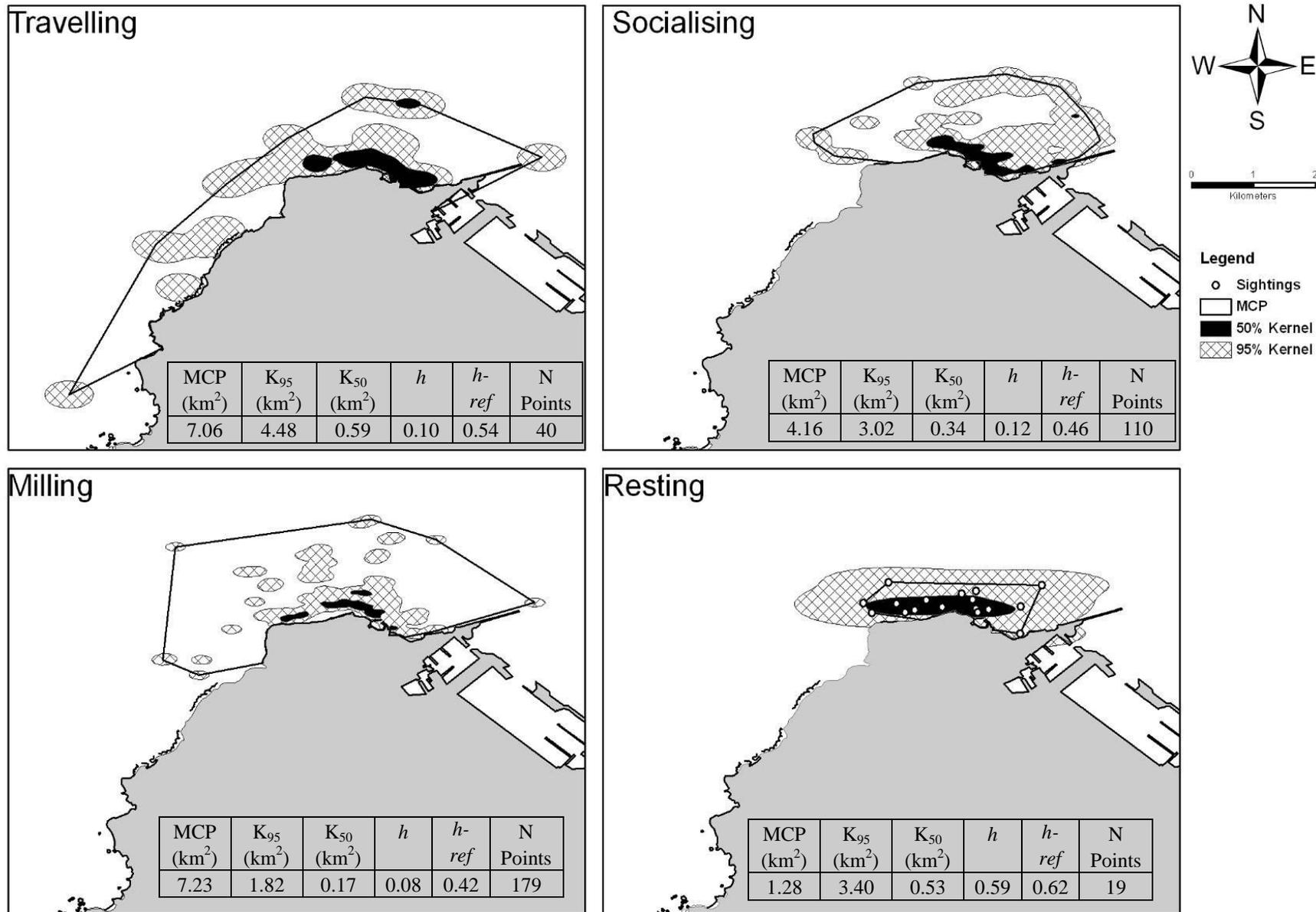
Figure 4.3: Comparison of behavioural activity range and core area sizes of Heaviside's dolphins using the minimum convex polygon and kernel methods (50 % kernel: K_{50} (solid) and 95 % kernel: K_{95} (hatched)). Adaptive Kernel Density Estimates were constructed by using Home Range Tools ArcGIS 9 extension, based on the least-squares cross-validation technique and automatically generated smoothing parameter h which is based on the h-ref value and the number of points (N points) used to construct kernels.
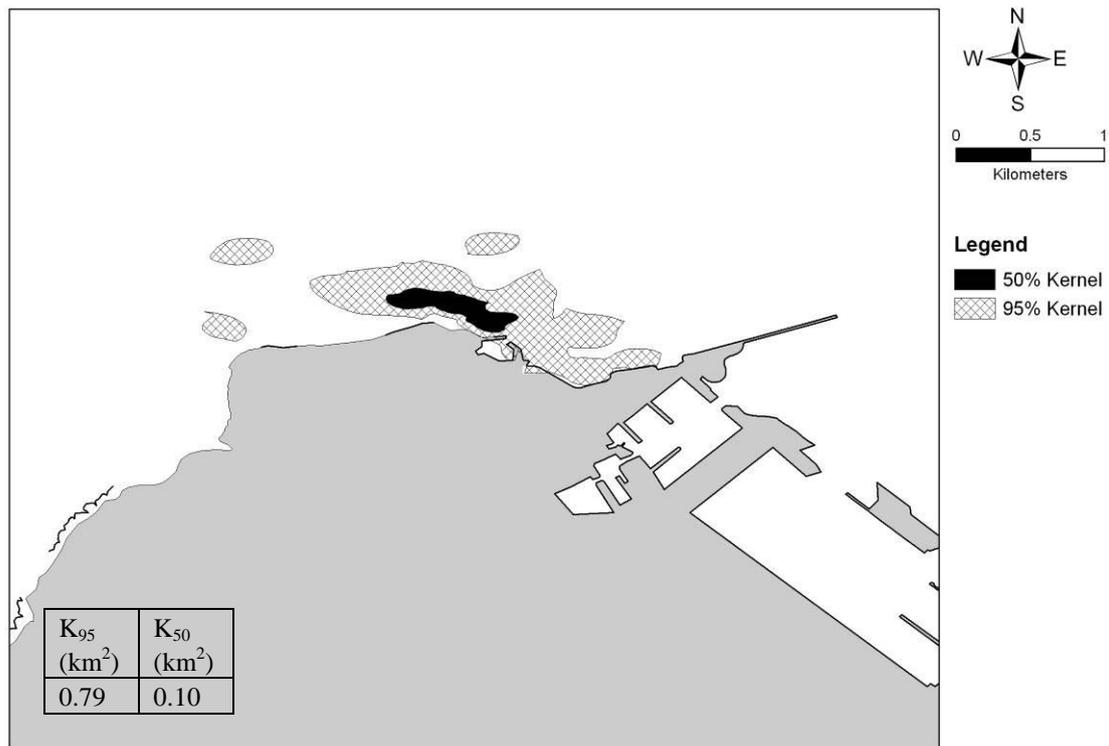
Figure 4.4: Kernel density estimate constructed of the overlapping areas for all four behaviours (travelling, milling, socialising and resting) displayed by Heaviside's dolphins from January to May 2009.

There is no significant difference between area size and group activity at the different levels (Kruskal-Wallis test: MCP: $H (3, N = 19) = 1.32$, $p = 0.72$; K_{95}: $H (3, N = 14) = 4.11$, $p = 0.25$ and K_{50}: $H (3, N = 14) = 4.10$, $p = 0.25$).

The best fitting model with the lowest AIC output (W_{AIC}, $= 0.55$, Table 4.3), was compiled of two variables Latitude, and Depth and were consistently predictive variables throughout most of the various models (Table 4.3), yielding the lowest AIC output as well as all of explanatory variables producing statistical significant interactions (Table 4.4). The estimated Latitude and Depth contributed a significant proportion of the variance found in the model to describe the probability of non-travelling (Table 4.4).

The probability of non-travelling increased to the north (increase in Y) of the study site, whilst probability of non-travelling increased in shallow areas (negative slope in estimate variable of Depth).

Table 4.3: Statistical outputs of the seven models according to the lowest AIC, explaining variation in the probability Non-travelling ~ Travel in the Table Bay area. Components featuring in model outputs are as follow: Latitude (LAT), Longitude (LONG), depth of locality during the encounter (DEPTH), the month of the encounter (MONTH), the hour of the day when the encountered occurred (HOUR) and the habitat (HAB). For all models we included the encounter (1|GROUP) as a random factor in the model.

Model	AIC	ΔAIC	W_{AIC}
LAT + DEPTH	213.7	0.00	0.55
LAT * DEPTH + LONG	215.3	1.60	0.17
LAT * DEPTH + HOUR + LONG	216.3	2.60	0.12
LAT * DEPTH + MONTH + HOUR + LONG	218.3	4.60	0.05
LAT * DEPTH + HOUR + HAB + LONG	223.2	9.50	0.01
LAT * DEPTH + MONTH + HOUR + HAB	225.1	11.40	0.00
LAT * LONG * DEPTH + HOUR + HAB	232.8	19.10	0.00

Table 4.4: Linear mixed effects model output for the truest fit model for analysis on Non-travelling (1) and Travel behaviour (0). Model variables are as follows: Components featuring in model outputs are as follow: Latitude, depth of locality during the encounter (DEPTH). For all models we included the encounter (1|GROUP) as a random factor in the model.

