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Identification and characterisation of
foraging areas of seabirds in upwelling systems:
biological and hydrographic implications
for foraging at sea

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Der Dekan

...dass es keinen Grund gibt, Angst zu haben vor der offenen See.
Denn in ihr zu ertrinken ist allemal besser,
als an der Küste geblieben zu sein.

DANIEL KEHLMANN

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Summary

This thesis investigates the foraging behaviour of three seabird species, the African penguin (*Spheniscus demersus*) and the Cape gannet (*Morus capensis*) in the Benguela upwelling system as well as the Peruvian booby (*Sula variegata*) in the Humboldt Current. Biological and hydrographic parameters were considered when evaluating the characteristics of foraging areas and the behaviour of the species studied. Foraging areas used by the birds as well as the birds' diving behaviour were assessed by using data logger technologies and results obtained through these methods were combined with diet sampling and observations from ship-based surveys. Seabirds in both upwelling regions are confronted with changes in environmental conditions and the birds' reaction to alterations in hydrography as well as food limitations have been evaluated.

African penguins in Namibia were studied at three breeding colonies which differ in numbers of breeding pairs as well as in oceanographic parameters due to distinct bathymetry. At Mercury Island, studies were performed in two consecutive years allowing for inter-annual comparisons, especially taking into account differences in food availability due to sulphide eruptions in 2005. African penguins at Mercury Island showed similar foraging behaviour as conspecifics in South Africa (Wilson, 1985; Wilson et al., 1988; Ryan et al., 2004; Petersen et al., 2006), foraging within a range of maximum 32 km from the colony (median of 22 and 21 km in 2005 and 2006) and diving to maximum depths of about 75 m. Considering only dives deeper than 10 m depth (defined as foraging dives), most dives reached depths of 25 – 35 m. In both years, birds frequented the same area north-west of the island in order to forage. In 2005, sulphide eruptions caused hypoxic conditions in the entire water column, dissolved oxygen concentrations being as low as 2 ml/l in surface waters and below 0.2 ml/l at the sea bottom. Birds were almost exclusively feeding on pelagic goby (*Sufflogobius bibarbatus*), a demersal fish species able to tolerate low-oxygen conditions (Currie et al., submitted). In 2006, birds were feeding on anchovy (*Engraulis capensis*) and sardine (*Sardinops sagax*) in addition to pelagic goby. The higher percentage of pelagic prey was also reflected in the diving behaviour, birds diving to lower depths during foraging dives (median 35 vs. 27 m in 2005 and 2006, respectively). Studies at Halifax and Possession Islands included only small numbers of birds, but differences in foraging behaviour as well as in diet composition were observed and may be related to varying bathymetry around the islands. Food limitation seems to affect African penguins at all breeding colonies along the Namibian coast, not only during sulphide eruptions, and has to be considered as a key factor for the population decline observed in Namibia.

In order to monitor environmental conditions, the use of seabirds as indicators has been proposed (Wilson, 1992; Montevecchi, 1993; Wilson et al., 1994; Weimerskirch et al., 1995; Wilson et al., 2002; Fedak, 2004). In this study, the use of data loggers enabled fine-scale

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temperature measurements during the diving in penguins. These *in situ* measurements of water temperature were included in an oceanographic model, showing small scale variations in spatial as well as temporal extensions. Cold upwelling cells were identified along the coast and the impact of local wind patterns on processes of temperature distribution became apparent. Relatively small numbers of logger-equipped birds would be needed for synoptical oceanographic monitoring around penguin colonies and would lead to a better understanding of oceanographic processes influencing seabird foraging.

The ability to cover larger distances within single foraging trips and its implication for foraging in areas of reduced food abundance was studied in Cape gannets in the Benguela system. Lower prey availability during the breeding season 2005 due to sulphide eruptions led to diving activity over larger areas and birds were feeding on smaller prey individuals. Birds' foraging took place mainly along the coast but several birds covered large areas offshore. They foraged over water masses with different temperature regimes and presumably encountered a different prey composition over the shelf break. Birds reached distances of almost 200 km away from the colony and about 80 km off the coast. Site fidelity presented by several birds feeding at similar sites in consecutive trips indicates predictable prey but, as in the case of African penguins, numbers of gannet breeding pairs show declining trends in Namibia which is presumably also due to food limitation.

Peruvian boobies breeding in northern central Chile were observed foraging almost exclusively in coastal waters. Food availability seemed to be favourable within large bays due to localised upwelling at protruding points and birds left for short foraging trips, which indicates high food abundance. A high variability in prey organisms obtained by the birds was observed between several years studied. Numbers of breeding pairs at Isla Pájaros varied strongly between years and breeding ceased completely during an El Niño year in 2002. Nonetheless, seabirds in the Humboldt upwelling system show fast population recoveries after strong El Niño events which indicates their adaption to this frequently occurring phenomenon.

The importance of predictable food abundance in upwelling systems for seabird foraging is pointed out in this study. All species studied showed similar foraging behaviours, commuting between colonies and predictable feeding sites, foraging mostly over coastal upwelled waters. Additionally, site fidelity underlined the predictability of prey patches within the upwelling systems. Birds were able to switch to different prey items and to adapt foraging and diving behaviour to varying environmental conditions. Nonetheless, it may be doubted whether birds will successfully cope with alterations in the ecosystems that could lead to further reduced prey abundance in the future.

Zusammenfassung

Die vorliegende Arbeit untersucht die Ernährungsweisen dreier unterschiedlicher Seevogelarten: des Afrikanischen Pinguins (*Spheniscus demersus*) und des Kaptölpels (*Morus capensis*) im Auftriebsgebiet des Benguelastroms vor der südwestlichen Küste Afrikas und des Guanotölpels (*Sula variegata*) im Auftriebsgebiet des Humboldtstroms vor der Westküste Südamerikas. Die Arbeit berücksichtigt sowohl biologische als auch hydrographische Parameter für die Beurteilung der Nahrungsgebiete auf See und des Verhaltens der genannten Arten. Zur Datenerhebung diente die Loggertechnologie; die erlangten Ergebnisse wurden durch Nahrungsproben sowie Beobachtungen auf See komplementiert. Seevögel in beiden Auftriebsgebieten sind von Veränderungen in ihrer Meeresumwelt betroffen. Die daraus resultierende Nahrungsverknappung und das dadurch bedingte Verhalten der Tiere wurden untersucht.

Die Untersuchungen am Afrikanischen Pinguin wurden in drei Brutkolonien entlang der namibischen Küste durchgeführt. Unterschiede sind sowohl in der Anzahl der Brutvögel in den Kolonien zu finden als auch in den ozeanographischen Bedingungen in der Umgebung der Brutinseln.

Das Verhalten der Pinguine auf Mercury Island wird vor allem im Hinblick auf unterschiedliche Nahrungsverfügbarkeit, verursacht durch Schwefelausbrüche im Jahre 2005, in zwei aufeinanderfolgenden Jahren verglichen. Das Ernährungsverhalten der Afrikanischen Pinguine in Namibia ist vergleichbar mit dem ihrer Artgenossen in Südafrika (Wilson, 1985; Wilson et al., 1988; Ryan et al., 2004; Petersen et al., 2006). Das Nahrungsgebiet der Pinguine auf Mercury Island erstreckte sich über eine maximale Distanz zur Kolonie von 32 km (mediane Distanzen 22 und 21 km in 2005 und 2006) und die maximal erreichte Tauchtiefe betrug 75 m. Während Nahrungstauchgängen, definiert als Tauchgänge mit einer Mindesttiefe von 10 m, erreichten die Tiere vorzugsweise Tiefen von 25 bis 35 m. In beiden Jahren frequentierten die Tiere ein Gebiet nordwestlich der Brutinsel Mercury Island.

Im Jahr 2005 verursachten Schwefelausbrüche hypoxische bis anoxische Verhältnisse in der Wassersäule; Konzentrationen von gelöstem Sauerstoff betragen weniger als 2 ml/l an der Oberfläche und weniger als 0.2 ml/l in größeren Tiefen. Die Pinguine erbeuteten fast ausschließlich Meeresgrundeln (*Sufflogobius bibarbatu*s), eine bodennah lebende Fischart, die geringe Sauerstoffmengen im Wasser toleriert (Currie et al., submitted). Im Jahr 2006 bestand die Nahrung der Pinguine hingegen neben Meeresgrundeln aus Sardellen (*Engraulis capensis*) und Sardinen (*Sardinops sagax*). Der höhere Anteil pelagischer Beutearten spiegelte sich auch im Tauchverhalten der Tiere wider. Pinguine tauchten in geringere Tiefen (Median 35 vs. 27 m in 2005 und 2006) während der Nahrungssuche. Die nur wenige Tiere umfassenden Studien auf Halifax und Possession Island ließen Unterschiede im Ernährungsverhalten und in der Nahrungszusammensetzung zwischen den

Zusammenfassung

Kolonien erkennen. Dies kann auf Unterschiede in der Bathymetrie in der Umgebung der verschiedenen Inseln zurückgeführt werden. Afrikanische Pinguine scheinen in allen Brutkolonien entlang der namibischen Küste von Nahrungsverknappung betroffen zu sein. Dies ist nicht nur während Schwefelausbrüchen der Fall, wie im Jahre 2005 beobachtet, sondern stellt ein Kernproblem dar, welches der wichtigste Faktor für die dramatische Abnahme des Pinguinbestandes in Namibia ist.

Die Überwachung von ökologischen Parametern durch Untersuchungen an Seevögeln wurde bereits mehrfach diskutiert (Wilson, 1992; Montevecchi, 1993; Wilson et al., 1994; Weimerskirch et al., 1995; Wilson et al., 2002; Fedak, 2004). Die in dieser Studie verwendeten Datenlogger erlauben eine feinskalige Analyse der Wassertemperaturen in den Nahrungsgebieten der Afrikanischen Pinguine. Die während der Tauchgänge gemessenen Temperaturen wurden mit Hilfe eines ozeanographischen Modells interpoliert, welches feinskalige Veränderungen räumlicher sowie zeitlicher Form im Untersuchungsgebiet aufzeigt. Kältere, vom Auftrieb herrührende Wasserlinsen befanden sich entlang der Küste, wohingegen Wassermassen fernab der Küste höhere Temperaturen aufwiesen. In größeren Tiefen erfolgte eine zunehmende Durchmischung. Bereits relativ wenige mit Datenloggern ausgerüstete Pinguine liefern ausreichend Daten, um die ozeanographischen Bedingungen in der Umgebung der Brutkolonien zu beurteilen. Die daraus resultierenden Kenntnisse der Auftriebsprozesse tragen zu einem besseren Verständnis der Nahrungsökologie der Tiere bei.

Kaptöpel im Auftriebsgebiet des Benguelastroms sind in der Lage, durch Flüge über große Distanzen ihre Nahrungssuche zu optimieren und gegebenenfalls Nahrungsknappheit zu umgehen. Während der Schwefelausbrüche im Jahr 2005 nutzten die Tiere größere Gebiete zur Nahrungssuche und die Nahrungsbestandteile bestanden aus kleineren Beuteindividuen. Die Tiere erbeuteten ihre Nahrung in unterschiedlichen Wassermassen entlang der Küste und an der Schelfkante. Die maximalen Entfernungen von der Kolonie betrugen 200 km und die Tiere erreichten bis zu 80 km von der Küste entfernte Meeresgebiete. Das Aufsuchen gleicher Gebiete bei aufeinander folgenden Nahrungsflügen deutet auf eine vorhersehbare Beuteverfügbarkeit hin. Dennoch ist, wie auch im Fall des Afrikanischen Pinguins, eine drastische Bestandsabnahme des Kaptöfels in Namibia zu beobachten, die vermutlich ebenfalls von Nahrungsverknappung herrührt.

Guanotöpel im Humboldtstrom suchten fast ausschließlich entlang der Küste ihre Nahrung. Die Nahrungsverfügbarkeit scheint positiv von Küstenlinie und von Buchten beeinflusst zu sein, die einen verstärkten Auftrieb und eine Ansammlung von Nahrungsorganismen verursachen. Die Töpel unternahmen zahlreiche, relativ kurze Nahrungsflüge und erbeuteten unterschiedliche Fischarten in den verschiedenen Jahren. Auch die Anzahl der auf der Isla Pájaros brütenden Guanotöpel variiert jährlich. Im Jahr 2002, einem Jahr mit einem ausgeprägtem El-Niño-Phänomen, wurde die bereits begonnene Brut aufgegeben. Trotz solcher Ereignisse scheinen die Vögel im Humboldtstrom an Veränderungen angepasst, u.a. verdeutlicht durch den schnellen Anstieg der Brutpaarzahlen.

Das Vorkommen von vorhersehbaren Nahrungsquellen in Auftriebsgebieten scheint von großer Bedeutung für die hier untersuchten Arten zu sein. Das Ernährungsverhalten der unterschiedlichen Arten ähnelt sich in beiden Auftriebsgebieten. Die Tiere begeben sich relativ direkt von ihren Brutkolonien zu den Nahrungsgebieten auf See und suchen ihre

Nahrung hauptsächlich an Auftriebszellen entlang der Küste oder der Schelfkante. Die Vorhersehbarkeit von Nahrungsansammlungen in diesen Gebieten wird auch durch das wiederholte Aufsuchen der gleichen Gebiete unterstrichen. Die untersuchten Seevogelarten können zwischen verschiedenen Nahrungsorganismen wechseln und ihr Such- und Tauchverhalten unterschiedlichen Gegebenheiten anpassen. Trotzdem kann bezweifelt werden, dass die hier untersuchten Seevogelarten in der Lage sind, fortschreitende Veränderungen in ihrer Umgebung und die daraus vermutlich resultierende Nahrungsknappheit zu verkraften.

Zusammenfassung

Chapter outline

This thesis identifies and characterises important foraging areas of three endemic seabird species in two coastal upwelling systems. The foraging and diving behaviour of the African penguin and the Cape gannet in the Benguela system and of the Peruvian booby in the Humboldt system are studied. Biological and hydrographic parameters affecting the foraging behaviour are evaluated and assumptions on the potential of seabirds for environmental monitoring are made.

Chapter 1 (page 1) gives a short general introduction on seabird ecology and poses the questions addressed in this thesis. Background information is given about logger technology, seabird-at-sea observations and about the upwelling systems in which the study was carried out. The Benguela and Humboldt systems are further described with special focus on their respective particularities. Furthermore, the study species, especially their distribution and population status, and the study colonies are presented.

Chapter 2 (page 13) investigates the foraging areas used by the African penguin (*Spheniscus demersus*) and its diving behaviour at different breeding colonies along the Namibian coast. General foraging and diving parameters are presented, focusing particularly on inter-annual differences within one colony (Mercury Island) and on differences between colonies along a latitudinal gradient (Possession, Halifax and Mercury Islands). The results are compared to the foraging behaviour of African penguins in South Africa and to that of other penguin species, interpreting population trends from differences in foraging behaviour.

Diving behaviour of African penguins at Mercury Island is further analysed in relation to sulphide eruptions in Chapter 3 (page 45). Sulphidic waters, which cause limited prey availability, influenced the foraging and diving behaviour of the birds in 2005. This chapter shows how birds are directly affected by hydrographic phenomena and how seabird foraging studies may be used to detect and monitor changes of environmental conditions.

The methods and devices used in this study allow a detailed analysis of water temperature structures, using penguins as *oceanographers*. In Chapter 4 (page 61), the temperature data obtained from foraging penguins at Mercury Island, Namibia, are used in an oceanographic model usually applied in fishery science. The model allows to detect small scale changes in water masses and presents the opportunity to combine oceanographic studies with studies concerning the foraging ecology of seabirds.

Chapter 5 (page 79) focuses on the foraging behaviour of Cape gannets (*Morus capensis*) breeding at Mercury and Possession Islands. The potential advantages of flying large distances and the use of different water masses are investigated and their implications for exploring limited food sources are discussed. Foraging tracks are analysed focusing on presumable predictability of prey.

Chapter outline

In comparison to Cape gannets in the Benguela system, Peruvian boobies (*Sula variegata*) were studied in the Humboldt upwelling system at Isla Pájaros, Chile. Their foraging and diving behaviour is presented in Chapter 6 (page 107). Peruvian boobies are regularly affected by El Niño phenomena and their diet composition and distribution at sea may be correlated with changing environmental conditions over several years.

The conclusions (Chapter 7, page 125) link the results of the different parts of the study to the questions asked in the introductory chapter. Similarities in foraging behaviour of the species studied within and across system boundaries are discussed. The global importance of this study in terms of environmental monitoring and conservation of species within upwelling systems is specified.

The appendices (Appendix A, page 133 and Appendix B, page 141) include a manual for logger attachment and a proposal for a Marine Protected Area (MPA) in Namibia. The first forms part of a manual for seabird monitoring techniques which was compiled for a Benguela Large Marine Ecosystem (BCLME) project on top predators as indicators of ecosystem health. The second appendix provides an overview over the proposed Marine Protected Area (MPA) in southern Namibia, of which the design is partly based on penguin foraging distribution identified during this study.

1 Introduction and background information

1.1 General introduction and study aim

1.1.1 Seabird foraging ecology

Seabirds spend most of their life at sea feeding on marine organisms. They return to land for breeding, where they often form large colonies in coastal areas or at offshore islands. During non-breeding, they may cover vast areas of the ocean foraging (Briggs and Chu, 1986; Weimerskirch and Robertson, 1994) but even when they are forced to return to land regularly during breeding, some species cover substantial distances during single foraging trips (Weimerskirch et al., 2002; Hyrenbach et al., 2006). Offshore foragers may spend several days to weeks at sea before returning to their nests in order to feed their offspring (Weimerskirch et al., 1994a; Wienecke and Robertson, 2006), whereas inshore foragers usually stay closer to their colonies, often returning within one day from single foraging trips (Shealer, 2001; Davis and Renner, 2003). Prey depletion may occur around very large colonies due to inter- and intraspecific competition and may lead to larger foraging ranges (Furness and Monaghan, 1987; Lewis et al., 2001; Grémillet et al., 2004a). The distribution of seabirds at sea is not homogeneous but is strongly influenced by prey distribution and abundance (Schneider and Piatt, 1986; Brown, 1988; Hunt et al., 1990). Hydrographic structures such as upwelling, fronts and eddies enhance food availability for seabirds and birds may often be observed in higher numbers in the vicinity of those structures (Haney, 1986a; Hayes and Baker, 1989; Schneider, 1990). When foraging at sea, seabirds use different methods in order to obtain their food; e.g. some species feed exclusively at the sea surface (e.g. gulls and terns) while others dive to great depths (e.g. penguins and alcid; Ashmole, 1971). Seabirds are strongly affected by alterations in the marine environment that lead to changes in prey availability. Because seabirds often react quickly to such changes, e.g. by changing prey or foraging behaviour or by reducing reproductive output, they may be used to monitor environmental changes (Montevecchi, 1993; Weimerskirch et al., 1995) and prey availability (Cairns, 1987; Weimerskirch et al., 1994b; Cherel and Weimerskirch, 1995).

1.1.2 Study aim

Upwelling systems are known to host large numbers of seabirds; similar oceanographic features often support similar seabird faunas as may be observed in the Benguela and Humboldt systems (Duffy, 1989a; Crawford and Jahncke, 1999; Gaston, 2004; Crawford et al., 2006b). The Benguela system along the southern African coast and the Humboldt

1 Introduction and background information



Figure 1.1: Study areas along the western coasts of South America and southern Africa.

system off the coasts of Peru and Chile (Fig. 1.1) are known as areas of strong upwelling. They are characterised by cold water masses, high primary production and great fish abundance (Idyll, 1973; Shannon, 1985; Schwartzlose et al., 1999; Boyer and Hampton, 2001; Mann and Lazier, 2006). Large numbers of seabirds occur in both systems, relying on the high productivity for food especially during breeding (Duffy and Siegfried, 1987; Duffy, 1989a; Berruti, 1995; Crawford and Jahncke, 1999). Several seabird families are present in both systems comprising closely related species. The family *Spheniscidae* is represented by the African penguin (*Spheniscus demersus*) in the Benguela and by the Humboldt penguin (*Spheniscus humboldti*) in the Humboldt system. The family *Sulidae* includes the Cape gannet (*Morus capensis*) in the Benguela and the Peruvian booby (*Sula variegata*) in the Humboldt system. Changes in the marine environment lead to reduced prey abundance in these productive ecosystems and seabirds living in these systems are often confronted with food shortage. The combination of environmental changes and overfishing has led to large population declines in several species living in upwelling systems (Kemper et al., 2001; Roux, 2003; Crawford et al., 2007).

1.1 General introduction and study aim

The aim of this thesis is to investigate the foraging behaviour of seabirds in two major upwelling regions and to assess how birds might cope with food shortages and alterations in the environment. The following key questions are posed:

- What are the characteristics of the foraging behaviour of some of the most important seabird species breeding in the Benguela and Humboldt upwelling systems?
- Is foraging behaviour related to biological and hydrographic parameters of the upwelling system?
- How do the birds react to changes in the system, e.g. to differences in hydrographic parameters and prey availability?
- Can data of oceanographic parameters recorded by the birds themselves be used in oceanographic models? Can they give information about the hydrographic situation in the area and be used for environmental monitoring?

In order to answer these questions, different methods were applied on seabirds living in upwelling systems. Remote-sensing logger technology was used in combination with diet studies and observations within the colonies. Additionally, at-sea observations and hydrographic sampling was undertaken where possible.

Diving birds in particular are able to supply important information about water structures beneath the water surface, a habitat usually not easily accessible by simple observations. Penguins, gannets and boobies were therefore chosen as study species. Furthermore, they constitute some of the most numerous seabird species within the respective upwelling systems (Schlatter, 1984; Kemper et al., 2001; Simeone et al., 2003; Crawford et al., 2007) and consume large amount of fish (Furness, 1981; Furness and Cooper, 1982; Laugksch and Duffy, 1984; Duffy and Siegfried, 1987; Crawford et al., 1991), thus playing a key-role in the ecosystems. Penguins, being unable to fly, spend their entire time at sea in the water, reaching large depths when diving (Burger, 1991; Davis and Renner, 2003). Gannets and boobies are able to fly large distances in short time periods, reaching water masses in further distances to their colonies. They also reach water depths of several metres due to their ability to plunge-dive (Nelson, 1978). The use of marine organisms such as seabirds and marine mammals as platforms for surveying oceanographic conditions has been widely proposed (Wilson, 1992; Weimerskirch et al., 1995; Watanuki et al., 2001; Wilson et al., 2002; Charrassin et al., 2004; Fedak, 2004). The species selected and the methods used in this study may be valuable for small scale environmental monitoring and permit insights into the birds' biology as well as about other biological and hydrographic parameters in the systems.

The study in Namibia was undertaken in 2005 and 2006, allowing a comparison between two years with different oceanographic conditions. Additionally, African penguins and Cape gannets breeding at the same colonies were investigated simultaneously. Their foraging behaviour could therefore be compared for the same hydrographic situations and locations. The study on Peruvian boobies in Chile includes data from several years with the main data collecting taking place during 2004. Although it would have been desirable to include the Humboldt penguin into the study in order to compare its behaviour to its

1 Introduction and background information

congeneric, the African penguin, this was not possible due to logistic difficulties and ethic concerns. The Humboldt penguin is known for its nervous reaction to humans (Mattern et al., 2004), especially during handling for logger deployment (A. Simeone pers. comm.) and disturbance during logger deployment would have had a major impact on the birds. Several studies dealing with the at-sea behaviour of Humboldt penguins have already been carried out (Luna Jorquera, 1996; Culik and Luna Jorquera, 1997b; Culik et al., 1997; Luna Jorquera and Culik, 1999; Culik et al., 2000; Culik, 2001; Hennicke, 2001; Simeone, 2003; Hennicke and Culik, 2005). This information may be incorporated when evaluating the response of seabird species to changes in the Humboldt upwelling system.

In the following sections I will give some background informations on logger technology and on seabird-at-sea observations, informations on the Benguela and Humboldt upwelling systems with their respective particularities, as well as on the study species, the African penguin, the Cape gannet and the Peruvian booby. This is followed by a brief description of the study sites.

1.2 Background information

1.2.1 Logger technology

Most studies evaluating the foraging behaviour of seabirds are limited to observations at breeding sites and to ship-based observations. Studying individual foraging behaviour of seabirds and especially diving behaviour of diving birds became possible with the development of telemetry and remote-sensing logger technology. The development of logger technology has started in the 1960s and has rapidly evolved since then. Identification of foraging areas and distribution at sea were achieved at first mainly using radio-telemetry (Culik et al., 1998; Henkel et al., 2003) and satellite telemetry (Weimerskirch and Robertson, 1994; Sagar and Weimerskirch, 1996; Culik and Luna Jorquera, 1997b), the first being limited to relatively small distances, the latter leading to relatively broad positional informations. Another method being used especially during winter migration is geolocation. This method does not give accurate positional information but identifies migration patterns and large-scale overwintering areas (Phillips et al., 2004). Relatively good positional information is obtained using compass loggers. Incorporating dead-reckoning and a known flight speed, positions of birds at sea may be calculated and their at-sea behaviour determined using these relatively small devices (Wilson et al., 1991).

A highly accurate positioning of birds at sea became available with the development of the Global Positioning System (GPS). The devices incorporating GPS enable a fine-scale analysis of space utilisation by seabirds, identifying foraging areas and behavioural aspects of at-sea distribution (Petersen et al., 2006; Weimerskirch, 2007). Further minimisation of devices will allow further studies on smaller and lighter seabird species. Until now, studies have been limited to large and heavy birds such as albatrosses and penguins but smaller species, such as petrels, are increasingly deployed with small size loggers (Iguar et al., 2005). Constraints of logger technology still consist in limited energy supply and data storage in combination with maximum size and weight of the device possible

to attach to seabirds without causing a major impact on the birds' foraging behaviour. Depending on the device used, birds often need to be recaptured in order to retrieve the logger and to download the data. Therefore, most studies take place during breeding when birds are regularly returning to their nest sites. For studies covering longer periods, including non-breeding seasons, attachment might present a problem, because most devices are attached to the feathers (Wilson et al., 1997) and would be lost during moult.

Besides the position of the birds at sea, many other aspects of the birds' foraging behaviour may be studied using remote-sensing. Many different sensor types have been invented, enabling the study of physiological as well as behavioural aspects of the animals life (see Ropert-Coudert and Wilson, 2005, and citations therein).

1.2.2 Seabird-at-sea observations

Seabird-at-sea observations are widely used to assess the distribution of birds at sea (Jehl, 1973; Garthe and Hüppop, 1994; Jahncke et al., 1998a; Camphuysen and van der Meer, 2005). Different observer platforms, such as aircraft or ship, may be used. The use of aircrafts allows the coverage of large areas within short periods of time and to estimate numbers of species that would flee from approaching ships. Disadvantages of aircraft-based observations are that some birds may not be identified to species level (e.g. gulls and terns) and that behavioural observations are not feasible (Garthe and Skov, 2006). Ship-based seabird-at-sea observations allow to assess the birds' behaviour at sea as well as environmental data simultaneously (Weichler et al., 2004; Schwemmer and Garthe, 2005), but only smaller areas may be covered within short periods of time. The methodology applied in this study followed Tasker et al. (1984), Garthe et al. (2002) and Camphuysen and Garthe (2004) for standardised ship-based observations. Densities of birds at sea were calculated and special emphasis was placed on the foraging behaviour of species included in this study.

1.2.3 Coastal upwelling

Wind-induced upwelling along the coast leads to high biological productivity due to upwelled nutrients from deeper waters reaching the euphotic zone (see Mann and Lazier, 2006). Major upwelling areas are located along the coasts of North and South America (i.e. the California and the Humboldt Currents in the Pacific Ocean) and along the coast of Africa (i.e. the Canary and the Benguela Currents in the Atlantic Ocean). All four currents run along the western coasts of the continents. Another coastal upwelling area, which is located along the eastern coast of northern Africa, is the Somalia Current.

Coastal upwelling takes place because of equatorward winds parallel to the coast. Due to the Coriolis force and the Ekman drift, surface water is moved to the left of the wind direction in the southern hemisphere (to the right in the northern hemisphere). Water from deeper layers replaces the water drifted offshore and the upwelling creates a current parallel to the coast in the same direction as the wind. A front between the colder upwelled water close to the coast and the warmer offshore waters may often be observed (Arntz and Fahrback, 1991; Mann and Lazier, 2006). Upwelling intensity is influenced

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by wind strength, the vertical structure of the water and the bathymetry and may vary strongly between days, months and years.

1.2.4 Benguela upwelling system

The Benguela upwelling system along the north-western coast of South Africa and the southern part of Namibia (approximately between 15°S and 34°S, see Bianchi et al., 1999) is characterised by strong upwelling. The upwelling cell off the Lüderitz region (26°50'S) is known to be of major strength (Shannon, 1985, 1995; Demarcq et al., 2003; Roux, 2003; Lett et al., 2006). The Benguela Current may be divided into a southern and a northern branch, separated by the upwelling cell off Lüderitz (Agenbag and Shannon, 1988; Bianchi et al., 1999; Weeks et al., 2004), which acts as an environmental barrier for marine organisms. Upwelling in the Benguela Current may vary spatially and temporally due to different wind patterns. Upwelling along the Namibian coast is strongest during the spring and summer; along the South African coast, major upwelling takes place during the summer (Shannon, 1985). Optimal biological productivity occurs when strong upwelling is followed by several days of weaker wind stress allowing the phytoplankton biomass to increase using the upwelled nutrients in the euphotic zone (Demarcq et al., 2003; Mann and Lazier, 2006).

Global warming might influence upwelling intensities. Bakun (1990) found an increase in wind stress at several coastal upwelling regions. Winds are generated by temperature differences between the warmer air over land and the cooler air over the sea (Mann and Lazier, 2006). Global warming could therefore also lead to a reduced upwelling, which would result in a reduced productivity (see Roux, 2003). In Namibian waters, southerly wind speeds, favourable for upwelling, were below the long term average for the past seven years (1998 – 2005) (Peard et al., 2005), possibly as an effect of higher sea surface temperatures (SST) due to global warming.

Fisheries

In former times the Benguela Current hosted large amounts of shoaling fish, especially sardine (*Sardinops sagax*¹; see Lluch-Belda et al., 1989; Bianchi et al., 1999; Schwartzlose et al., 1999). Sardine catches peaked in 1968 with 1.4 million tons taken. The stock was overfished by the end of the 1960s and catches declined sharply. The sardine stock has never recovered since in the northern Benguela (see Fig. 1.2; Bianchi et al., 1999; Roux and Shannon, 2004; Cury et al., 2005). Since then, no other fish species has reached the population size of the former sardine biomass although anchovy (*Engraulis capensis*) had replaced sardine for some time during the 1970s (Matthews and Berruti, 1983). The fisheries for Cape hake (*Merluccius capensis* and *M. paradoxus*) and horse mackerel (*Trachurus trachurus capensis*) are currently the most important ones in Namibia (Roux and Shannon, 2004; Gordo et al., 2006). By the beginning of the 20th century catch rates in Namibia were at their lowest rate since these were recorded (Roux and Shannon, 2004; Cury et al., 2005).

¹also considered as *Sardinops ocellatus*; see Bianchi et al. (1999)

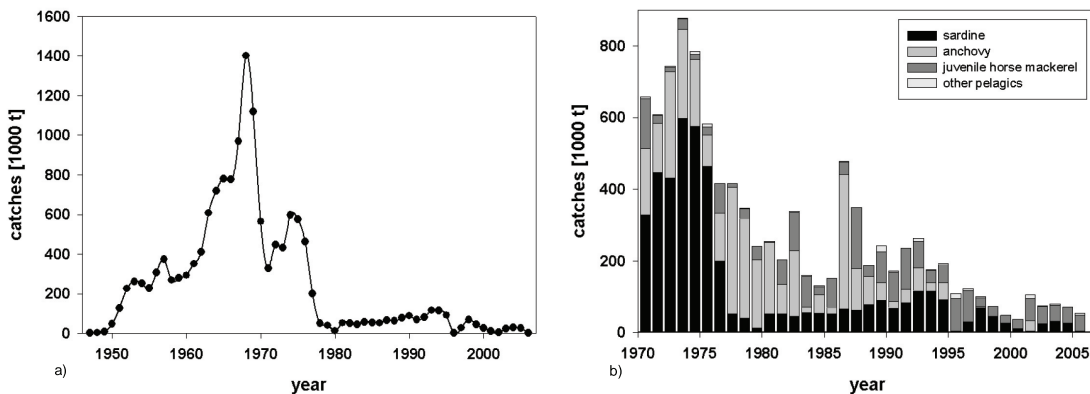


Figure 1.2: Catches [1000 t] of a) sardine fisheries between 1947 – 2006 and b) purse seine fisheries between 1971 – 2006 in Namibia. Purse seine catches include sardine, anchovy, juvenile horse mackerel and other pelagics (mainly redeye). Data by courtesy of Dr. J.-P. Roux, Ministry of Fisheries and Marine Resources, Namibia.

A decrease in fish biomass may also have indirect effects on ecosystem processes and may eventually lead, especially in combination with climatic changes, to a regime shift (Roux, 2003; Cury et al., 2005). The northern Benguela ecosystem has changed from supporting large stocks of pelagics to non-exploited species such as pelagic goby (*Sufflogobius bibarbatus*) and jellyfish (Roux and Shannon, 2004; Cury et al., 2005).

Benguela Niño

An equivalent to the Pacific El Niño phenomenon is the Benguela Niño which occurs on a smaller scale and less frequently than its Pacific counterpart (Shannon, 1985, 1995). During the event, positive water temperature anomalies may be observed as well as a deepening of the thermocline. Benguela Niños are caused by large-scale changes in wind patterns that lead to a southward intrusion of warm and highly saline waters from Angola into Namibian coastal waters (Gammelsrød et al., 1998). Recent Benguela Niño events took place in 1972, 1984 and 1995 and had a large impact on fish abundance in the Benguela marine ecosystem, especially in combination with high fishing efforts having led to overfished stocks (Laugksch and Adams, 1993; Bianchi et al., 1999; Gammelsrød et al., 1998). A reduction in stock size during such an event also resulted in breeding failures of seabirds (Kemper et al., 2001).

Sulphide eruptions

Due to the high productivity of the system, large amounts of phytoplankton sink to the bottom where they are degraded (Bianchi et al., 1999). Since the absence of large stocks of planktivorous fish species, such as sardine and anchovy, a higher percentage of the primary production is not entirely consumed in the water column (Roux, 2003; Weeks

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et al., 2004) and is decomposed by bacteria at the sea floor. This, in addition to low-oxygen water from the poleward undercurrent causes an hypoxic environment. Anaerobic sulphate-reducing bacteria metabolise organic matter, thus producing hydrogen sulphide (Currie et al., submitted). Sulphide is normally precipitated by reactive iron but iron does not occur in large quantities along the Namibian coast due to little input of terrestrial material (Emeis et al., 2004; Brüchert et al., 2006; Currie et al., submitted). Another source for sulphide removal are sulphide-oxidising bacteria such as *Thiomargarita namibiensis* and *Beggiatoa* ssp. (Emeis et al., 2004; Currie et al., submitted) which cover large area of the sea floor (Schulz et al., 1999). Bacterial sulphate reduction only takes place in the top 10 cm of the sediment and hydrogen sulphide accumulates together with methane in pore water in the shelf sediment (Emeis et al., 2004; Brüchert et al., 2006) from where it erupts regularly, especially during the austral summer (Emeis et al., 2004; Weeks et al., 2004). Eruptions of hydrogen sulphide from gas pockets inside the diatomaceous mud layer are probably triggered by changes in the atmospheric and oceanographic pressure fields, occurring during both weakened and strengthened upwelling (Emeis et al., 2004; Weeks et al., 2004). Hydrogen sulphide strips dissolved oxygen from the water column causing hypoxic and anoxic conditions that affect marine organisms (Weeks et al., 2002, 2004). Sulphide eruptions can even be detected through satellite remote sensing and it has been shown that those events last longer and are more extensive then previously thought (Weeks et al., 2002, 2004). The milky water colouring seen at the surface is caused by micro-granules of sulphur (Weeks et al., 2004).

Sulphide eruptions also seem to play an important role in the functional separation between the northern and southern branch of the northern Benguela system preventing fish species from crossing this area of low oxygen (Weeks et al., 2004). Anoxic events can cause mortality and displacement of crustaceans and fish species such as rock lobster (*Jasus lalandii*) and Cape hake (*Merluccius capensis*) (Hamukuaya et al., 1998; Weeks et al., 2004).

Eruptions occur quite frequently along the Namibian coast. The phenomenon is known since the early 20th century (Currie, 2005); the frequency differs between years and seasons. Weeks et al. (2004) observed 16 events between March 2001 and 2002.

1.2.5 Humboldt upwelling system

The Humboldt upwelling system is located along the South American coast; the Humboldt Current flows equatorwards between 38°S off central Chile, along the Peruvian coast and reaching Ecuador. The exact extent differs between seasons. Off central Chile, the upwelling peaks during late spring and summer. Wind stress is relatively constant and not very strong, leading to a shallow wind-induced mixing of the euphotic zone (Mann and Lazier, 2006). Along the Chilean coast, upwelling depends on bottom topography as well as coastline geometry and local wind forcing (Moraga, 1996; Strub et al., 1998; Marín et al., 2003; Mesías et al., 2003). Localised upwelling at protruding points and retention of planktonic organisms in bays lead to chlorophyll filaments along the coast (Marín and Moreno, 2002; Marín et al., 2003). Along the Peruvian and Chilean coasts, upwelling usually continuous during the entire year but ceases almost completely

in some years, known as the El Niño phenomenon and as part of the El Niño - Southern Oscillation (ENSO) (Mann and Lazier, 2006).