	Estimate	Std.	Error	z value	P
(Intercept)	5225.576	1505.528	3.471	0.001	< 0.001
Depth	-0.078	0.031	-2.515	0.012	< 0.05
Latitude	154.071	44.412	3.469	0.001	< 0.001

Discussion

In this study Heaviside's dolphins were not observed further than 2 km offshore and were predominantly seen in the shallow (< 15 m), coastal waters of Granger Bay. The dolphins were observed milling and socialising more often than travelling and resting, while foraging was not observed, yielding a highly concentrated core area of use.

Heaviside's dolphins have been seen up to 83 km offshore but are most abundant in waters inshore of the 100m isobath (Findlay et al. 1992). From 1979 to 1984, there are opportunistic sightings of these dolphins in the basin of Table Bay and around Robben Island (Rice and Saayman 1984), which does seem to suggest that the broader Table Bay area is used, but there are core areas (such as Granger Bay). Similarly, the closely related Chilean, Commerson's and Hector's dolphins are associated with

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swallow waters (Goodall 1994, Lescrauwaet et al. 2000, Bejder and Dawson 2001). Bräger et al. (2003) suggested that habitat preference for Hector's dolphins is influenced by environmental factors such as water clarity, depth and sea surface temperature and environmental structures such as river mouths, underwater reefs and prominent headlands. However, the current study did not look at the influence of these factors on area use and it is recommended that these should be included in future studies.

The kernel density estimates (50 %) show that the dolphins were observed using several small core areas of Granger Bay for travelling, socialising, milling and resting, which indicates a high preference for this area (Figure 4.3). All the core areas are located within 0.5 km offshore. The predominant behaviour on the western side of the study area (Green Point to Camps Bay) was travelling. Observations of the dolphins in this area indicate that they generally tend to be travelling in the direction of Granger Bay (C. Behrmann, per. obs.). There is no significant difference between the area size and the group activity indicating that there is little overlap (5.89 %) of the core areas used for the different behaviours. The general linear modelling indicates that the north east part of the study area (Granger Bay) is where the dolphins were most likely to display non-travelling behaviour (socialising, resting and milling), which supports the observed behaviours and the KDE.

As indicated, all the core areas are located in Granger Bay within 0.5 km from the shore and have very little overlap. This indicates that these dolphins are highly site-specific for certain behaviours, at least on a short temporal scale, which in turn indicates that Granger Bay is an important area for Heaviside's dolphins.

Studies on coastal dolphins suggest that habitat selection patterns occur firstly as a function of the distribution, movement and abundance of their prey species and secondly as a shelter from predators (Stevick et al. 2002) and the utilization of specific resources.

However, foraging was never observed in Table Bay during this study which is similar to Elwen et al. (2009) findings in St Helena Bay. This, in addition to the dolphins moving offshore in the early afternoons, supports the suggestion that

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Heaviside's dolphins are foraging offshore at night; when their prey is easier to catch (Elwen et al. 2006). Juvenile shallow water cape hake (*Merluccius capensis*), their main prey item, has a diurnal movement where they move closer to the surface at night making it easier for predators to feed on them (Payne 1989, Sekiguchi et al. 1992). Diurnal feeding patterns has also been observed for dusky dolphins (*Lagenorhynchus obscurus*) and spinner dolphins (*Stenella longirostris*) (Würsig and Würsig 1980, Würsig et al. 1994).

Studies have shown that most cetaceans will choose environments that are safe from predators and harsh environmental conditions when resting (Norris and Dohl 1980, Whitehead and Moore 1982, Smultea 1994, Elwen and Best 2004, Lammers 2004, Heithaus and Dill 2006). Spinner dolphins stay inshore during the day to rest and socialise , probably to reduce the chance of shark predation in deepwater (Norris and Dohl 1980). While bottlenose dolphins (*Tursiops aduncus*) move offshore at night in response to the inshore movement of same shark species at dusk (Cockcroft et al. 1989). Therefore predator avoidance (killer whale *Orcinus orca* and sharks) may be a explanation of Heaviside's dolphins movement inshore when not feeding (Elwen et al. 2009a). As killer whales are rarely sighted along the South African coastline (Findlay et al. 1992) and several Heaviside's dolphins have been sighted bearing shark inflicted scars (Best and Abernethy 1994), therefore shark predation is possibly a higher risk to these dolphins than killer whale predation.

With tourist attractions such as the Victoria & Alfred waterfront situated close by, Granger Bay is used for various tourist activities. One such activity is the adrenaline-seeking ride in a high-powered speed boat. These boats, amongst others, have been observed racing towards and away from dolphin groups thus indicating a possible risk of vessel collisions. The South African Marine Living Resources Act (Act No. 18 of 1998) protects cetaceans from harassment, capture and intentional killing by vessels and humans. However, there are no restrictions on how close vessels can approach dolphins provided that the vessel does not deliberately move through a school of dolphins.

Since there seem to be little overlap between areas where Heaviside's dolphins display various behaviours (50 % kernel) these animals appear to be behaviourally highly site

specific, at least on a short temporal scale. This indicates that Granger Bay is an important area for this species in Table Bay. It should therefore be recommended that management strategies be implemented that will reduce the speed of boats in this area such as a 'go slow' zone where motorised vessels are limited to travelling at a maximum speed of 2 knots (e.g. Karczmarski et al. 1998). As milling and socialising were the most exhibited behaviours in Granger Bay, the "go slow" (reduce speed) zone should cover the core areas (50 % Kernel) of these two behaviours, and the area along the shore from the Green Point lighthouse to the tip of the harbour wall, and 0.5 nautical mile wide (Figure 4.5) seems appropriate.
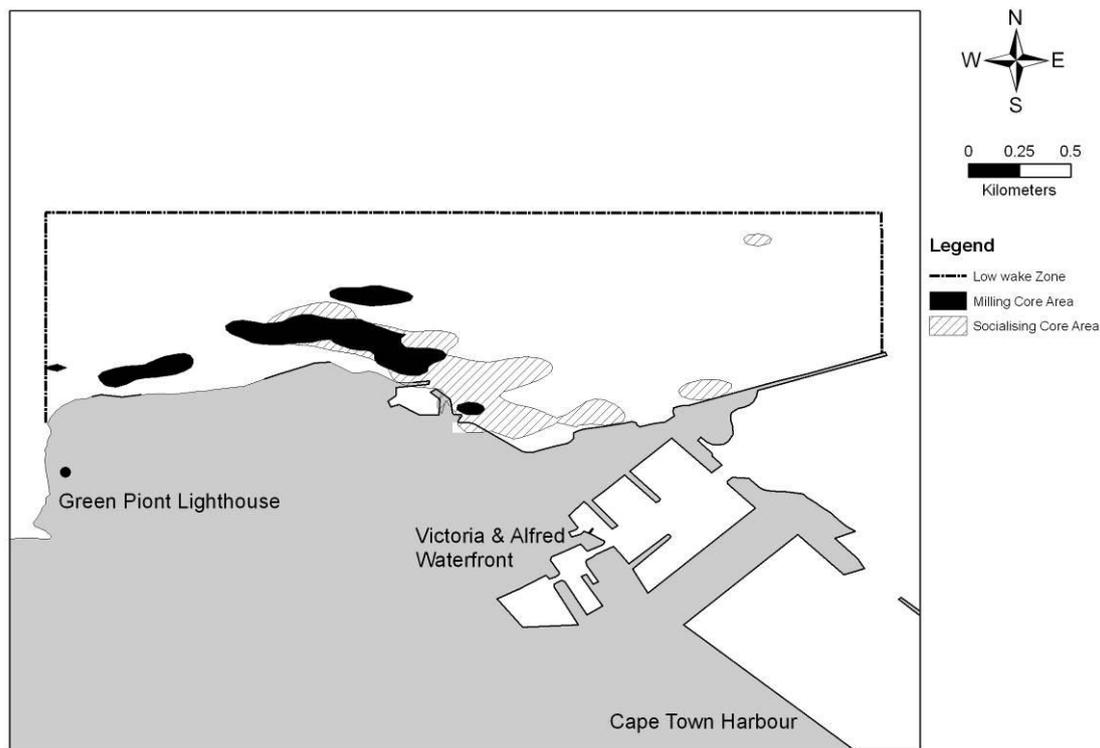
Figure 4.5: Recommended location of 'go slow' zone where motorised vessles should be limited to travelling at 2 knots. The core areas (50 % kernels) for milling (solid) and socialising (hashed) are shown.