Fisheries

The Humboldt upwelling system once produced 22 % of all fish caught in the world (Idyll, 1973). Anchovy (*Engraulis ringens*) was caught almost exclusively until 1975, catches reaching almost 13 million tons in 1970 (Schwartzlose et al., 1999). When the anchovy stock began to decrease, sardine (*Sardinops sagax*) was caught in higher numbers. Sardine catches began to decrease in 1986 and anchovy catches began to increase again. In 1995 and 1996, about eight million tons of anchovy were caught off Peru and Chile (Lluch-Belda et al., 1992; FAO, 1997; Schwartzlose et al., 1999). Fish stocks were strongly affected by El Niño events; during the 1983 El Niño, no anchovy at all was caught off Chile (Schwartzlose et al., 1999). A combination of human exploitation and environmental changes has led to a strong reduction of fish stocks within the system, strongly impacting seabird populations (Duffy, 1983, 1989b).

El Niño

The El Niño phenomenon affecting the Humboldt Current is part of a global oscillation, called the Southern Oscillation (SO), a pressure gradient between regions of high pressure in the eastern equatorial Pacific and low pressure regions in the area of Indonesia. A lower-than-average gradient between those two regions causes El Niño conditions with warmer water masses along the Chilean and Peruvian coasts whereas a higher-than-average gradient causes the so called La Niña phenomenon with cooler water along the South American coast. In El Niño years, trade winds weaken or reverse and the thermocline sinks to greater depths. Although the Ekman transport still causes coastal upwelling, the upwelled water is much warmer and less rich in nutrients, resulting in a reduction of productivity with severe effects on organisms in the region, such as seabirds and mammals (Cane, 1983; Mann and Lazier, 2006). The beginning of an El Niño event may usually be detected by a raise in SST along the South American coast, although this may not always be the case, as seen in the 1982 – 83 event (Cane, 1983).

1.2.6 Study species

African penguin

The African penguin (*Spheniscus demersus*), formerly also known as jackass or black-footed penguin, belongs to the genus of the *Spheniscus* penguins. This genus also includes the Magellanic (*S. magellanicus*) and the Humboldt penguin (*S. humboldti*) breeding along the South American coast of Argentina and Chile and the Galápagos penguin (*S. mendiculus*), breeding at the Galápagos Archipelago in the Pacific Ocean. The African penguin is endemic to southern Africa, breeding between Bird Island on the south-eastern coast of South Africa and Hollamsbird Island, off central Namibia. Birds breed at nine island colonies and two mainland sites between Hollamsbird Island (24°38'S, 14°32'E) in

1 Introduction and background information

the north and Sinclair Island (27°40'S, 15°31'E) in the south along the southern Namibian coast (Fig. 2.1). Several colony sites have been abandoned during the last century, of which some have been recolonised recently (Roux et al., 2003). The population of African penguins has been reduced by 72 % since the 1950s and numbers continue to decrease at almost all colonies in Namibia (Kemper et al., 2001). The decline of population numbers for African penguins is closely related to the over-exploitation of pelagic fish stocks (Crawford and Shelton, 1978; Randall and Randall, 1986). Numbers of breeding African penguins have been severely reduced at all Namibian breeding sites, the adult population had decreased at a rate of 2.6 % per year between 1996 and 2001 (Kemper et al., 2001) and continues to decrease (Kemper, 2006). The regional Namibian population of African penguins is listed as *Endangered* (Kemper, 2006). The South African population is listed as *Vulnerable* and numbers had been increasing slightly in South Africa during the last years² but since 2005 the population there has further declined (Koenig, 2007). African penguins breed throughout the year and peak breeding varies between breeding colonies and between years (Kemper, 2006). At Mercury Island, peak breeding takes place between October and January whereas most birds at Halifax breed during July and August. Breeding at Possession Island is less seasonal. Penguins have been observed laying replacement clutches as well as second clutches after they have successfully raised chicks (Kemper, 2006).

Cape gannet

The Cape gannet (*Morus capensis*) is endemic to the southern African coast where it breeds at only six breeding colonies, three of which are located at islands in Namibian waters. Ichaboe Island (26°17'S, 14°56'E) hosts the largest number of breeding Cape gannets in Namibia with an estimated number of 8600 breeding pairs (Crawford et al., 2007). About 1400 pairs are breeding at Mercury Island and only 350 at Possession Island (Crawford et al., 2007). Different methods have been used to estimate population numbers and figures vary between different authors (see Lewis et al., 2006; Crawford et al., 2007; Kemper, in press b). Numbers of breeding gannets at all Namibian islands have been much higher in the past (Nelson, 1978), numbers fell by 95 % between 1956 – 57 and 2005 – 06 (Crawford et al., 2007) and currently, the Cape gannet is listed as *Endangered* in Namibia (Kemper, in press b). The entire population of South Africa and Namibia is listed as *Vulnerable* (IUCN, 2006). The population decline is considered to be partly due to food shortage especially after the main prey, sardine, collapsed due to overfishing (Crawford et al., 2007). Numbers of Cape gannets are strongly correlated with the abundance of sardine and diet monitoring of Cape gannets has been used in order to assess fish stocks (Crawford and Shelton, 1978; Crawford et al., 1992). In South Africa, numbers of breeding Cape gannets are currently increasing, mostly due to a better food availability (Lewis et al., 2006; Crawford et al., 2007). Cape gannets are annual breeders and usually raise one chick. Breeding is relatively synchronised and breeding takes place between September and April. Replacement clutches may be laid during this period (Nelson, 1978; Kemper, in press b).

²http://web.uct.ac.za/depts/stats/adu/species/sp003_09.htm

Peruvian booby

The Peruvian booby (*Sula variegata*) is endemic to the Humboldt upwelling system and breeds along the coasts of Peru and Chile. It is one of the most numerous seabird species in this upwelling system and belongs to the so-called *guano birds*. Cape gannets are seasonal breeders, breeding taking place between October and February and birds may lay between one to four eggs. Most birds raise two to three chicks. Numbers of adult Cape gannets have always fluctuated strongly; decreases in numbers being related to low fish abundance but also to human disturbance during guano exploitation and bird and egg harvesting (Nelson, 1978). Recent estimates of Peruvian boobies in Chile state 18000 breeding pairs (Simeone et al., 2003). During El Niño years, birds might abandon breeding (Jahncke and Goya, 2000) but this usually does not affect adult population numbers (Crawford and Jahncke, 1999; Jahncke and Goya, 2000). The species is listed as of *Least concern* (IUCN, 2006).

1.2.7 Study colonies

Namibia

Mercury Island

Mercury Island (25°43'S, 14°50'E) is located about 100 km north of the harbour town of Lüderitz, situated within Spencer Bay in range of sight of the mainland. The 3 ha island currently hosts the largest breeding colony of African penguins in Namibia with about 12000 adults. Additionally, large numbers of Cape gannets and Cape cormorants (*Phalacrocorax capensis*) breed on the island as well as bank (*P. neglectus*) and crowned cormorants (*P. coronatus*). In the vicinity, a small Cape fur seal (*Arctocephalus pusillus pusillus*) breeding colony is located. Seals used to occupy the island before being chased off by staff of the Ministry of Fisheries in the 1980s. The island is manned and public access is strictly regulated. Lobster fishery takes place within a few metres to the island and oiled birds are regularly found and taken in for rehabilitation.

Halifax Island

Halifax Island (26°37'S, 15°04'E) is located about 200 m from the mainland, just south of Lüderitz. It used to host one of the largest breeding colonies of African penguins with about 10000 adults in 1956 (Rand, 1963) but by 2004 the maximum number of nests during peak breeding numbered 800. Besides penguins, crowned cormorants, African black oystercatchers (*Haematopus moquini*), swift terns (*Sterna bergii*), kelp gulls (*Larus dominicanus vetula*) and Hartlaub's gulls (*L. hartlaubii*) breed on the island. Due to its close vicinity to the mainland, the island is occasionally visited illegally. Ship-based tourism takes place around the island.

1 Introduction and background information

Possession Island

Possession Island (27°01'S, 15°12'E) is the largest of the Namibian islands (90 ha), being located 40 km south of Lüderitz within Elizabeth Bay. The island hosts breeding African penguins as well as Cape gannets but both species occur in much smaller numbers than historically known (Cordes et al., 1999; Crawford et al., 2007). Possession Island used to host the largest population of African penguins in Namibia with an estimated 46000 adults (Rand, 1963). By 2004 the maximum number of nests numbered 109 (Kemper, 2006). Large numbers of kelp gulls breed on the island, occasionally predated on eggs and chicks of other seabird species. Several cormorant species, swift terns and African black oystercatchers also breed on the island. The island is manned and access is limited. Mining activities are taking place on the mainland adjacent to Elizabeth Bay and mining effluent, consisting mainly on fine sediment, is regularly pumped into the bay (Simmons, 2005). The installation of aquaculture infrastructure in the bay has been proposed.

Chile

Isla Pájaros

Isla Pájaros (29°35'S, 71°33'W) is located about 40 km north and 25 km offshore of La Serena in northern central Chile (Fig. 6.1). The island is situated at the shelf break with water depths of up to 200 m east of the island towards the mainland and water depths of more than 1000 m towards the west (Moraga, 1996). Localised upwelling takes place at protruding points along the coast, which form a large bay in which Isla Pájaros is located, and at the island itself (Marín et al., 2003). The island hosts large numbers of breeding Peruvian boobies, kelp gulls (*Larus dominicanus*) and Humboldt penguins and large numbers of rats are present. Numbers of breeding Peruvian boobies vary strongly between years (see Chapter 6, Simeone et al., 2003). Fishermen regularly visit the island to spend the night.

2 Foraging areas and diving behaviour of African penguins (*Spheniscus demersus*) along the Namibian coast

2.1 Introduction

The African penguin (*Spheniscus demersus*) is endemic to southern Africa, breeding between Bird Island on the south-eastern coast of South Africa and Hollamsbird Island, off central Namibia. In Namibia, African penguins breed along the southern Namibian coast at nine island colonies and only two mainland sites between Hollamsbird Island (24°38'S, 14°32'E) in the north and Sinclair Island (27°40'S, 15°31'E) in the south (Fig. 2.1). Several colony sites have been abandoned during the last century, of which some have been recolonised recently (Roux et al., 2003). The northern Benguela Current, in which all breeding sites are located, is known for its high productivity but also for its temporal and spatial variability (Shannon, 1995). Differences in the hydrography and hence differences in food availability around breeding colonies may lead to large differences in breeding numbers and breeding success (Tremblay and Cherel, 2003; Chiaradia et al., 2007). The population of African penguins has been reduced by 72 % since the 1950s and numbers continue to decrease at almost all colonies (Kemper et al., 2001). Studies concerning the at-sea behaviour of African penguins have so far only been carried out in South Africa (Wilson, 1985; Wilson et al., 1988; Ryan et al., 2004; Petersen et al., 2006). Little is known about African penguins in Namibia outside their breeding colonies. Recent studies have dealt with population trends and breeding ecology (Kemper, 2006) but no informations about diving behaviour and foraging areas used by the birds in Namibian waters were available before this study. Inter-annual variations of foraging areas and of the birds' foraging behaviour have to be considered when implementing protection measures as well as possible impacts of climate change and events, such as sulphide eruptions and Benguela Niños, have to be taken into account.

In this chapter, I investigate the foraging areas and the diving behaviour of chick-rearing African penguins at three different breeding colonies, considering inter-annual differences at Mercury Island and latitudinal differences between birds from Possession, Halifax and Mercury Islands. The use of data loggers provides detailed insight in the birds' behaviour at sea. Foraging behaviour and diet composition during this critical stage of the breeding period are used to deduce on the food availability and the environmental conditions encountered by the penguins in Namibian waters.

2.2 Methods and study sites

Study sites Field work was conducted at several breeding sites at three islands along the Namibian coast, these being Mercury, Halifax and Possession Islands (Fig. 2.1). Mercury Island (25°43'S, 14°50'E) currently hosts the largest breeding colony of African penguins. Numbers had been slightly increasing in the 1990s (Kemper et al., 2001) but are recently decreasing at a rate of 3.7 % per year, about 12500 adults being present at the island in 2004 (Kemper, 2006). At Halifax Island (26°37'S, 15°04'E), about 6000 adult African penguins have been counted in 2004, being the only colony with increasing numbers today (Kemper, 2006) although the island formerly hosted about 10000 adults in the 1950s (Rand, 1963). Possession Island (27°01'S, 15°12'E) used to be the largest breeding colony for African penguins in Namibia in the 1950s with an estimated 46000 adult birds (Rand, 1963), today only 1400 adults are present at the island and no more than 500 active nests are found during the peak breeding season (Kemper, 2006). For further details on the breeding colonies refer to Chapter 1, page 11.

Data logger deployment GPS TDlog data loggers (earth&OCEAN technologies, Kiel, Germany) were used, recording the bird's position at sea, the diving depth (measured from water pressure) and the water temperature *in situ*. The hydrodynamic shaped aramid-fibre housing of the device is 96 mm long, 39 x 27 mm in profile and weighs 75 g including the battery (for further details see Ryan et al., 2004). GPS receivers were programmed to get positional fixes every two to 15 minutes (settings varied between deployments) when the birds were at the colony or drifting at the surface and after every surfacing following each dive. The positional accuracy using this intermittent mode lies between ten and 20 m (product information earth&OCEAN technologies and Ryan et al., 2004). Pressure and temperature sensors record water depth and temperature with an accuracy of 4 mbar and 5 mK, respectively. Both sensors were set to store data every second, allowing a detailed analysis of diving patterns and water temperature structure. Attachment of data loggers followed the procedure described in Wilson et al. (1997) and Appendix A, page 133, using Tesa® tape to stick the device to the birds lower back. Birds were captured by hand at the nest site shortly after the partner returned from the sea and deployment took place at the border of the colony. Birds were weighed and held by one person while the other person attached the logger. The total procedure did not last more than ten minutes before the bird was returned to the nest. Sex determination was only realised when obvious; no measurements were taken. Data loggers were retrieved after the bird returned from the foraging trip usually the following day, therefore only one trip per bird was recorded. Only one partner of each nest was handled in order to reduce a possible impact on food delivery to the chicks. Chicks were not handled at all, but age was estimated by visual clues, such as size and feather stages.

In 2005, 13 birds were equipped at Mercury Island between the 12th and the 26th of February (Table 2.1¹) and five birds at Possession Island between the 6th and the 11th of March (Table 2.5). In 2006, two birds were equipped at Halifax Island on the 7th of

¹ tables may be found following the discussion of each chapter

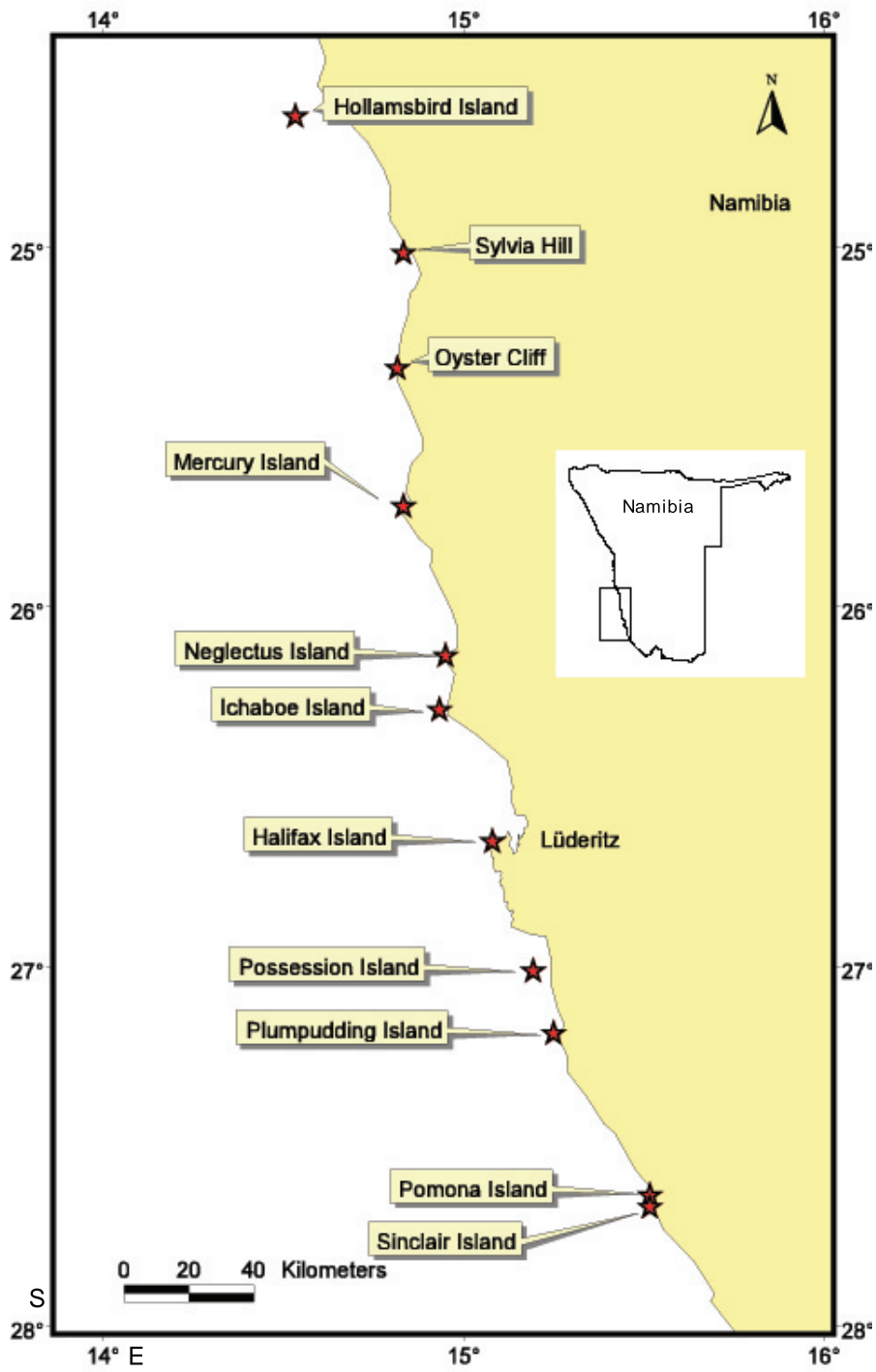


Figure 2.1: Breeding colonies of African penguins in Namibia.

2 Foraging areas and diving behaviour of African penguins

February (Table 2.5) and 14 birds at Mercury Island between the 15th and the 27th of February (Table 2.2). All birds were raising one or two chicks of three to eight weeks of age.

Data analysis Positional data were analysed using ArcView GIS 3.2[®]. The foraging range was defined as the maximum distance away from the colony (Wilson et al., 1989b). Tracks between known positions were interpolated in order to calculate the total distance travelled. A straight line between positions was assumed which leads to a possible underestimation of the total distance travelled. A loop factor was calculated by dividing the total distance travelled by the maximum distance away from the colony. The closer this value is to 2, the more directly the bird swam towards its feeding area. The analysis of diving parameters was conducted using Matlab[®], running a personal designed script written by T. Mattern and L.-G. Ellenberg. Dives were defined as such when the depth was ≥ 3 m and the duration ≥ 3 s. Dives were separated into travelling and foraging dives following Ydenberg and Clark (1989) (see also Luna Jorquera and Culik, 1999; Tremblay and Cherel, 2003) on the basis of a well-defined mode in the dive frequency distribution. Diving efficiency was calculated as

$$\text{diving efficiency} = \frac{\text{bottom duration}}{\text{dive duration} + \text{post-dive surface time}}$$

(see Ydenberg and Clark, 1989; Cherel et al., 1999; Tremblay and Cherel, 2003). A higher value for dive efficiency presumably indicates a higher food intake (Tremblay and Cherel, 2003). Foraging efficiency was defined as the time spent diving as percentage of the time spent at sea during the entire trip (Cherel et al., 1999). The vertical distance was calculated as the sum of all dive depths multiplied by two, comprising the descending and ascending distances.

Statistical tests were carried out using the program R 2.4.1[®]. The median was calculated for all birds combined for one year if not stated differently. When the mean was calculated, values for standard deviation are given. Statistical tests applied were general linear models (GLM) using a quasipoisson distribution and linear models (LM) as well as linear mixed-effects models fit by REML (restricted maximum likelihood) (LMER), taking into account the variance between birds within one year when comparing results between two years or two islands.

Diet analysis Diet samples were taken at Mercury Island in 2005 and 2006 and at Possession Island in 2005 during the study periods, capturing birds returning from the sea with visibly filled stomachs. Logger equipped birds were not sampled in order to avoid additional stress. Stomach flushing, as described by Wilson (1984), was conducted in order to obtain the stomach contents. A soft tube was orally inserted into the bird's stomach and lukewarm water was poured in until the natural vomiting reflex was triggered. Regurgitated stomach contents were drained through a sieve and later weighed and analysed. Birds were weighed and immediately released after not more than ten minutes. A total of 24 stomach samples were obtained at Mercury in 2005 over a period

of three weeks, eight birds being sampled on one day per week. Nine birds were sampled on one day at Possession Island in 2005. In 2006, a total of 16 samples were obtained on two occasions at Mercury Island. For Mercury Island, diet information since 1998 is available at the Ministry of Fishery and Marine Resources, Lüderitz, Namibia, obtained with the same method as used in this study. Diet components were identified to species level using Bianchi et al. (1999) and measured if specimens were complete. For each species, the percentage of the total mass of the sample was calculated.

2.3 Results

2.3.1 Mercury Island

In 2005, of all 13 birds equipped with GPS TDlog data loggers, data obtained from twelve birds was included in the following analysis (Table 2.1). The 13th bird only returned after four days at sea, travelling over 60 km in the first 27 hours, after which the battery ran flat and no further positional and sensor data could be obtained. Therefore, the bird was excluded from the following analysis.

In 2006, 14 birds were equipped with GPS TDlog data loggers of which one logger did not deliver any usable information at sea. Three other devices did not record data for the entire trip but two of these birds were already on their return trip when the battery ran out so that the maximum distance reached could be calculated for a total of twelve birds. The exact trip duration was known for eleven birds (Table 2.2). Dive analysis was performed on complete dive data sets for entire trips. These were available from ten birds.

Trip duration

2005 Birds at Mercury Island spent on average 13 hrs 34 min away from the colony ($n = 12$; range 10 hrs 57 min – 27 hrs 18 min) in 2005 (Table 2.3). The one bird not included in this analysis had a trip duration of 83 hrs 05 min. Three out of the 13 birds studied in 2005 left the colony in the evening hours, two within ten minutes after logger deployment and one about three hours later. Average trip duration for birds leaving in the early morning and returning the same day (following referred to as one-day trips) was 12 hrs 53 min ($n = 9$; range 10 hrs 57 min – 14 hrs 59 min). They all left between 4:00 and 6:45 h in the morning and all birds, including birds leaving in the evening hours, returned to their nest sites between 17:30 and 20:45 h. Only one bird returned at 22:11 h.

2006 In 2006, birds at Mercury Island had an average trip duration of 15 hrs 12 min ($n = 11$; range 9 hrs 56 min – 25 hrs 27 min; Table 2.3). For three birds, trip durations could not be calculated because the devices did not record the return of the birds and the exact return times were not observed in the field. Of the 13 birds for which the departure time is known, one left at 2:21 h; the majority of the birds left between 5:54 and 7:05 h ($n = 8$), two birds left the colony around midday at 13:57 and 14:27 h and two birds left the colony in the evening hours at 18:00 and 18:33 h, both leaving within 30 minutes

2 Foraging areas and diving behaviour of African penguins

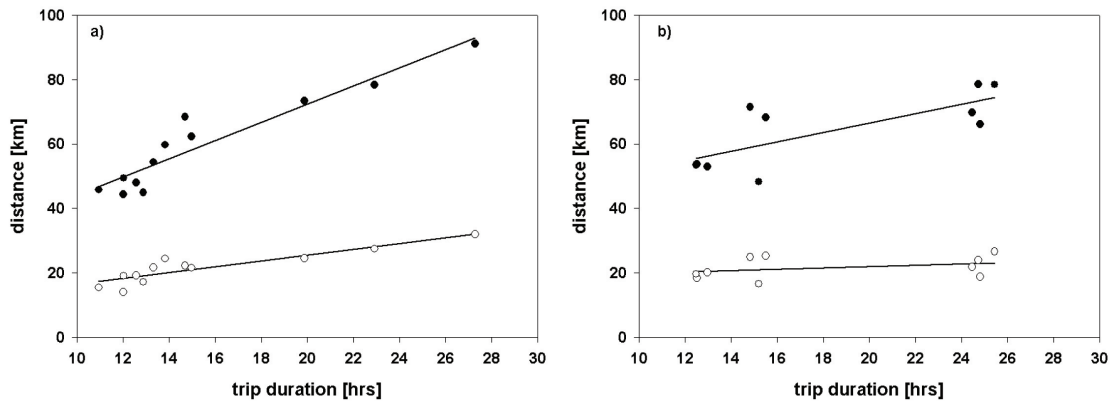


Figure 2.2: Correlation between trip duration [hrs] and foraging range (maximum distance away from the colony) [km] (white circles) and the total distance travelled (black circles) for African penguins from Mercury Island, Namibia, in a) 2005 ($n = 12$ birds) and b) 2006 ($n = 10$ birds).

after logger deployment. The average trip duration for one-day trips was 13 hrs 54 min \pm 1 hrs 59 min ($n = 7$; range 9 hrs 56 min – 15 hrs 30 min).

There was no significant difference in average trip duration between 2005 and 2006 ($n = 12$ and 11 birds, respectively; $p = 0.414$; GLM; Table 2.3).

Foraging area

2005 All birds in 2005 swam in a north-westerly direction from the colony (Fig. 2.3). Median foraging range (i.e. the maximum distance away from the colony) was 21.6 km ($n = 12$; range 14.1 – 31.9; Table 2.3). The median distance travelled was 57.0 km ($n = 12$; range 44.4 – 91.1; Table 2.3).

Dividing the total distance travelled by the foraging range for each bird indicates how directly the foraging area was reached. This factor, the so-called loop factor, had a median of 2.9 for all birds in 2005.

Foraging range as well as total distance travelled were positively correlated with trip duration ($p < 0.001$; $R^2 = 0.807$; $p < 0.001$; $R^2 = 0.893$, respectively; LM; Fig. 2.2a). Birds that stayed away from the colony overnight had greater foraging ranges and travelled further distances compared to birds returning the same day ($p < 0.01$ and $p < 0.001$, respectively, GLM).

2006 In 2006, birds used almost the identical area to forage and passed through the same area as in 2005 (Fig. 2.4). The foraging range could only be calculated for twelve birds, since one device did not record any positional information during the trip and for one bird the maximum distance recorded presumably underestimated the total foraging range of the trip. The median foraging range was 20.9 km ($n = 12$; range 16.6 – 26.6; Table 2.3).

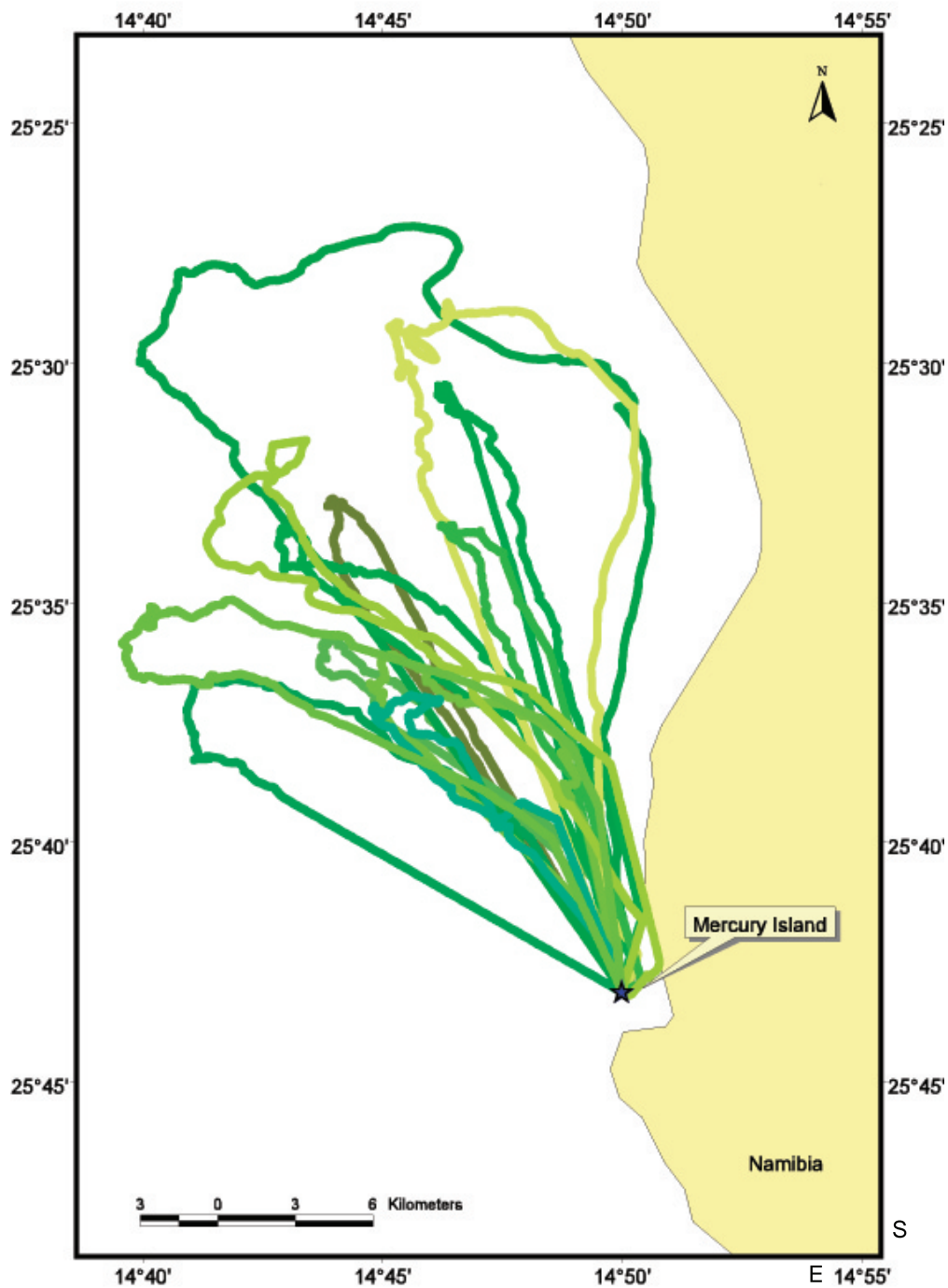


Figure 2.3: Foraging tracks of twelve African penguins from Mercury Island, Namibia, equipped with GPS TDlog between the 12th and 26th of February 2005. Each colour represents an individual foraging trip of a single bird.

2 Foraging areas and diving behaviour of African penguins

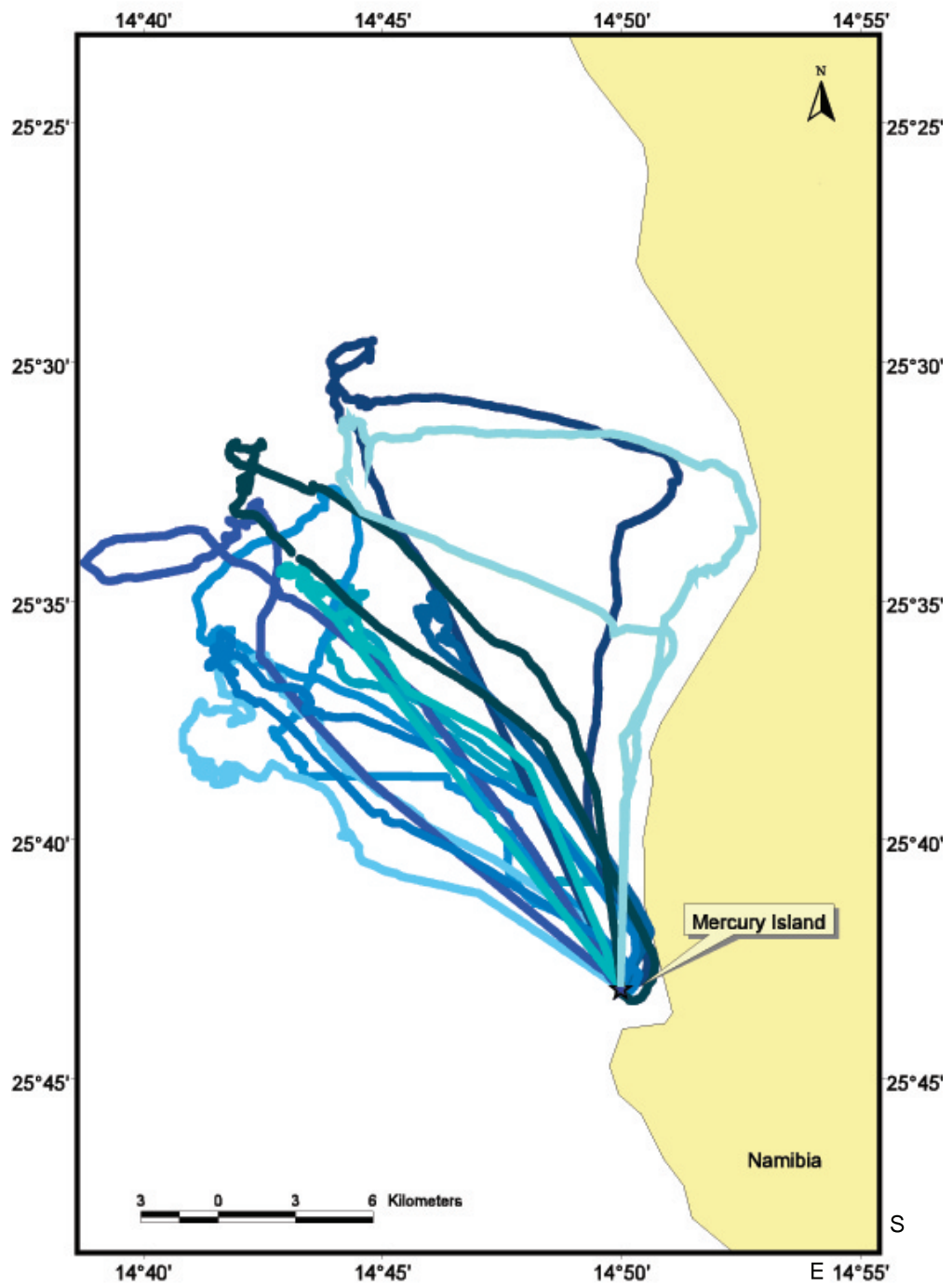


Figure 2.4: Foraging tracks of twelve African penguins at Mercury Island, Namibia, equipped with GPS TDlog between the 15th and 27th of February 2006. Each colour represents an individual foraging trip of a single bird.

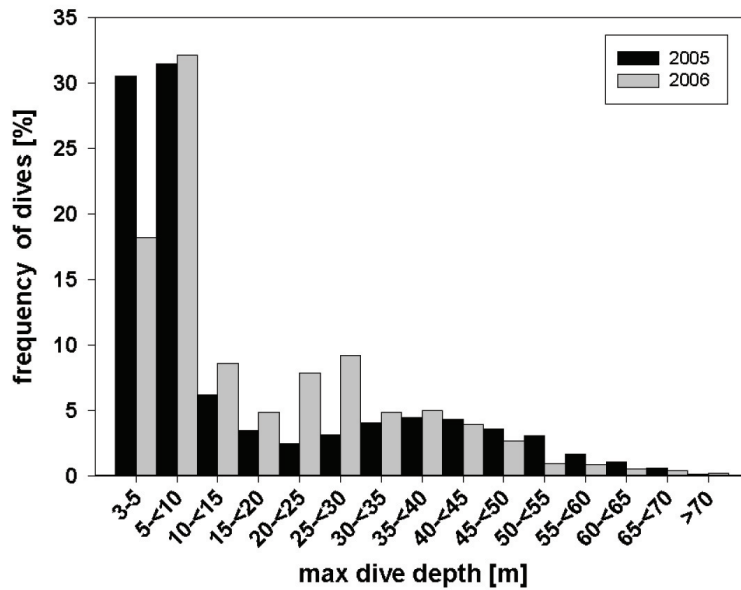


Figure 2.5: Dive frequency in 5 m intervals (the first interval comprises $\geq 3 - < 5$ m) for African penguins from Mercury Island, Namibia, in 2005 and 2006.

The median distance travelled for birds in 2006 was 60.8 km ($n = 12$; range 47.0 – 78.4; Table 2.3). The loop factor had a median of 2.9 ($n = 12$; range 2.4 – 3.5; Table 2.3).

The foraging range of birds in 2006 was not significantly correlated with trip duration (n.s.; $p = 0.3$; $R^2 = 0.135$; LM; Fig. 2.2b) and no significant differences were found in the foraging ranges of birds staying away overnight compared to birds leaving on one-day trips (n.s.; $p = 0.407$; GLM). Significant correlations were found considering the total distance travelled and the trip duration ($p < 0.05$; $R^2 = 0.573$; LM; Fig. 2.2b) and birds staying away overnight covered larger distances ($p < 0.05$; GLM).

There were no significant differences found neither in the foraging range, the total distance travelled nor in the loop factor calculated between both years ($n = 12$ birds for each year; $p = 0.939$, $p = 0.727$ and $p = 0.356$, respectively; GLM; Table 2.3).

Diving parameters

In 2005 and 2006, 4125 and 3573 dives deeper than three metres were recorded for twelve and ten penguins, respectively (Fig. 2.5). Dives shallower than ten metres were considered travelling dives whereas dives equal or deeper than ten metres were considered foraging dives in the following analysis. This differentiation between travelling and foraging dives was made following Ydenberg and Clark (1989) (see also Luna Jorquera and Culik, 1999; Tremblay and Cherel, 2003) due to the well-defined mode in the dive frequency distribution (Fig. 2.5).