Vessel collisions contribute to many mortalities of several marine species including turtles (e.g. Hazel & Gyuris 2006), manatees (e.g. Laist and Shaw 2006), dugongs (Greenland and Limpus 2006) and whales (e.g. Knowlton and Kraus 2001). One method of trying to reduce the amount of such collisions is the introduction of a "go slow" zone where vessels are restricted to low speeds. Such "go slow" zones have been suggested for green turtles (*Chelonia mydas* - Hazel et al. 2007), manatees (*Trichechus manatus latirostris* - Laist and Shaw 2006), humpback dolphins (*Sousa*

chinensis - Karczmarski et al. 1998) and Indo-Pacific bottlenose dolphins (*Tursiops aduncus* – Steckenreuters et al. 2012a). Preliminary results indicate that the go slow zone for the Florida manatees is a success (Laist and Shaw 2006). Hazel et al. (2007) found that green turtles have a greater chance of avoiding collisions when the vessels were travelling at a slower speed (<4 km.h^{-1}) and would therefore probably benefit from the implementation go slow zones. Unfortunately the "go slow" zone for the humpback dolphins in Algoa Bay, South Africa has never been implemented therefore it is impossible to say if this management strategy would have proven to be successful. Steckenreuters et al. (2012b) investigated the effectiveness of the go slow zones (speed restriction zone (SRZ)) implemented in the Port Stephens - Great Lakes Marine Park in Australia for the Indo-Pacific bottlenose dolphin. They found that the dolphins had a seasonal shift in their feeding areas, in winter they fed outside the SRZ, which could be as a result of the increase in whale watching vessels in the SRZ during winter or their preference for a different foraging habitat in winter. Therefore the SRZ were not effective at minimising the impact of boats on the dolphins and were not a great management tool. This study seems to focus more on the effect of boat presence on the dolphin's behaviour in- and outside of the SRZ and not on the effect of the boats speed on the dolphin's behaviour. Another thing to bear in mind is that the SRZ were only implemented 16 months before starting their research and therefore it is possible that this is too short a time period to notice a significant influence of the SRZ on the dolphin behaviour. They do suggest that the SRZ be monitored for another five years before making a decision as to whether or not the SRZ is a successful management tool in this area.

Steckenreuters et al. (2012b) investigations bring to mind an important fact about whether the "go slow" zone should be seasonal or annual. The study presented in this dissertation only looked at the habitat use of the dolphins during the summer methods. Thus the winter months will also need to be studied in order to determine if the go-slow zone should be restricted to the summer months (seasonal) or present all-year round.

"Go slow" zones are usually located around important feeding areas of dolphins (e.g. Karczmarski et al. 1998, Steckenreuters et al. 2012b). Heaviside's dolphins have never been observed foraging in the Granger Bay area (C. Behrmann per. obs.)

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However this study indicates that Granger Bay is an important area for the Heaviside's dolphins in Table Bay. Until the source of the attraction to this area can be identified, and a more refined management strategy be suggested, it is advised to adopt the precautionary principle and implement conservation and management strategies. Although there have been no reports of vessel collisions with Heaviside's dolphins in the Granger Bay area, there have been reports in Namibia where close proximity of whale watching and recreational boats probably resulted in a boat propeller injury observed on a Heaviside's dolphin (Elwen and Leeney 2010). The implication of the "go slow" zone could reduce the possibility of these injuries while dolphins are involved in behaviours such as milling and socialising. Outside the suggested "go slow" zone travelling was the main behaviour recorded and thus in this behavioural state the dolphins are probably more likely to detect and avoid approaching boats.

It need to be stressed, however, that the current study had a rather short duration and as such it needs to be seen as preliminary; further research is needed to refine the patterns and recommendations presented in this chapter.

Conclusion

Granger Bay certainly does not represent the entire home range of Heaviside's dolphins, but it appears to serve as an important summer inshore core area within the overall home range. The current pattern of area use and preference indicate that implementation of coastal management strategies would be beneficial in facilitating suitable environment for the animals. Further continuing research will build on this initial study to deepen our understanding of Heaviside's dolphin ecology and the pattern of area use in South African coastal habitats.

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Chapter 5

Short-term group dynamics of Heaviside's dolphins (*Cephalorhynchus heavisidii*) in Table Bay, South Africa

Abstract

Little is known about the behavioural ecology of Heaviside's dolphins. The current study investigated short-term group dynamics of this species in Table Bay, Western Cape, South Africa. Photo-ID surveys were conducted from January to April 2008; 95 recognizable individuals were identified and catalogued. Sighting frequencies varied substantially, with 24.2 % of the individuals seen only once and 73.7 % sighted less than five times; two most frequently resighted individuals were seen 11 times. Groups varied in size from one to 26 animals with a median of five. In a short-term (four months), the group structure appears to be highly dynamic, with great lability in group sizes and membership, weak inter-individual bonds, and weak site fidelity. Further research is needed to decipher the mechanism that shapes Heaviside's dolphin group dynamics and social structure.

Introduction

Interactions between conspecifics make up the social structure of a population and are important in influencing the fitness, gene flow and spatial pattern of the population (Wilson 1975). Individuals of the same species often compete for the same resources; as members of a group, however, they might cooperate to attain or defend a resource or reduce the risk of predation (Gowans et al. 2008) by defending each other from predators.

For management and conservation purposes it is informative to know patterns of behaviour and social organisation to better understand population processes that might contribute to population/species vulnerability (Karczmarski 2000). The individual's social and sexual behaviour affects the population's reproductive rate which may help explain how the reproductive rates vary with population size (e.g. Whitehead 1987). Thus by understanding individual behaviours we can understand the population and possibly predict how the population will respond to demographic changes or anthropogenic impacts (Gowans et al. 2008).

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Delphinid social organisation has been studied for a number of species and is known in a reasonable detail for certain populations of killer whales (*Orcinus orca*), bottlenose dolphins (*Tursiops sp.*) and spinner dolphins (*Stenella longirostris*). The group structures range from stable family pods in the killer whales (Heimlich-Boran 1986, Bigg et al. 1990) to relatively fluid groups in most dolphins (Würsig 1989). Among the genus *Cephalorhynchus*, Hectors dolphins (*Cephalorhynchus hectori*) and Chilean dolphins (*Cephalorhynchus eutropia)* display a fission-fusion social organisation that appears to be broadly similar to the bottlenose dolphin (Slooten et al. 1993, Christie 2005 as cited in Heinrich 2006). Commerson's dolphins (*Cephalorhynchus commersonii*) at the Kerguelen Islands are seen in groups from one to 15 individuals (Borsa 1997) and have no definite group structure (de Buffrenil et al. 1989). While Commerson's dolphins in Argentina are seen in larger groups ($\bar{x} = 18$, SE = 26) and display a fission-fusion society (Coscarella 2005, Coscarella et al. 2010).

Heaviside's dolphins are endemic to the west coast of southern Africa (Findlay et al. 1992) and have apparently a relatively small population estimated at 6 345 individuals (Elwen et al. 2009b). In the St Helena Bay area, South Africa, they were reported to have fluid short-term associations (Elwen 2007); however, with the exception of general group size data, very little is known about the ecology and behavioural biology of this elusive species. The aim of the current study is to provide baseline information on their short-term group dynamics in Table Bay, South Africa.

Materials and Methods

Data Collection

Photo-identification boat surveys were conducted in the inshore waters of Table Bay, Western Cape, South Africa (Figure 3.1) from January to April 2008. Surveys typically started within an hour of dawn and ended between mid-day and mid-afternoon or earlier if weather conditions deteriorated significantly (Beaufort scale $\geq$ 4). Surveys were undertaken using a 6 m semi-rigid, out-board powered inflatable boat. Once a group or solitary individuals of dolphins were located a photographic survey begun with the boat generally moving at 2 - 3 knots alongside the dolphin group. Photographs were taken using Cannon EOS 1D Mark II camera with a variable length (zoom 100 – 400 mm) image-stabilised lens at a distance of less than

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10 m from the animals. All individuals in a group were photographed irrelevant of their individual markings to reduce unequal catchability bias. The group size was recorded at the beginning, the end and throughout the encounter if a change in group size and membership was noted. At the end of the encounter, these recorded group sizes were used to get the best overall estimate of the maximum group size present during the encounter; which was recorded as the "group size". This was done by consensus amongst the personal present on the boat and the final decision was always done by the same person to avoid observer bias.

Definitions

Each time the boat went out searching for dolphins is referred to as a survey. Only one survey was conducted per day. A group is defined as a spatial aggregation of dolphins involved in similar (often the same) activities that interact over time scales sufficiently short so that there are few changes in the group membership (Whitehead and Dufault 1999). Each time a dolphin group was located is referred to as an encounter. An encounter lasted until 100 % photographic coverage of the group was obtained or the animals were lost. All animals photographed within an encounter where considered part of the same group.

Three age classes were distinguished: calf (including neonates), juvenile and adult. Calves were defined as an animal three quarters or less the length of an adult and were accompanied by a larger animal assumed to be the mother. Small individuals with visible foetal folds were regarded as neonates. Juveniles were defined as animals between three quarters to full adult length, but visibly more slender than adults and often independent from their mothers. Adults were defined as animals 1.5 to 1.7 m in length and completely independent

Photographic analysis

The proportion of identifiable individuals was estimated using all photographic records of an encounter, following the procedures of Karczmarski et al. (2005). All photographs were assessed for image quality and assigned a quality grade from one to 100; images graded < 70 were considered too low of a quality for reliable identification with equal catchability. Image graded 70 - 79 were of good quality but generally had part of the dorsal fin below the water. Only images graded ≥ 80 were

considered suitable for further analysis. This ensured that all photographs used in this study were in focus, well-exposed and the entire dorsal fin was visible above the water with no or only moderate cases of parallax.

Each photograph graded ≥ 80 was assessed for distinctiveness (D) of the individual (following the principles described in Friday et al. 2000 and Karczmarski et al. 2005) and were assigned a distinctiveness grade from one to five which are as follows: 1) Unmarked, 2) Slight marking but cannot ensure re-sighting, 3) Marked enough to ensure re-sighting if an ≥ 80 quality photos is taken, 4) Distinctive markings which allows for confident re-sighting of the individual even with a poor photograph, 5) Very distinctive markings that allow for easy individual identification at a first sight. A photo-ID catalogue was produced using the highest quality image of each individual with distinctiveness ≥ 2. Nicks and other dorsal fin mutilations are long-lasting and are a very useful tool for long-term individual identification (Lockyear and Morris 1990), and in the present short-term study the changing of marks was considered negligible.

Individuals with distinctiveness ≥ 3 were classified as suitable to be included in the photo-ID data set for analysis. However, previous studies of Heaviside's dolphins (Elwen 2007) and Hector's dolphins studies (Slooten et al. 1993, Bejder et al. 1998, Bräger 1999) used only the highly distinctive individuals in the analysis which approximates the distinctiveness ≥ 4 in this study; therefore for comparison all analysis were also conducted on a subset of data using only the identified 'non-calf' individuals with distinctiveness ≥ 4 (n = 33).

Statistical analysis
The search per unit effort (SPUE) for each of the lunar months was calculated by dividing the total hours spent actively searching for the dolphins by the total number of surveys conducted in that lunar month.

The association pattern of individuals were quantified using a simple ratio index (Ginsberg and Young 1992) that was calculated using the social analysis software program SOCPROG 2.4[1] (Whitehead 2009). For rationale see Appendix A.

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[1] The compiled version of SOCPROG 2.4 was used which does not require MATLAB to run.

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The Manly/Bejder et al. procedure (Manly 1995, Bejder et al. 1998) was used to determine whether the patterns of associations between individuals are significantly different from random. Using SOCPROG 2.4 both long term (between sampling periods) and short term (within sampling periods) preferred associations were tested using the 'permutation of groups within sampling periods' method.

Standardised lagged association rates were calculated to measure the temporal stability of associations (Whitehead 1995). Models of temporal permanence of associations were fitted to the data using the maximum likelihood and quasi-Akaike information criterion (QAIC) to determine the most parsimonious model (Akaike 1973, Burnham and Anderson 2002, Whitehead 2007). The precision of each estimate is indicated by the standard error (SE) which was calculated for each model using the jackknife procedure. The lagged association rates were calculated for all the 'non-calf' individuals with a moving average of 9000 to smooth the curve.

Lagged identification rates were calculated to measure the residence rate of individuals. Models of residency were fitted to the data using the maximum likelihood and Akaike information criterion (AIC) methods to determine the best fit model. The 95 % confidence intervals and the SE were calculated using the bootstrap procedure. The lagged identification rates were calculated for all 'non-calf' identifiable dolphins.

A sociogram generated with SOCPROG 2.4 was used to investigate the relationship between individuals, the thicker the line between the individuals the stronger the association.

See Appendix A for further explanation into the statistical analysis used in this study.

Results

During 29 surveys (195 hours of search effort), Heaviside's dolphins were seen on all surveys with 61 encounters (95 hours of direct observations), of which nine encounters recorded only individuals with distinctiveness of 2. Almost 18000 photographs were taken of which 2840 images were of a quality $\geq$ 80.

Three of the four months (January, March and April) have similar SPUE (Table 5.1) while in February the SPUE was low due to inclement weather (rain and fog) and the research team spending 15 days at a secondary research area (St. Helena Bay, Western Cape, South Africa).

Table 5.1: Number of Heaviside's dolphin sightings per unit effort (SPUE) per month in Table Bay for January to April 2008.

Lunar Month	Gregorian Calendar Dates	Search per Unit Effort
January	8 Jan – 6 Feb	0.425
February	7 Feb – 6 Mar	0.156
March	7 Mar – 5 Apr	0.554
April	6 Apr – 4 May	0.529

The cumulative number of photographically identified individuals with distinctiveness ≥ 3 showed first signs of apparently reaching plateau after 20 surveys (Figure 5.1, continuous line) although individuals with distinctiveness of 2 continued to be identified and this discovery curve does not show signs of asymptote (Figure 5.1, dashed line). After 29 surveys, there are 96 identified individuals with a distinctiveness ≥ 3 (95 'non-calf' individuals and one calf) and 21 'non-calf' individuals with a distinctiveness of 2. Nine encounters had only individuals rated as non-marked (D = 2) and unmarked clear fin (D = 1). The overall proportion of identifiable animals (D ≥ 3) in this study is 59.5 % (SE: 27.2).
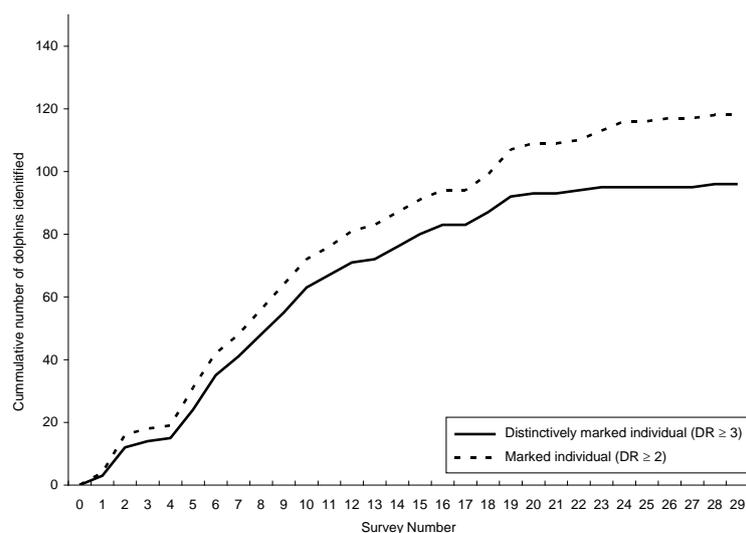
Figure 5.1: Discovery curve for all individuals identified in surveys conducted between January and May 2008. The solid line represents individuals with distinctiveness ≥ 3 and the dashed line represents individuals with distinctiveness ≥ 2 (see text for detailed description).

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Of the 95 identified individuals, 24.2 % were seen only once and 73.7 % less than five times (Figure 5.2). Two individuals were seen 11 times. Group size varied from one to 26 animals ($\bar{x}$ = 7.4, SD = 6.3 and median = 5) and was seldom larger than 13; solitary individuals had the highest sighting frequency (n = 9; 18.0 %) across all the groups seen (Figure 5.3).
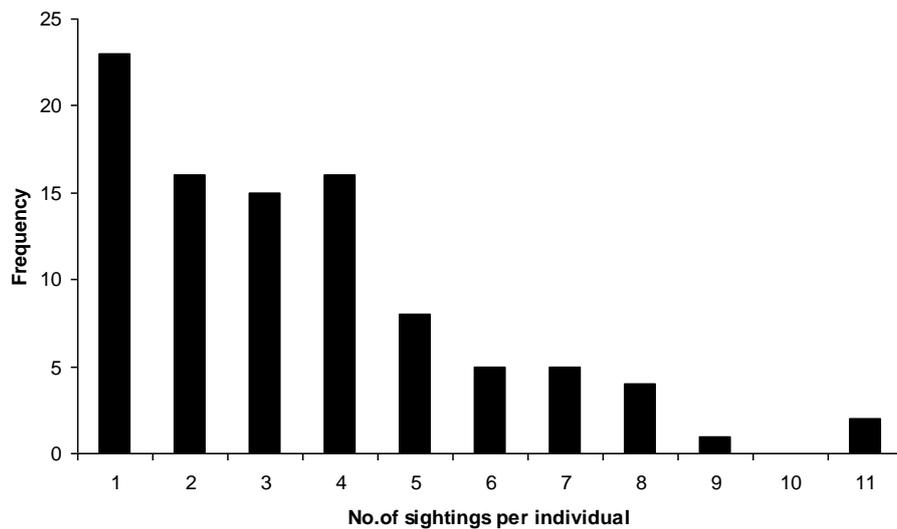
Figure 5.2: Individual sighting frequency of all the marked Heaviside's dolphins seen in Table Bay between January and April 2008 (n = 95).
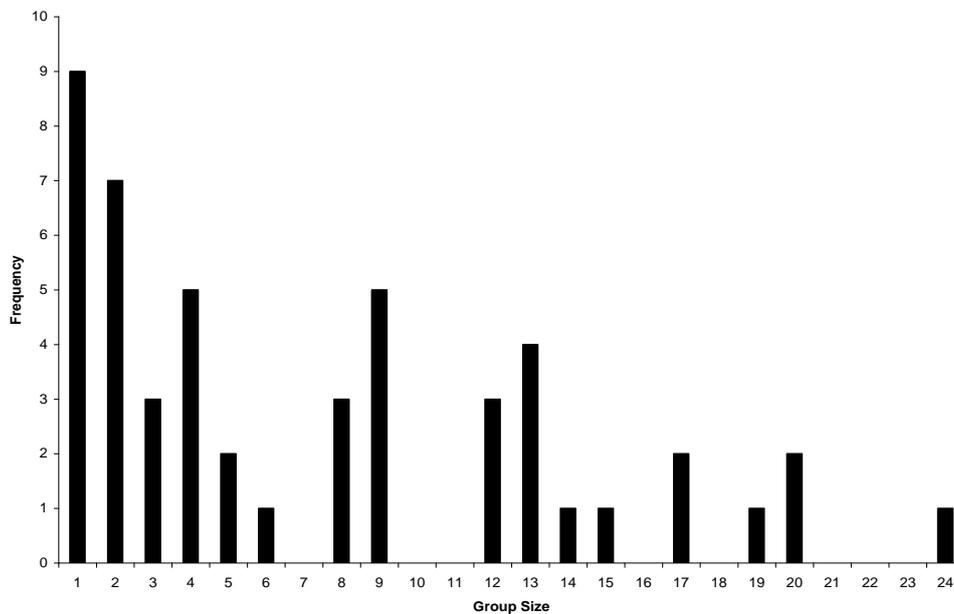
Figure 5.3: Group size frequency distribution of Heaviside's dolphins in Table Bay between January and April 2008.