2 Foraging areas and diving behaviour of African penguins

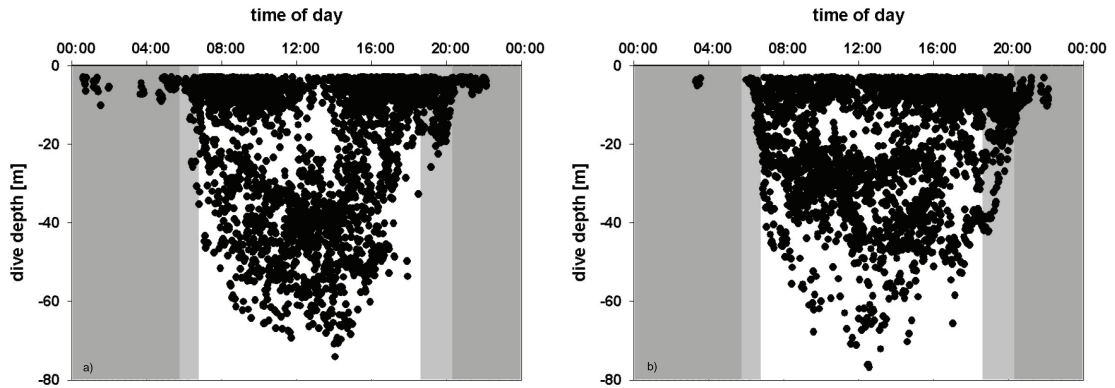


Figure 2.6: Maximum dive depth [m] for African penguins from Mercury Island, Namibia, in relation to time of day. Dark grey represents night hours, light grey represents nautical twilight and white represents daylight. Circles represent maximum depth of dives a) in 2005 and b) in 2006.

2005 For birds at Mercury Island in 2005, the median number of dives per foraging trip was 487 ($n = 12$ birds; range 94 – 605; Table 2.3). For birds staying away from the colony only for one day, the average number of dives was 404 dives per trip ($n = 9$ birds; range 94 – 447) whereas for birds staying away overnight, the median number of dives was 546 per trip ($n = 3$ birds, range 418 – 605). No diving took place later than 21:00 h (representing the end of the nautical twilight) by birds staying at sea overnight. Dives late in the evening and early in the morning were almost exclusively travelling dives (Fig. 2.6a). All three birds exhibiting overnight trips left in the late afternoon or night, swam and drifted towards their later foraging area where they foraged the following day. On this second day at sea, these birds dived 32.6 times per hour during daylight whereas birds on on-day trips dived 27.1 times per hour.

The majority of dives were recorded in the morning hours between 6:00 and 10:00 h and in the afternoon between 14:00 and 18:00 h (Fig. 2.7a). These include travelling dives of less than 10 m of depth because most birds commuted between the colony and the foraging area during those times (see 2.3.1, page 17). For foraging dives, the maximum number of dives was recorded between 14:00 and 16:00 h (Fig. 2.7b).

The median maximum depth reached by birds from Mercury Island in 2005 was 53.0 m ($n = 12$; range 41.6 – 74.1; Table 2.3). Median dive depth for all dives deeper than three metres was 7.0 m (mean of all dives 16.3 ± 16.85 m; $n = 12$ birds and 4125 dives) in 2005 (Table 2.3). Of all dives, 49.7 % were deeper than ten metres ($n = 1571$ dives) and can be considered as foraging dives (for definition see above). Thus, foraging dives reached on average a depth of 34.8 m. The deepest dives took place between 12:00 and 14:00 h (Fig. 2.8), representing the foraging dives in the main foraging area reached during midday.

Median dive duration for all dives deeper than three metres in 2005 was 42.0 s (mean of all dives 51.3 ± 28.5 s; $n = 12$ birds and 4125 dives; range 4 – 142; Table 2.3). For foraging

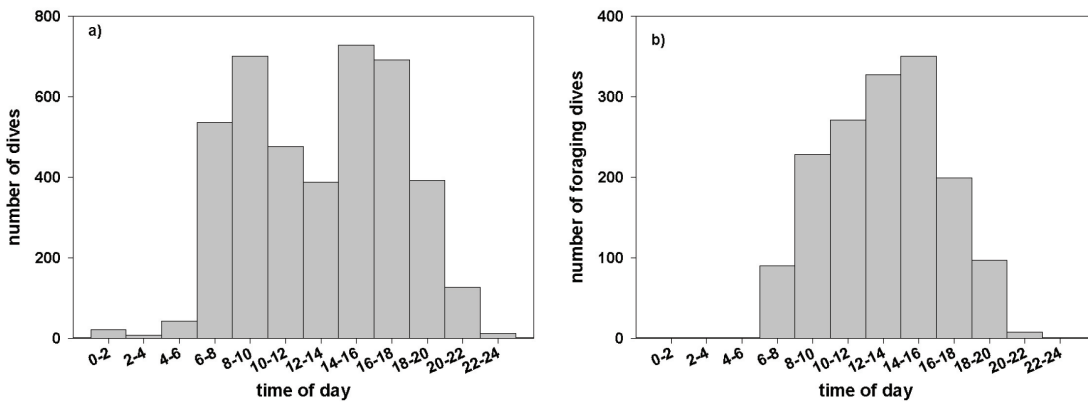


Figure 2.7: Relationship between number of dives and time of day for African penguins from Mercury Island, Namibia, in 2005 ($n = 12$ birds); a) including all dives ≥ 3 m; b) only foraging dives ≥ 10 m.

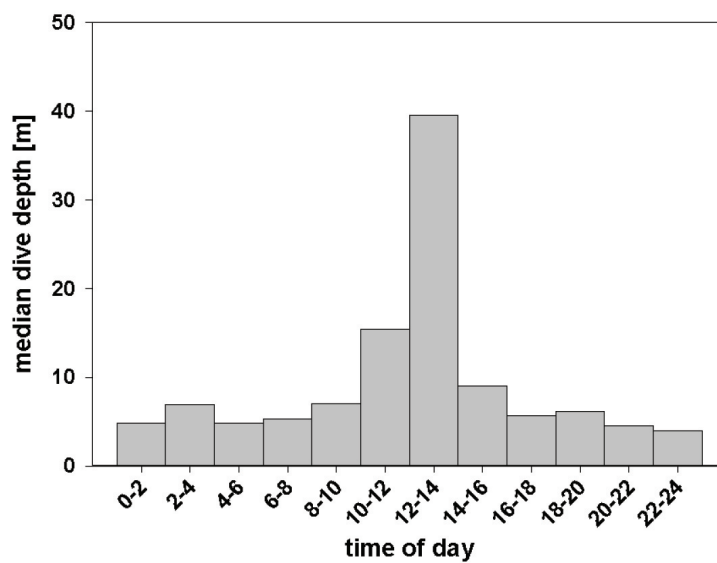


Figure 2.8: Distribution of dives ≥ 3 m of African penguins ($n = 12$ birds) from Mercury Island, Namibia, in 2005 in relation to time of day. Grey bars indicate median values.

2 Foraging areas and diving behaviour of African penguins

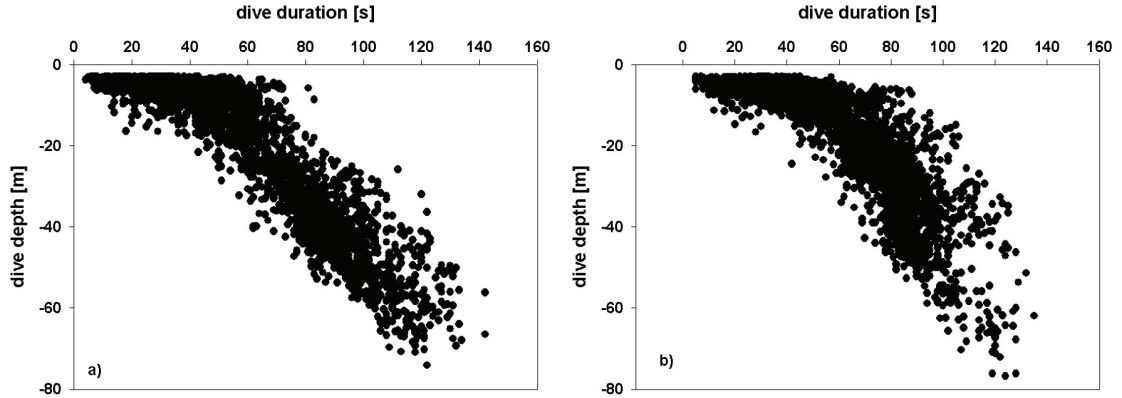


Figure 2.9: Relationship between dive duration [s] and dive depth [m] for African penguins from Mercury Island, Namibia, a) in 2005 and b) in 2006. Plotted are all dives ($n = 4125$ and 3573 dives) for twelve and ten birds in 2005 and 2006, respectively.

dives, the median dive duration was 82.0 s ($n = 1571$ dives; range $13 - 142$; Table 2.3). Dive duration was significantly correlated with dive depth ($p < 0.001$; $R^2 = 0.851$; LM; Fig. 2.9a).

2006 In 2006, the median number of dives per trip was 357 dives ($n = 10$ birds; range $173 - 559$; Table 2.3). For one-day trips the average number of dives per trip was 277 ($n = 6$ birds; range $173 - 476$) whereas birds staying away overnight dived 420 per trip ($n = 4$ birds; range $324 - 559$). More dives per hour were performed by birds staying at sea overnight when only considering daylight hours than by birds during one-day trips (median 28.3 vs. 20.4 dives/hour daylight).

Most dives were recorded between $16:00$ and $18:00$ h but dives were numerous between $6:00$ h in the morning and $20:00$ h in the evening and no prominent peaks as in 2005 could be observed (Fig. 2.10a). Foraging dives were recorded in large numbers between $8:00$ and $16:00$ h (Fig. 2.10b), which again corresponded to the time of deepest diving during the day (Fig. 2.6b and Fig. 2.11).

The deepest dives occurred between $12:00$ and $14:00$ h as in 2005 but dives to depth of at least 20 m occurred from $8:00$ until $16:00$ h (Fig. 2.11).

The median dive depth of the ten birds considered in this analysis was 10.0 m (mean of all dives 17.2 ± 14.53 m; $n = 3573$ dives; range $3.0 - 76.8$; Table 2.3). The average maximum diving depth was 53.7 m ($n = 10$ birds; range $35.1 - 76.8$). Of all dives, 38.1% were deeper than ten metres ($n = 1775$ dives) and therefore considered foraging dives. Foraging dives reached an average depth of 27 m (mean of all foraging dives 28.6 ± 12.86 m; $n = 1775$ dives; Table 2.3).

The median dive duration in 2006 was 55.0 s (mean of all dives 58.7 ± 25.5 s; $n = 10$ birds and 3573 dives; range $5 - 135$; Table 2.3). For foraging dives, the median duration was 80 s ($n = 1775$ dives; range $12 - 135$). Dive duration was significantly correlated with dive depth ($p < 0.001$; $R^2 = 0.731$; LM; Fig. 2.9b).

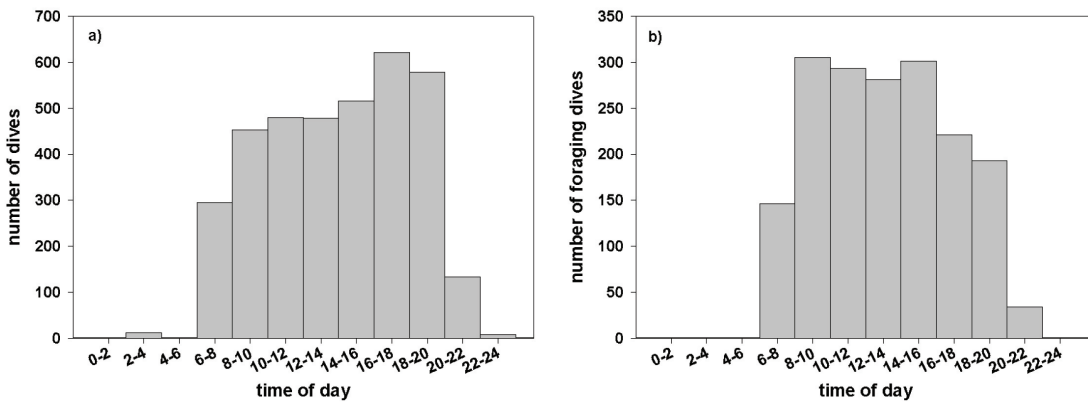


Figure 2.10: Relationship between number of dives and time of day for African penguins from Mercury Island, Namibia, in 2006 (n = 10 birds); a) including all dives ≥ 3 m and b) only foraging dives ≥ 10 m.

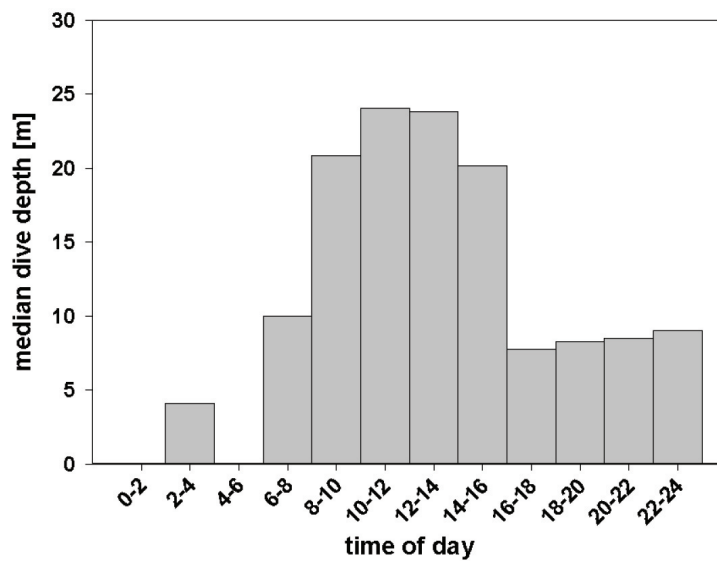


Figure 2.11: Distribution of dives ≥ 3 m of African penguins (n = 10 birds) from Mercury Island, Namibia, in 2006 in relation to time of day. Grey bars indicate median values.

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None of the diving parameters considered differed significantly between years (Table 2.3).

Diving and foraging efficiency

Foraging behaviour was analysed in further detail using the foraging and diving parameters considered above. Calculating, for example, the diving efficiency and the foraging efficiency may give an indication of prey availability and the success of the birds capturing this prey. Birds spent on average 15 ± 13 s ($n = 12$; range 0 – 89; median 12 s) and 19 ± 15 s ($n = 10$; range 0 – 79; median 16 s) in 2005 and 2006, respectively, at the bottom of their dives. So-called V-dives (see Wilson et al., 1996) with bottom times less than 2 s made up only 18.3 and 13.2 % of all dives in 2005 and 2006, respectively. Considering only foraging dives, the mean bottom time was 23 ± 15 s (median 24 s) in 2005 and 27 ± 15 s (median 29 s) in 2006. The bottom duration divided by the dive duration plus the post-dive surface time is defined as diving efficiency. The mean diving efficiency was 0.16 ± 0.14 (range 0 – 0.80) for birds from Mercury Island in 2005 and in 2006, mean diving efficiency was 0.18 ± 0.13 (range 0 – 0.70). For foraging dives (≥ 10 m) the diving efficiency was on average 0.16 ± 0.11 (range 0 – 0.62) in 2005. In 2006, the diving efficiency for foraging dives was 0.20 ± 0.12 (range 0 – 0.70). Considering the diving efficiency for different depth intervals, peaks in dive efficiency were found for dives of 15 – 25 m depth and 30 – 40 m depth in 2005 (dive efficiency = 0.18 and 0.17, respectively; Fig. 2.12). In 2006, the highest diving efficiency was found for dives 15 – 30 m deep (dive efficiency = 0.23 – 0.25; Fig. 2.12). Dive efficiency was overall higher (0.18 – 0.20) for dives up to depth of 45 m in 2006 than for any depth interval in 2005. For deep dives (50 – 75 m of depth), the dive efficiency was higher for birds in 2005 compared to 2006 (0.14 – 0.15 vs. 0.07 – 0.11, respectively; Fig. 2.12). Bottom times and diving efficiencies were significantly different between both years for all dives and for foraging dives ($p < 0.0001$, GLM). Means were calculated for dives of all birds combined for each year.

Foraging efficiency was defined here as the time spent diving as percentage of the time spent at sea during the entire trip. In 2005, birds spent on average 30.6 % ($n = 12$; range 14.2 – 49.6; Table 2.3) of their time at sea diving. For birds presenting one-day trips, the median foraging efficiency was 36.1 % ($n = 9$; range 14.2 – 49.6). For birds spending the night at sea, the median foraging efficiency was lower (25.5 %; $n = 3$; range 22.4 – 31.9), because birds did not dive during the night hours. Taking into account only hours, when the birds were actively diving (excluding drift hours during the night), birds spent 43.2, 33.1 and 49.3 % of the daylight hours diving, the foraging efficiency being above or similar to one-day trip birds.

In 2006, birds spent 29.5 % ($n = 10$; range 23.7 – 52.6; Table 2.3) of their time at sea diving. During one-day trips, birds dived on average 36.0 % ($n = 6$; range 28.0 – 52.6) of their time whereas birds during two-days trips dived 26.9 % ($n = 4$; range 23.7 – 30.7) of the entire time at sea. Considering only hours when diving took place, the median foraging efficiency was 47.2 % ($n = 4$; range 39.9 – 52.6), higher than during one-day trips.

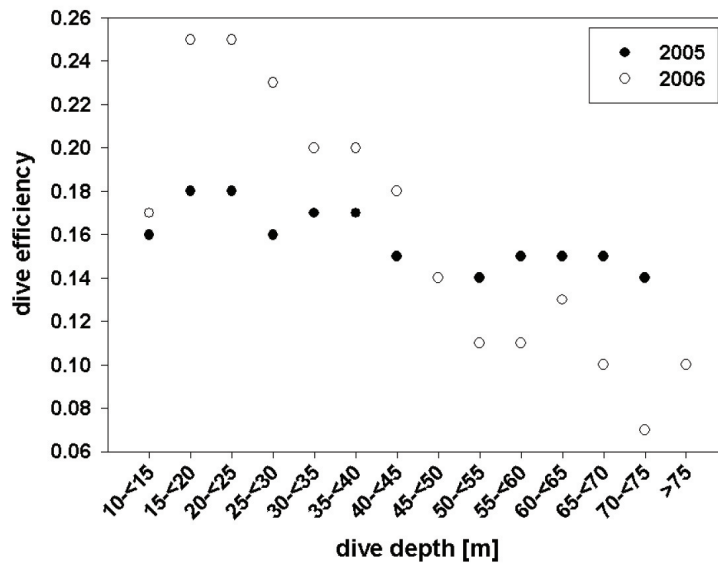


Figure 2.12: Relationship between dive depth [m] and dive efficiency for foraging dives of African penguins from Mercury Island, Namibia, in 2005 and 2006.

The total vertical distance travelled was used as an indicator for foraging effort (see Cherel et al., 1999; Tremblay and Cherel, 2003). The median vertical distance was 10.9 km ($n = 12$; range 5.0 – 20.1) in 2005 and 11.5 km ($n = 10$; range 8.0 – 18.3) in 2006 (Table 2.3).

The foraging efficiency and the vertical distance travelled did not differ significantly between 2005 and 2006 ($n = 22$ birds; $p = 0.766$ and $p = 0.528$, respectively; GLM; Table 2.3).

Diet

2005 All 24 stomach samples from birds breeding at Mercury Island contained pelagic goby (*Sufflogobius bibarbatus*). This species made up 84.0 % of the total mass of all samples. Other species occurring in the diet were anchovy (*Engraulis capensis*; 7.6 % by mass) and horse mackerel (*Trachurus capensis*; 4.4 %). Redeye (*Etrumeus whiteheadi*), Cape hake (*Merluccius capensis* and *M. paradoxus*, see Gordo et al., 2006), squid (unidentified) and sardine (*Sardinops sagax* or *S. ocellatus*, see Bianchi et al., 1999) were found in minor quantities (2.1 %, 1.1 %, 0.7 % and 0.03 %, respectively; Table 2.4).

2006 In 2006, pelagic goby was again the most important prey species in terms of the percentage of total mass of all 16 stomach samples. Pelagic goby made up 42.6 % of the total mass, but anchovy also contributed 34.8 %. Sardine, nearly absent in 2005, made up 19.1 % of the total prey mass. Other species found in the stomach samples were squid,

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horse mackerel and saury (*Scomberesox saurus scombroides*) (1.6 %, 1.2 % and 0.7 %, respectively; Table 2.4).

2.3.2 Possession and Halifax Islands

On Possession and Halifax Islands, only few penguins were equipped with GPS TDlog data loggers in 2005 and 2006, respectively.

Between the 6th and the 13th of March 2005, five chick-rearing African penguins were equipped with data loggers at the main breeding colony at Possession Island (Table 2.5). One of the birds did not leave to sea and the logger was taken off without recording any foraging trip. One bird stayed away for nine days and only data for the first two days at sea were recorded. For three remaining birds, data were obtained for complete foraging trips. The following analysis considers informations derived from these three birds, unless otherwise indicated.

In 2006, two breeding birds were equipped with data loggers at Halifax Island on the 7th of February 2006 (Table 2.5). One bird left the colony before the device started to work, therefore diving information is incomplete. This bird went on another foraging trip before the logger was detached, therefore two complete and one incomplete foraging trips were recorded for the two birds at Halifax Island.

Foraging area and trip duration

Possession Island At Possession Island, the three birds stayed east of the island within the area of Elizabeth Bay between the island and the Namibian coast (Fig. 2.13).

Two birds foraged exclusively north of the island whereas the third bird (bird 59-120305) travelled south at first, later reaching the same foraging area north of the island as the other two. The bird which stayed away for nine days, left Elizabeth Bay in a north-easterly direction, travelling north past Halifax and Ichaboe Islands, where other penguin colonies are located. When the recording stopped, after two days at sea, the bird had reached a distance of 118 km away from the colony. Whether the bird travelled further north or stayed in this area is unknown. The foraging ranges for the three birds staying within the bay were 6.2, 10.4 and 11.4 km (mean 9.3 ± 2.8 km; $n = 3$; Table 2.6). One bird left the following morning after logger deployment and returned the same afternoon after being at sea for 8 hours. This individual also showed the least foraging range. The other two birds left the colony in the evening hours, one within one hour after logger deployment and the other one the next day. Both birds stayed one night at sea, resulting in trip durations of 25 hrs 53 min and 27 hrs 33 min, reaching similar maximum distances of 10.4 km and 11.4 km away from the colony. The total distances travelled were 34.4, 61.0 and 76.1 km (mean 57.2 ± 21.1 km). The loop factor averaged 6.0 ± 0.5 for all three birds ($n = 3$; 5.6, 5.9 and 6.7; Table 2.6).

Halifax Island At Halifax Island, both birds equipped with data loggers swam in a north-westerly direction away from the colony (Fig. 2.13). The bird which made two trips had foraging ranges of 5.3 km and 5.5 km, whereas the second bird travelled further

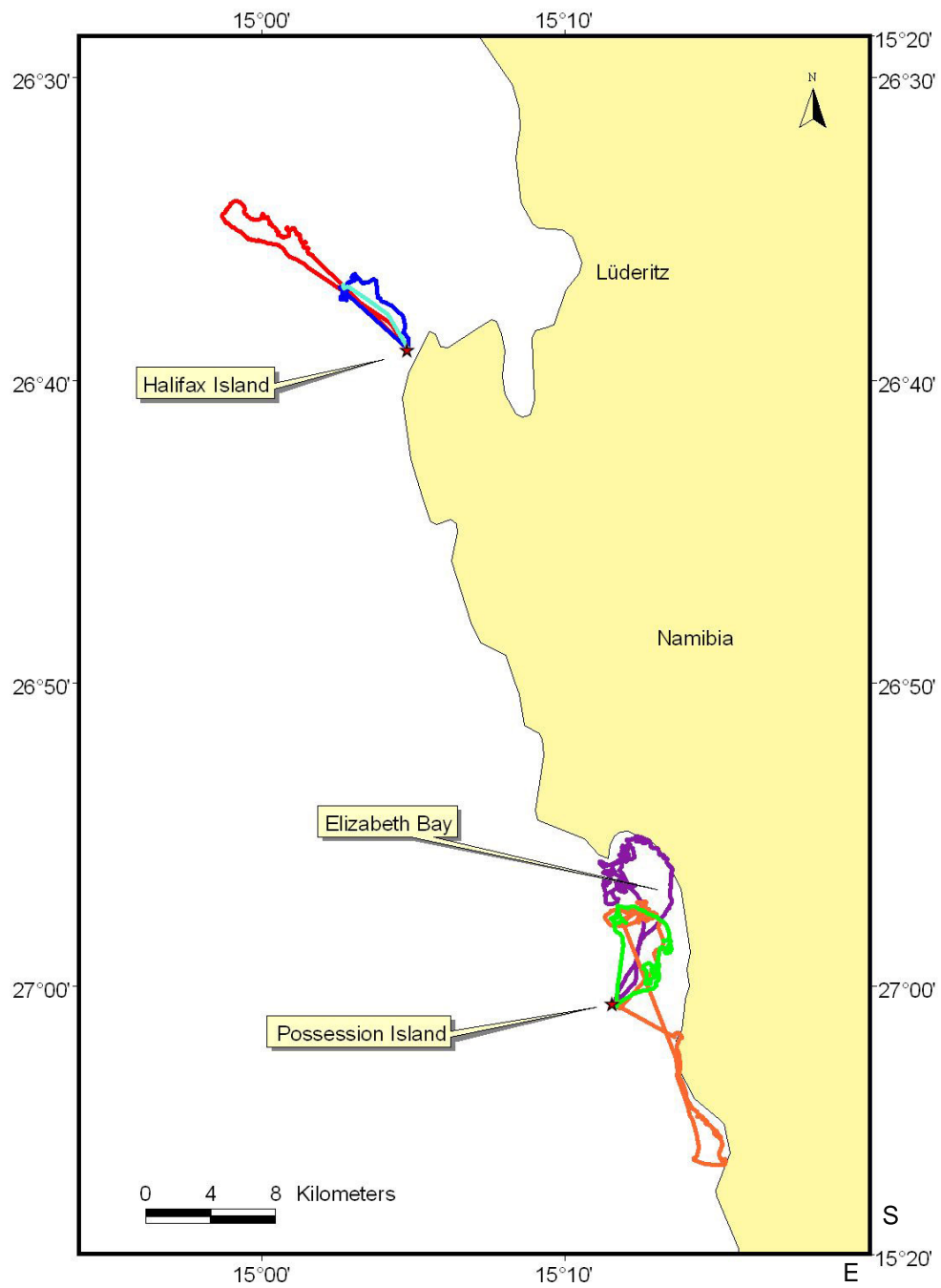


Figure 2.13: Foraging tracks of African penguins from Halifax and Possession Islands, Namibia. Birds at Halifax Island were equipped with GPD TDlog data loggers in 2006 and at Possession Island birds were equipped in 2005.

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away, reaching a maximum distance of 13.2 km. Actual distances travelled were 11.6 km and 17.7 km for the first bird and 35.7 km for the second bird (Table 2.6). The loop factor averaged 2.7 ± 0.5 ($n = 3$; 2.2, 3.2 and 2.7). Even though the device had not started to record when the first bird left to sea, departure time was known because the bird was observed leaving to sea. The first trip took place the same evening after deployment and lasted 3 hrs 29 min. The duration of the second trip, which started at midday the following day was 6 hrs 45 min. The second bird left early in the morning, arriving back at the colony in the evening of the same day after 12 hrs 12 min at sea.

Diving

Possession Island Birds at Possession Island dived 338, 849 and 747 times per trip (mean 645 ± 270 dives). The three birds reached maximum depths of 25.7, 33.4 and 27.6 m (mean 28.9 ± 4.0 m). The median depths were 8.7, 6.2 and 7.3 m (median of all dives 6.7 m; mean 9.7 ± 6.7 m; $n = 1934$ dives; Table 2.6). For foraging dives, the median dive depths were 15.4, 20.0 and 16.8 m (median of all dives 16.4; $n = 654$ dives) and the median dive durations were 56.0, 52.5 and 57 s (median of all dives 56.0 s) for foraging dives and 40.5, 27.0 and 38.0 s (median 33.0 s; mean 35.6 ± 20.6 s) for all dives (including travelling dives). For the bird staying away only during the day, 47.9 % of all dives were deeper than ten metres whereas for the two birds staying away overnight, only 28.5 and 33.5 % of all dives were foraging dives. Bottom time for all dives was on average 14 s (18, 12 and 15 s for each bird; mean 15.5 ± 12.7 s; $n = 1934$; range 0 – 73); for dives deeper than ten metres, the median bottom time was 17 s (27, 19 and 25 for each bird; $n = 654$; Table 2.6). The mean dive efficiency was 0.24 ± 0.18 (range 0 – 0.73) for all dives and 0.28 ± 0.13 (range 0 – 0.68) for foraging dives. Birds spent on average 34.9 ± 10.7 % of their time at sea diving. The bird being at sea only during the day had a foraging efficiency of 42.3 %, whereas the birds that stayed overnight had foraging efficiencies of 29.0 and 28.4 %. Considering only hours with diving activities, this increased to 42.1 and 47.0 %, respectively. The vertical distances travelled were 6.8, 16.6 and 14.3 km (mean 12.6 ± 5.1 km; Table 2.6).

Halifax Island For the two complete trips at Halifax Island, the number of dives were 317 and 336 per trip. The maximum diving depth reached was 52.5 and 46.5 m and the median depths were 5.4 m (mean 10.6 ± 13.2 m) and 14.5 m (mean 20.9 ± 15.1 m). The median dive durations were 26 s (mean 36.4 ± 29.1 s; $n = 317$ dives; range 9 – 131) and 53 s (mean 56.8 ± 26.5 s; $n = 336$ dives; range 7 – 112; Table 2.6). For dives deeper ≥ 10 m, the median dive depths were 41.8 and 36.3 m and the median durations for foraging dives were 105 and 80 s. The bottom times were 14 and 15 s on average for all dives and 35.5 and 25.0 s for foraging dives. Mean diving efficiency was 0.32 ± 0.18 and 0.17 ± 0.12 for all dives and 0.21 ± 0.13 and 0.19 ± 0.1 for foraging dives. The two birds spent 47.5 and 43.5 % of their time at sea diving and vertical distances of 3.4 km and 7.0 km were covered, respectively (Table 2.6).

Diet

Diet samples were only taken at Possession Island during the study period in 2005 and there is no diet information available for birds breeding at Halifax Island. Almost 90.0 % of the total mass of all nine stomach samples taken at Possession Island were made up by unidentified fish larvae. Other prey species found were anchovy (8.3 %) and squid (1.7 %) and small quantities of pipefish and *Nereis* sp.. The mean drained mass of individual stomach samples was 56.1 ± 61.8 g (range 0.1 – 190; Table 2.4). It is possible that this is an underestimate, because not necessarily all stomach contents are collected using the stomach flushing technique.

2.4 Discussion

The results presented here are considered to represent the natural foraging behaviour of African penguins. Nonetheless, possible consequences of data logger deployment on foraging in penguins are discussed in the following section. Foraging areas and diving behaviour of birds at Mercury Island are compared between both study years and differences to African penguins breeding at South Africa are pointed out. Subsequently, differences between the foraging behaviour of birds from the three different colonies studied are highlighted and the different behaviour is discussed in relation to hydrographic variability between the sites and to differences in colony sizes.

Device effects Negative effects (e.g. increased energetic cost of swimming and decreased diving efficiency) of externally attached devices on penguins have been reported by various authors (Wilson and Culik, 1992; Ropert-Coudert et al., 2007). The impact of logger attachment on the studied individuals was tried to be reduced in several ways during this study. Devices were attached according to Bannasch et al. (1994) on the lower back in order to reduce drag. Handling time was reduced to a minimum and birds were returned to their nests immediately after handling. Observations made in the colony showed that birds behaved in the same way as unequipped birds, usually leaving in the early morning hours, returning in the evening of the same day. The birds' departures shortly after attachment might have been due to stress induced by handling the bird or due to pecking by the partner when the device was noticed. Except for one bird at Mercury Island in 2005 and one bird at Possession Island, all birds returned to their nests within the expected time frame and returned to normal chick-rearing behaviour. Breeding failure of equipped birds was within the same margin as of unequipped birds. Longer foraging trip duration for equipped birds has been observed in other penguin species (Wilson et al., 1989a) but observations of unequipped birds in the colony led me to conclude that trip duration of unequipped birds was similar to that of equipped birds in this study. Birds only carried the device during one foraging trip with the exception of one bird at Halifax Island which performed two short trips within 24 hours. Only one partner per nest was equipped, therefore minimal impact on chick growth may be considered. Penguins breeding at the outer edges of colonies have been found to be less successful breeders (Kemper, 2006). They are often young and unexperienced birds, who

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might show a different (and potentially less successful) foraging behaviour. In order to minimise colony disturbance, most birds equipped were breeding within a few metres from the edge of the colony. Earlier studies on African penguins found reduced swimming speeds for birds fitted with larger devices (Wilson et al., 1986). Devices used in this study have been deployed on African penguins by Ryan et al. (2004) and Petersen et al. (2006) and no obvious effects on foraging behaviour have been recorded. A reduction in swimming speed without an increase in foraging trip duration would have led to a reduced foraging range. Ship-based surveys revealed highest penguin numbers in the same area as equipped birds were foraging a few days earlier. This implies that equipped birds did neither make longer foraging trips nor covered smaller distances owing to reduced swimming speed.

Possible underestimation of distance travelled The GPS devices used in this study provide positional information with an accuracy of less than 20 metres in intermittent mode (as used in this study; Ryan et al., 2004). Positions between recorded GPS fixes were interpolated, assuming a straight line in-between fixes. Large gaps between fixes occurred mostly during travelling, when birds are known to displace highly directional into the foraging area or back to the colony (Wilson, 2002; Ryan et al., 2004). The parameter *distance travelled* may still be considered as an underestimate of the total distance travelled by the bird because non-linear movements between known positions are not considered. Even though, it is still more accurate than earlier considerations taking into account only foraging trip duration and calculating the distance possibly covered during this time or when only considering the maximum distance reached away from the colony (Wilson, 1985; Wilson et al., 1988).

2.4.1 Mercury Island - Inter-annual comparison

Trip duration Being central place foragers, chick-rearing penguins are restricted to foraging areas close to their colony. African penguins, as well as the other *Spheniscus* species, are known to forage during the day, in most cases returning to their nest sites in the evening hours when brooding chicks (Wilson et al., 1988; Culik et al., 1998; Otley et al., 2004; Petersen et al., 2006; Steinfurth et al., submitted). The pattern of early morning departures and late evening returns for breeding African penguins was identical for birds in this study in Namibia and for birds in South Africa (Wilson et al., 1988; Wilson and Wilson, 1990; Petersen et al., 2006). Exceptions from this pattern could be due to stress or to extrinsic factors such as weather conditions at land or at sea. Because all birds in this study were surface-nesting without any protection against sun radiation (Kemper, 2006), the two birds in 2006 might have left the colony during the day due to heat stress. Trip duration was not significantly different between both years and correlated positively with the foraging range and the total distance travelled, especially for birds in 2005. Overnight trips resulted in larger foraging ranges, possibly as a result of the birds' drifting towards the foraging area during the night. Whether birds intentionally leave in the evening in order to reach further distances or whether this behaviour is due to other factors mentioned above, remains unclear. Birds spending the night at

sea had higher dive rates during daylight hours, presumably taking advantage of the fact that they were already closer to their foraging area after spending the night at sea. But thermoregulative costs of drifting at night must be considered (Humphreys et al., 2007) although penguins might be able to apply mechanisms to save energy in cold water (Wilson and Grémillet, 1996, G. Luna Jorquera unpubl. data). Higher dive rates on the second day at sea might be necessary to make up for energy lost during the night. Petersen et al. (2006) found trip duration to be a good proxy for foraging effort in African penguins, with longer trip duration indicating reduced food availability. Penguins breeding at Mercury Island spent more time at sea compared to birds in South Africa (Petersen et al., 2006), indicating a possibly reduced food availability around the island.

Foraging area The inability of penguins to fly and to cover vast areas looking for sparse and unpredictable prey within limited time forces them to rely on spatially and temporal predictable prey in foraging areas relatively close to their colony (Wilson, 1985; Tremblay and Cherel, 2003). Foraging areas used by the birds from Mercury Island in 2005 and 2006 were almost identical, being located about 20 km north-west of the island. No significant differences were found in foraging ranges or in distances travelled between 2005 and 2006. In 2005, some birds reached an area slightly further away than in 2006, but the main area used for foraging was identical in both years.

Areas where birds are found to spend most of their time at sea can be considered important feeding areas (Weimerskirch, 2007). Birds usually commute directly between colony and foraging area, with shallow dive sequences and highly directional travel indicating commuting patterns, followed by reduced speed and increased vertical movements without large horizontal displacement when actively foraging (Culik et al., 1998; Wilson, 2002; Ryan et al., 2004; Petersen et al., 2006). When spending the night at sea, birds drift slowly, remaining longer in one single area. Although passage-ways are not important for the birds in terms of their feeding behaviour, the identification of those highly frequented areas is important when considering possible threats, such as oiling or entanglement in fishing gear. Birds leaving the island travelled almost directly towards their eventual foraging area, also demonstrated by loop factors very close to the value 2, which means that birds did not roam before reaching their final destination. After spending some time diving and presumably feeding, they swam more or less directly back to the colony. This indicates predictable food availability in the area frequented by the birds during the time of this study. Humboldt penguins in the south-east Pacific also travelled in a straight line towards the eventual feeding area in some cases but birds from Pan de Azúcar (breeding colony in central Chile) were found to be circling, covering larger area. No preference for specific marine areas or for certain foraging strategies were found by Culik et al. (1998) for Humboldt penguins.