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Encounters consisted mostly of adults with occasional sightings of calves and juveniles. Of the 43 calves seen, only one calf had individually recognisable markings but was seen only once. Juveniles were seen 27 times. Although juveniles could be distinguished in the field, during the subsequent analyses of the photographs collected it was difficult to confirm the age due to the similar body and dorsal fin sizes as compared to small adults; therefore the photographed individuals were classified as either calf (including neonate) or 'non-calf' individuals. For the purpose of this study only identifiable 'non-calf' individuals (distinctiveness ≥ 3, n = 95) were used for further analysis.

The sex was determined for 22 (15 confirmed and seven probable but not confirmed) of the 95 identified 'non-calf' individuals (23.2 %). Four females and 11 males were identified from direct observation of the genital area, DNA testing[2] or assumed from consistently close association with a young calf. Six possible females were seen with an older, more independent calf, making it difficult to confirm whether the individual seen with the calf is indeed the mother. One possible male was identified from a jump photograph showing the side profile of the genital area.

Associations between 69 individuals seen twice or more were calculated using the simple ratio index. The overall frequency distribution of association index shows that 40 % of the possible associations were seen and the majority of these associations were weak (Figure 5.4). The frequency distribution of the maximum and the mean values of association indices is shown in Figure 5.5; the overall mean of the mean values was 0.09 (SD = 0.04) and mean of the maximum values of AI was 0.48 (SD = 0.14).

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[2] The DNA tests were performed as part of an on-going study (PhD study by K. Gopal, University of Pretoria, under the supervision of L. Karczmarski, K. Tolley and M. Keith); the description of genetic sampling and analytical procedures is not included in this thesis.
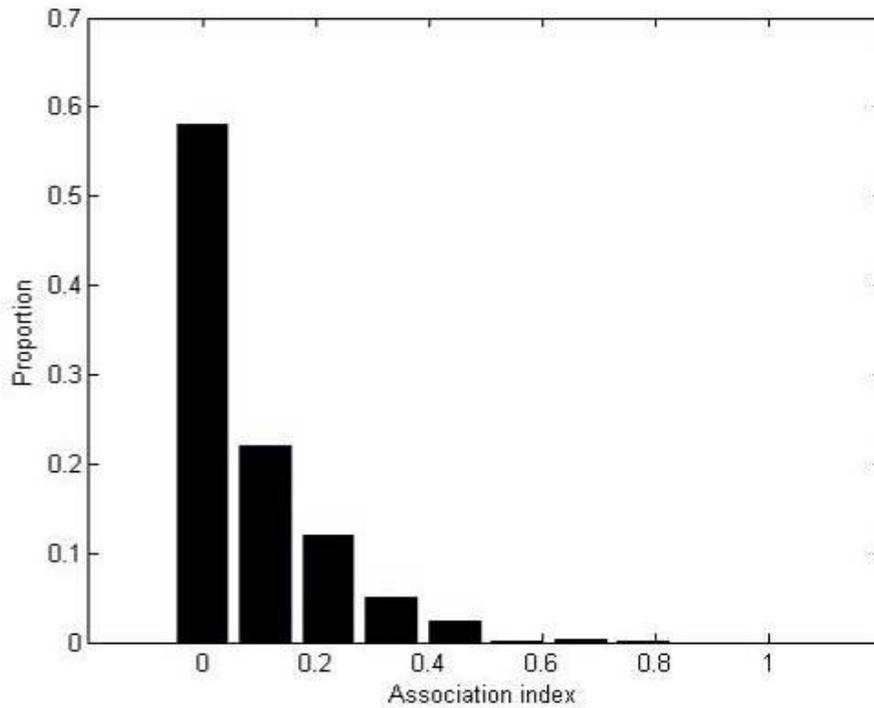
Figure 5.4: Overall frequency distribution of association index using simple ratio for identified 'non-calf' Heaviside's dolphins seen twice or more in Table Bay from January to April 2008 (n = 69).
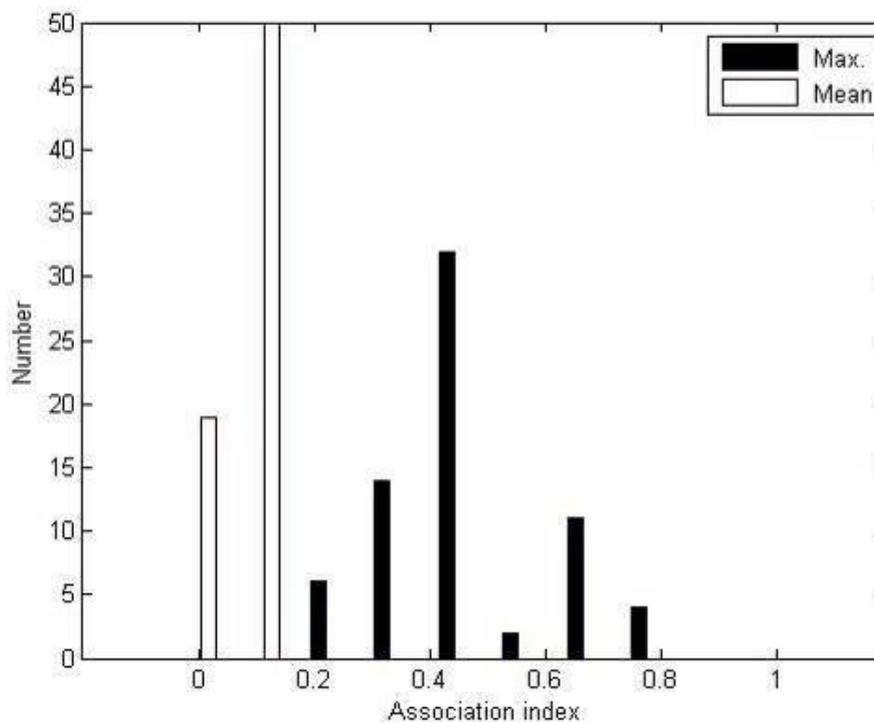
Figure 5.5: Frequency distribution of the mean (white bars) and maximum (black bars) association indices using simple ratio for 'non-calf' Heaviside's dolphins seen twice or more in Table Bay from January to April 2008 (n = 69).

Permutation tests for preferential associations within sampling periods (18000 permutations with 1000 trails per permutation to stabilise the *p*-value), performed for 'non-calf' dolphins seen twice or more (n = 69, Table 5.2) indicated that the mean observed association index did not differ significantly from the randomly permuted data. The observed SD and the CV of the mean association index were not significantly higher than the randomly permuted data. The values were the same as anticipated by chance alone in both short-term (within sampling period) and long-term (between sampling periods).

Table 5.2: Results of permutation tests for preferential companionship using modified Manly/ Bejder et al. procedures (Manly 1995, Bejder et al. 1998, Whitehead 2008) on Heaviside's dolphins seen twice or more in Table Bay from January to April 2008 (n = 69).

	Mean association index	SD of mean association index	CV of mean association index
Observed data	0.086	0.123	1.437
Random data	0.087	0.124	1.425
p Value	0.081	0.344	0.800

Standardised lagged association rates calculated for all 'non-calf' individuals are shown in Figure 5.6. Using the maximum likelihood and the QAIC methods the casual acquaintance model (QAIC = 3702.720, green line in Figure 5.6) was selected as the best fit model. The two levels of acquaintance model (QAIC = 3702.910, red line in Figure 5.6) was the second best fit with a ΔQAIC < 2. The lagged association rate intersects the null association rate at approximately 40 days.

Similarly calculated lagged identification rates (Figure 5.7) show a rapid decrease, reaching a half of their initial values within a time lag of just three days. Subsequently the rate of decrease was not as rapid but remained evident. The maximum likelihood and the AIC methods indicates the 'emigration, re-immigration and mortality' model as the most parsimonious (AIC = 5193.666, blue line in Figure 5.7).

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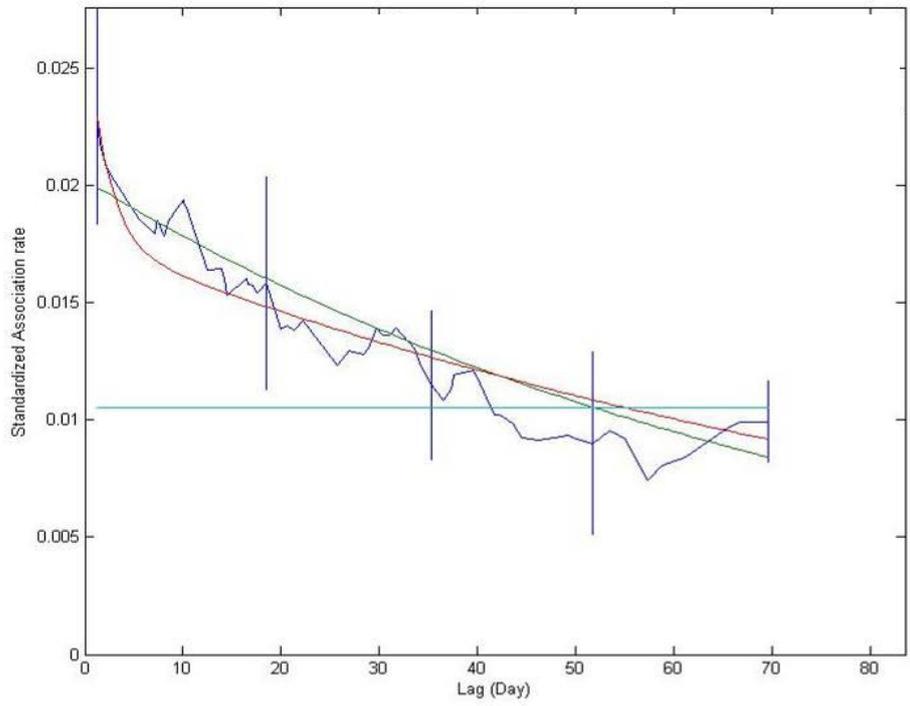
Legend:

━━━ Lagged Association Rate   ━━━ Null association rate

━━━ Casual acquaintance   ━━━ Two levels of acquaintance

Figure 5.6: Standardised lagged association rate of 'non-calf' Heaviside's dolphins in Table Bay (blue line), with vertical lines indicating jackknifed error bars. The null association rate is represented by the aqua line. The best fitting models of casual acquaintance (green line) and two levels of acquaintance (red line) are also shown.
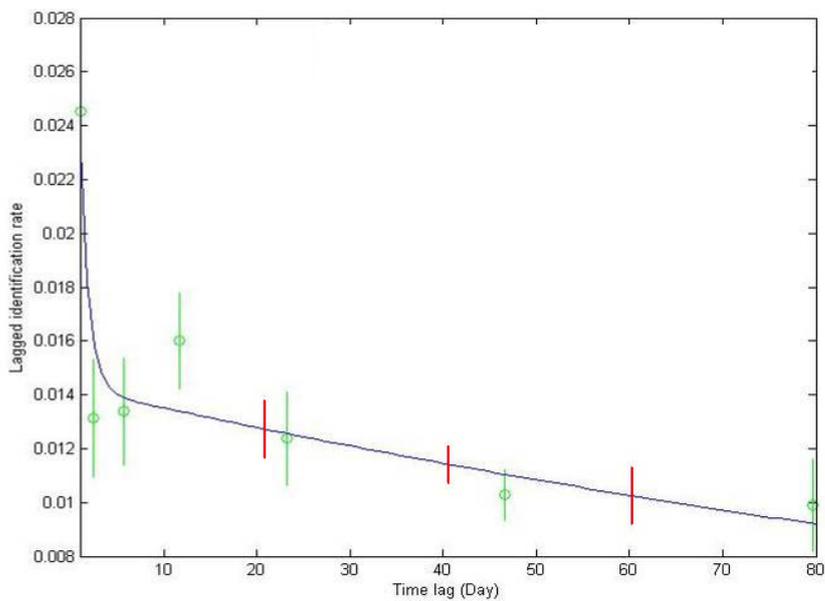
Figure 5.7: Lagged identification rates of all 'non-calf' Heaviside's dolphins in Table Bay from January to April 2008 (n = 95, green data points). The vertical red lines represent the bootstrap error bars. The best fitting model of emigration, re-immigration and mortality is shown by the blue line.

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The results of all model fit and selection performed on both the standardised lagged association rate (Table B.3) and lagged identification rate (Table B.4) are listed in Appendix B.

The sociogram, representing the pattern of association between 17 'non-calf' dolphins seen more than four times in Table Bay from January to April 2008, indicates no clear pattern of association between the individuals (Figure 5.8). The majority of the associations are 'weak' (thin lines) although there are a few `strong` associations indicated by the thicker lines between the individuals.
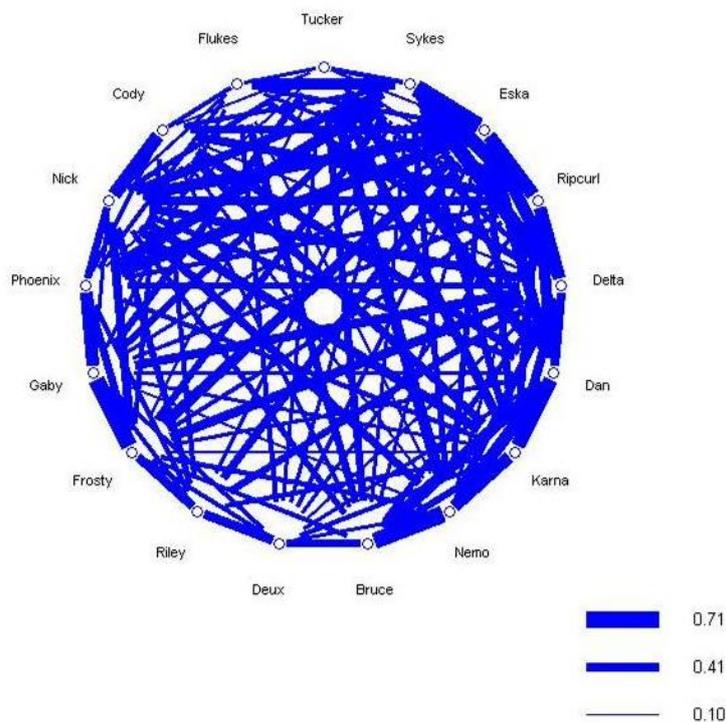
Figure 5.8: Sociogram showing associations between 'non-calf' Heaviside's dolphins seen five times or more in Table Bay from January to April 2008 (n = 17). The thicker the line the stronger the association.

Discussion

Heaviside's dolphins are frequently seen in Table Bay with sightings on all surveys (n = 29) over a period of four summer-autumn months (January – April 2008). In addition a high proportion (59.5 %) of Heaviside's dolphins in this area is individually identifiable. Groups of dolphins varied in size from one to 26 animals with a median of five animals. During some of the encounters the size of the group increased and

then decreased as animals joined and then left the group. Since the exact time of arrival and departure of these animals could not be determined these animals where considered as part of the group for that encounter. Best and Abernethy (1994) found Heaviside's dolphins in small groups from one to 10 animals with an average of 3.2 animals, although occasionally these groups would combine into one large group. Analysis of sex-specific associations (e.g. male-male, female-male or female-female associations) could not be conducted due to the small sample sizes (n = 22 sexed; 24.6 % of identified).

It seems apparent that the dolphins seen in Table Bay form fluid groups with short-lasting associations and low site fidelity. Both socio-behavioural models that best fit the data indicate that the animals associate on a casual basis, frequently disassociate and then may re-associate again in the future. After 40 days the lagged association rate intersects the null association rate indicating that after 1.5 months the observed association pattern does not differ from associations by chance alone. However, the short duration of the current study calls for caution when interpreting this data as a longer period of surveys could likely result in further identifications and re-identifications and if so the observed and modelled pattern of associations could possibly change. There were a few strong associations that may be consequent to the short time-span and small sample size but could possibly indicate some long-term associations between specific individuals. A larger temporal dataset would be required to reliably assess the pattern of association between individuals.

In short temporal scales, Heaviside's dolphins in the St Helena Bay area also displayed fluid association pattern which did not differ from random (Elwen 2007). Weak associations between individuals have also been shown for Hector's dolphins (Slooten et al. 1993, Bejder et al. 1998, Bräger 1999) which generally tend to have associations that are not significantly different from random. Of the five studied populations of Hector's dolphin (Banks Peninsula - Slooten et al. 1993; Porpoise Bay - Bejder et al. 1998; Moeraki, Jackson Bay and Kaikoura - Bräger 1999) only the Jackson Bay population displayed significantly higher associations.

However Slooten et al. (1993), Bejder et al. (1998), Bräger (1999) and Elwen (2007) have a low proportion of identifiable individuals and used only the highly distinctive

individuals in their analysis (equivalent to distinctiveness ≥ 4 in this study). The difference in the proportion of identifiable individuals could be as a result of the difference in the camera equipment used (auto-focus, digital cameras in this study compared to manual-focus, film camera in the St Helena Bay and Hector's dolphin studies). The Heaviside's dolphins in St Helena Bay seem to be less marked (smaller or fewer nicks) than in Table Bay (C. Behrmann, pers. obs.) thus making the lower proportion of identifiable individuals plausible. In comparison with St Helena Bay and Hector's dolphin studies (Slooten et al. 1993, Bejder et al. 1998, Bräger 1999, Elwen 2007) the subset of data (i.e. identified 'non-calf' individuals with distinctiveness ≥ 4, n = 33), displayed similar patterns to that present in the above studies. The 33 'non-calf' individuals showed fluid, short-term associations with the association not being significantly different from random. The lack of long-term associations can explain the inconclusive results of the sociogram.