Wilson (1985) and Petersen et al. (2006) found similar foraging ranges for African penguins breeding at South African colonies, although birds breeding at Robben and Dassen Islands travelled shorter distances and had smaller foraging ranges than birds breeding at a mainland site (Petersen et al., 2006). The loop factor was also much higher

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for birds breeding at Robben and Dassen Islands. This was found to be due to intensive foraging close to the island without long commuting into foraging areas. Humboldt penguins off the Chilean coast were found to feed within a 20 – 25 km range from the breeding colony (Culik et al., 1998; Boersma et al., 2007), comparable to birds at Mercury Island. Galápagos penguins were found to feed closer to their nest sites, often within one kilometre off the coast (Steinfurth et al., submitted).

Short foraging trips and foraging areas close to the colony during the chick rearing period indicate predictable marine resources (Tremblay and Cherel, 2003). Birds in South Africa were feeding closer to their colonies (Petersen et al., 2006) than birds at Mercury Island. Their main prey consisted of anchovy and sardine (Petersen et al., 2006), high-energetic prey, which is almost absent from Namibian waters due to overfishing (Cury et al., 2005). Penguins at Mercury Island spent more time foraging in areas further away from their colony than birds in South Africa and their prey consisted of less-energetic fish species. Nonetheless, birds fed in the same area in both years which indicates a predictable food source. But continuously decreasing numbers of breeding pairs demonstrate that food availability is not sufficient in order to sustain the breeding population at Mercury Island. Penguin numbers had been increasing slightly in South Africa within the last years², which seemed to be due to a better food availability after fishery restrictions prevented the total collapse of pelagic fish stocks (Kemper et al., 2001; Cury et al., 2005; Crawford et al., 2006a). An eastward shift of prey species has led to an anew population decline of African penguins in South Africa and to changes in the distribution of breeding sites just recently (Koenig, 2007).

Diving behaviour in relation to prey Penguins are visual foragers, therefore most diving activity takes place during daylight hours (Green et al., 1998; Jansen et al., 1998; Luna Jorquera and Culik, 1999; Tremblay and Cherel, 1999). This is also the case in African penguins in Namibia, with all foraging dives being performed between sunrise and sunset or within nautical twilight (when the sun is less than 12° below the horizon) (Fig 2.6).

The deepest dives in this study were observed during midday. This may have several reasons. For example, the main foraging region (and therefore the area where dives were likely to be the deepest) was reached during midday. Alternatively, increased illumination and light penetration during midday allows penguins to detect their prey further down the water column (Luna Jorquera and Culik, 1999). In addition, vertical migration of prey organisms may force penguins to dive deeper during midday hours.

Basic diving parameters, such as dive depth and dive duration, did not differ between 2005 and 2006 and agree well with other studies on African penguins (Wilson, 1985; Petersen et al., 2006). Petersen et al. (2006) found a mean maximum dive depth of 50.6 and 52.1 m with a maximum dive depth of 69.4 m, similar to the median maximum dive depth for birds at Mercury Island (55.3 and 55.5 m in 2005 and 2006, respectively). The maximum dive depth recorded in Namibia was 76.8 m, although a maximum dive depth of 130 m has been recorded for African penguins using a depth gauge (Wilson,

²http://web.uct.ac.za/depts/stats/adu/species/sp003_09.htm

1985). Factors such as dive depth and dive duration might be physiologically limited (Kooyman and Kooyman, 1995) and might therefore be less useful for gauging prey availability although parameters, such as undulations during bottom time, may be used for determining prey capture events (see Simeone and Wilson, 2003).

Differences in diving behaviour and in parameters derived from diving patterns, such as diving efficiency, foraging efficiency and vertical distance, may be related to different prey being available in both years at Mercury Island. Birds in 2006 showed a higher diving efficiency during foraging dives (0.20 ± 0.12 in 2006 vs. 0.16 ± 0.11 in 2005), especially in depths between 15 and 45 m. For dives deeper than 50 m, dive efficiency in 2005 was higher than in 2006. It appears that birds in 2006 did not have to dive as deep as birds in 2005 in order to reach their prey and had therefore a better dive efficiency for lower dives (due to longer bottom phases representing food intake; see Ropert-Coudert et al., 2000, 2001). Birds in 2006 were feeding to a large extent on anchovy and sardine, both strictly pelagic species found in the upper 30 m of the water column. Birds in 2005 were almost exclusively feeding on pelagic goby, a demersal species whose juveniles may also be found within the water column. Birds in 2005 showed deeper dive depth presumably feeding on more demersal prey and some dives might have been benthic dives, as has been found for other penguin species (Tremblay and Cherel, 2000). The shelf edge region in which birds were feeding is on average 350 m deep (Bianchi et al., 1999), but birds were mostly feeding within the 100 m isobath and in some areas the sea bottom could have been reached (see Chapter 3). Since pelagic goby has a lower energy content than anchovy and sardine (Crawford et al., 1985; Mecenero et al., 2006a), deep diving for less energetic food indicates poorer food availability and probably the absence of other prey species during the study period in 2005 (see also Chapter 3). Birds in both years spent between 30 and 50 % of their time at sea diving. Values for other penguin species may be as high as 79 % (see Cherel et al., 1999, for rockhopper penguins) and lower food availability could hardly be compensated by increased diving in that case. In the case of birds from Mercury Island, a relatively low foraging effort is due to the long commuting between the colony and the feeding area and it is doubtful whether diving time could be increased if food availability would further decrease.

2.4.2 Mercury, Possession and Halifax Islands - Latitudinal comparison

Sample sizes of birds equipped with data loggers at Possession and Halifax Islands were smaller than at Mercury Island but differences in foraging behaviour between the islands were nevertheless clear. Distinct environments are the main component in shaping foraging behaviour of seabirds (Tremblay and Cherel, 2003). Prey availability might differ around colonies due to differences in the topographic locations of colonies (in-shore/offshore) or hydrographic characteristics (Hamer et al., 2001b; Garthe et al., 2007b). This seems to be the case for the different penguin breeding islands off the Namibian coast. Although, all of them are located within the Benguela upwelling system, differences in hydrography, bathymetry and hence different prey availability result in different foraging patterns.

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Foraging trip durations were shorter and maximum foraging ranges were smaller for birds at Halifax Island than for birds at Mercury Island, but the overall behaviour was similar for birds at both islands. Birds travelled in a north-westerly direction, directly reaching their feeding grounds (loop factor of 2.7 compared to 2.8 and 2.9 for Mercury) and reached similar diving depths as birds at Mercury Island. Diving patterns were similar to birds at Mercury Island, although commuting distances were shorter at Halifax Island. The strength of the Lüderitz upwelling cell inhibits large phytoplankton growth because of strong wind-induced mixing and a deeper surface layer (Demarcq et al., 2003). Diet of birds at Halifax Island might therefore differ from birds at Mercury Island but the foraging behaviour observed indicates a comparable food availability. Although breeding success at Halifax Island is the lowest in Namibia, it is the only breeding site in Namibia where numbers of adults are increasing (Kemper, 2006). This increase is likely to be due to the immigration of young, inexperienced breeders from other areas (Whittington et al., 2005; Kemper, 2006); poor breeding success at this site might therefore not necessarily be due to limited food availability.

The foraging behaviour of birds from Possession Island differed from that of birds at Mercury and Halifax Islands. Birds stayed within Elizabeth Bay and foraging ranges were small although total distances travelled were long for single individuals. Birds used large areas within the bay and one bird even foraged south and north of the island within one trip, leading to a loop factor of 6, more than twice as high as for birds from Mercury and Halifax Islands. The main prey taken by birds breeding at Possession Island was fish larvae which is thought to have a very small energy content. Fish larvae are often caught by juvenile penguins due to their inability to catch fast swimming prey (Wilson, 1985). Chiaradia et al. (2007) found a higher fledging success for little penguins (*Eudyptula minor*) foraging in shallow waters due to a more efficient prey capture close to the seabed (Ropert-Coudert et al., 2006). Prey availability seems poor in the vicinity of Possession Island, despite a favourable bathymetry, and is likely to be responsible for the rapid decline in penguin numbers there (Kemper et al., 2001; Kemper, 2006). The large numbers of penguins breeding at Possession Island in former times were presumably feeding on sardines (Crawford, 1999). In the 1980s, Crawford et al. (1985) found birds feeding almost exclusively on cephalopods. Pelagic goby is not present around the island; goby distribution shows a gap between south of Lüderitz and the Orange River (Cruickshank et al., 1980). In addition, fish availability is considered to be low due to mining activity within Elizabeth Bay, as demonstrated by low reproductive output and reduced feeding activity of shorebirds breeding along the bay's beaches (Simmons, 2005).

The Lüderitz upwelling cell divides the northern Benguela Current into two regions with different prey composition north and south of the cell (Mecenero et al., 2006b). Birds at Halifax and Mercury Islands seem to be profiting from enhanced upwelling and higher productivity around the islands. Predominant foraging in a north-westerly direction of the islands might be explained by possible small scale upwelling due to the bathymetry around the islands and a downstream increase in prey availability (Marín et al., 2003). Prey abundance and distribution varies spatially due to the complex system of upwelling cells in the Benguela Current. Differences in diet composition and resulting differences in foraging behaviour of birds from different colonies may therefore be expected. Diet

studies in Cape fur seals (*Arctocephalus pusillus pusillus*) along the Namibian coast have found fewer horse mackerel in the diet of seals south of Lüderitz. In contrast, in the north, horse mackerel constituted one of the main prey items (Mecenero et al., 2006b). Fish stocks are mainly concentrated between Lüderitz and the Angola-Benguela Front in the north (Roux, 2003). Since seasonality is known for possible prey species in the study area (de Bruyn et al., 2003; Mecenero et al., 2006c) and the Benguela marine ecosystem is known to be highly variable (Roux, 2003), results presented here may only be considered for the study period of February and March 2005 and 2006. Seasonal differences in diet composition, as well as the diet of non-breeding birds and associated foraging behaviour need to be further investigated. Diet data from the Ministry of Fisheries and Marine Resources indicate a more diverse diet in the pre-breeding season in some years. Differential prey availability at different latitudes and colonies may account for colony-specific breeding seasonality patterns (Kemper et al., 2001). Numbers of breeding African penguins have been severely reduced at all Namibian breeding sites, the adult population had decreased at a rate of 2.6 % per year between 1996 and 2001 (Kemper et al., 2001) and continues to decrease (Kemper, 2006). Mercury Island hosts the largest number of penguins in Namibia. The population increased between the early 1990s and 1996 but has declined by 3.7 % per year between 1996 and 2004 (Kemper, 2006). The increase of the number of birds breeding at Mercury Island during the early 1990s has partly been ascribed to the availability of pelagic goby after the collapse of the sardine stock (Crawford et al., 1985; Crawford, 1998). However, it appears that current fish stocks in the vicinity of Mercury Island have been insufficient since the mid-1990s. Although penguin numbers have decreased by 75 % since the 1950s at Halifax Island, recent counts show an increase of 8.9 % per year between 1996 and 2004. In contrast, numbers at Possession Island, once the largest breeding colony of African penguins in Namibia, declined by 8.0 % per year between 1996 and 2004 (Kemper, 2006). Positive population trends at Halifax might be due to better food availability, indicated by short foraging trip duration and direct commuting to foraging areas nearby. More studies concerning feeding behaviour and diet of penguins breeding at Halifax Island are necessary.

Differences in colony size and foraging distances Besides food availability, competition for food might also be an important factor when considering differences between Namibian breeding sites.

Due to intra-specific competition for food, seabirds from larger colonies usually have to forage further away from their colony, exploiting larger areas in order to obtain food (Lewis et al., 2001). Mercury Island supports the largest number of breeding African penguins in Namibia. This study shows that birds from Mercury Island forage further away than birds from smaller colonies, such as Halifax and Possession Islands. If this was due to limited food sources reduced by intra-specific competition, birds would have to use a larger area around the colony in order to escape competition. All study birds from Mercury Island foraged in a limited area. Predictable food availability rather than a need to outmanoeuvre potential competitors seems to be the reason for the larger foraging range. Competition appears to be negligible at Possession Island following a

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strong population decline of African penguins there. This lack of competition may explain the small foraging ranges of penguins from Possession Island. Taking into account the poor quality of the diet, it seems more reasonable to assume that prey availability is low within the possible foraging range. Energetic limitations prevent birds from increasing their foraging range. At this stage, due to the small sample size and the lack of dietary information, it is not possible to make any conclusive statements about the potential role of competition and food availability for birds at Halifax Island.

While breeding space is not a limiting factor for the growth of this depleted regional population of African penguins, lack of food appears to be a key factor in preventing an increase in penguin numbers in Namibia.

Table 2.1: Logger deployment, departure and arrival times and trip duration for 13 African penguins from Mercury Island, Namibia, equipped with GPS TDlog data loggers in 2005.

Bird ID	Deployment		Departure		Arrival		Trip duration hours
	Date	Time	Date	Time	Date	Time	
58-130205	12.2.05	17:00	13.2.05	6:28	13.2.05	19:48	13:20
58-150205	14.2.05	18:11	15.2.05	5:57	15.2.05	19:46	13:49
59-150205	14.2.05	18:22	14.2.05	18:31	15.2.05	17:27	22:56
58-170205	16.2.05	19:00	17.2.05	6:02	17.2.05	18:55	12:53
59-170205	16.2.05	18:41	17.2.05	6:24	17.2.05	18:58	12:34
58-190205	18.2.05	18:53	19.2.05	6:18	19.2.05	18:20	12:02
59-190205	18.2.05	19:05	19.2.05	6:45	19.2.05	17:42	10:57
58-210205	20.2.05	18:35	20.2.05	18:53	21.2.05	22:11	27:18
59-210205	20.2.05	18:25	21.2.05	6:19	21.2.05	18:20	12:01
58-230205	22.2.05	18:23	23.2.05	4:08	23.2.05	19:07	14:59
59-230205	22.2.05	19:55	22.2.05	23:16	23.2.05	19:09	19:53
59-260205	25.2.05	17:40	26.2.05	4:34	26.2.05	19:16	14:42
58-010305	25.2.05	17:10	26.2.05	6:25	1.3.05	17:30	83:05

Table 2.2: Logger deployment, departure and arrival times and trip duration for 13 African penguins from Mercury Island, Namibia, equipped with GPS TDlog data loggers in 2006. *Unknown* refers to devices not having worked properly.

Bird ID	Deployment		Departure		Arrival		Trip duration hours
	Date	Time	Date	Time	Date	Time	
58-160206	15.2.06	18:09	16.2.06	7:04	16.2.06	17:00	9:56
74-160206	15.2.06	18:20	16.2.06	2:21	16.2.06	17:33	15:12
59-180206	16.2.05	17:29	17.2.06	13:57	18.2.06	14:46	24:49
135-170206	16.2.05	17:38	17.2.06	6:13	17.2.06	19:11	12:58
58-180206	17.2.06	17:31	18.2.06	5:49	18.2.06	18:20	12:31
74-180206	17.2.06	17:40	17.2.06	18:00	18.2.06	18:45	24:45
58-220206	21.2.06	17:33	unknown	unknown	22.2.06	unknown	unknown
74-220206	21.2.06	17:45	22.2.06	6:27	22.2.06	21:17	14:50
59-240206	22.2.06	17:42	23.2.06	14:27	24.2.06	15:17	24:50
135-240206	22.2.06	17:51	23.2.06	6:42	23.2.06	22:12	15:30
58-250206	23.2.06	17:56	24.2.06	6:40	24.2.06	unknown	unknown
74-250206	23.2.06	18:09	25.2.06	6:15	25.2.06	18:44	12:29
59-280206	27.2.04	18:02	27.2.06	18:33	28.2.06	20:00	25:27
135-280206	27.2.06	18:30	28.2.06	6:11	28.2.06	unknown	unknown

Table 2.3: Foraging and diving parameters for African penguins from Mercury Island, Namibia, equipped with GPS TDlog data loggers in 2005 and 2006.

	Mercury Island 2005			Mercury Island 2006			Statistics 2005 vs. 2006	
	n	median	range	n	median	range	test	p-value
Trip duration [hrs:min]	12	13:34	10:57 - 27:18	11	15:12	9:56 - 25:27	GLM	p = 0.414
Foraging range [km]	12	21.6	14.1 - 31.9	12	20.9	16.6 - 26.6	GLM	p = 0.939
Distance travelled [km]	12	57.0	44.4 - 91.1	12	60.8	47.0 - 78.4	GLM	p = 0.727
Loop factor	12	2.9	2.4 - 3.2	12	2.9	2.4 - 3.5	GLM	p = 0.356
Number of dives per trip	12	487	94 - 605	10	358	173 - 559	GLM	p = 0.823
Maximum dive depth [m]	12	53.0	41.6 - 74.1	10	53.7	35.1 - 76.8	GLM	p = 0.963
Overall dive depth [m]	12	7.0	3.0 - 74.1	10	10.0	3.0 - 76.8	LMER	p = 0.982
Foraging dive depth [m]	12	34.8	10.0 - 74.1	10	27.0	10.0 - 76.8	LMER	p = 0.148
Overall dive duration [s]	12	42.0	4 - 142	10	55.0	5 - 135	LMER	p = 0.79
Foraging dive duration [m]	12	82.0	13 - 142	10	80.0	12 - 135	LMER	p = 0.054
Overall bottom time [s]	12	12.0	0 - 89	10	16.0	0 - 79	LMER	p < 0.0001
Foraging bottom time [s]	12	24.0	0 - 89	10	29.0	0 - 79	LMER	p < 0.0001
Foraging efficiency [%]	12	30.6	14.2 - 49.6	10	29.5	23.7 - 52.6	GLM	p = 0.766
Vertical distance [km]	12	10.9	5.0 - 20.1	10	11.5	8.0 - 18.3	GLM	p = 0.528

Table 2.4: Diet composition of African penguins at Mercury and Possession Islands, Namibia. Given are the percentages of each species of the entire mass of all stomach samples combined, n indicates the number of stomach samples taken in each year and at each colony.

Common name	Scientific name	Mercury 2005		Mercury 2006		Possession 2006	
		n = 24	% of total mass	n = 16	% of total mass	n = 9	% of total mass
Pelagic goby	<i>Sufflogobius bibarbatus</i>	84.0		42.6		0.0	
Anchovy	<i>Engraulis capensis</i>	7.6		34.8		8.3	
Sardine	<i>Sardinops sagax</i>	0.03		19.1		0.0	
Cape hake	<i>Mertuiccius capensis</i>	1.1		0.0		0.0	
Horse mackerel	<i>Trachurus capensis</i>	4.4		1.2		0.0	
Saury	<i>Scomberesox saurus scomberoides</i>	0.0		0.7		0.0	
Redeye	<i>Etrumeus whiteheadi</i>	2.1		0.0		0.0	
Pipefish	unidentified	0.1		0.0		0.02	
Squid	unidentified	0.7		1.6		1.7	
Fish larvae	unidentified	0.0		0.0		89.9	

2 Foraging areas and diving behaviour of African penguins

Table 2.5: Logger deployment, departure and arrival times and trip duration for five African penguins from Possession Island, Namibia, in 2005 and two African penguins from Halifax Island, Namibia, in 2006 equipped with GPS TDlog data loggers.

Island	Bird	Trip	Deployment		Departure		Arrival		Trip duration hours
			Date	Time	Date	Time	Date	Time	
Possession	59-070305	1	6.3.05	18:51	7.3.05	8:45	7.3.05	16:44	7:59
Possession	59-090305	1	8.3.05	17:10	8.3.05	18:29	9.3.05	20:22	25:53
Possession	59-120305	1	10.3.05	17:00	11.3.05	17:49	12.3.05	21:22	27:33
Possession	59-140305	1	13.3.05	19:14					
Possession	59-150305	1	6.3.05	18:19	7.3.05	7:00	15.3.05	18:06	410:06
Halifax	58-080206	1	7.2.06	16:08	7.2.06	17:00	7.2.06	20:29	3:29
Halifax		2			8.2.06	12:20	8.2.06	19:05	6:45
Halifax	74-080206	1	7.2.06	15:55	8.2.06	5:48	8.2.06	18:00	12:12

Table 2.6: Foraging and diving parameters for African penguins from Possession and Halifax Islands, Namibia, in 2005 and 2006, respectively.

	Possession individual birds		Halifax individual birds	
	59-070305	59-090305	59-120305	58-080206 ¹ 58-080206 ² 74-080206
Trip duration [hrs:min]	7:59	25:53	27:33	3:29 6:45 12:12
Foraging range [km]	6.2	10.4	11.4	5.3 5.5 13.2
Distance travelled [km]	34.4	61.0	76.1	11.6 17.7 35.7
Loop factor	5.6	5.9	6.7	2.2 3.2 2.7
Number of dives per trip	338	849	747	incomplete 317 336
Maximum dive depth [m]	25.7	33.4	27.6	incomplete 52.5 46.5
Overall dive depth [m]	8.7	6.2	7.3	incomplete 5.4 14.5
Foraging dive depth [m]	15.4	20.0	16.8	incomplete 41.8 36.3
Overall dive duration [s]	40.5	27.0	38.0	incomplete 26.0 53.0
Foraging dive duration [s]	56.0	52.5	57.0	incomplete 105.0 80.0
Overall bottom time [s]	18.0	12.0	15.0	incomplete 14.0 15.0
Foraging bottom time [s]	27.0	19.0	25.0	incomplete 35.5 25.0
Foraging efficiency [%]	47.3	29.0	28.4	incomplete 47.5 43.5
Vertical distance [km]	6.8	16.6	14.3	incomplete 3.4 7.0

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3 Sulphide eruptions and their implication for foraging in African penguins (*Spheniscus demersus*)

3.1 Introduction

Seabirds are strongly influenced by harsh weather conditions as well as changes in the marine environment (Furness and Monaghan, 1987). Breeding is often negatively affected by either unfavourable weather (Velando et al., 1999; Schreiber, 2001) or by limited food availability due to changes in their marine habitat (Duffy et al., 1984; Dann et al., 2000; Crawford et al., 2006a).

Large scale phenomena, such as the El Niño Southern Oscillation (ENSO), affect all trophic levels within the marine ecosystem, often leading to food limitations for seabirds and thus breeding failures during such events (Boersma, 1998; Vandenbosch, 2000; Simeone et al., 2002). Changes of biological and hydrographic parameters affecting only small scale localised areas and therefore only single colonies, might often occur without being noticed by scientists. Birds are often capable of buffering unfavourable environmental conditions. By switching to different prey, increasing their foraging range or feeding less frequently, they are able to successfully raise their chicks even though food is limited (Croxall et al., 1988; Hennicke and Culik, 2005; Clarke et al., 2006; Quillfeldt et al., 2007). Otherwise, unfavourable conditions lead to a reduced breeding output or even to complete breeding failures.

A phenomenon which affects small scale areas of the ocean but occurs quite frequently along the southern Namibian coast especially during austral summer is the so-called sulphide eruption (Emeis et al., 2004; Weeks et al., 2004, see Chapter 1). Such events influence all trophic levels due to the hypoxic or even anoxic conditions in the water column following the eruptions of hydrogen sulphide gas chambers in the sediment (Weeks et al., 2002, 2004). Many organisms cannot support such low oxygen levels and either die or migrate away from the affected area (Hamukuaya et al., 1998; Weeks et al., 2004). It can therefore be assumed that sulphide eruptions have strong influence on fish assemblages and thus on the foraging behaviour of seabirds in Namibia.

In this chapter, the effects of sulphide eruptions on the foraging behaviour of African penguins breeding at Mercury Island are investigated. Foraging areas of penguins overlap with areas where sulphide eruptions are known to occur. Presumably, diving and feeding behaviour of African penguins should be correlated to the conditions within the water column during such events. Hydrographic conditions are considered as a main

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factor influencing seabird foraging ecology and may also be reflected in the birds' diet composition.

3.2 Methods and study site

Data logger deployment During the breeding season 2005, 13 African penguins were equipped with GPS TDlog data loggers (earth&OCEAN technologies, Kiel, Germany) at Mercury Island (25°38'S, 14°50'E) between the 13th and the 26th of February 2005. Devices used in this study allow the identification of areas frequented for foraging, the diving behaviour of each individual bird and, by measuring the water temperature *in situ* while the birds are at sea, allow the characterisation of temperature distribution within the water column. Pressure and temperature sensors record water depth and water temperature with a precision of 4 mbar and 5 mK, respectively. The positional accuracy using the intermittent mode lies between ten and 20 m (product information earth&OCEAN technologies and Ryan et al., 2004). For further details on device dimensions and deployment in the field see Chapter 2 and Appendix A.

Dive analysis Data from twelve birds are included in the following analysis (see Chapter 2). General dive analysis was performed as described in Chapter 2. Analysis of benthic dive behaviour followed Tremblay and Cherel (2000), taking into account dives reaching depths within $\pm 10\%$ of the previous dive depth. Those dives presumably reach the sea bottom, therefore only dives deeper than 50 m were considered for this analysis due to the bathymetric characteristics of the foraging area. The vertical distance was calculated as the sum of all dive depths multiplied by two, comprising the descending and ascending distances. Water temperature analysis was carried out for foraging dives (≥ 10 m of depth) using the data obtained by the temperature sensor incorporated in the logger. The sea surface temperature (SST) was determined at the beginning of each dive when the bird started to submerge. The start of the bottom time was used for the measurement of water temperature within the water column at the maximum depth of each dive.

Satellite images For the detection of sulphide eruptions in the study area and study period, NASA satellite images¹ were analysed for visible clues of sulphide, i.e. milky water colouring of the sea surface (Weeks et al., 2004). Water masses influenced by sulphide eruptions around Mercury Island were also detected by personal observation from the island and water samples were taken for later analysis (carried out by the Ministry of Fisheries and Marine Resources, Lüderitz, Namibia).

Hydrographic survey A hydrographic survey was performed on the 4th of March 2005, leading into the main penguin foraging area identified by analysis of the GPS logger data (see Fig. 3.1). At six stations (Table 3.1), a CTD (Conductivity Temperature

¹MODIS Rapid Response Project at NASA/GSFC; <http://rapidfire.sci.gsfc.nasa.gov/subsets/?NBenguela>

Depth) cast was used to measure water temperature and salinity levels within the water column. To determine dissolved oxygen concentrations, water samples were taken and later analysed by scientists from the Ministry of Fisheries and Marine Resources, Lüderitz, Namibia (MFMR).

Water temperature and dissolved oxygen concentrations as well as temperature data obtained from data loggers were interpolated using the ordinary kriging option in Golden Software Surfer 8[®] along transect lines running from south-east to north-west (including stations 1 – 3 and 6) and from east to west (including stations 4 – 6). In order to compare CTD based temperature measurements with water temperatures encountered by the penguins, data of one bird equipped with a GPS logger (individual 58-210205) was chosen. This penguin had been travelling roughly along the transect lines covered during the hydrographic survey (Fig. 3.1).

Diet Diet samples were taken at Mercury Island, capturing birds returning from the sea with visibly filled stomachs. Logger equipped birds were not sampled in order to avoid additional stress. Stomach flushing, as described by Wilson (1984), was used in order to obtain the stomach contents. A soft tube was orally inserted into the bird's stomach and lukewarm water was poured in until the natural vomiting reflex was triggered. Regurgitated stomach contents were drained through a sieve and later weighed and analysed. Birds were weighed and immediately released after no more than ten minutes. A total of 24 stomach samples were obtained over a period of three weeks between the 15th of February and the 1st of March 2005, with eight birds sampled on one day per week. For Mercury Island, additional diet information since 1998 is available at the Ministry of Fishery and Marine Resources, Lüderitz, Namibia, obtained with the same method as used in this study. Diet components were identified to species level (following Bianchi et al., 1999) and measured if specimens were complete. For each species, the percentage of the total mass of the sample was calculated.

3.3 Results

All twelve birds in 2005 travelled north-west of the island, where the main foraging area is located (see Chapter 2). During the study period in 2005, strong sulphide eruptions were observed within the area frequented by foraging African penguins from Mercury Island (Fig. 3.2). The presence of sulphide in the water column was noted from the island as a milky colouring of the water in combination with bad odours and was confirmed by satellite images during the same period. Water samples taken during the study period confirmed high sulphide concentrations in the water and low oxygen levels (unpubl. data MFMR, Lüderitz).

3.3.1 Foraging area

All twelve African penguins from Mercury Island foraged north-west of the breeding colony (Fig. 3.2) and the deepest dives were recorded mainly at the furthest positions away from the colony towards the north-west (Fig. 3.3).

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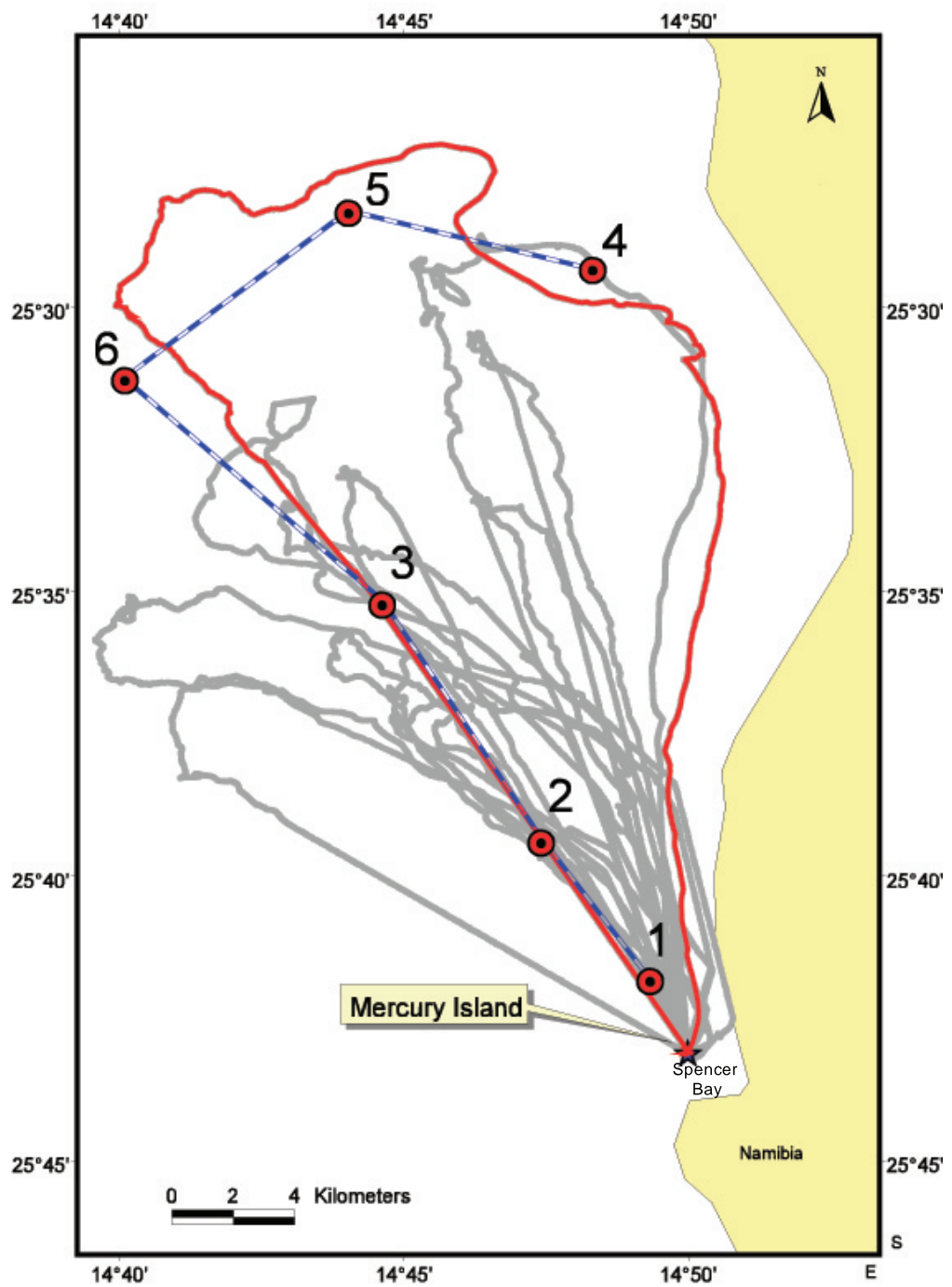


Figure 3.1: CTD stations (numbered red dots) and hydrographic transects (blue-white lines) in relation to foraging tracks (grey) of African penguins from Mercury Island, Namibia, equipped with GPD TDlog data loggers in 2005. Track marked in red corresponds to the penguin individual 58-210205, referred to in the text.

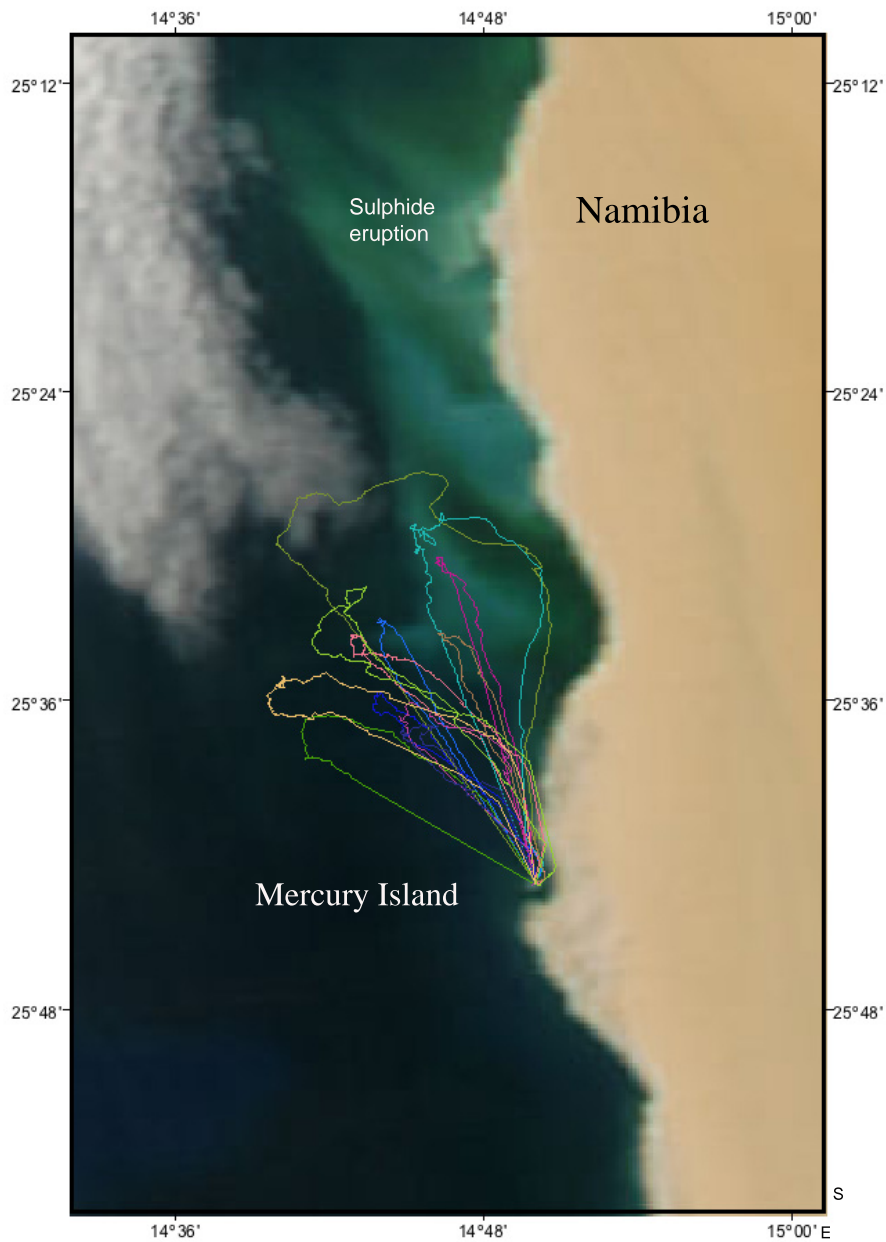


Figure 3.2: Satellite image showing a sulphide eruption (indicated by the milky green colouring of the water) and foraging tracks from twelve African penguins from Mercury Island, Namibia, in 2005. The satellite image corresponds to the 27th of February and penguin tracks were recorded between the 13th and 26th of February 2005.

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Satellite images show sulphide eruptions along the southern Namibian coast during the entire month of February and the first weeks of March 2005 (the image of the 27th of February was only chosen as an example). The main eruption sites seemed to be located north of the penguin foraging range for birds from Mercury Island but an overlap of penguin tracks and satellite images show that birds from Mercury Island actually came into contact with sulphidic waters (Fig. 3.2). Satellite images only represent the surface layer and not the entire water column and birds might have been affected throughout their dive range of a maximum depth of 75 m. Birds which travelled into more easterly direction from the colony did not come into contact with sulphidic surface waters (Fig. 3.2), but might have encountered sulphidic waters deeper in the water column.

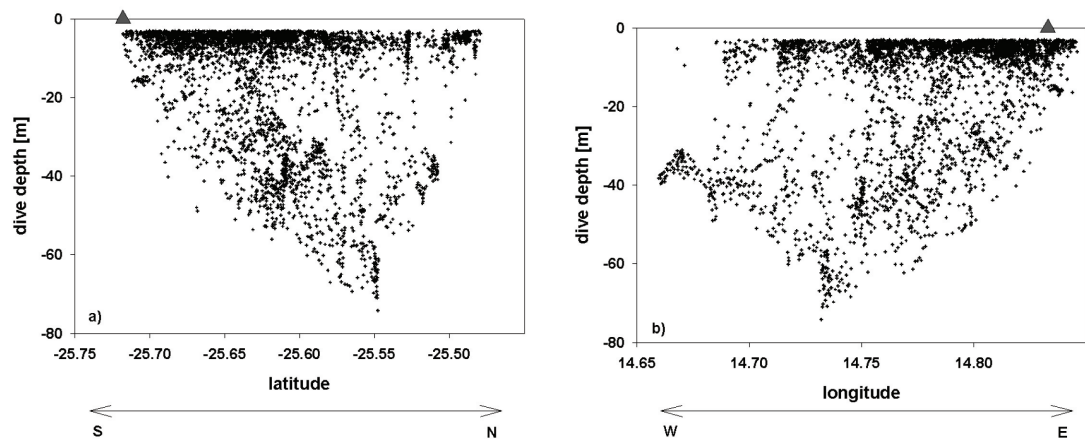


Figure 3.3: All dives of African penguins ($n = 12$) equipped in 2005 along a) latitudinal and b) longitudinal gradient. Black crosses indicate the maximum dive depth [m] of each dive and the triangles indicate the location of Mercury Island, Namibia.