Although Heaviside's dolphins were seen regularly in Table Bay, the individuals photographed displayed a very low or perhaps no site fidelity, albeit over a short temporal scale. Four satellite tagged Heaviside's dolphins (females) in St Helena displayed high site fidelity with a small home range of < 2000 km^2 for the summer months (Elwen et al. 2006, Elwen 2007). Hector's and Chilean dolphins display strong site fidelity over several years (Bräger et al. 2002, Heinrich 2006). Commerson's dolphins have been observed to migrate seasonally (> 200 km) (Coscarella 2005) which is thought to be due to the variation in prey abundance (Goodall et al. 1988b).

There are two possible explanations for the low site fidelity recorded for individuals in Table Bay. Firstly, Chapter 4 shows that the dolphins have a preference for Granger Bay which is smaller (4 km^2) than the home range indicated by Elwen et al. (2006). Rice and Saayman (1984) reported sightings of Heaviside's dolphins within the main part of Table Bay and 3 nautical miles from Robben Island. Therefore it is possible that the Heaviside's dolphins' home range includes other areas within Table Bay and the dolphins are utilising these other areas (e.g. shore around Robben Island) when they are not sighted in Granger Bay.

Secondly, the short temporal scale of the current study did not provide sufficient power to produce sufficiently reliable analyses of the site fidelity pattern. In the context of the on-going photo-identification study (L. Karczmarski, study in progress), there are at least 12 identified individuals with D ≥ 3 that have been seen in Table Bay at least once every summer (Nov through April) for each of the three years between 2008 and 2010. This indicates a possibility of higher site fidelity on a long-term. It is therefore important to consider both short and long temporal scales and assess how fidelity and social association change over these time durations. Heaviside's dolphins appear to have a well-defined diurnal behaviour cycle (Elwen et al. 2006) and can only be reliably photographed in the morning while they are closer to shore as they are hard to find and follow in deeper waters (C. Behrmann, pers. obs.). In order to better ascertain the home range and site fidelity of Heaviside's dolphins in Table Bay, satellite tagging of known individuals, or extended photo-ID surveys with multiple sites for immigration/emigration modelling (L. Karczmarski, study in progress) would likely be the most effective approach.

Conclusion

In a short temporal scale, Heaviside's dolphins in Table Bay display an apparent fission-fusion society with a few possible strong associations between individuals and low site fidelity. Even though the site fidelity is low, the area of Table Bay is still regularly used by these animals; therefore a management strategy for Table Bay needs to consider the ecological and behavioural needs of Heaviside's dolphins. More research is needed to find out what exactly is attracting Heaviside's dolphins to Table Bay; a larger dataset will be required to get a greater understanding of the long-term group dynamics and pattern of geographic fidelity.

Chapter 6

Conclusions and Recommendations

Conclusions

Along the southern African coastline there are 18 different species of dolphins (Family Delphinidae) but only the Heaviside's dolphin (*Cephalorhynchus heavisidii*) is endemic (Findlay et al. 1992). This small dolphin is only found along the west coast of southern Africa from Cape Point, South Africa (34°S) to Angola (17°S). Heaviside's dolphins are found in the coastal zone from the breakers to about 45 nautical miles offshore and in waters shallower than 200 m (Findlay et al. 1992). To date, Heaviside's dolphins are one of the least known cetaceans with almost all aspects of its population dynamics and behavioural ecology remaining unknown. The Heaviside's dolphin status remains Data Deficient (DD) since it was included on the IUCN Red List in 1988 (Reeves et al. 2008b).

This study investigated three elements of the population structure, namely the spatial distribution, behavioural patterns and the short term group dynamics of Heaviside's dolphin in Table Bay, South Africa, the southern limit of their distribution in the summer months of 2008 and 2009.

Granger Bay is not the entire home range of these dolphins but it appears to serve as an important summer habitat within the overall home range. The dolphins display a heterogeneous use of the area and were observed in a well-defined 7 km^2 area on the south side of Table Bay along a 3 km east-west stretch of coast. The dolphins were seen within 2 km from shore. For the array of behaviours observed (milling, socialising, travelling and resting), the core areas (50 % Kernel) were observed close to shore (< 0.5 km from the shoreline) in the Granger Bay area. There was very little (6 %) overlapping between these core areas of displayed behaviour indicating that Granger Bay area is an important area for Heaviside's dolphins. Milling and socialising were exhibited more often than travelling and resting. Foraging was never observed in areas close to shore, which supports earlier studies suggesting that these dolphins forage primarily offshore (Sekiguchi et al. 1992).

This current study assembled the first, although still incomplete photo-ID catalogue of Heaviside's dolphins in Table Bay, including 117 individuals identified in the first field season of a larger scale on-going research. Only 95 of these individuals were classified distinct enough to be included in the analysis of this study (Distinctive rating $\geq$ 3). Twenty three individuals (24.2 %) were seen only once, the majority of individuals (73.7 %) were seen less than five times (n = 70) and two individuals were seen 11 times. Table Bay has a high proportion (59.5 %) of individually identifiable dolphins. Analysis of sex-specific associations (e.g. male-male, female-male or female-female associations) could not be conducted due to small sample sizes (n = 22 sexed; 24.6 % of identified).

Groups of dolphins varied in size from one to 26 animals with a median of five animals and were seldom larger than 13. Best and Abernethy (1994) found Heaviside's dolphins in small groups from one to 10 animals (average of 3.2 animals), although occasionally these groups would combine into one large group. The group structure documented in the study reported here appears to be highly dynamic, with great lability in group sizes and membership, suggesting a fluid social system with mostly weak inter-individual bonds. This is similar to the findings of Heaviside's dolphins in St Helena Bay (Elwen 2007) and the closely related Hector's dolphins (Slooten et al. 1993, Bejder et al. 1998, Bräger 1999).

Although Heaviside's dolphins are frequently seen in Table Bay, individuals display low site fidelity, at least in the short-term. This is a contradiction to the high site fidelity of Heaviside's dolphins in St Helena Bay (Elwen et al. 2006) and is most probably due to the short temporal span of this study.

Future work

This project represents an initial, exploratory phase of a larger-scale multifaceted research (L. Karczmarski, University of Pretoria and University of Hong Kong; study in progress) which, among other, includes a recently completed acoustics component (Morisaka et al. 2011), on-going genetic component (K. Gopal, PhD candidate at University of Pretoria), spatial modelling, further mark-recapture work, and socio-behavioural and conservation ecology research.

This study indicates that Granger Bay is an important area for Heaviside's dolphins. As several other studies indicate, habitat use in delphinids is often influenced by environmental factors and fine-scale structures (e.g. Croll et al. 1998, Bräger et al. 2003, Garaffo et al. 2011). Therefore future studies should investigate how environmental variables (e.g. water clarity, depth, sea surface temperature, chlorophyll-a etc.) and other environmental structures (e.g. prominent headlands, kelp beds etc.) influence habitat use of Heaviside's dolphins in Table Bay and other sites within the population range.

Seasonal differences in habitat preferences have been displayed for many delphinid species including the other members of the genus *Cephalorhynchus* (Goodall et al. 1995, Borsa 1997, Maze and Würsig 1999, Bräger et al. 2003). The Western Cape has a mediterranean climate and the high winter rainfall and stormy season limits the amount of boat-based surveys that could be conducted during winter. The incorporation of land-based observations and passive acoustic monitoring may provide information regarding the surface and subsurface activities at times when the boat-based work is logistically impossible.

The results of the association patterns in this study indicate that there are a few strong associations between individuals. Four of the five populations of Hector's dolphins (*Cephalorhynchus hectorii*) that have been studied displayed weak associations between individuals (Slooten et al. 1993, Bejder et al. 1998, Bräger 1999). A larger temporal photo-ID dataset, which is already existing thanks to the on-going research (L. Karczmarski, study in progress), will allow for detailed investigations of the association patterns on a long-term basis. This will allow researchers to investigate if and how the pattern of group dynamics changes across greater temporal scales. A greater duration of research might also facilitate comparisons with patterns such as the Jackson Bay's population of Hector's dolphins which displayed higher associations (Bräger 1999).

Knowledge of the population size is crucial for the development of conservation and management strategies for any species. The application of mark-capture-recapture techniques on considerably larger temporal scales and larger dataset will allow for the refinement of the current population estimate.

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Heaviside's dolphins are sexually dimorphic in the colouration patterns around the genital area (see Chapter 1 for detailed description). However it is difficult to sex these dolphins in the field. The incorporation of an under-water camera could assist with sexing of known individuals as both the dorsal fin and the genital areas could be captured on film. The relatively poor water clarity in the areas inhabited by Heaviside's dolphins might be a logistical obstacle hard to overcome. However, the knowledge of the sex of the individually catalogued animals could further refine population models and contribute to the knowledge of population's reproductive rate which in turn is important for the creation of effective conservation and management strategies.