3.3.2 Dive analysis

The median maximum diving depth for birds in 2005 was 53.0 m ($n = 12$ birds, range 41.6 – 74.1). The total area covered by the birds was about 520 km² and the total vertical distance of all birds was 134.5 km.

Penguins mainly foraged in areas with a water depth of 50 – 100 m. The analysis of dives deeper than 50 m revealed some dive series with consecutive dives reaching similar depths (so-called intra-depth zone (IDZ), see Tremblay and Cherel, 2000), possibly reaching the sea floor. Of all foraging dives (≥ 10 m), 13.9 % were within the IDZ of the previous dive and therefore considered as possibly benthic dives ($n = 219$ out of 1571 foraging dives). Of all dives deeper than 50 m ($n = 266$ dives), 82.3 % were considered to be benthic.

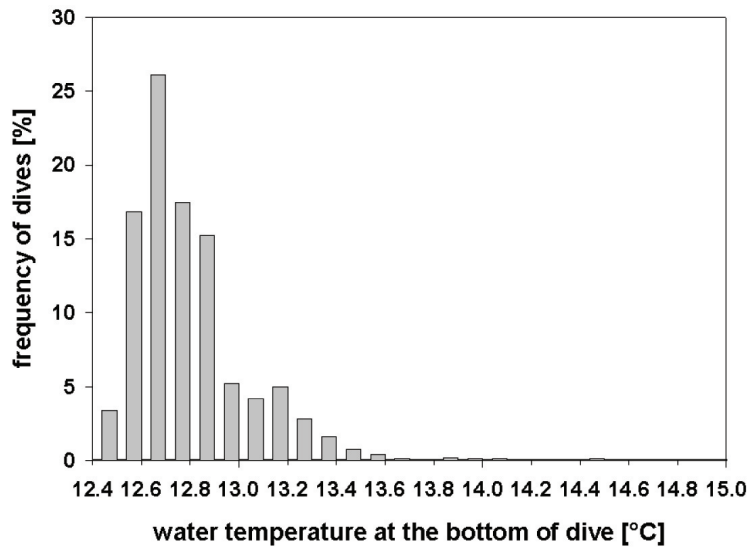


Figure 3.4: Frequency of foraging dives related to the water temperature [°C] at the bottom of each dive for African penguins from Mercury Island, Namibia, in 2005.

3.3.3 Temperature measurements obtained from diving penguins

The temperature sensor integrated in the GPS TDlog data logger allowed the *in situ* measurement of the water temperature. Characteristics of the water column used by the birds during foraging were related to their diving behaviour and to environmental conditions.

Considering the water temperature at the beginning of each dive as a measure of sea surface temperature (SST), the median water temperature at locations where diving took place was 13.9°C (range 12.5 – 19.8) in 2005. Besides the SST, the water temperature at the bottom of each dive was analysed, representing the water masses in which birds are presumably feeding. Temperatures at the bottom of all dives were significantly lower compared to SST values at the beginning of each dive ($p < 0.001$; GLM; Fig. 3.5) and were within a very small temperature range (Fig. 3.4). 80.8 % of all foraging dives were into water masses with temperatures between > 12.5 and < 13.1 °C (Fig. 3.4) and the median dive depth of those dives was 36.8 m compared to 34.8 m for all foraging dives. The median water temperature at the bottom of all foraging dives was 12.7°C (range 12.4 – 17.6).

3.3.4 Hydrographic survey

A hydrographic survey in the main penguin foraging area was carried out on the 4th of March 2005, six days after the last foraging trip was recorded. Oxygen samples and water temperature measurements using a CTD cast were taken at six stations located within the main foraging area (Fig. 3.1 and Table 3.1).

3 Sulphide eruptions and their implication for foraging in African penguins

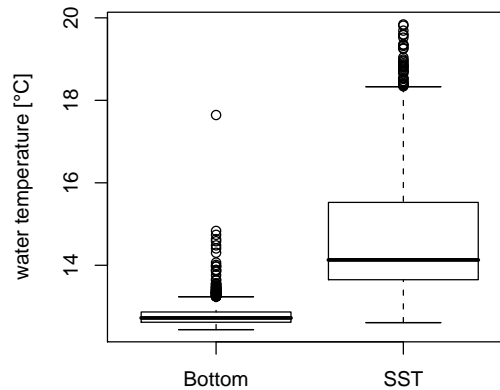


Figure 3.5: Differences in water temperature [°C] at the bottom of each dive and the sea surface temperature (SST) at the beginning of each dive for all dives of African penguins from Mercury Island, Namibia, in 2005.

Oxygen contents were lower than 2 ml/l at most stations even in surface waters and decreased with increasing depth (Fig. 3.6b), reaching concentrations of less than 0.2 ml/l in greater depth. Concentrations higher than 2 ml/l oxygen were only found in the upper five and eight metres at stations five and six, respectively (Table 3.2). Oxygen concentrations of less than 0.2 ml/l were reached in water depths of six metres (station one) and 50 metres (station three; Table 3.2). Surface temperatures were between 13.0 and 13.5°C at all stations, decreasing with increasing depth, reaching a minimum temperature of 12.3°C at a depth of 97 m at station six (Fig. 3.6a; Table 3.3).

Comparison of penguin and CTD derived data

Since environmental conditions may change within days due to different wind and upwelling patterns, it is doubtful whether temperature and oxygen conditions encountered during the survey were still similar to the period of penguin logger deployment several days before. In order to compare penguin and CTD derived data, a penguin track was chosen that coincided well with the south-north and the east-west transect between stations of CTD sampling (Fig. 3.1). The water temperature within the water column was compared for both sampling methods (penguin based and CTD) along the two transects.

The general structure of the water column was similar between the hydrographic survey and the time the penguin was at sea (Fig. 3.7). The upper water layer was characterised by warmer temperatures. Beneath a depth of about 30 – 40 metres, cooler water masses were found on both occasions. Water temperature and oxygen conditions encountered by the birds may therefore be compared to those during the oceanographic survey.

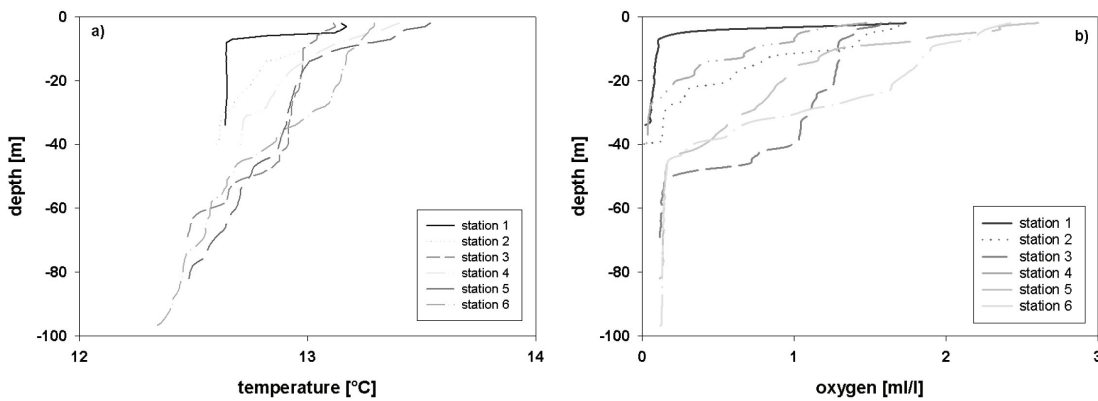


Figure 3.6: Water temperature [$^{\circ}\text{C}$] (a) and oxygen content [ml/l] (b) at six CTD stations north-west of Mercury Island, Namibia, on the 4th of March 2005.

Devices deployed on penguins are not yet able to measure oxygen concentrations but only record water temperature at specific depths. Considering the similarities of the temperature regime during both the CTD measurements and the birds' foraging (Fig. 3.7), similar oxygen conditions may be assumed for the time of logger deployment on the birds. Satellite images during the study period support this assumption, showing similar extensions of sulphidic waters during logger deployment and the hydrographic survey.

Oxygen levels were low within the entire water column and oxygen was almost absent beneath a depth of 30 – 40 metres (Fig. 3.8). Superimposing the dives performed by the penguin used as an example and the measured oxygen levels during the hydrographic survey indicates that birds dived into water which contained almost no oxygen (Fig. 3.8).

3.3.5 Diet

Pelagic goby (*Sufflogobius bibarbatus*) constituted the main prey item during the study period, which was present in all 24 stomach samples. 84.0 % of the total mass of all diet samples combined were pelagic goby; anchovy (*Engraulis capensis*) and horse mackerel (*Trachurus capensis*) made up only 7.6 and 4.4 % of the mass, respectively, and were present in seven stomach samples each. Sardine (*Sardinops sagax*) was found only in one sample and made up 0.03 %. Cape hake (*Merluccius capensis*) was also found in seven stomach samples but only made up 1.1 % of the entire mass. Other species found in the samples were redeye (roundherring, *Etrumeus whiteheadi*), pipefish, squid and crustaceans (the latter three all remaining unidentified to species level) in smaller amounts.

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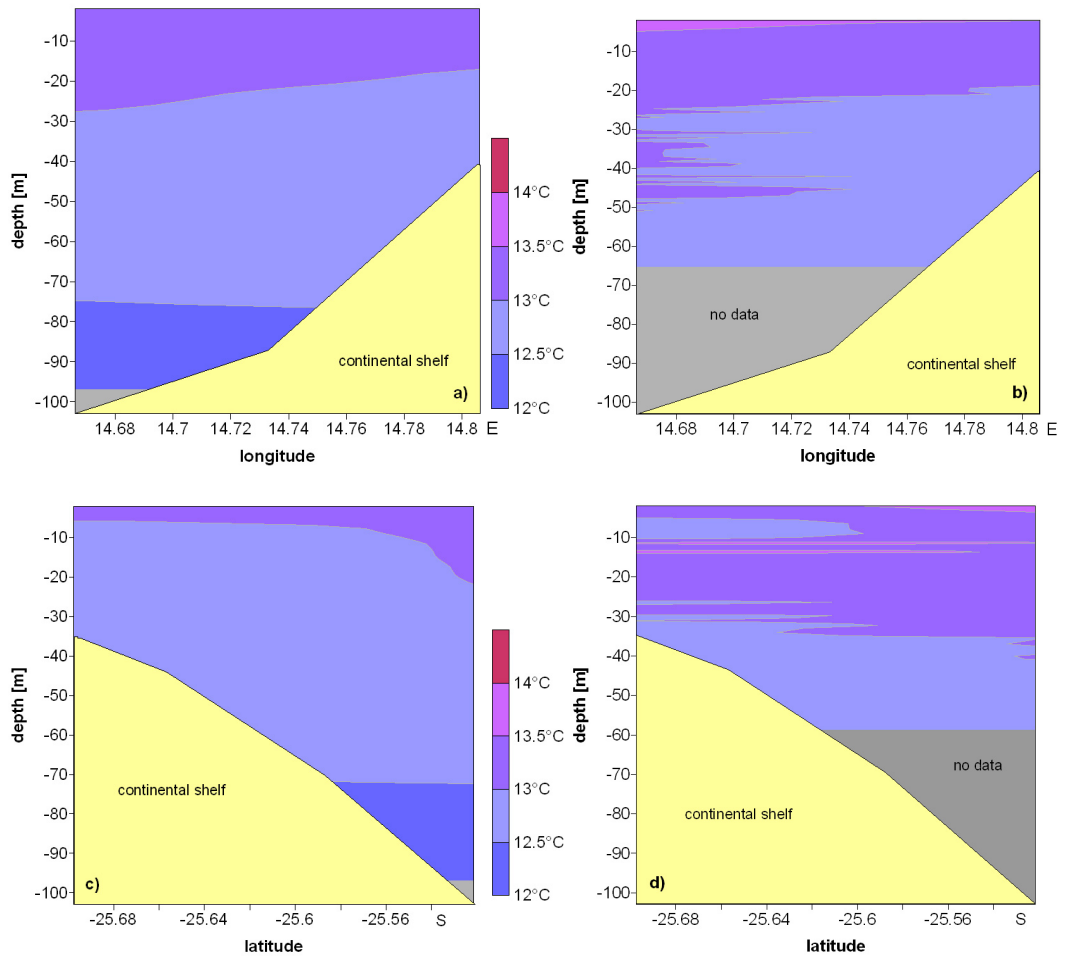


Figure 3.7: Water temperature [$^{\circ}\text{C}$] measured at CTD stations during a hydrographic survey on the 4th of March 2005 and by an African penguin carrying a GPS TDlog data logger on the 21st of February 2005. Compared are two transects; a) hydrographic survey, stations 4 – 6; b) penguin data, E – W; c) hydrographic survey, stations 1-3 & 6; d) penguin data, SE – NW.

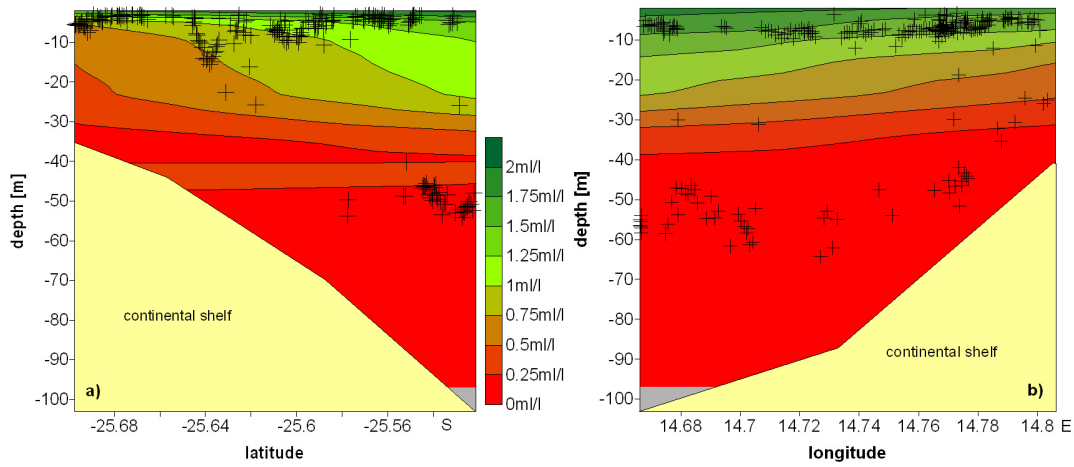


Figure 3.8: Oxygen levels [ml/l] measured during a hydrographic survey on the 4th of March 2005 along two transects north-west of Mercury Island, Namibia; a) station 1 – 3 & 6 and b) stations 4 – 6. Black crosses indicate the maximum dive depths of the African penguin individual 58-210205 foraging on the 21st of March 2004.

3.4 Discussion

Sulphide eruptions are frequently occurring phenomena along the Namibian coast (Emeis et al., 2004; Weeks et al., 2004) and this study shows that areas affected by those eruptions overlap with main foraging areas of African penguins breeding at Namibian islands. Earlier considered to be of minor importance, satellite remote sensing has indicated that sulphide eruptions are of greater extent and of longer duration than previously thought (Weeks et al., 2002). They have strong effects on the Benguela marine ecosystem, especially on the predominant fish species (Hamukuaya et al., 1998; Weeks et al., 2004) and thus on their predators, such as penguins.

The areas used for foraging by African penguins breeding at Mercury Island overlapped to a great extent with areas where sulphide eruptions took place during the study period. Even in areas where no milky, sulphidic waters were visible on the satellite images, diving birds might have been affected deeper down in the water column, since eruptions occur at the sea floor and subsurface water tends to be hypoxic over vast areas (Emeis et al., 2004).

During sulphide eruptions, dissolved oxygen is stripped from the water during the process of oxidation of hydrogen sulphide. Hypoxic or even anoxic conditions are the usual result and may cause fish die-offs or displacement of fish shoals into waters with higher oxygen concentrations (Hamukuaya et al., 1998). African penguins were feeding almost exclusively on pelagic goby during the presence of sulphidic waters. Pelagic goby is a demersal fish species which may tolerate very low oxygen levels and sulphidic waters as experiments in the laboratory have demonstrated (Currie et al., submitted). It is also known that pelagic gobies are associated with sulphidic muds along the Namibian coast (Currie et al., submitted) and that they prefer temperatures between 11 and 15°C², the water temperature range in which feeding penguins were observed. Pelagic goby is abundant in Namibian waters and it is found up to 60 km off the coast (Cruikshank et al., 1980).

Juvenile gobies live more pelagic than adults (Crawford et al., 1985) and both juveniles and adults were found in the diet. The high percentage of apparently benthic dives possibly reaching the sea bottom shows that birds adapted their diving behaviour to demersal prey. In 2006, fewer dives reached depth ≥ 50 m and fewer benthic dives were recorded, which coincides well with the more pelagic prey found in the birds' diet in 2006 (see Chapter 2). Penguins are usually thought to be pelagic feeders (Wilson, 1985; Davis and Renner, 2003) but benthic diving as well as benthic prey has been observed in other penguin species, such as gentoo (*Pygoscelis papua*), emperor (*Aptenodytes forsteri*) and rockhopper (*Eudyptes chrysocome*) penguins (Croxall et al., 1988; Kooyman and Kooyman, 1995; Tremblay and Cherel, 2000).

As the food load of penguins usually reflects the availability of local marine resources (Tremblay and Cherel, 2003), prey availability seemed to be restricted to pelagic goby during this study period. It is uncertain whether gobies actively accumulate in areas of sulphide eruptions, minimizing their own risk of predation by other fish species that

²<http://www.fishbase.org>

cannot tolerate low-oxygen conditions or whether they are widely distributed, as found by Cruickshank et al. (1980). If pelagic goby actively accumulates, penguins might travel into areas of sulphide eruption intentionally in order to feed on pelagic goby. Alternatively, the area constitutes their usual feeding ground and availability of other prey species is limited during sulphide events. The latter assumption is supported by the fact that in 2006 birds were foraging in the same area where they fed on anchovy and sardine in addition to pelagic goby (see Chapter 2). Pelagic goby has lower energetic contents than other pelagic fish species (Cruickshank et al., 1980; Crawford et al., 1985) and may be used as an alternative prey for lack of higher energetic fish. Breeding on islands usually enables birds to theoretically forage in an area extending 360° around the island (Furness and Monaghan, 1987). Even though Mercury Island is located within Spencer Bay and the potential foraging area is limited by the mainland to the east, foraging would still be possible north, west and south of the island. It is unclear why African penguins only forage north-west of the island even in years with sulphide eruptions and poor food availability. Prey distribution around the island is unknown, but during periods of sulphide eruptions, vast areas around the island might be exhausted of pelagic fish species. Penguins would therefore benefit from the presence of pelagic goby in hypoxic waters. The actual extent of low-oxygen water masses is unknown and distances to areas with other prey might be out of reach for penguins breeding at Mercury Island. Cape gannets, which are able to fly and therefore able to cover longer distances when foraging, did encounter sardine and other high-energy food items during the same study period in 2005 (see Chapter 5).

Long-term diet analyses show that pelagic goby has been the main prey in penguin diet at Mercury Island for at least a decade (Ministry of Fisheries and Marine Resources, Lüderitz, Namibia). Studies from the 1950s still indicate anchovy and sardine as main prey items but already in the 1970s, after the collapse of the anchovy and sardine stocks, goby became the main prey for penguins (Crawford et al., 1985). Diet studies of seabirds may be used to monitor prey availability and changes in the ecosystem (see Berruti, 1983; Montevecchi, 1993). Laugksch and Adams (1993) studied the diet of African penguins in South Africa between 1980 and 1990 which consisted mainly of anchovy. The abundance of this species in penguin diet samples reflected the interannual variance in the local anchovy population (Laugksch and Adams, 1993). In the northern Benguela ecosystem, the presence of pelagic goby and the absence of pelagics such as sardine and anchovy, are indications for a regime shift with an on-going degradation of the ecosystem and possibly increasing occurrence of sulphide eruptions (Bakun and Weeks, 2004). Recruitment of sardine and other pelagic fish species are negatively affected by low oxygen concentrations (Ekau and Verheye, 2005), worsening the food availability for penguins. Diet studies of birds breeding along the Namibian coast should be used to monitor changes in the ecosystem.

Different scenarios about possible consequences of global change are considered by Roux (2003), mostly with negative consequences for African penguins. Penguins breeding along the Namibian coast would be further threatened if, in addition to global changes, pelagic goby would be considered as a future target species for the fish meal industry, as is currently contemplated in Namibia (J.-P. Roux pers. comm.). Pelagic goby may not

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be adapted to compensate for loss through commercial fishery, due to its life history with late maturity and longevity (Melo and Le Clus, 2005). The regional Namibian population of African penguins is listed as *Endangered* (Kemper, in press a) and is currently heading towards extinction if no drastic conservation management actions are taken such as the implementation of a set of Marine Protected Areas (MPAs) (see Appendix B; Kemper, 2006).

Table 3.1: Geographic positions of six CTD stations during a hydrographic survey on the 4th of March 2005 off the coast of southern Namibia.

Station	Position	
	Latitude	Longitude
1	25° 41.85' S	14° 49.33' E
2	25° 39.42' S	14° 47.41' E
3	25° 35.24' S	14° 44.62' E
4	25° 29.35' S	14° 48.32' E
5	25° 28.35' S	14° 44.03' E
6	25° 31.29' S	14° 40.10' E

Table 3.2: Oxygen concentration [ml/l] at six sampling stations north-west of Mercury Island, Namibia, on the 4th of March, 2005 using CTD measurements.

Depth [m]	Oxygen [ml/l]					
	Station 1	Station 2	Station 3	Station 4	Station 5	Station 6
2	1.74	1.63	1.57	1.48	2.61	2.42
3	1.18	1.69	1.54	1.28	2.36	2.33
4	0.54	1.62	1.41	1.15	2.36	2.26
5	0.26	1.52	1.40	1.05	2.19	2.23
6	0.16	1.45	1.37	1.02	1.97	2.20
7	0.11	1.43	1.32	1.00	1.85	2.16
8	0.10	1.42	1.29	0.97	1.73	2.04
9	0.11	1.40	1.29	0.80	1.46	1.93
10	0.10	1.32	1.29	0.73	1.29	1.90
11	0.10	1.11	1.30	0.68	1.23	1.89
12	0.09	0.89	1.29	0.67	1.18	1.87
13	0.09	0.82	1.30	0.64	1.16	1.84
14	0.09	0.79	1.29	0.45	1.15	1.82
15	0.08	0.75	1.28	0.38	1.04	1.81
16	0.08	0.68	1.28	0.36	1.00	1.79
17	0.08	0.63	1.27	0.34	0.97	1.76
18	0.08	0.61	1.27	0.34	0.96	1.74
19	0.08	0.60	1.27	0.31	0.95	1.71
20	0.08	0.56	1.27	0.23	0.93	1.68
21	0.08	0.51	1.26	0.20	0.89	1.65
22	0.07	0.34	1.25	0.18	0.88	1.64
23	0.07	0.31	1.21	0.17	0.86	1.63
24	0.07	0.29	1.15	0.16	0.85	1.57
25	0.07	0.28	1.15	0.14	0.83	1.46
26	0.06	0.28	1.14	0.10	0.81	1.39
27	0.06	0.23	1.12	0.06	0.79	1.32
28	0.05	0.17	1.12	0.05	0.76	1.22
29	0.06	0.16	1.11	0.05	0.74	1.11
30	0.05	0.15	1.11	0.05	0.69	1.04
31	0.05	0.14	1.09	0.04	0.63	0.96
32	0.05	0.14	1.06	0.04	0.60	0.82
33	0.05	0.14	1.05	0.04	0.57	0.72
34	0.02	0.14	1.04	0.04	0.56	0.66
35		0.14	1.04	0.04	0.54	0.62
36		0.14	1.04	0.04	0.51	0.58
37		0.13	1.04	0.04	0.49	0.56
38		0.14	1.03	0.04	0.47	0.53
39		0.13	1.03	0.03	0.44	0.40
40		0.00	0.99	0.03	0.41	0.33
41			0.93		0.37	0.30
42			0.79		0.32	0.29
43			0.77		0.24	0.28
44			0.73		0.19	0.21
45			0.72		0.17	0.17
46			0.71		0.16	0.16
47			0.58		0.16	0.16
48			0.39		0.16	0.16
49			0.27		0.15	0.16
50			0.19		0.15	0.16
51			0.16		0.15	0.15
52			0.15		0.15	0.15
53			0.14		0.15	0.15
54			0.14		0.15	0.15
55			0.13		0.14	0.15
56			0.13		0.15	0.15
57			0.13		0.15	0.14
58			0.12		0.14	0.14
59			0.13		0.14	0.15
60			0.13		0.15	0.14
61			0.13		0.14	0.14
62			0.12		0.14	0.14
63			0.12		0.14	0.14
64			0.12		0.14	0.14
65			0.12		0.14	0.14
66			0.12		0.14	0.14
67			0.12		0.14	0.14
68			0.11		0.14	0.14
69			0.12		0.13	0.14
70			0.11		0.14	0.13
71					0.14	0.14
72					0.14	0.14
73					0.14	0.14
74					0.14	0.13
75					0.14	0.13
76					0.14	0.13
77					0.14	0.13
78					0.13	0.13
79					0.13	0.13
80					0.13	0.13
81					0.13	0.13
82					0.12	0.13
83						0.13
84						0.13
85						0.13
86						0.13
87						0.13
88						0.13
89						0.13
90						0.13
91						0.13
92						0.13
93						0.13
94						0.13
95						0.13
96						0.13
97						0.12

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Table 3.3: Water temperature [°C] at six sampling stations north-west of Mercury Island, Namibia, on the 4th of March, 2005 using CTD measurements.

Depth [m]	Water temperature [°C]					
	Station 1	Station 2	Station 3	Station 4	Station 5	Station 6
2	13.15	13.15	13.11	13.40	13.54	13.29
3	13.17	13.16	13.12	13.36	13.52	13.29
4	13.15	13.15	13.10	13.33	13.43	13.27
5	13.12	13.11	13.06	13.27	13.40	13.26
6	12.82	13.05	13.04	13.24	13.39	13.25
7	12.67	13.03	13.04	13.19	13.36	13.24
8	12.65	13.02	13.02	13.15	13.29	13.23
9	12.65	13.01	13.00	13.11	13.21	13.22
10	12.65	12.99	12.98	13.08	13.15	13.20
11	12.64	12.96	12.98	13.05	13.10	13.18
12	12.64	12.92	12.98	13.03	13.07	13.17
13	12.64	12.88	12.98	13.01	13.04	13.17
14	12.64	12.82	12.98	12.99	13.01	13.17
15	12.65	12.81	12.98	12.97	13.00	13.17
16	12.65	12.80	12.98	12.94	12.99	13.16
17	12.65	12.79	12.98	12.93	12.98	13.15
18	12.65	12.78	12.97	12.91	12.97	13.15
19	12.65	12.77	12.97	12.90	12.96	13.15
20	12.65	12.76	12.97	12.90	12.96	13.14
21	12.65	12.76	12.97	12.88	12.95	13.14
22	12.65	12.74	12.97	12.87	12.95	13.12
23	12.65	12.73	12.96	12.86	12.94	13.12
24	12.65	12.71	12.95	12.85	12.94	13.11
25	12.65	12.70	12.94	12.84	12.93	13.11
26	12.65	12.68	12.94	12.83	12.93	13.10
27	12.65	12.68	12.93	12.83	12.93	13.10
28	12.64	12.68	12.93	12.82	12.92	13.08
29	12.64	12.66	12.93	12.81	12.92	13.04
30	12.64	12.63	12.93	12.78	12.92	13.02
31	12.64	12.62	12.93	12.73	12.91	13.01
32	12.64	12.62	12.93	12.72	12.91	12.98
33	12.64	12.62	12.92	12.72	12.91	12.97
34	12.64	12.62	12.92	12.72	12.91	12.95
35		12.62	12.92	12.72	12.90	12.91
36		12.62	12.92	12.72	12.89	12.89
37		12.62	12.92	12.71	12.89	12.87
38		12.61	12.92	12.71	12.88	12.86
39		12.61	12.92	12.71	12.88	12.86
40		12.60	12.92	12.71	12.88	12.85
41			12.91		12.87	12.82
42			12.89		12.87	12.80
43			12.88		12.85	12.78
44			12.88		12.84	12.76
45			12.88		12.80	12.71
46			12.86		12.78	12.69
47			12.85		12.77	12.68
48			12.83		12.76	12.68
49			12.80		12.75	12.67
50			12.75		12.75	12.66
51			12.71		12.74	12.65
52			12.68		12.73	12.65
53			12.67		12.72	12.65
54			12.66		12.71	12.64
55			12.65		12.71	12.63
56			12.65		12.70	12.62
57			12.65		12.70	12.59
58			12.64		12.70	12.58
59			12.62		12.69	12.58
60			12.58		12.69	12.57
61			12.53		12.67	12.58
62			12.51		12.66	12.57
63			12.50		12.65	12.57
64			12.50		12.65	12.56
65			12.49		12.64	12.56
66			12.48		12.64	12.55
67			12.48		12.63	12.56
68			12.48		12.61	12.55
69			12.48		12.60	12.55
70			12.48		12.59	12.54
71					12.58	12.52
72					12.57	12.51
73					12.56	12.49
74					12.56	12.47
75					12.56	12.47
76					12.54	12.46
77					12.51	12.46
78					12.50	12.46
79					12.49	12.46
80					12.49	12.45
81					12.48	12.45
82					12.48	12.45
83						12.45
84						12.44
85						12.44
86						12.43
87						12.42
88						12.41
89						12.41
90						12.41
91						12.40
92						12.40
93						12.39
94						12.38
95						12.37
96						12.36
97						12.33

4 Penguins as oceanographers: insight into small scale temperature distribution

4.1 Introduction

The use of seabirds for monitoring environmental conditions has been proposed by various authors (Wilson et al., 1993; Weimerskirch et al., 1995; Charrassin et al., 2004; Sokolov et al., 2006). Depending on the at-sea behaviour of the bird species, either large areas may be monitored, such as in the case of wandering albatrosses (*Diomedea exulans*) (Weimerskirch et al., 1995) or smaller areas at higher resolution and including vertical structures as in the case of penguins (Wilson et al., 1994; Charrassin et al., 2002, 2004; Sokolov et al., 2006) and other diving seabirds (Watanuki et al., 2001).

Informations about environmental parameters, such as sea surface temperature, chlorophyll a or oxygen concentration (see Chapter 3) are scarce for the northern Benguela region. Satellite images may provide useful informations (Demarcq et al., 2003; Weeks et al., 2004) but data coverage is often limited due to cloud cover. The spatial scale of satellite-based data is rather large and not appropriate for very small scale aspects (Cole and McGlade, 1998; Weeks et al., 2006). Ship-based surveys are costly and may therefore not be realised very frequently. High resolution monitoring, even of basic parameters such as water temperature, would be needed to better understand the biological and physical variability in the Benguela system (Cole and McGlade, 1998). The use of bird-borne devices for measuring oceanographic parameters constitutes a small scale, high resolution solution for covering important foraging areas of seabirds in this coastal upwelling system. It allows an environmental monitoring at relatively low cost, combining studies about the foraging behaviour of seabirds with hydrographic measurements.

In this chapter, water temperature measurements obtained by foraging African penguins are presented in an area of approximately 300 km² north-west of Mercury Island. The water column is sampled down to depths of 70 m. *In situ* measurements were used to run an oceanographic model, calculating the water temperature within the water column for an area frequently visited by penguins and other seabird species.

4.2 Methods

Data collection African penguins were equipped with GPS TDlog data loggers at Mercury Island in 2005 and 2006 (for further details see Chapter 2). The devices recorded water temperature and pressure (for depth calculations) every second with a precision

of 5 mK and 4 mbar, respectively. These data were combined with the positional information obtained through the GPS function which was interpolated between known locations. Single tracks of individual penguins were plotted using Matlab 7.0.1[®] (scripts written by T. Mattern and S. Zankl). For the oceanographic model, data from twelve and 13 birds in 2005 and 2006, respectively, were included.

Oceanographic model A grid was designed, limited by 25.52°S and 25.70°S in the north and south, respectively and by 14.67°E and 14.83°E in the west and east, respectively (Fig. 4.1). The dimension of each grid cell is 0.6 x 0.6 minutes and the grid contains a total of 272 grid cells. Each grid cell covers about 1.1 km² and the total grid has a dimension of approximately 300 km². The water column was divided into ten meter depth intervals. Data for depths less than one meter were excluded, leading to intervals of 1 – < 10 m, 10 – < 20 m etc. up to a maximum depth of 70 m. The temperature data measured by the equipped birds during the study period of about two weeks (13th to 26th of February 2005 and 16th to 28th of February 2006) were combined and treated as if being quasi-synoptic for each year.

Horizontal maps of water temperature in each depth interval were constructed interpolating the observed data onto the regular grid by objective analysis (Bretherton et al., 1976). A Gaussian isotropic covariance function

$$f(r) = \sigma^2 \exp(-r^2/R^2)$$

was chosen where $R = 2.5$ km; σ is the variance and r the distance between data points. Only grid cells for which the expected root mean square (r.m.s.) error in interpolation was < 75 % of the standard deviations of the grid were considered for the statistical analysis. Each grid cell represents the analysed temperature data centered around it. Objective analysis provides a smoothed version of the original data. Model programming and runs was carried out by Hans-Harald Hinrichsen at the IFM-Geomar, University of Kiel, Germany.

Statistical analysis for temperature distribution between both years was performed using linear mixed-effects models fit by REML (LMER) in the program R 2.4.1[®], comparing the temperature within each depth interval between years.

Grid cells visited by at least one bird and therefore having contributed original data into the model were added up over the time of the study and over the number of birds for which data were already included. Hence, the number of birds that are necessary to be at sea in order to receive original data for a certain number of grid cells synoptical was calculated.

Short term variations within years In each year, different wind patterns were observed at Mercury Island within the study period. In order to assess short term variations between different wind patterns, birds were grouped according to the predominant wind direction while the birds were at sea. In 2005, the study period was divided into four wind periods, alternating between southerly and northerly wind conditions. During one period, only one bird was at sea and this period was thus excluded from further analysis.

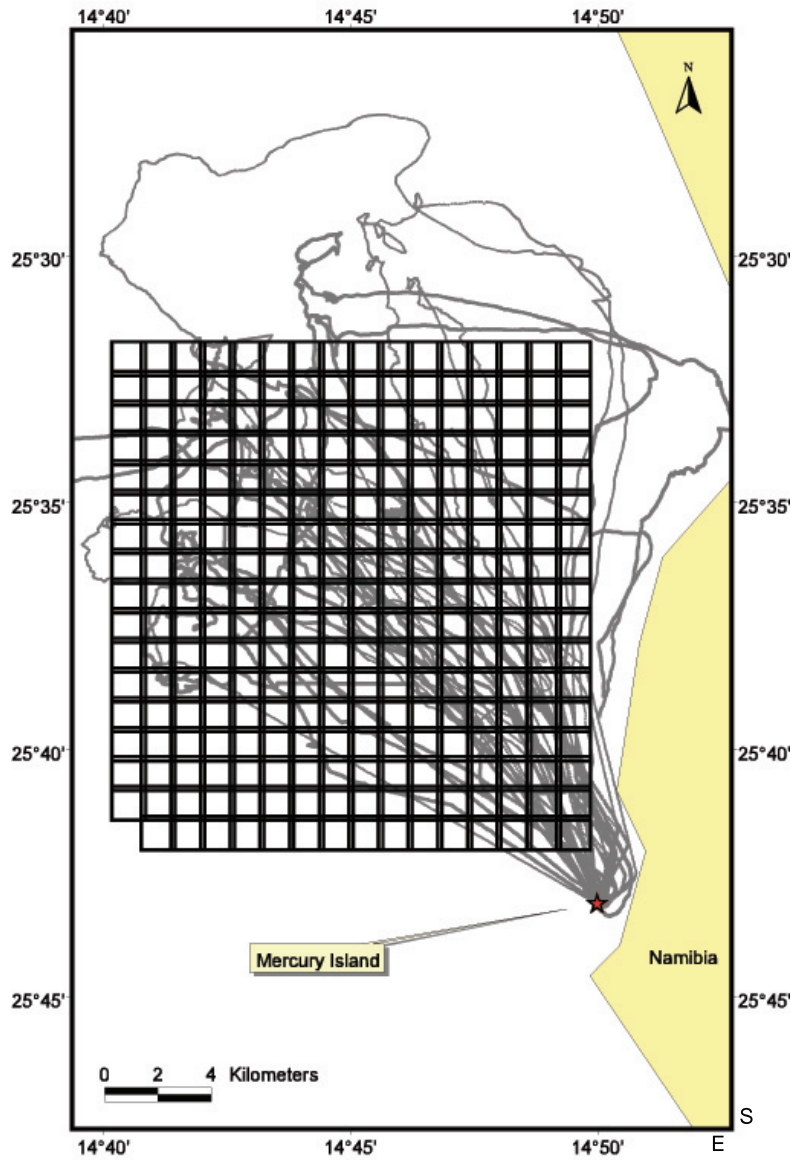


Figure 4.1: Grid designed for oceanographic modelling. Foraging tracks of African penguins from Mercury Island, Namibia, in 2005 and 2006 are shown in light grey.

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The other three groups contain birds foraging between the 15th and the 17th of February (group 1, predominant northerly wind conditions), between the 19th and 21st of February (group 2, southerly wind conditions) and between the 22nd and 26th of February (group 3, a mixture of northerly and southerly winds).

In 2006, the study period could be again divided into four distinct periods, of which three were included in the oceanographic model. Four birds being at sea between the 16th and the 17th of February were included in group 1, encountering mainly southerly winds. Group 2 included three birds being at sea during northerly wind conditions between the 23rd and 24th of February. Wind changed direction again to southerly and the three birds being at sea between the 25th and the 28th of February were combined to group 3. The model was calculated down to a depth of 50 m for group 1 and down to depths of 70 m for groups 2 and 3.

Environmental conditions Sea surface temperature was measured at Mercury Island at eight o'clock every morning during the entire study period. Wind direction and wind speed were recorded three times a day. For simplification, wind directions were assigned to either southerly (including S, SW and SE) or northerly (including N, NW and NE) winds in order to evaluate the predominant wind pattern. The division into separate groups for the oceanographic modelling was based on these wind patterns.

4.3 Results

4.3.1 Individual foraging tracks

Water temperatures were measured during the entire trip of each bird by the devices attached. Together with the diving depths, also measured every second, and the geographical positions, a three-dimensional picture of the temperature distribution within the water column was obtained (Fig. 4.2). Birds were travelling in warmer surface waters and reaching colder depths when diving in both years. Birds were generally swimming in warmer water in 2006 than in 2005. This method uses the original temperature data along the track of each individual and presents the actual water temperature encountered by each bird. In order to assess the water temperature regime of the entire area, an oceanographic model would be more useful, as demonstrated in the following section.

4.3.2 Oceanographic modelling

Using the temperature data from twelve and 13 birds in 2005 and 2006, respectively, a three-dimensional model was calculated for the main foraging area of African penguins breeding at Mercury Island. Birds in both years were foraging within a range of 30 km north-west of the island, the grid covering the main foraging area frequented by the most birds in both years (see Fig. 4.1). The temperature distribution within the defined grid in ten metres intervals down to a maximum depth of 70 m (limited by the maximum diving depth of the birds) may be presented in a three-dimensional model (Fig. 4.3). Even though birds were deployed with data loggers over a period of about two weeks, all

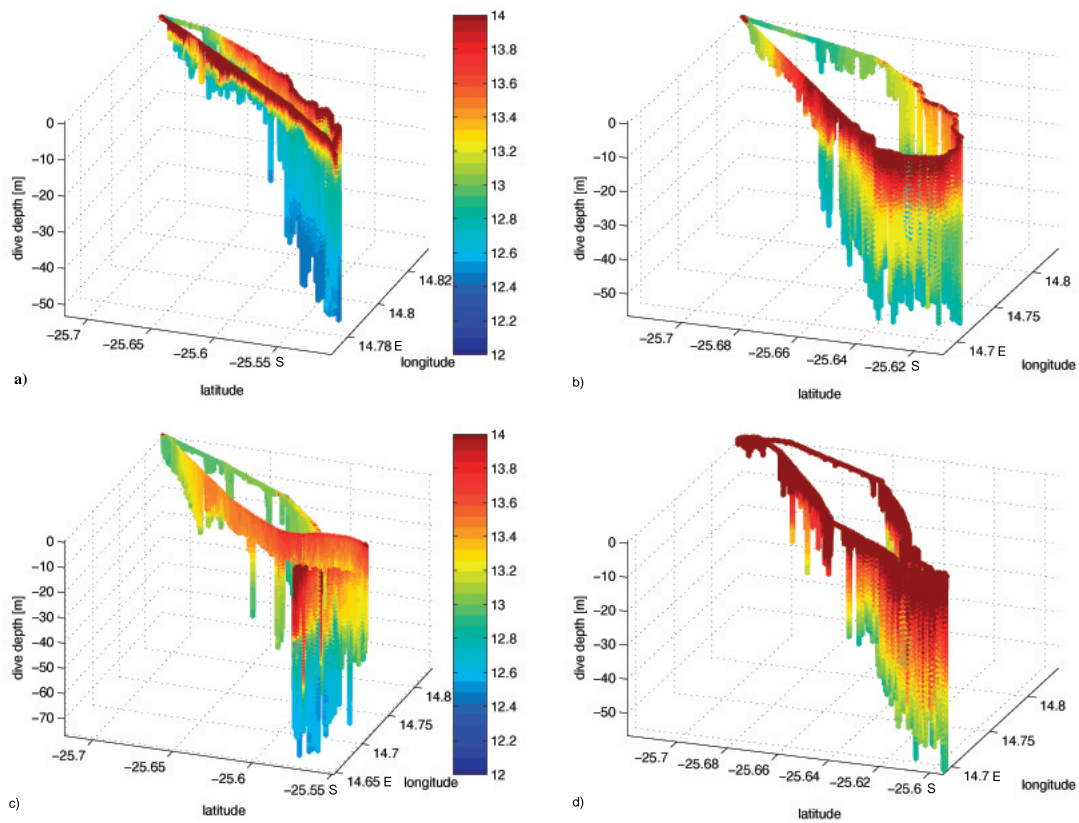


Figure 4.2: Temperature distribution along foraging tracks of African penguins from Mercury Island, Namibia, equipped with GPS TD data loggers. Two birds were chosen as examples in a) and b) 2005 and in c) and d) 2006.

4 Penguins as oceanographers: insight into small scale temperature distribution

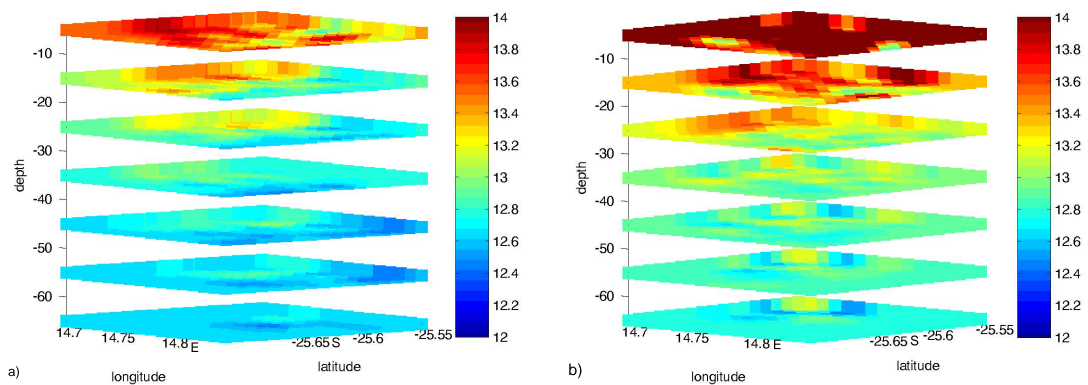


Figure 4.3: Three-dimensional water temperature distribution in the main African penguin foraging area north-west of Mercury Island, Namibia, a) in 2005 and b) in 2006. Original data were interpolated using an oceanographic model.

data were included per year, assuming a quasi-synoptic sampling. Differences in smaller time scales will be dealt with later in this chapter.

Considering the temperature distribution for each depth interval compared between both years, differences were found down to a depth of 60 m. Average water temperature in each layer was significantly higher in 2006 than in 2005, especially in upper water layers ($p < 0.01$; LMER; Fig. 4.4).

Considering each depth interval separately, characteristic temperature distributions especially along a longitudinal gradient, i.e. the distance to the coast, may be observed.

2005 In 2005, the upper water level (1 – < 10 m) was characterised by warm water especially offshore and by cells of colder water along the coast. Warmer water masses continued to be visible in offshore waters up to a depth of 30 m; colder water masses along the coast extended further to the west with increasing water depth. Deeper down in the water column, starting at a depth of 40 m, differences in water temperature became smaller between inshore and offshore waters and also between further depth intervals (Fig. 4.5).

2006 In 2006, water temperatures were higher within the entire water column, especially in the upper levels (Fig. 4.5). Differences were of about 1°C in the upper water level and decreased towards lesser temperature differences deeper down in the water column. Warmer water was found offshore as in 2005, being still visible in the north-western corner of the grid down to a depth of 70 m.

Grid coverage

The number of grid cells being frequented by the birds are accumulated over the study period (Fig. 4.6). Numbers of equipped birds contributing data to each depth interval are

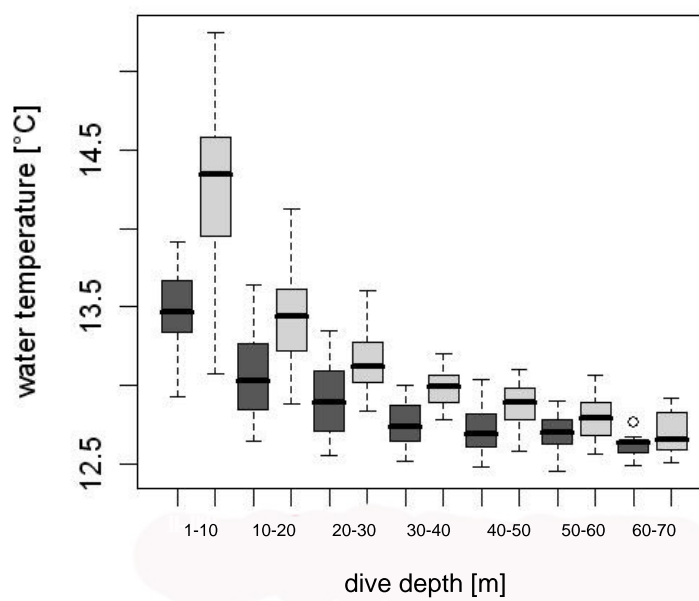
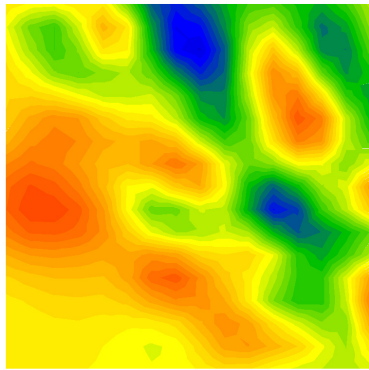
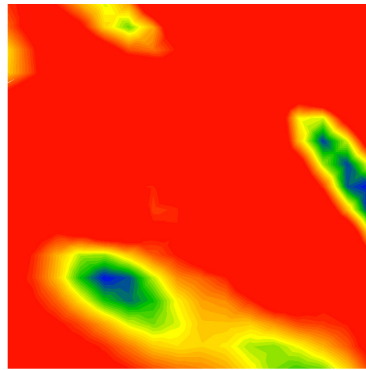


Figure 4.4: Average water temperature [°C] for each depth interval (1 – 10 m, 10 – 20 m, etc) in 2005 (dark grey) and 2006 (light grey).

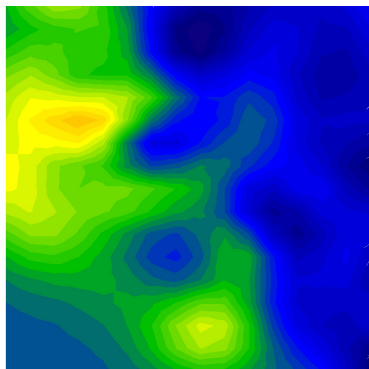
4 Penguins as oceanographers: insight into small scale temperature distribution



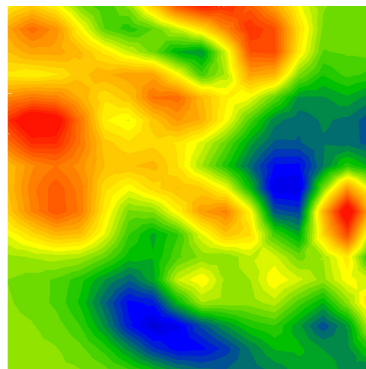
(a) $1 < T < 10$



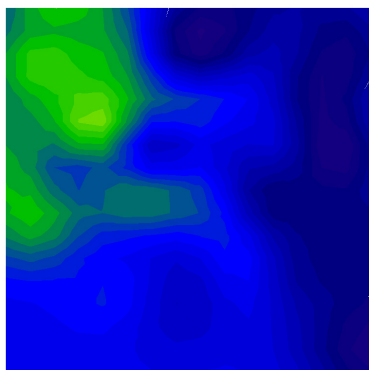
(b) $1 < T < 10$



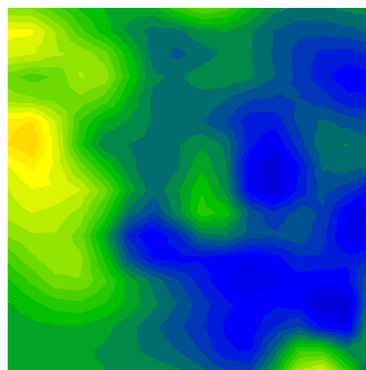
(c) $10 < T < 20$



(d) $10 < T < 20$

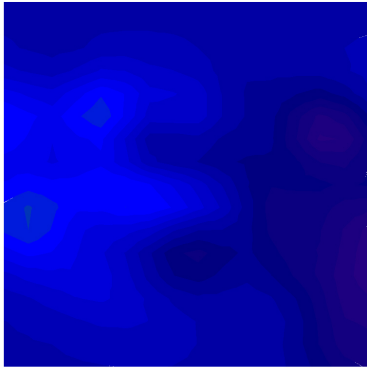


(e) $20 < T < 30$

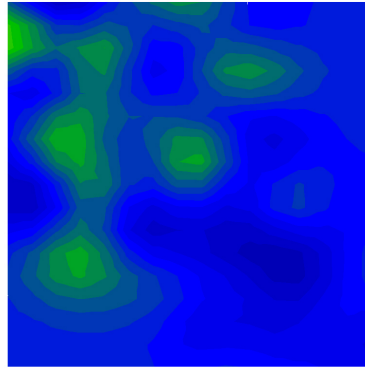


(f) $20 < T < 30$

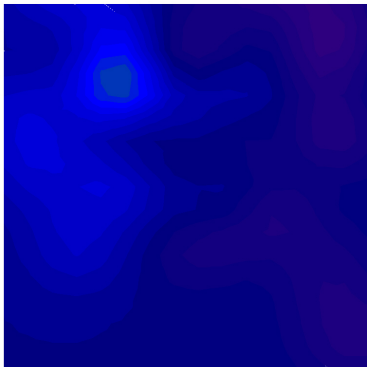
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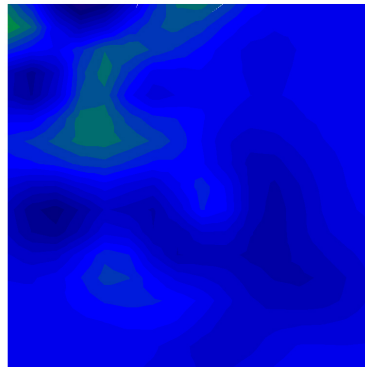
(g) $30 - < 40$



(h) $30 - < 40$



(i) $40 - < 50$



(j) $40 - < 50$



(k) $50 - < 60$



(l) $50 - < 60$

continues...

4 Penguins as oceanographers: insight into small scale temperature distribution

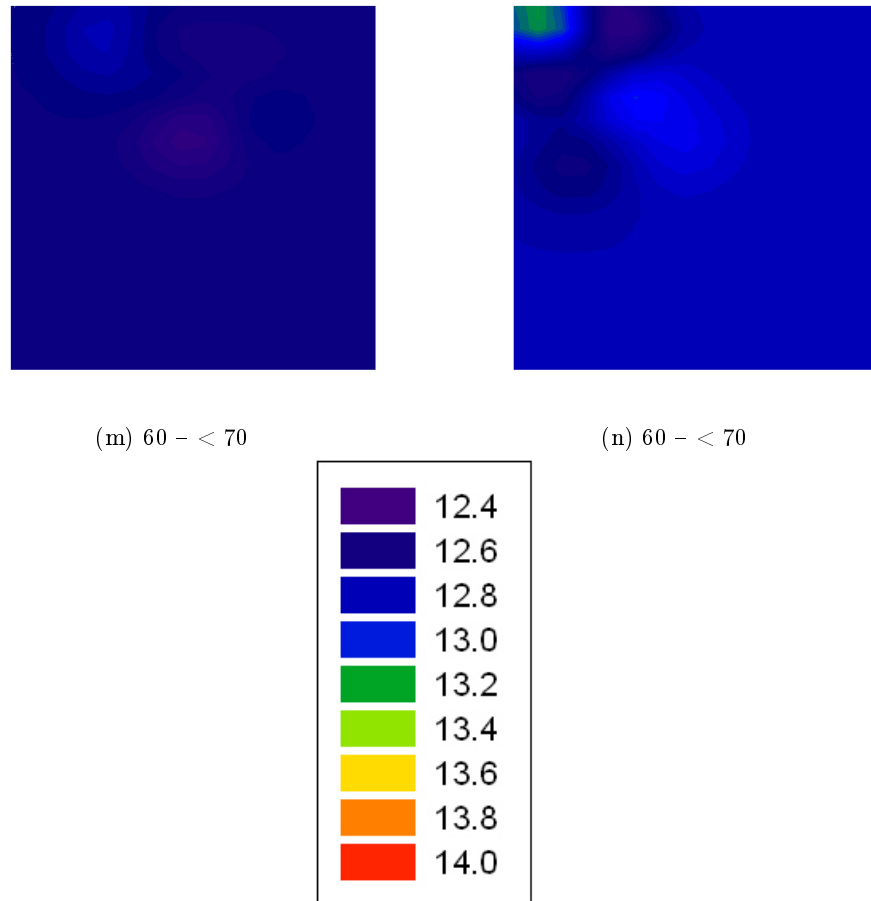


Figure 4.5: Water temperature [$^{\circ}\text{C}$] derived by an oceanographic model based on temperature measurements by logger equipped African penguins from Mercury Island, Namibia. Left column represents 2005, right column represents 2006.

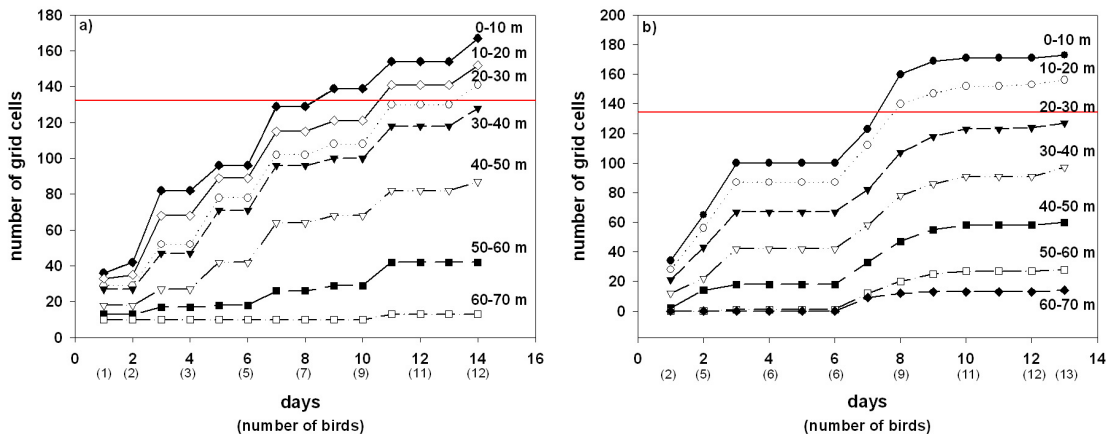


Figure 4.6: Accumulative numbers of in the model included grid cells a) in 2005 and b) in 2006. Days represent the ongoing study period with the numbers of African penguins included in parentheses. The red line indicates half of the total number of grid cells ($n = 136$).

added up. Already small numbers of equipped birds cover a great number of grid cells, as may be seen for the upper water level (1 – 10 m). With increasing water depth, the number of birds necessary in order to cover large number of grid cells increases because birds visit greater depth less frequently and only at specific positions for feeding (see Chapter 2). In 2005, seven birds covered almost half of the entire grid in the upper water level; in 2006, this was accomplished by six birds (Fig. 4.6).

Short term variation within years

2005 In 2005, three groups of birds were analysed separately according to the predominant wind directions during their time at sea.

Group 1 included four birds being at sea between the 15th and the 17th of February during north wind conditions. Water temperatures in the upper depth interval (1 – 10 m) were quite high compared to the other groups. Sea surface temperatures (SST) were also higher than SST values calculated for the entire study period (compare Fig. 4.8 and Fig. 4.5). Warm water masses were present in the upper level; in the following depth interval (10 – 20 m), water temperatures were already colder than average and the water column seemed well-mixed in all deeper depths (Fig. 4.8). For group 1, the model was only generated up to a depth of 50 m.

The number of data points allowed to model the water temperature down to a depth of 60 m for group 2. This group includes four birds foraging between the 19th and 21st of February during south wind conditions (Fig. 4.7). Warmer water could be observed down to a depth of 20 m, being not as warm as during north wind conditions but extending further down in the water column. Cooler water intruded from the south-east in 10 – 20 m depths, extending further towards the north-west in deeper water layers (Fig. 4.8).

4 Penguins as oceanographers: insight into small scale temperature distribution

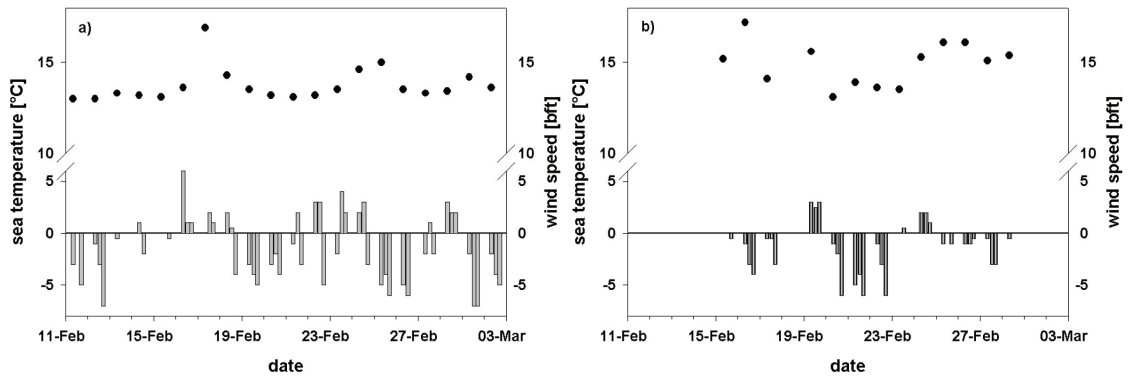


Figure 4.7: Sea surface temperature [°C] (dots) and wind speed [bft] (bars, negative values indicate southerly winds, positive values indicate northerly winds) a) in 2005 and b) in 2006 measured at Mercury Island, Namibia.

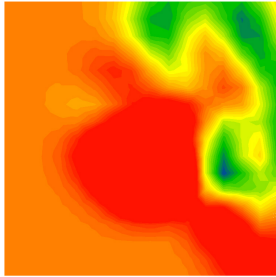
During the third period which includes three birds being at sea between the 22nd and 26th of February, warmer water masses extended even further down in the water column, reaching depths up to 30 m. During this period, a combination of southerly and northerly winds was recorded in the study area (Fig. 4.7). Cool water intruded from the south-east, spreading northwards between 20 to 30 m depths; a well-mixed cold water mass was found in 40 m depth and deeper (Fig. 4.8). Temperature distribution was significantly different between group 1 and group 2 as well as between group 1 and group 3 ($p < 0.0001$; LMER), no significant difference was found between groups 2 and 3.

2006 Surface waters were warmest for group 1 and group 3, whereas group 2 encountered cooler water masses at the surface, especially towards the coast (Fig. 4.9). With increasing depth, water temperatures for group 1 decreased, especially due to cold water cells appearing in the south. Cold water was present within the entire grid at depths deeper than 20 m. The water column for group 3 was characterised by warmer waters all the way down to depths of 50 – 60 m, with only a few cold water cells present. Group 2 encountered colder water cells already in the surface layer. Further down in the water column, warmer water masses were only found in the western part of the grid (Fig. 4.9).

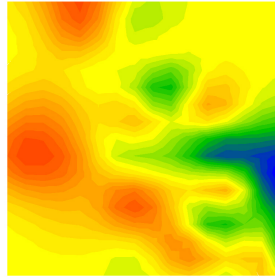
Temperature distribution was significantly different between the three groups ($p < 0.0001$; LMER).

4.3.3 Environmental conditions

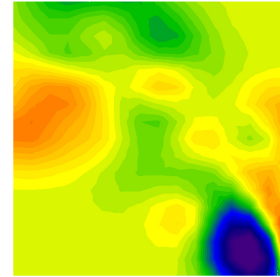
Sea surface temperatures and wind regimes varied between days during the study period (Fig. 4.7). Predominant winds were southerly (negative bars indicating winds coming from S, SE or SW in Fig. 4.7), interrupted by northerly winds in both years. Sea surface temperatures varied between days but water temperatures were overall higher in 2006 than in 2005 (Fig. 4.7).



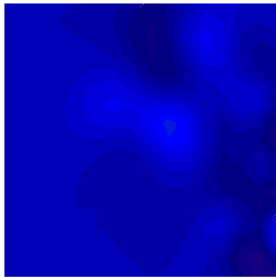
(a) $1 - < 10$



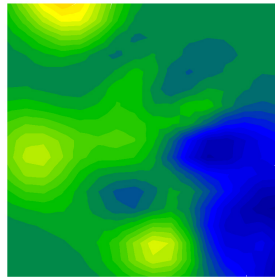
(b) $1 - < 10$



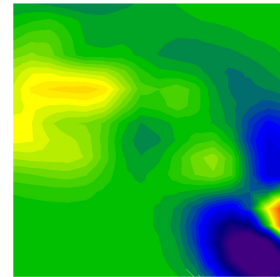
(c) $1 - < 10$



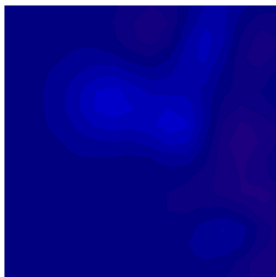
(d) $10 - < 20$



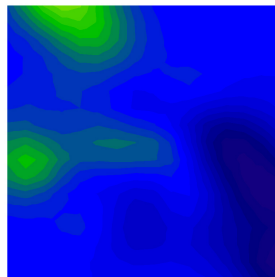
(e) $10 - < 20$



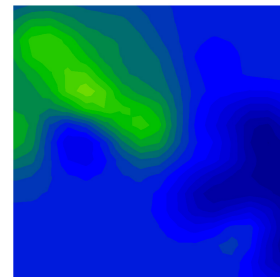
(f) $10 - < 20$



(g) $20 - < 30$



(h) $20 - < 30$



(i) $20 - < 30$

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4 Penguins as oceanographers: insight into small scale temperature distribution

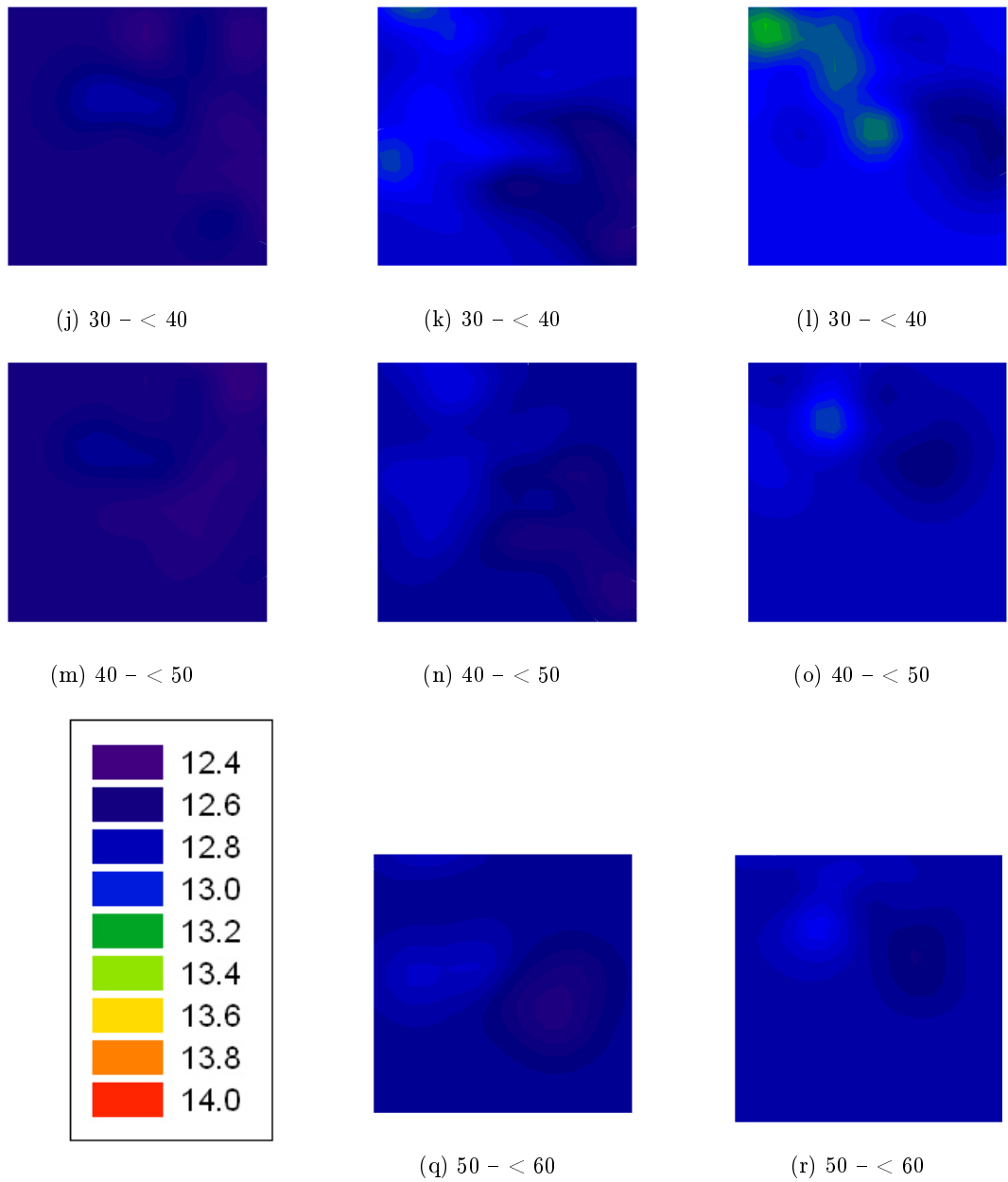
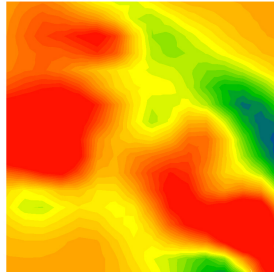


Figure 4.8: Water temperature [$^{\circ}\text{C}$] derived by an oceanographic model based on temperature measurements by logger equipped African penguins from Mercury Island, Namibia, in 2005. Left column represents group 1, centre column represents group 2 and right column represents group 3.



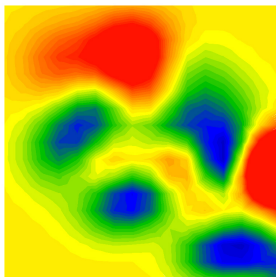
(a) $1 - < 10$



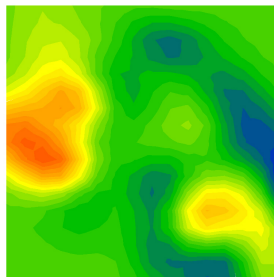
(b) $1 - < 10$



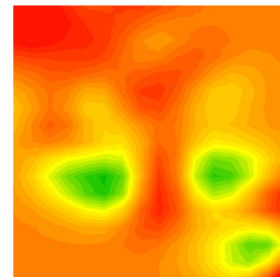
(c) $1 - < 10$



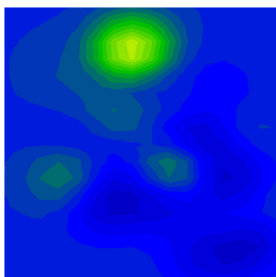
(d) $10 - < 20$



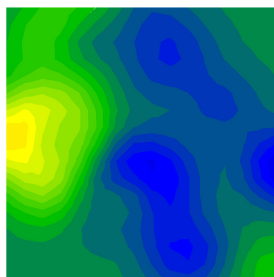
(e) $10 - < 20$



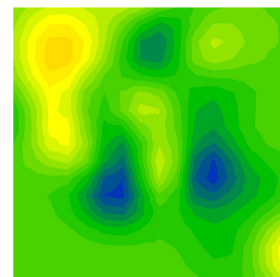
(f) $10 - < 20$



(g) $20 - < 30$



(h) $20 - < 30$



(i) $20 - < 30$

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4 Penguins as oceanographers: insight into small scale temperature distribution

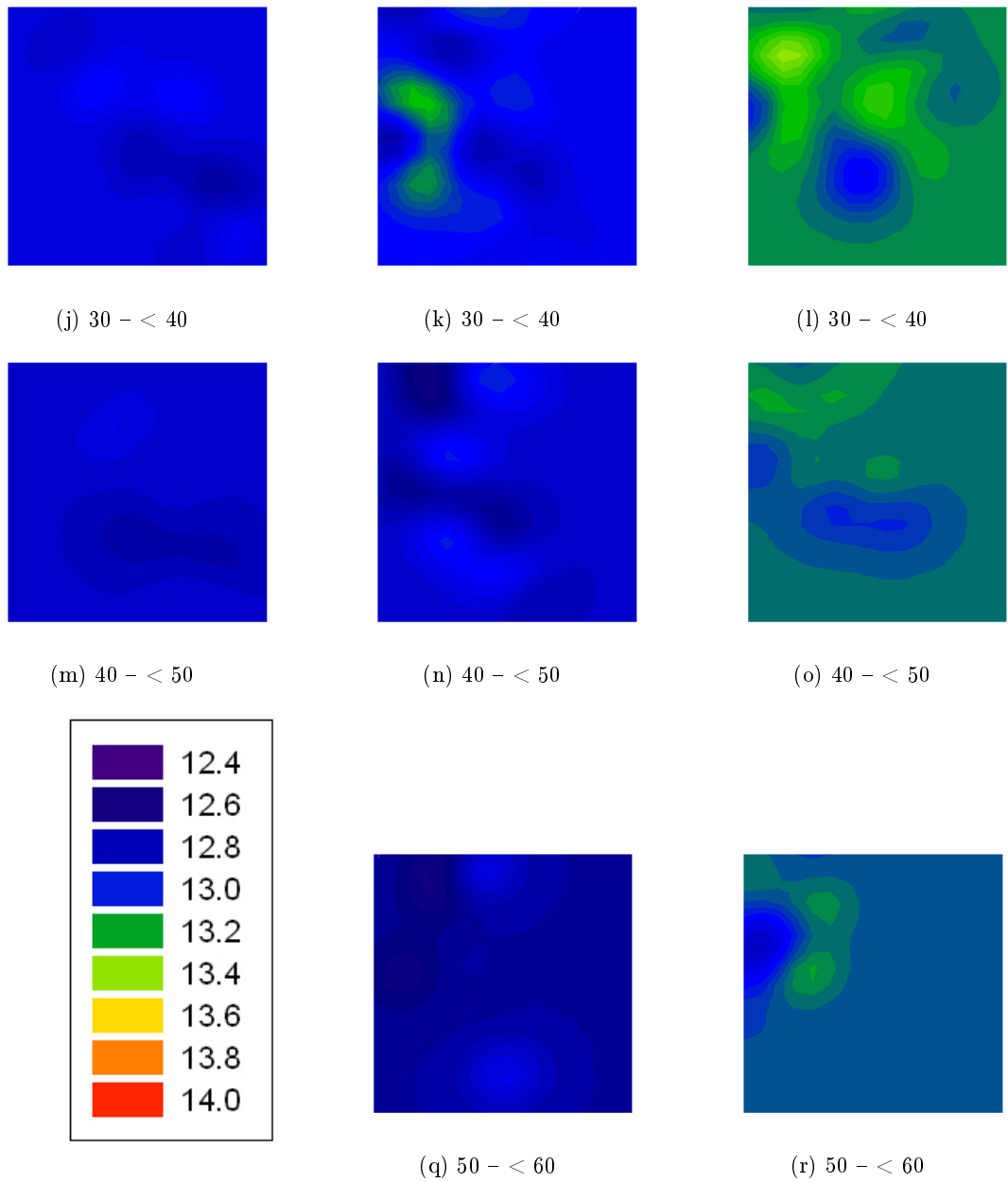


Figure 4.9: Water temperature calculated using an oceanographic model based on temperature measurements by logger equipped African penguins from Mercury Island, Namibia, in 2006. Left column represents group 1, centre column represents group 2 and right column represents group 3.

4.4 Discussion

The results presented in this chapter show that temperature data obtained from bird-borne devices may be effectively used for oceanographic modelling. Already small numbers of birds supply sufficient data to allow a reliable analysis of water temperatures and water mass structures within a limited area, such as the study area. Penguins from Mercury Island are very convenient *oceanographers* since they foraged in a well-defined area that was frequently visited by the majority of the birds even in consecutive years. This fact allowed the comparison of water temperature structures in different years but also on a smaller time scale between days with different wind patterns. The approach of using an oceanographic model instead of solely the single data points allows a larger area to be characterised and a better comparison between seasons or years. It allows the mapping of temperature regimes within an entire area without the need of a total coverage by the birds (Charrassin et al., 2004).

A quasi-synoptic sampling was assumed for data collected by the birds within a time period of about two weeks in each year. This might imply some difficulties since the Benguela system is known for its high spatial and temporal variances (Demarcq et al., 2003; Roux, 2003). Wind patterns change within days or even during a single day and affect the sea surface temperature (see Fig. 4.7; Shannon, 1985; Peard et al., 2005). Nevertheless, large scale differences between both study years regarding the entire foraging area of African penguins from Mercury Island became visible. The entire water column was comprised by warmer water in 2006 than in 2005. This difference was most predominant in the surface layer but differences in water temperatures were significant down to 60 m, thus almost for the entire water column used by diving penguins.

The general distribution of water masses shown in the model reflects the typical coastal upwelling pattern (Demarcq et al., 2003; Mann and Lazier, 2006). The sea surface temperature along the Namibian coast south of Walvis Bay is always $< 16.7^{\circ}\text{C}$ due to persistent coastal upwelling (Demarcq et al., 2003). A temperature gradient may be found between warmer offshore waters in the west and colder coastal waters further east closer to the coast. This gradient is especially obvious around the Lüderitz upwelling cell (Demarcq et al., 2003).