Although Heaviside's dolphins were seen regularly in Table Bay, the individuals photographed displayed a very low or perhaps no site fidelity. The other members of the genus *Cephalorhynchus* as well as Heaviside's dolphin in St Helena Bay have exhibited high individual site fidelity (Bräger et al. 2002, Elwen et al. 2006, Heinrich 2006). It is suggested that the most probable reason for the low site fidelity seen in this study is the very short period of research and resulting small sample size. Satellite tagging of known individuals or extended photo-ID surveys with multiple sites are two possible methods to address this problem.

Conservation and managements implications

These findings, although from a short study period, increase our understanding of the area use, behaviour and group dynamics of Heaviside's dolphins in Table Bay. The results have a potential to be applied to coastal conservation and management in the region.

Granger Bay is located close to the Victoria & Alfred waterfront, a major tourist attraction, and is used for various tourist activities. One such activity is the adrenaline-seeking ride in a high-powered speed boat. These boats, amongst others, have been observed racing towards and away from dolphin groups. The South African Marine Living Resources Act (Act No. 18 of 1998) protects cetaceans from harassment, capture and intentional killing by vessels and humans. However, there are no restrictions on how close vessels can approach dolphins provided that the vessel does not deliberately move through a school of dolphins.

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The regular sightings of dolphins within small areas where certain behaviours are displayed, and little overlap of these core areas indicates that Granger Bay is an important area for Heaviside's dolphin. Therefore it is recommended that management strategies be implemented that will reduce the speed of boats in this area such as a 'go slow' (reduced speed) zone where motorised vessels are limited to travelling at 2 knots. Milling and socialising were the most exhibited behaviours in Granger Bay therefore the reduced speed zone should cover the core areas (50 % Kernel) of these two behaviours. The area should extend along the shore from Green Point lighthouse to the tip off the harbour wall and at least 0.5 nautical mile seawards from shore. See Figure 4.5 for a map showing the recommended location of the go slow zone.

Any development or expansion of the Cape Town harbour or any coastal development in the area should consider the impact on Heaviside's dolphins, specifically since these animals are displaying high site-specific behaviours.

Appendices

Appendix A: Detailed explanation of methods

The association pattern of individuals are generally quantified using either a simple ratio index (Ginsberg and Young 1992) and a half-weight index (Cairns and Schwager 1987):

$$\text{Simple ratio index} = \frac{x}{x + y_{AB} + y_A + y_B}$$

$$\text{Half-weight Index} = \frac{x}{x + y_{AB} + \frac{1}{2}(y_A + y_B)}$$

where: x = number of sampling periods with A and B observed associated, y_{AB} = number of sampling periods with A and B identified but not associated, y_A = number of sampling periods with just A identified, y_B = number of sampling periods with just B identified. Both these indexes have a range from zero (two individuals never seen together) to one (two individuals always seen together) and assume that the associations observed in different sampling periods are independent (Whitehead 2008).

The assumptions of the ideal data set are 1) the recorded association is a symmetric 1:0 measure of whether the members of a dyad are or are not associated in a sampling period, 2) the recorded associations are accurate, 3) if one individual is identified in a sampling period, then all its associates are identified and 4) the members of a dyad are equally likely to be identified whether they are associated or not associated (Whitehead 2008).

If these assumptions hold then Ginsberg and Young (1992) recommend that the simple ratio index be used as it will give an unbiased estimate of the proportion of time two individuals spend together (Ginsberg and Young 1992).

If the individuals are more likely to be identified when they are apart then Cairns and Schwager (1987) suggest using the half-weight index to give the least biased estimate of the proportion of the time two individuals spend together. The half-weight index tends to overestimate the level of associations (Ginsberg and Young 1992) and is

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more commonly used in dolphin social structure studies (e.g. Wells et al. 1987). In this study, the small group sizes seen during encounters allowed for achieving a 100 % photographic coverage of the group on majority of the encounters. Therefore the simple ratio index was chosen for analysis. Studies using the simple ratio index can still be compared with studies using the half-weight index provided that overall pattern (e.g. shape of curves, pattern of dendrograms, etc.), and not the numerical values of the associations is used.

The social analysis software program SOCPROG 2.4 (Whitehead 2009) can be used to calculate both the simple ratio and half-weight indices.

Preferred associations

The Manly/Bejder et al. procedure (Manly 1995, Bejder et al. 1998) is used to determine whether the patterns of associations between individuals are significantly different from random. This procedure, for each sampling period, inverts the intersection of two rows and two columns randomly chosen from the association matrix while keeping the total number of individuals and groups constant. Each flip makes the new data set only slightly different from the previous data set therefore the two data sets are not independent from each other. This requires more permutations to be performed until the *p*-value stabilises (Whitehead 2008).

Both long term (between sampling periods) and short term (within sampling periods) preferred associations were tested using the permutation of groups within sampling periods method. This method uses a modification of the Manly/ Bejder et al. procedure (Manly 1995, Bejder et al. 1998) in which, at each step, a sampling period is randomly chosen within which the data are to be flipped (Whitehead 2008). This test does account for situations where not all the individuals are present in each sampling period (because of birth, death, migration, etc), but does not account for differences in gregariousness between individuals. The results of simulations, using either half-weight or simple ratio association indices, suggest the short-term associations are indicated by a significantly low mean of the real association indices whereas the long-term preferred associations are indicated by a significantly high SD or CV of the real association indices (Whitehead et al. 2005). If there are short-term associations, the mean and SD of the associations tends to be lower therefore it may

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be better to use the CV of associations as a test statistic for long-term associations (Whitehead et al. 2005). The null hypothesis is that there are no preferred or avoided associations (individuals who preferentially group together or avoid one another) given the number of groups each individual was seen in during each sampling period (Whitehead 2009).

If the association is defined by groups there are more possibilities however this method ('permuting groups with samples') makes more assumptions than the 'permutation of associations' method. Whitehead (2008) believes that the permutation of associations method ('permuting associations within samples') should be generally preferred, however this method only tests for long-term preferred associations. Due to the short temporal nature of this project it was decided to not run the 'permutation of associations' method.

Temporal pattern and community structure

Lagged association rates were calculated to measure the temporal stability of associations (Whitehead 1995). The association rate, for any time lag *t,* represents the probability of the same two individuals still being associated after lag *t* units later (Whitehead 1995). The null association rate indicates the expected lagged association rate if the associations are by chance alone i.e. there are no preferred associations. A jackknife procedure was used to measure the precision of the estimated lagged association rate. The jackknife procedure works by running the analysis several times and omitting a sampling period each time. The analysis is run until all the sampling periods have been removed once (Efron and Stein 1981, Whitehead 1995). In this study the sampling period is one day. Models of temporal permanence of associations were fitted to the data using the maximum likelihood and quasi-Akaike information criterion (QAIC) to determine the best fit model (Akaike 1973, Burnham and Anderson 2002, Whitehead 2007). The precision of each estimate is indicated by the standard error (SE) which was calculated for each model using the jackknife procedure. The lagged association rates were calculated for all the 'non-calf' individuals Heaviside's dolphins with a moving average of 9000 to smooth the curve.

Lagged identification rates were calculated to measure the residence rate of individuals. The lagged identification rates show the probability of an individual

being identified at lagged time *t* and that same individual being identified again in the same location (in this case the study area) after lagged time *t* units later (Whitehead 2001). Models of residency were fitted to the data using the maximum likelihood and QAIC methods to determine the best fit model. The 95 % confidence intervals and the SE were calculated using the bootstrap procedure. The lagged identification rates were calculated for all 'non-calf' individuals Heaviside's dolphins.

Sociogram

A sociogram can be used to illustrate the relationship between two individuals, the thicker the line between the individuals the stronger the association. Sociograms drawn in SOCPROG 2.4 of more than 25 individuals become cluttered and difficult to interpret (Whitehead 2009). The number of individuals in the sociogram was limited to those seen five time or more (n = 17) to reduce the bias of a small sample size.

Appendix B: Lagged association and identification rate models

Results of all the models conducted for lagged association rate (Table B.3) and lagged identification rate (Table B.4).

Table B.1: Statistical outputs of all models conducted for lagged association rate of 'non-calf' Heaviside's dolphins seen in Table Bay from Janurary to April 2008 (n = 95). The models are in ascending order of ΔQAIC. The model with the lowest QAIC is the best fitting model

Model	AIC	QAIC	ΔQAIC
Casual acquaintance	9636.632	3702.720	0.000
Two level of casual acquaintance	9630.717	3702.910	0.191
Constant companions + casual acquaintance	9655.694	3711.275	8.555
Constant companions	9702.261	3726.702	23.982

Table B.2: Statistical outputs of all models conducted for lagged identification rate of 'non-calf' Heaviside's dolphins seen in Table Bay from Janurary to April 2008 (n = 95). The models are in ascending order of ΔAIC. The model with the lowest AIC is the best fitting model.

Model	AIC	QAIC	ΔAIC
Emigration + re-immigration + mortality	5193.666	5191.666	0.000
Emigration/mortality	5197.714	5195.714	4.048
Closed: emigration + re-immigration	5199.641	5197.641	5.975
Closed	5214.218	5212.218	20.551

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