Short term variations Seasonal patterns of sea surface temperature variability are not very pronounced around Lüderitz due to relatively constant upwelling (Demarcq et al., 2003), but small scale differences may be observed within days and at small spatial scales. Spatial and temporal variations in temperatures were studied by Demarcq et al. (2003) over limited areas within the Benguela Current using satellite images, thus only considering sea surface waters. Areas were about 20 x 20 km of size. Areas analysed based on the penguin derived data were about 1 km², including the water column down to a depth of 70 m. Such a small scale approach is of major importance when considering organisms that do not travel large distances and that depend on a patchy distributed prey (Hunt and Schneider, 1987). In the case of breeding penguins, birds forage over limited areas due to their need to return to the colony (Davis and Renner, 2003).

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In 2005, elevated surface temperatures corresponded to north wind conditions, although this affected solely the upper ten metres of the water column (see group 1 in Fig. 4.8) due to surface stratification during calm conditions (Peard et al., 2005). In the following period with predominant south wind conditions, overall temperatures were lower but warm water extended further down in the water column. Surprisingly, in 2006, the periods with the highest surface water temperatures occurred during south wind conditions when upwelling took place. The period with the warmest water temperatures in greater depths was the one following previous north wind conditions. Apparently, wind induced mixing took place, combining warm surface waters with cold upwelled water in further depths. While northerly wind conditions led to higher SST values in 2005 and following south wind events dispersed warm surface waters into greater depths, in 2006, a lag in temperature responses to wind patterns was observed, possibly due to the overall higher water temperatures. A delayed signal in water temperature was also observed after the 1995 Benguela Niño when temperatures decreased not until several days of southerly winds causing upwelling of colder water (Gammelsrød et al., 1998).

The short term approach, running the oceanographic model with data corresponding to times of certain wind patterns, shows the ability to detect small scale changes occurring within days. The relatively small number of birds necessary in order to cover large extents of the studied grid (see Fig. 4.6) provides the possibility to study short term events with a very high resolution. Only few birds, equipped with data loggers synchronously, would be sufficient to provide useful data for detailed oceanographic analysis.

Outlook Temperature measurements obtained from device carrying penguins have been correlated with prey distribution (Wilson et al., 1994). This aspect may be of special importance for the evaluation of isolated areas and non-commercially used prey, which distribution is often unknown. Temperature and salinity are main factors influencing prey distribution at sea and seabird distribution is known to be related to those factors (Schneider, 1990; Garthe, 1997; Weichler et al., 2004). I found African penguins in Namibia to be foraging in water masses of a narrow temperature range (see Chapter 3). The present oceanographic model shows that water masses with temperatures falling within this range may be found in different depths depending on wind and circulation patterns. Penguins apparently prey on fish species that are associated with certain water temperatures and therefore with different water masses. Because African penguins seem to be sensitive to water temperature distribution, they might face problems when temperatures raise due to global warming (Roux, 2003).

An extensive monitoring of hydrographic conditions in the Benguela ecosystem using seabirds would be useful for detecting changes in the environment and for assessing their implications for the birds. The knowledge of foraging areas, prey composition and physical parameters would also provide valuable information on the biology of prey species, such as pelagic goby (*Sufflogobius bibarbatu*s), an important and not commercially used fish species in the Benguela ecosystem.

A combination of logger deployments on penguins, other seabird species and possibly marine mammals in the area of the Benguela upwelling system would present a relatively low-cost monitoring device for a very important marine ecosystem, being affected by local and global changes.

5 Is the ability to fly an advantage for Cape gannets (*Morus capensis*) when facing food shortage?

5.1 Introduction

Breeding seabirds may cover large distances during foraging even though they are forced to return to their breeding colony regularly in order to feed their chicks (Weimerskirch, 2001; Weimerskirch et al., 2002; Hyrenbach et al., 2006). Within their foraging range, different oceanographic environments and therefore different prey types may be encountered (Stahl et al., 1985; Cherel and Weimerskirch, 1995; Sokolov et al., 2006; Garthe et al., 2007a,b). Depending on the predictability of the prey, birds exhibit different foraging patterns, commuting directly between colonies and feeding areas or looping over vast areas at sea, searching for food and increasing their activity when a food patch is encountered (Weimerskirch, 2007). Several seabird species present an alternation of short and long foraging trips (Weimerskirch et al., 1994a; Ropert-Coudert et al., 2004c) and a bimodal distribution in trip duration has been observed in northern gannets (*Morus bassanus*¹) (Garthe et al., 2003) as well as in Cape gannets (*Morus capensis*) (Adams and Klages, 1999). Different foraging strategies may also be used in order to compensate for reduced prey abundance. Birds might exhibit larger foraging ranges and an increase in trip durations (Monaghan et al., 1996; Ropert-Coudert et al., 2004a) as well as different prey composition (Klages et al., 1992; Crawford and Dyer, 1995) when confronted with reduced prey availability. Birds either leave intentionally on longer foraging trips in order to reach areas with more profitable prey or might be forced to prolong their foraging due to low success rates in foraging during their first day at sea (Garthe et al., 2003; Ropert-Coudert et al., 2004a). Diving patterns and dive frequencies may be used as indicators of prey availability because birds may adapt their behaviour to the conditions encountered at sea (Garthe et al., 2003; Ropert-Coudert et al., 2004a; Garthe et al., 2007a). Lewis et al. (2004c) found tropical boobies adjusting their diving activity according to the time available for foraging.

Cape gannets, breeding at three islands along the Namibian coast, have to cope with limited food abundance (Crawford et al., 2007), especially since the collapse of the sardine stock in the late 1960s (see Chapter 1, Bianchi et al., 1999). Reduced prey availability seems to be one of the main causes for the drastic declines in populations of African

¹also named *Sula bassana*, see Bauer et al. (2005); nomenclature for *Sulidae* in this work follows Friesen and Anderson (1997)

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penguins (*Spheniscus demersus*) and Cape gannets in Namibia (Berruti, 1995; Crawford, 1998; Crawford et al., 2001; Kemper et al., 2001; Crawford et al., 2007).

Since gannets are able to fly, they may explore food patches located outside of the range of African penguins and might therefore be less affected by changes in the marine environment that cause localised prey depletion. The foraging behaviour of Cape gannets and their diet may be used as indicators of food abundance. The number of Cape gannets breeding in South Africa and the abundance of sardine (*Sardinops sagax*) in their diet have been correlated with the abundance of this fish species in the southern Benguela system (Crawford and Shelton, 1978; Crawford et al., 1992). Sardine also used to be the main prey of Cape gannets in Namibian waters (Matthews and Berruti, 1983), but as the sardine stock collapsed, birds had to switch to other prey species, such as anchovy (*Engraulis capensis*) and saury (*Scomberesox saurus scomberoides*) (Crawford et al., 1985), and numbers of breeding pairs decreased (Lewis et al., 2006; Crawford et al., 2007).

In this chapter, the foraging behaviour of chick-rearing Cape gannets at Mercury Island is presented for two consecutive years. Sulphide eruptions presumably enhanced food scarcity around the breeding colony in 2005 (see also Chapter 3) and low food availability may be represented in both foraging areas and diving patterns shown by the birds. The use of different water masses for foraging and the reasons for vast ranging flight patterns are investigated. The deployment of data loggers on Cape gannets at Possession Island enables a comparison of foraging behaviour for different breeding colonies, taking into account colony size, intra- and inter-specific competition and hydrographic differences.

5.2 Methods and study sites

Study sites Field work was conducted at Mercury and Possession Islands, two of three breeding colonies of Cape gannets in Namibia. Mercury Island (25°43'S, 14°50'E) currently hosts about 1400 breeding pairs (Crawford et al., 2007), being the second largest colony in Namibia. At Possession Island (27°01'S, 15°12'E), only 350 breeding pairs have been counted in 2005 – 06 (Crawford et al., 2007), making it the smallest of all Cape gannet breeding sites. Numbers of Cape gannets decreased strongly since the collapse of sardine stocks in the 1960s (Crawford et al., 1983), having declined by 95 % at the Namibian colonies since 1956 – 57, whereas South African breeding colonies show increasing numbers in breeding pairs (Crawford et al., 2007). For further details on the study colonies see Chapter 1, page 11.

Data logger deployment GPS TDlog data loggers (earth&OCEAN technologies, Kiel, Germany) were used, recording the bird's position at sea, the diving depth (measured from water pressure) and the water temperature *in situ*. Data loggers used had a streamlined aramide fibre/epoxy-composite housing (100 x 48 x 24 mm) and had a total mass of 70 g. The GPS receiver settings for obtaining positional data differed between individual deployments and between years. Positional information was obtained at 2 – 10 min intervals, switching to continuous mode for 0 - 10 min after a dive was recorded. In in-

intermittent mode, the error for positional fixes lies between ten and 20 m, for continuous mode it is less than 5 m (product information earth&OCEAN technologies and Ryan et al., 2004). Positions were later interpolated using Matlab 7.0.1[®] (script written by T. Mattern). Pressure and temperature sensors record water depth and temperature with an accuracy of 4 mbar and 5 mK, respectively. Both sensors were set to store data every second, allowing a detailed analysis of diving patterns and water temperature structure.

In 2005, nine breeding Cape gannets were equipped with GPS TDlog data loggers at Mercury Island between the 14th and the 25th of February 2005 (Table 5.1). Birds were rearing chicks of four to six weeks of age and were caught at the nest site shortly after the partner returned from its foraging trip. Loggers were attached following Garthe et al. (2007b) using Tesa[®] tape, attaching the device to the center tail feathers and the lower back of the bird. Observations in the colony showed that nest attendance and chick-rearing was not different for device carrying birds compared to other birds in the same colony. The same devices were used by Lewis et al. (2006) and no impact on the birds' behaviour was observed. Birds were recaptured at the nest site after returning from sea or when encountered in the colony after an observed absence of several hours, presumably having realised at least one foraging trip. Data loggers were detached by removing the tape and if necessary clipping the tips of the taped back feathers without harming the main tail feathers. Of the nine birds equipped, seven data loggers were recovered containing information on eight foraging trips as one bird realised two trips before the device was recovered. The remaining two loggers were lost; birds apparently had removed them with their bills. Birds returning without loggers continued breeding as did the other equipped birds.

In 2006, nine chick-rearing Cape gannets were equipped at Mercury Island following the same procedure as in 2005. Deployment took place between the 17th and 27th of February 2006 (Table 5.2). One bird did not return to the colony but all other devices were recovered within three days. A total of 14 foraging trips were recorded because several birds realised various trips (maximum four trips) before the devices were taken off (see Table 5.2); one data logger did not function properly.

At Possession Island, two birds were equipped with GPS TDlog data loggers on the 8th and 9th of March 2005 using the same method as at Mercury Island.

Data analysis Positional data were analysed using ArcView GIS 3.2[®]. The foraging range was defined as the maximum distance away from the colony. Tracks between known positions were interpolated, assuming a straight line which leads to a possible underestimation of the total distance travelled (see also discussion in Chapter 2, page 32). All changes in depth were considered as dives when ≥ 1 m of depth and ≥ 2 s of duration were recorded. The analysis of diving parameters was conducted using Matlab[®] (script written by T. Mattern and L.-G. Ellenberg). Dive rates were calculated for the time birds were at sea. For the analysis of daily dive rates, only daylight periods (between 6:00 and 21:00 h) were considered. Water temperature was measured by the temperature sensor included in the device when the birds were either swimming or diving. For the comparison of water temperature in- and offshore, the water temperatures at the locations

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where diving activity took place were analysed. In each year, mean temperatures for in- and offshore dives of individual birds were calculated. Some birds solely exhibited diving close to the coast, other dived exclusively more than 10 km off the coast. In both years, not all data loggers recorded valid temperatures and were thus excluded from analysis. A total of six and seven trips were included in the analysis for inshore and offshore waters, respectively, in 2005 and nine and seven birds in 2006, respectively. In order to determine the use of different water masses of single birds within individual foraging trips, one bird in each year exhibiting extensive diving close to the coast as well as offshore was analysed separately. Inshore waters were defined as within 10 km off the coastline with water depths of up to 100 m. Offshore waters were defined as being over 10 km away from the coast but mainly within the 200 m depth contour. Small scale bathymetry data were not available, therefore in- and offshore waters cannot be defined by water depth; Duffy (1989a) defined inshore foraging over waters < 50 m of depth for the Benguela Current. The area covered by all birds in each years refers to the outer line of all trips combined, not to the sum of foraging ranges of individuals. Statistical tests were carried out using the program R 2.4.1[®]. For the calculation of the median all data from all birds for one year were combined if not stated differently. Statistical tests applied were general linear models (GLM) using a quasipoisson distribution and linear models (LM) as well as linear mixed-effects models fit by REML (LMER). These take into account the variance between birds when comparing results between two years or two islands.

Diet Diet samples were obtained in both years and at both breeding colonies by capturing birds immediately after their arrival at the colony, holding the birds in-between the legs, massaging their stomach until the birds regurgitated their stomach contents. Samples were stored in plastic bags and analysed in the field. Species identification was conducted using Bianchi et al. (1999) and individual fish were measured and weighed to the nearest centimetre and gram when specimens were complete. In 2005, 17 birds were sampled on two occasions at Mercury Island on the 23rd of February and the 2nd of March. At Possession Island, five stomach samples were obtained from birds on the 12th of March 2005. In 2006, a total of 17 birds were sampled at Mercury Island on four days between the 28th of February and the 14th of March. Logger equipped birds were not sampled because the return of the birds was seldom observed and in order to avoid additional stress.

5.3 Results

5.3.1 Mercury Island

In both years, birds were equipped during daylight hours between 10:00 and 18:30 h. Some birds took off immediately after deployment, mostly bathing within sight from the island before taking off from the water towards the foraging area; others returned to their nests and left later the day or the following day to forage (Table 5.1 and Table 5.2).

Trip duration

The average trip duration for birds in 2005 was 23 hrs 53 min ($n = 8$ trips of 7 birds; range 4 hrs 10 min - 72 hrs 21 min) and 20 hrs 39 min in 2006 ($n = 14$ trips of 7 birds; range 3 hrs 18 min - 58 hrs 17 min; Table 5.3). There was no significant difference between the two years concerning the trip duration (n.s; $p = 1$; LMER). Birds stayed away mostly during the day only (three and six trips in 2005 and 2006, respectively); one bird in 2006 made two trips within one day. Birds spent the night at sea on four trips in 2005 and on six trips in 2006. Two birds spent two nights at sea in 2006 and one bird stayed away for three nights in 2005 (Table 5.2 and Table 5.1). Three out of the four birds leaving before midday in 2005 returned the same day to their nests whereas all birds that left after midday spent at least one night at sea (Table 5.1). In 2006, departure time did not seem to influence the time spent at sea. Of the six birds returning the same day, three left in the morning and three in the afternoon. Birds spending one or more nights at sea also left before or after midday (Table 5.2).

Foraging area

All birds in 2005 and 2006 left the island in a north or north-westerly direction (Fig. 5.1 and Fig. 5.2). Most birds flew along the coast, later turning offshore towards the west before returning to the colony. Locations reached further away from the coast than 10 km were considered as offshore in the following analysis. Almost all flight tracks of birds in 2005 and 2006 stayed within the 200 m depth contour. Two birds in 2005 reached areas with water depths of over 200 m but their diving took place along the 200 m depth contour and not over deeper waters (Fig. 5.1 and Fig. 5.6).

2005 Out of eight trips recorded in 2005, four represented a mixture of foraging over inshore and offshore waters (Fig. 5.3c). Birds travelled along the coast and turned offshore, later returning to the coast or directly to the colony. Diving took place mainly along the coast (Fig. 5.6 and Fig. 5.9), even during trips with large proportions spent flying offshore. Only one bird stayed inshore during the entire trip (Fig. 5.3a) and three trips were directed offshore without visiting inshore waters (Fig. 5.3b). Two of these three trips were made on consecutive days by the same bird. On the first day, the bird flew to a maximum distance from the colony of about 40 km where it intensively searched for food and frequently dived before returning back to the colony. On the second day, the bird travelled directly towards the same area but, without spending time searching or diving there, passed on to a maximum distance from the colony of about 95 km, travelling in a large loop with single dispersed dives (Fig. 5.5a).

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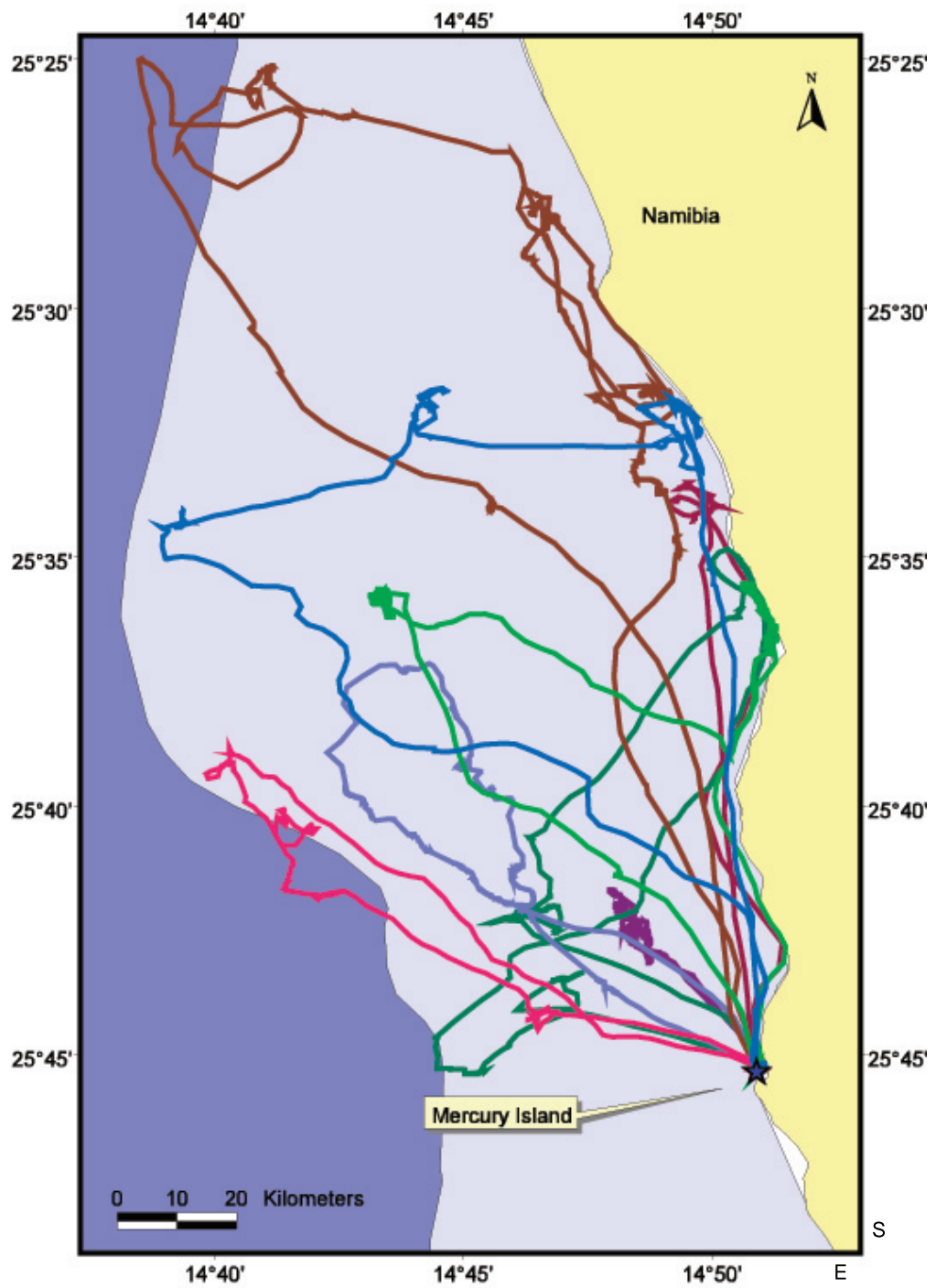


Figure 5.1: All foraging tracks of Cape gannets from Mercury Island, Namibia, equipped with GPS TDlog data loggers in 2005 (n = 8 trips of 7 birds). Each colour represents a single trip. Light blue areas correspond to water depths of 0 – 200 m and darker blue to water depths of 200 – 500 m.

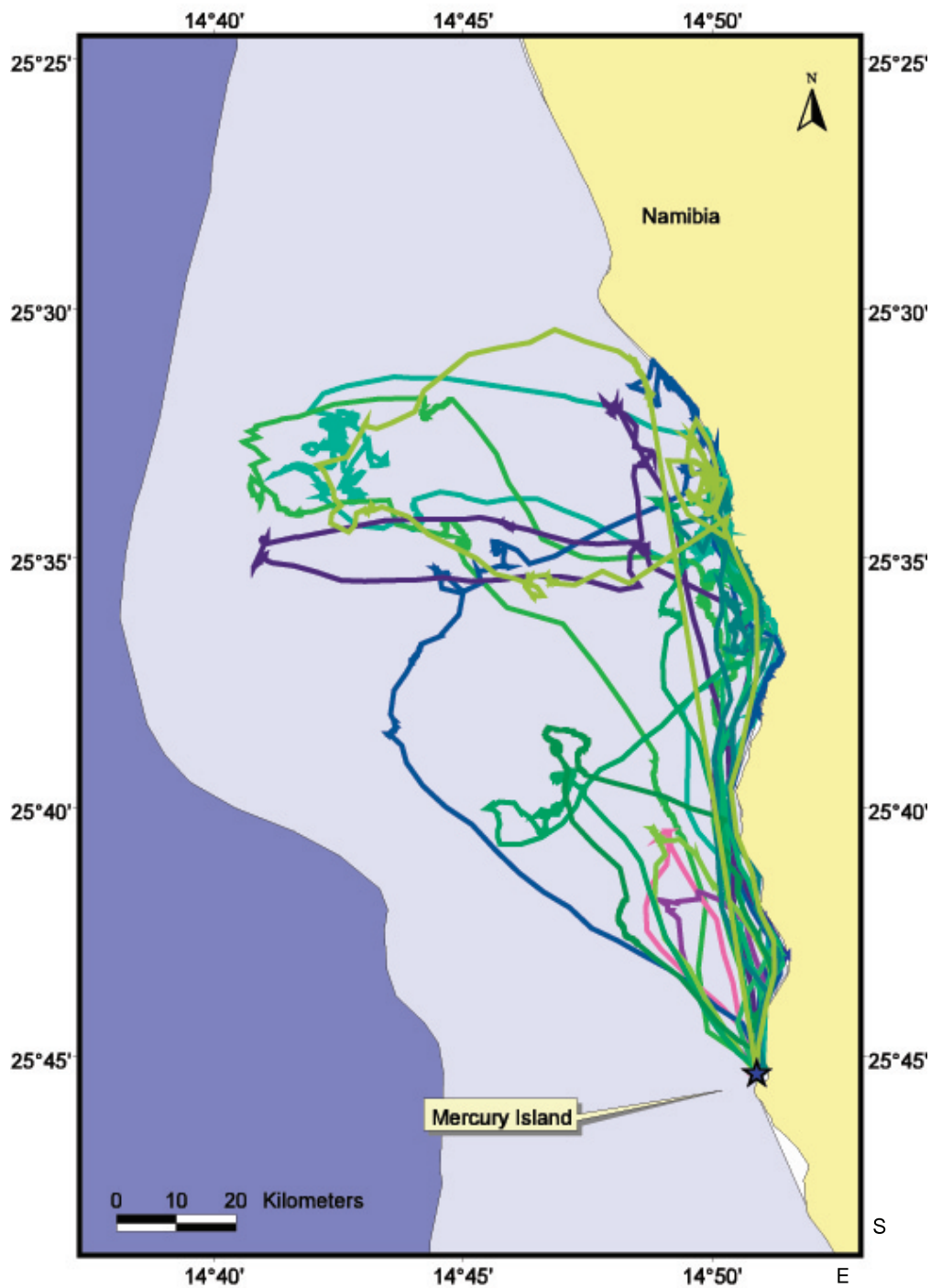


Figure 5.2: All foraging tracks of Cape gannets from Mercury Island, Namibia, equipped with GPS TDlog data loggers in 2006 ($n = 14$ trips of 7 birds). Each colour represents a single trip. Light blue areas correspond to water depths of 0 – 200 m and darker blue to water depths of 200 – 500 m.

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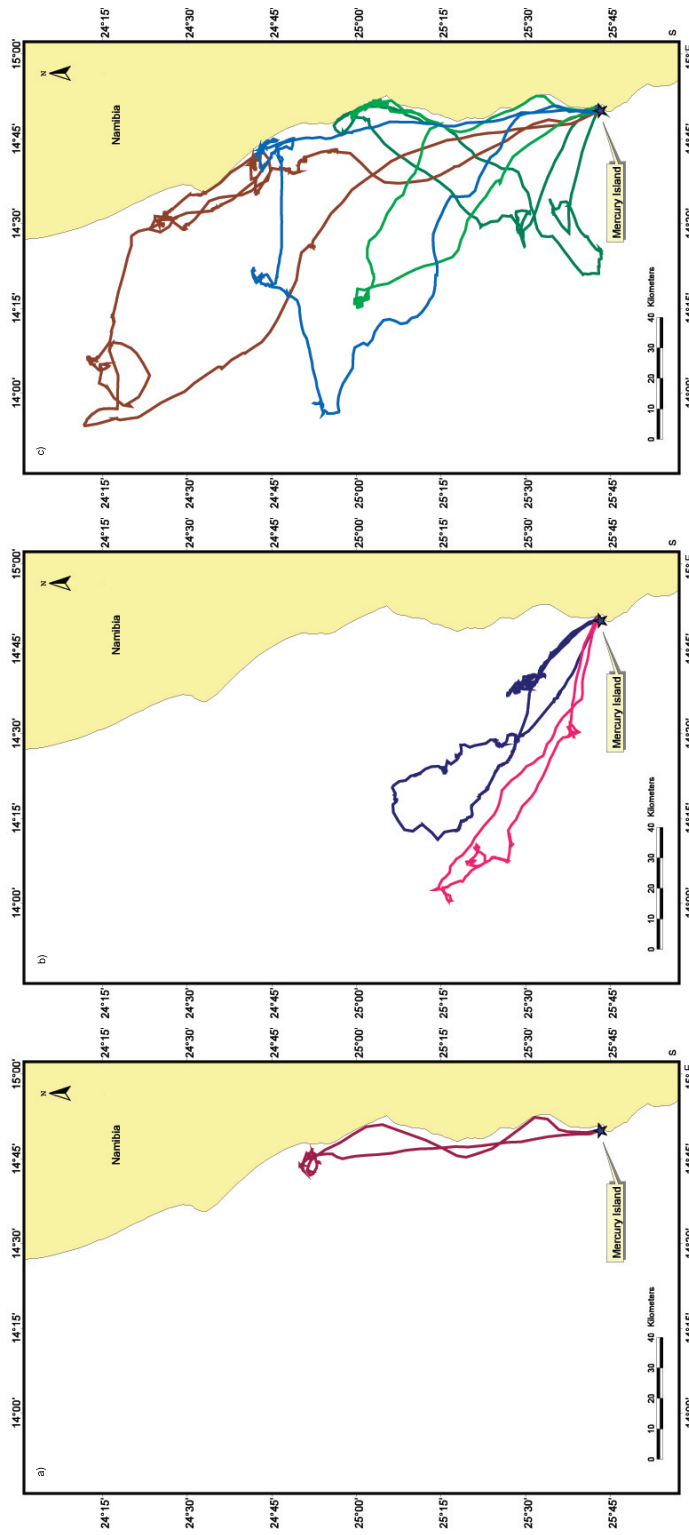


Figure 5.3: Single foraging tracks of Cape gannets from Mercury Island, Namibia, equipped with GPS TDlog data loggers in 2005. Birds foraged a) inshore, b) offshore and c) over in- and offshore waters.

2006 In 2006, seven out of the 14 recorded foraging trips covered only inshore waters (Fig. 5.4a). Four of these trips were conducted by the same bird, leaving for short foraging trips north of the island, almost reaching identical areas on each trip (Fig. 5.5b). Birds on the remaining seven trips reached in- and offshore waters (Fig. 5.4) and showed similar flight patterns as in 2005. Diving took place mostly along the coast (Fig. 5.6) but, nonetheless, birds covered vast areas offshore.

The median foraging range in 2005 was 97.8 km ($n = 8$ trips of 7 birds; range 37.4 – 193.2) and 98.2 km ($n = 14$ trips for 7 birds; range 26.2 – 131.0) for birds in 2006 (Table 5.3). Although there was no significant difference in the maximum distance reached for birds in 2005 and 2006 (n.s.; $p = 0.62$; LMER), the area covered by all birds in 2005 was about double the size than the area used by birds in 2006 (15300 vs. 7400 km²). The total distance travelled by each bird during one foraging trip was on average 352.1 km (range 155.4 – 815.6) in 2005 and 344.3 km (range 84.6 – 696.4) in 2006 (Table 5.3). There was a significant correlation between total distance travelled and the duration of a foraging trip ($p < 0.01$; $R^2 = 0.849$; LM) as well as between trip duration and the foraging range ($p < 0.001$; $R^2 = 0.858$; LM) in 2005 (Fig. 5.7a). The bird spending three nights away from the colony covered a distance of 815 km whereas the bird performing short foraging trips of four and nine hours of duration only travelled 155 and 283 km, also exhibiting the smallest foraging ranges of 37 and 89 km. On both trips, the bird flew directly towards its final foraging area located north-west of the island instead of flying northwards along the coast and later turning offshore like most of the other birds. In 2006, trip duration was correlated significantly with the total distance travelled ($p < 0.001$; $R^2 = 0.823$; LM) and with the foraging range ($p < 0.001$; $R^2 = 0.721$; LM; Fig. 5.7b). The number of dives were correlated significantly with trip duration in 2006 ($p < 0.01$; $R^2 = 0.542$; LM) but not in 2005 (n.s.; $p = 0.061$; $R^2 = 0.470$; LM).

Diving behaviour

In 2005, birds dived on average 42.5 times (range 20 – 95) and a median 35.5 dives per trip (range 1 – 106) were performed by birds in 2006. Birds in 2005 dived to a median depth of 3.3 m (dives ≥ 1 m; range 1.0 – 6.9) and to a median depth of 2.8 m in 2006 (range 1.0 – 8.0). The mean dive duration was 4.4 ± 0.5 s (range 2.0 – 21.0) in 2005 and 3.7 ± 1.0 s (range 2.0 – 22.0) in 2006. No significant differences were found in the parameter dive duration or in dive depth between 2005 and 2006 (n.s.; $p = 0.449$ and $p = 0.197$, respectively; LMER; Table 5.3). The median maximum dive depth was 6.0 m (range 4.9 – 6.9) in 2005 and 5.2 m (range 1.4 – 8.0) in 2006 (n.s.; $p = 0.367$; LMER). Maximum dive duration was 7.5 s (mean 9.6 ± 5.2 s; range 6 – 21) in 2005 and 7.5 s (mean 9.1 ± 5.9 s; range 2 – 22) in 2006 (n.s.; $p = 1$; LM; Table 5.3). All diving activity took place during daylight hours between 6:30 and 20:00 h. Birds during one-day trips dived frequently during midday whereas birds staying at sea overnight, often dived in the morning and evening hours. Diving was often interrupted during midday in birds that had spent the night at sea (Fig. 5.8).

Dive rates on the day of departure were different for birds during one-day trips compared to birds spending several days at sea in 2005. These birds dived on average 2.2

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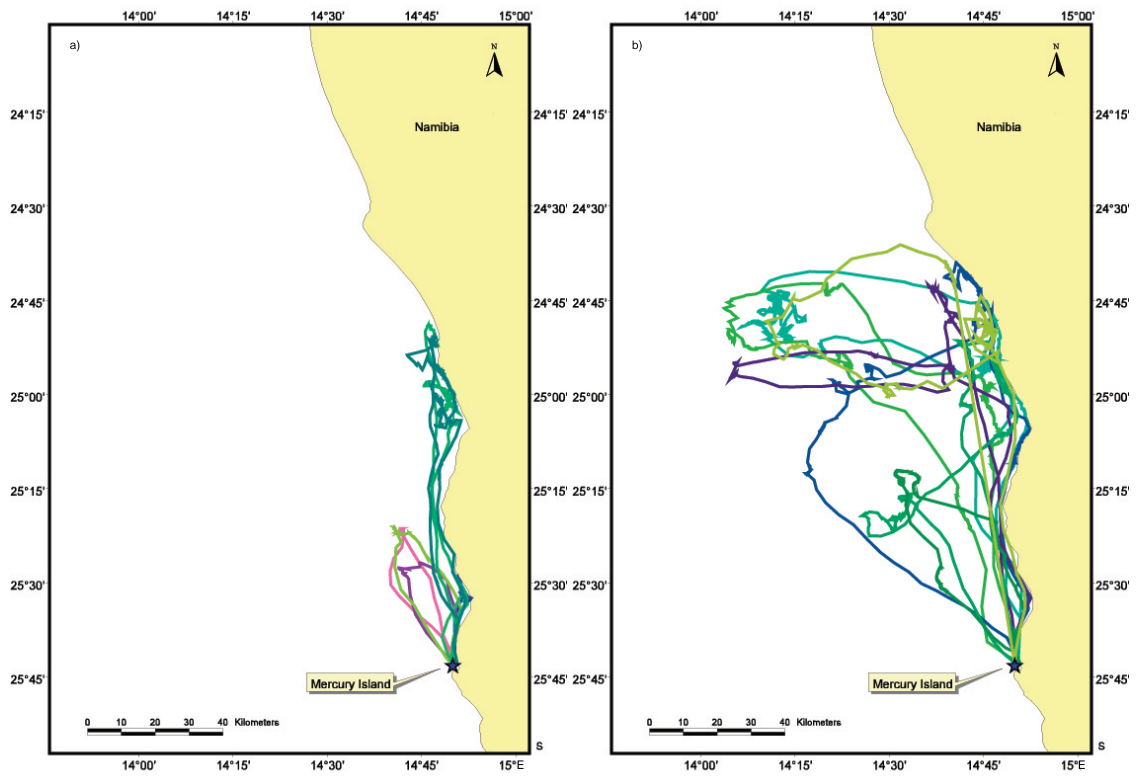


Figure 5.4: Single foraging tracks of Cape gannets from Mercury Island, Namibia, equipped with GPD TDlog data loggers in 2006. Birds foraged a) inshore and b) over in- and offshore waters.

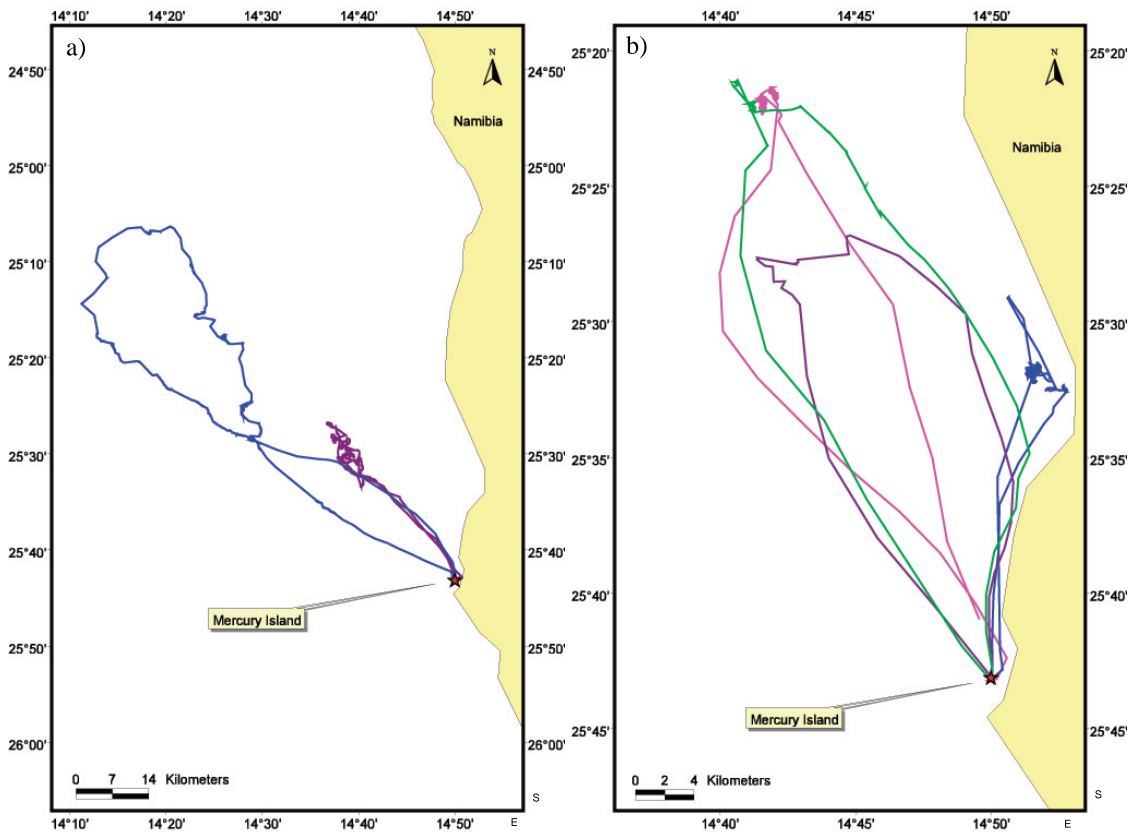


Figure 5.5: Site fidelity of Cape gannets from Mercury Island, Namibia. a) One bird (27-180205) foraging close to the colony on the first day, followed the same path on the second day but foraged further away. b) In 2006, four trips presented by the same bird (83-230206) in three consecutive days. Following one trip close to the coast, the bird reached almost identical areas on the three following trips.

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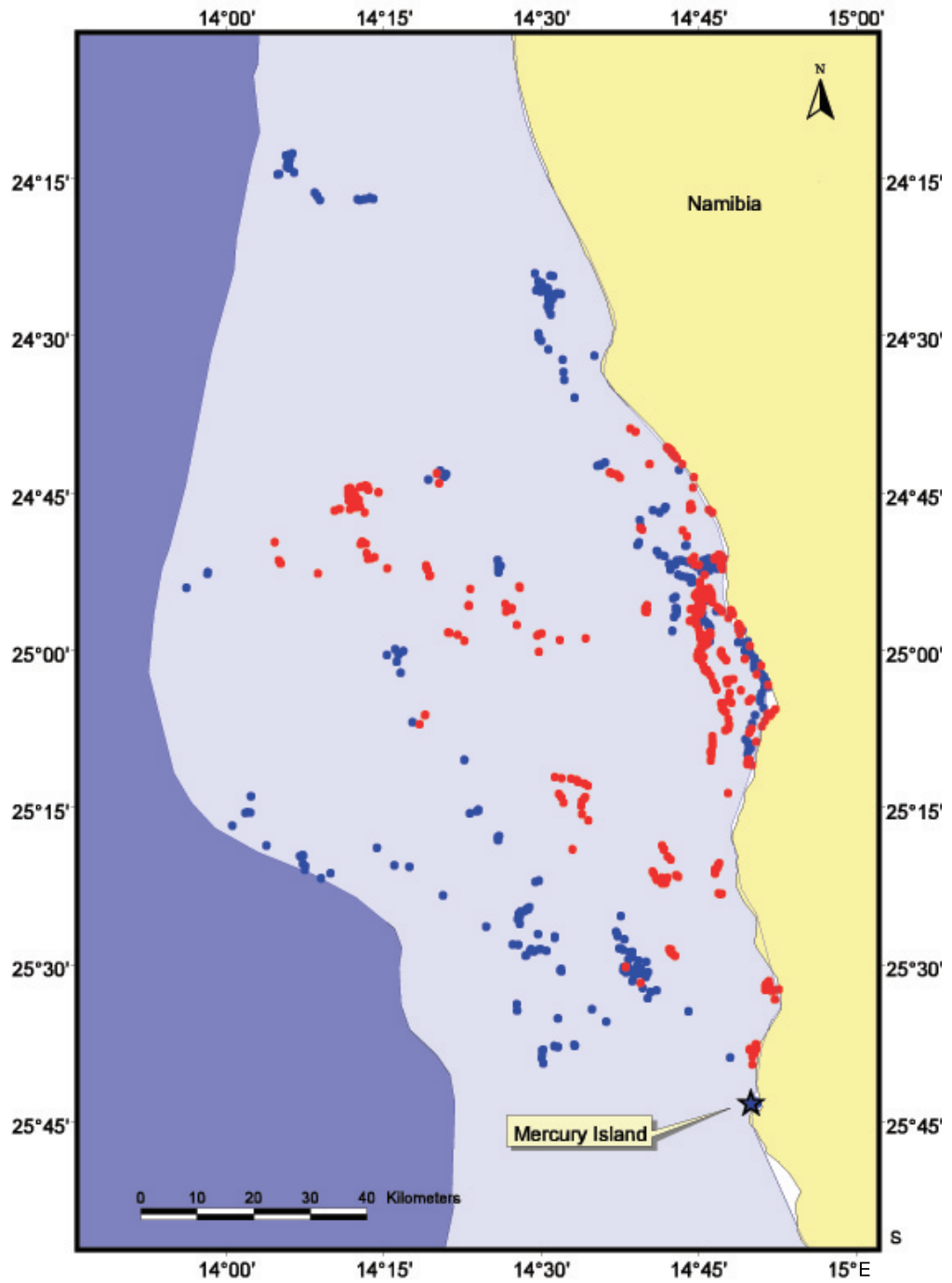


Figure 5.6: Dive locations of Cape gannets from Mercury Island, Namibia, equipped with GPS TDlog data loggers in 2005 (blue circles) and 2006 (red circles).

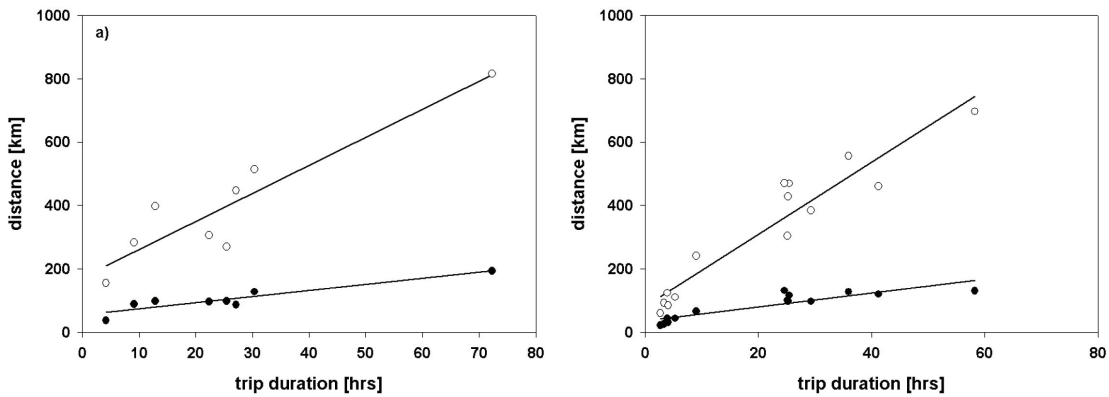


Figure 5.7: Correlation between trip duration [hrs] and foraging range [km] (black dots) and distance travelled (white dots) for Cape gannets from Mercury Island, Namibia, a) in 2005 ($n = 8$ trips) and b) in 2006 ($n = 14$ trips).

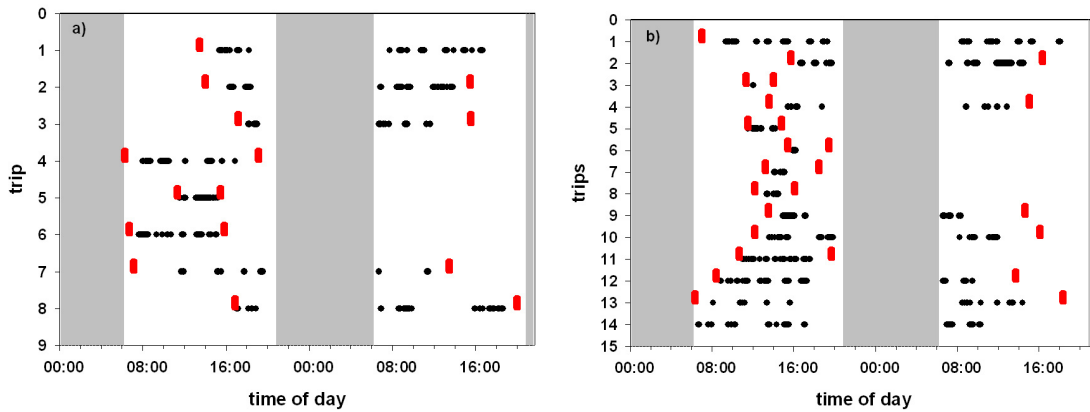


Figure 5.8: Dive events of Cape gannets from Mercury Island, Namibia, a) in 2005 and b) in 2006. Each row represents a single trip; in 2005 eight trips are presented according to Table 5.1 and in 2006 14 trips according to Table 5.2. For all birds only the first two days at sea are presented. Bird 14 in 2006 departed the night before and bird 1 in both years spent more than two days at sea. Circles represent single dive events, red bars indicate the beginning and end of the trip. Grey shaded areas indicate the night time between 21:00 and 6:00 h.

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times per hour ($n = 5$; range 0.5 – 3.7) on their first day compared to 4.4 dives/hour for birds on one-day trips ($n = 3$; range 3.5 – 9.4). However, these differences were not significant (n.s.; $p = 0.0793$; GLM) due to the small sample size. Significant differences were found in the dive rate over the entire trip. Birds on one-day trips dived more frequently than birds during longer foraging trips when considering all dives for the entire trip duration (4.4 vs. 1.3 dives/hour; $p < 0.05$; GLM) as well as when considering only daylight hours (4.4 vs. 1.7 dives/hour; $p < 0.05$; GLM). In 2006, no significant correlation was found between dive rate and trip duration. The dive rate on the first day did not differ significantly between one-day trips and birds that spent more time at sea; the latter diving more often (2.6 vs. 4.5 dives/hour; $p = 0.544$; GLM). Dive rates per hour for the entire trip duration as well as for daylight periods during the trip were similar for birds during one-day trips and overnight trips (2.6 vs. 2.3 and 2.6 vs. 3.4 dives/hour, respectively; n.s.; $p = 0.7381$ and $p = 0.621$, respectively; GLM).

Birds were diving in an average distance of 86.5 km to the colony ($n = 377$ dives; range 0.8 – 183.1) in 2005 and 73.9 km ($n = 690$ dives with known positions, range 0.9 – 116.9) in 2006 (Fig. 5.6 and Fig. 5.9a; n.s., $p = 1$; LMER). Excluding dives within the bay shortly after departure, birds flew on average about 60 km before diving; the same distance was covered after the last dive towards the colony in 2005. In 2006, birds covered an average distance of 55 km before the first dive and travelled on average 80 km after the last dive in order to return to the colony.

The distance between each diving location and the closest point on the coast shows a bimodal distribution. In 2005, 51.2 % of all dives were located within 10 km off the coast and 48.8 % were further away than 10 km from the coast ($n = 377$ dives from seven birds and eight trips; Fig. 5.6 and Fig. 5.9b). In 2006, diving tended to take place closer to the coast (Fig. 5.6). Of all dives, 74.2 % were located within 10 km off the coast ($n = 690$ dives from seven birds and 14 trips; Fig. 5.9b). The median distance of all dives in 2006 was 4.9 km away from the coast compared to 9.5 km in 2005 (n.s., $p = 1$; LMER).

Dive durations and dive depths differed between inshore and offshore areas in 2005. Dives made offshore were deeper and of longer duration. The differences were significant for both dive depth and dive duration ($p < 0.01$ and $p < 0.05$, respectively; LMER). Differences in dive depth and dive duration between inshore and offshore dives were not significant in 2006 ($p = 0.895$ and $p = 0.094$, respectively; LMER).

Inshore dives in 2005 were mostly to depths of 1 – 2 m and 2.5 – 3.5 m; dives deeper than 4 m took place mostly in offshore waters (Fig. 5.10a). In 2006, dives reached similar depth in inshore and offshore waters, most birds dived to depths of 1.5 – 2.5 m (Fig. 5.10b).

Water temperature in foraging areas

In 2005, the mean sea surface temperature at dive locations inshore was $16.0 \pm 1.3^\circ\text{C}$ ($n = 6$ trips; range 14.9 – 18.1) and offshore dives occurred in mean water temperature of $16.7 \pm 1.4^\circ\text{C}$ ($n = 7$ trips; range 15.1 – 19.2). Differences between the mean water temperatures in- and offshore were not significant (n.s.; $p = 0.393$; GLM) due to the high variability between trips. In 2006, differences in the water temperature measured during

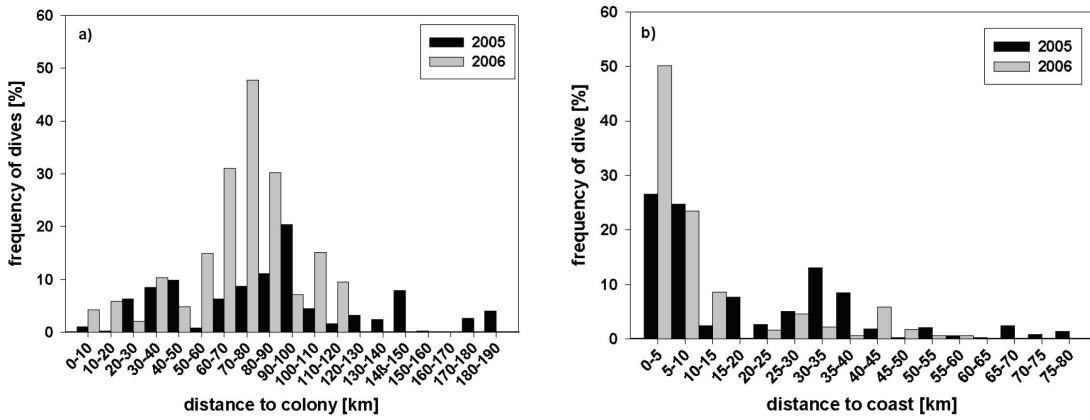


Figure 5.9: Frequency of dives a) in 10 km intervals from the colony and b) in 5 km intervals from the coast for Cape gannets from Mercury Island, Namibia, in 2005 (black bars) and 2006 (grey bars).

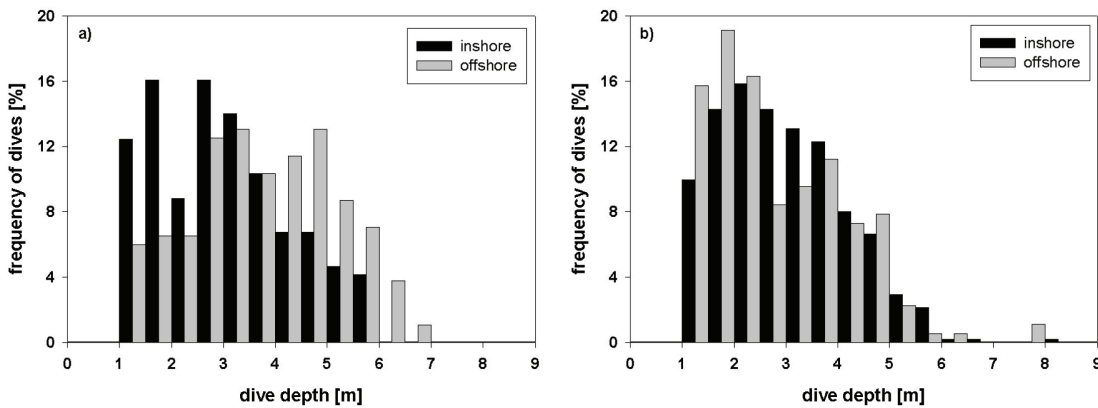


Figure 5.10: Frequency of dives in 0.5 m depth intervals for inshore (≤ 10 km off the coast) and offshore (> 10 km off the coast) dives of Cape gannets from Mercury Island, Namibia a) in 2005 ($n = 193$ inshore and 184 offshore dives) and b) in 2006 ($n = 508$ inshore and 182 offshore dives).

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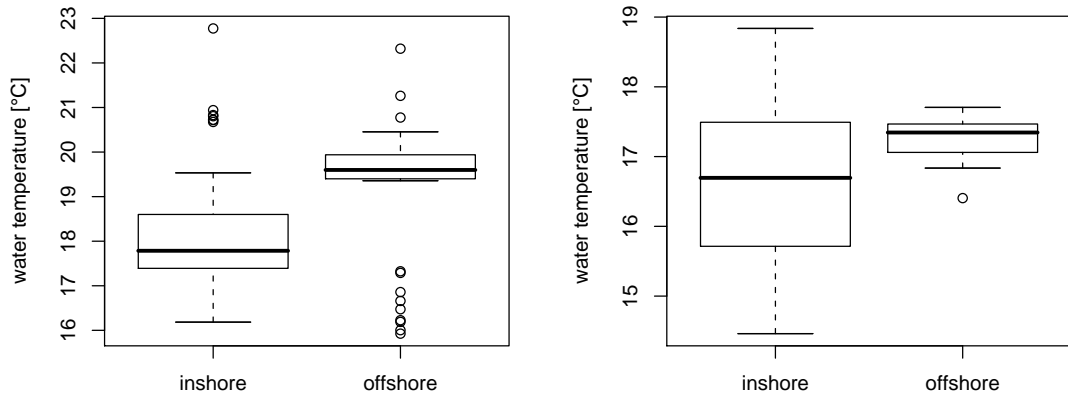


Figure 5.11: Water temperature [°C] at the bottom of inshore and offshore dives for Cape gannets a) bird 29-170205 and b) bird 57-200206 from Mercury Island, Namibia.

dives close to the coast and offshore were even less pronounced than in 2005 and did not differ significantly (n.s.; $p = 0.7$; GLM). Inshore waters where diving took place had a mean temperature of $15.7 \pm 1.1^\circ\text{C}$ ($n = 9$ trips; range 14.0 – 17.4) and offshore waters a mean temperature of $16.0 \pm 1.7^\circ\text{C}$ ($n = 7$ trips; 13.9 – 17.7).

For each year, a single bird was chosen that foraged over inshore as well as offshore waters during a single trip to assess differences of used water masses.

In 2005, bird 29-170205 spent over 72 hours at sea, travelling along the coast where it showed intense foraging behaviour, increasing its turning rate and diving frequently. On its third day at sea the bird moved offshore, diving further away from the coast and returning to the colony. The median water temperature at the bottom of each inshore dive was 17.8°C ($n = 53$ dives, range 16.2 – 22.8) and the median water temperature for offshore dives was 19.6°C ($n = 42$, range 15.9 – 22.3). Water temperatures differed significantly between these two areas ($p < 0.001$; GLM; Fig. 5.11a).

In 2006, only the first half of the trip of bird 57-200206 could be analysed because the temperature sensor did not work properly for the entire trip. A total of 88 dives were included in the water temperature analysis. Dives were either > 40 km or < 10 km away from the coast. The median water temperature at the bottom of each inshore dive was 16.7°C ($n = 70$; range 14.5 – 18.8) and for the offshore dives the median temperature was 17.3°C ($n = 18$; range 16.4 – 17.7). Water temperatures differed significantly between in- and offshore areas ($p < 0.05$; GLM; Fig. 5.11b).

Diet Birds sampled at Mercury Island in 2005 comprised of 13 chick-rearing individuals, one non-breeder and three birds of unknown breeding status. Sardine was the main food item found in the diet samples, constituting 60.9 % of the total mass and the highest

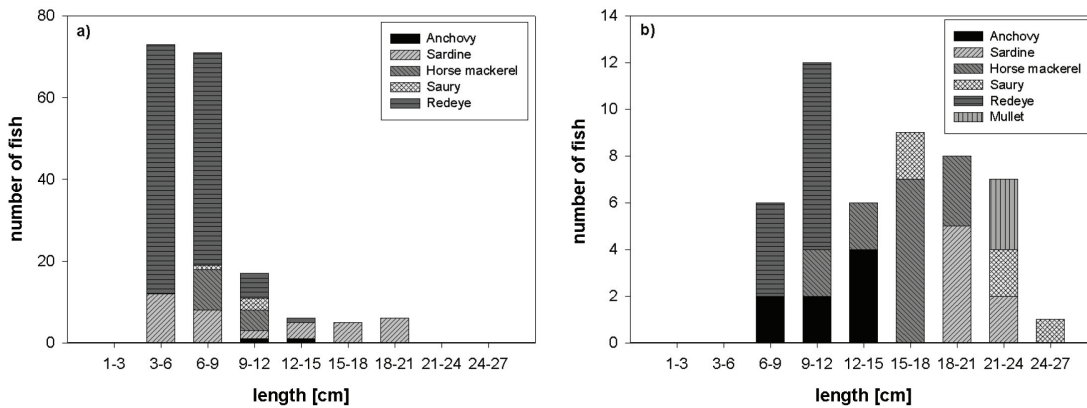


Figure 5.12: Length distribution of entire fish found in diet samples of Cape gannets at Mercury Island a) in 2005 and b) in 2006.

frequency of occurrence (Table 5.4). Horse mackerel (*Trachurus capensis*) and redeye (*Etrumeus whiteheadi*) made up 16.4 and 17.4 %, respectively. Saury (*Scomberesox saurus scombroides*) did not play an important role by mass but by frequency of occurrence (Table 5.4).

In 2006, samples obtained were of 14 chick-rearing adults, two birds of unknown breeding stage and one fledgling. Diet composition was more diverse in 2006 than in 2005 with eight fish species being present compared to only six in the previous year. Sardine and horse mackerel showed almost the same presence in the diet, making up 22.1 and 20.9 % of the total mass of all samples. Horse mackerel was more important than sardine in terms of occurrence (Table 5.4). Anchovy did not occur in large amounts in terms of mass but was found in 23.5 % of all stomach samples (Table 5.4).

Length distribution of complete fish found in the diet of birds differed between 2005 and 2006 (Fig. 5.12). In 2005, large numbers of relatively small redeye (median 5.9 cm, range 4.3 – 13.5) were found in the samples, one sample containing 56 intact individuals of this species. Sardines and horse mackerels found intact were smaller in 2005 than in 2006 (median length of 6.8 vs. 19.5 cm and 8.4 vs. 17.2 cm, respectively; Table 5.5 and Fig. 5.12).

5.3.2 Possession Island

Only two birds were equipped with GPS TDlog data loggers at Possession Island as part of a preliminary study. One bird left the colony, flew out in the bay and, without having dived, returned to its nests after only 14 minutes. The other bird departed at midday, returning the following day after 28 hrs 30 min at sea. The maximum distance reached away from the colony was 114.3 km and the distance travelled by the bird was 483.4 km (Fig. 5.14). During its foraging trip, the bird dived 47 times. The maximum diving depth was 6.6 m and the median diving depth was 5.0 m (range 2.3 – 6.6). The median dive

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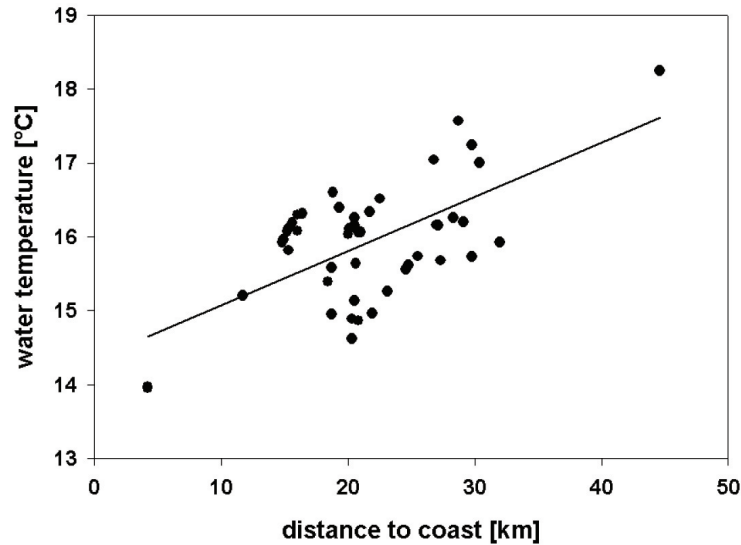


Figure 5.13: Relationship between distance to coast [km] and water temperature [°C] at the bottom of each dive for a Cape gannet from Possession Island, Namibia, in 2005.

duration was 5.0 s (range 2 – 9; Table 5.3). On average diving took place 20.5 km from the coast (range 4.2 – 44.6). Over 80 % of all dives were located between 15 and 30 km from the coast. Before the first and after the last dive, the bird commuted between 35 and 45 km in a relatively straight line away from and back to the colony. The bird stayed within the 200 m depth contour, as also observed for birds from Mercury Island. The median water temperature at the bottom of each dive was 16.1°C (range 14.0 – 18.2) and water temperature increased significantly with increasing distance to the coast ($p < 0.001$; $R^2 = 0.399$; LM; Fig. 5.13).

Diet Five birds were sampled at the breeding colony at Possession Island in 2005. Three samples contained saury, with 44.7 % of the drained weight being the main prey item. One sample consisted of horse mackerel (24.6 %) and one of Redeye (14.0 %). Sardine was found together with saury in one sample, constituting 16.8 % of the entire mass. Fishes found intact in the diet samples were mainly large individuals, especially saury with a median length of 24.0 cm (Table 5.5).

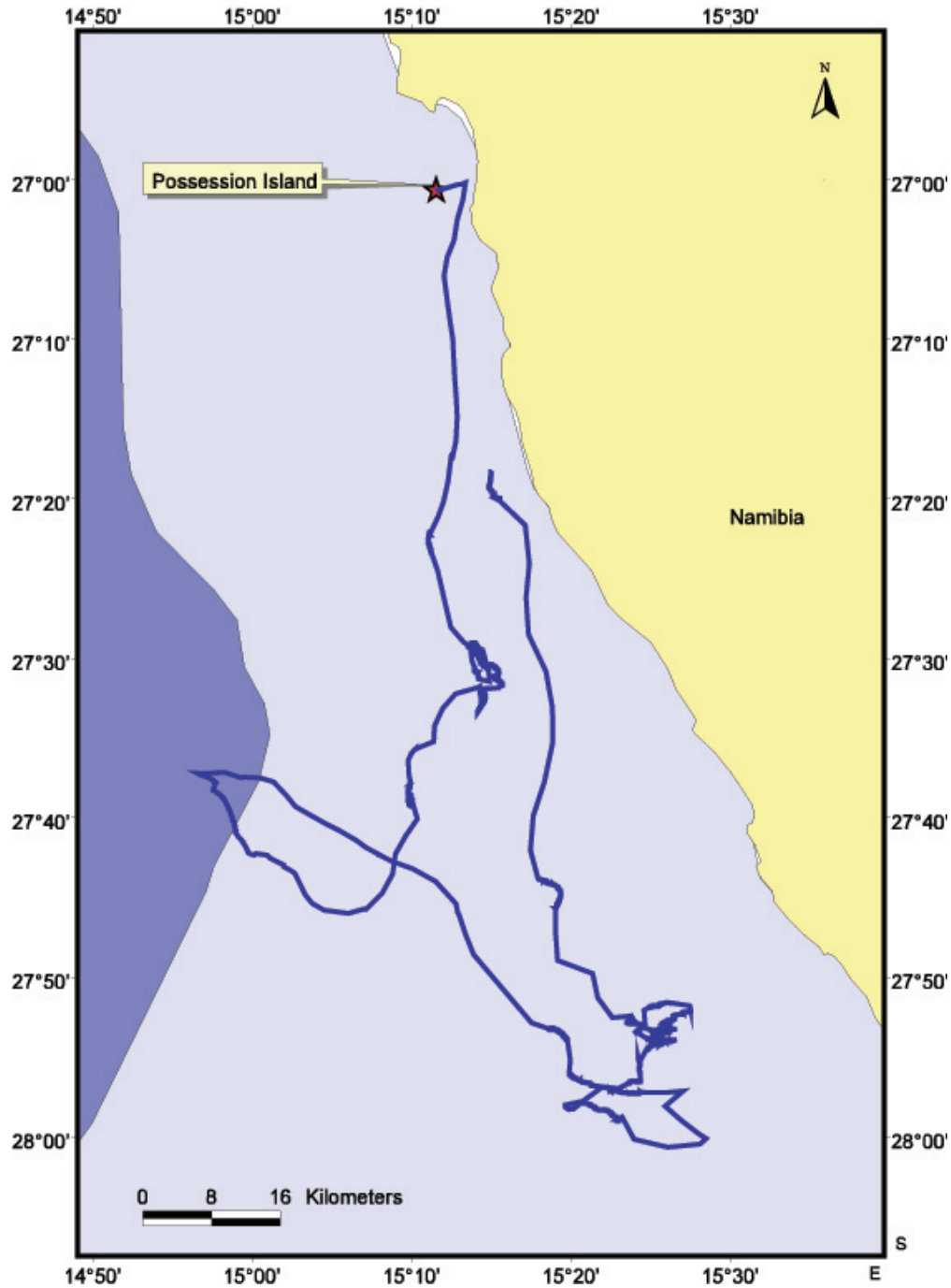


Figure 5.14: Foraging track of a Cape gannet equipped with GPS TDlog data logger at Possession Island, Namibia, in 2005.

5.4 Discussion

Gannets are able to search for food over large areas due to their ability to fly and may cover longer distances compared to swimming seabird species, such as penguins (Laugksch and Adams, 1993). They are able to commute directly to predictable foraging sites, increasing the search for food when entering such an area (Weimerskirch, 2007). The foraging behaviour of Cape gannets breeding at Mercury Island was investigated in two successive years. Although general foraging parameters, such as median trip duration, foraging range or total distance travelled, did not differ significantly between years, several aspects in the behaviour of individual birds reflected reduced prey availability. Cape gannets in this study showed a great flexibility in foraging trip duration and in distances covered during single trips. Trip durations lasted between two and 72 hours and the foraging range was between 20 and 200 km. In both years, birds were observed undertaking one-day trips as well as spending one or more nights at sea. Foraging trip length is strongly correlated with the foraging range (Hamer et al., 2000; Grémillet et al., 2004a; Ropert-Coudert et al., 2004a). This relationship was confirmed in this study where birds who spent more time at sea reached foraging areas further away in both years. Ropert-Coudert et al. (2004a) gives two possible explanations for longer trips, one being food shortage forcing the birds to prolong their initial one-day foraging trip, the other one being the presence of highly profitable prey patches further away. Both interpretations could apply for birds from Mercury Island.

Outmanoeuvring food shortage Sulphide eruptions in 2005 might have caused food shortage. These eruptions affected vast areas along the southern Namibian coast, including feeding areas of Cape gannets and African penguins breeding at Mercury Island (see also Chapter 3). During such sulphide events, hypoxic conditions are present within the entire water column and many organisms die or evacuate the area (Hamukuaya et al., 1998). Prey for seabirds becomes scarce during such events. Birds in 2005 covered a larger area during foraging and the diet consisted of smaller prey organisms, both indications of reduced prey abundance (Adams and Klages, 1999; Grémillet et al., 2004a). They also spent more time foraging and travelled longer distances, although these differences were not significant due to high variabilities in the behaviour of individual birds and relatively small data sets. In 2005, all birds returning the same day had left the colony before midday. It appears that the time available at sea for foraging was not sufficient to reach profitable foraging areas within one day when birds departed in the afternoon, because all individuals leaving later than 12:00 h made overnight trips. In 2006, several birds returning the same day had departed from the colony in the afternoon. Prey availability allowed birds to obtain sufficient food within shorter periods of time and within closer distance to the colony. Larger prey items were consumed in 2006 and dive rates were higher than in 2005. Whether birds prolong their foraging trips because of insufficient prey availability has been discussed for Cape gannets (Adams and Klages, 1999; Ropert-Coudert et al., 2004a) as well as for northern gannets (Garthe et al., 2003; Lewis et al., 2004a). Lewis et al. (2004a) found no evidence between the dive frequency at the beginning of the trip (as a measure of foraging success) and trip duration, concluding

that birds' decision to undertake longer trips was not affected by prey encounter rate. For birds at Mercury Island, the dive rate on the first day at sea was higher for birds returning the same evening than for birds staying at sea overnight. Birds on longer foraging trips exhibited fewer dives per hour over the entire trip than birds during one-day trips. This might indicate that birds with low dive rates encountered low prey abundance and had to stay at sea for several days in order to obtain sufficient prey. Prey availability seemed to have been better in 2006 when dive rates between one-day trips and longer lasting trips were similar and with birds on overnight trips diving more frequently than birds during one-day trips.

Predictability of foraging areas Similar to the African penguins breeding at Mercury Island, gannets left the colony in a north and north-westerly direction. Birds travelled long distances before starting to dive, showing highly directional flight patterns. This suggests direct commuting to presumably predictable foraging areas. Lewis et al. (2004a) found northern gannets to be foraging at the beginning and at the end of trips at Bass Rock, North Sea, thus feeding opportunistically. Garthe et al. (2003) identified different temporal patterns of diving activities in northern gannets at Funk Island, north-west Atlantic, birds diving either at midday on one-day trips or in the evening and morning hours during longer trips. The latter strategy indicates more predictable foraging areas from where birds either return after feeding on one-day trips or where they spend the night and continue feeding the next morning before they return to their colonies. A similar pattern could be observed in Cape gannets at Mercury Island, however birds also dived on their way towards the foraging area as well as on their way back, thus feeding more opportunistically. All diving took place only during daylight hours, as has been observed in Cape gannets and other gannet and booby species (Garthe et al., 1999; Ropert-Coudert et al., 2004a; Weimerskirch et al., 2005).

Birds that undertook several foraging trips while carrying the device often returned to the same foraging area on consecutive trips. Such foraging site fidelity indicates predictable food availability (Garthe et al., 2007a,b; Weimerskirch, 2007). Certain areas along the coast were visited by a number of birds in both years, indicating a predictable food supply even during times of food shortage such as in 2005 and over a period of several years. Bathymetric features are known to enhance upwelling, leading to higher productivity (Marín et al., 2001; Yen et al., 2004) and bays tend to retain planktonic organisms (Marín and Moreno, 2002; Marín et al., 2003), resulting in higher fish abundance and seabird foraging aggregations (Duffy, 1989a). As shown in this study, coastal areas stated important feeding sites for gannets from Mercury Island.

Offshore foraging Besides showing intense diving along the coast, birds in both years covered vast areas flying over offshore waters. Several birds visited coastal as well as more distant areas within single trips, however diving activity took place in much lesser intensity in the latter. The entire foraging area of Cape gannets lies within the 200 m depth contour, belonging to the continental shelf (Duffy, 1989a; Grémillet et al., 2004a). Birds were foraging at a maximum distance of about 80 km from the coast which allows

the birds to reach different water masses. Due to the coastal upwelling, a strong temperature gradient exists, especially around the Lüderitz upwelling cell, with warmer offshore waters and cold coastal waters with sea surface temperatures usually lower than 16.7°C (Demarcq et al., 2003). Water temperatures at the bottom of each dive were analysed but differences between dives in inshore and offshore waters were not found to be significant when considering the mean water temperature for all birds combined for each year. This might be due to the fact that birds were foraging over a time period of about two weeks. In the Benguela system, wind patterns and therefore upwelling intensity may change within days (Shannon, 1985; Peard et al., 2005) and affect the water temperature distribution (see also Chapter 4). During the entire study period, the extension of cold upwelled water masses may have fluctuated, some birds might have been foraging in these cold water masses further offshore while others fed in warmer water in the same distance off the coast. When considering single birds that foraged close to the coast as well as offshore within short periods of time (i.e. one foraging trip), a significant difference between water temperatures of inshore and offshore dives was observed. Although the location of prey capture is not known for diet samples collected at the islands, it is likely that different prey types are caught in different water masses. Warm-water species such as saury (Klages et al., 1992) were presumably preyed on in warmer offshore areas. Fronts caused by temperature gradients as well as shelf breaks result in accumulation of prey organisms (Lett et al., 2006) and constitute important feeding areas for seabirds (Haney, 1986a,b; Schneider, 1990; Camphuysen and van der Meer, 2005). Northern gannets have been observed off Mauretania feeding along the shelf edge (Camphuysen and van der Meer, 2005) and the relatively high numbers of offshore dives between 30 to 40 km off the coast observed in Cape gannets from Mercury Island may be related to such a bathymetric feature.

Diving was relatively scarce when birds travelled further offshore compared to the diving activity along the coast. This raises the question why birds spend so much time and energy leaving the coast where food availability is apparently high. This site fidelity to offshore waters might be linked to the use of discard from trawlers in offshore waters, as observed in Cape gannets in South Africa (Ryan and Moloney, 1988) and in northern gannets off Mauretania (Camphuysen and van der Meer, 2005). In the diet samples obtained from birds at Mercury Island in 2005 and 2006, no obvious offal such as single heads or intestines were found but the use of discard has been reported for Cape gannets breeding at Ichaboe Island, another large Namibian breeding colony (Lewis et al., 2006), and at other locations (Matthews and Berruti, 1983). Birds feeding on sardine dive deeper than birds feeding on hake behind commercial trawlers (Adams and Walter, 1993). Birds feeding offshore were diving deeper in 2005 when sardine was the main prey compared to 2006 when other species were present in the diet. Whether these were taken behind trawlers could not be determined. Besides being attracted by trawlers (Camphuysen et al., 1995; Camphuysen and van der Meer, 2005), gannets are also known to be attracted by conspecifics and might fly towards locations where other birds had been seen foraging (Nelson, 1978; Camphuysen et al., 1995; Camphuysen and Webb, 1999). Site fidelity over longer periods (several seasons) has been found for Cape gannets and other seabirds (Grémillet et al., 1999; Hamer et al., 2001a; Grémillet et al., 2004a). Cape gannets from

Mercury Island might frequent former commercial fishing grounds along the shelf break not being fished anymore due to reduced fish biomasses but still profitable for foraging gannets.

Flight direction Since only one foraging trip was recorded at Possession Island, general conclusions cannot be drawn about the foraging behaviour of those birds. Parameters such as trip length, foraging range and diving behaviour were similar to those measured from birds at Mercury Island. One difference was that birds at Mercury foraged in a north-westerly direction from the colony whereas the bird at Possession Island travelled south in order to reach its foraging area. Red-footed boobies use tail winds when flying towards their foraging areas (Weimerskirch et al., 2005). This would be true for birds at Mercury Island but not for the bird at Possession Island, since predominant winds are towards the north along the Namibian coast. In contrast, Grémillet et al. (2004a) and Adams and Navarro (2005) found gannets using tail winds on their way back to the colony. Prey availability seems to be a more important factor than wind direction in the case of Cape gannets in Namibia. The Lüderitz upwelling cell functions as a barrier for fish species (Agenbag and Shannon, 1988; Bianchi et al., 1999; Weeks et al., 2004) and birds from Possession Island might be more likely to encounter prey towards the south instead of having to cross an area relatively poor in fish in order to find food further north. A potential problem for birds foraging south of Possession Island might be caused by the bathymetry around the island. The shelf extends further offshore south of the island, making the shelf break with its potential prey accumulations less available to foraging birds.

Intra-specific competition An advantage for birds from Possession Island foraging south of the island might be the lack of intra-specific competition. Possession is the only Cape gannet breeding island south of the Lüderitz upwelling cell along the Namibian coast. The closest breeding colony towards the south with large numbers of gannets is Bird Island (Lambert's Bay) in South Africa, more than 500 km away. Towards the north, Ichaboe and Mercury Islands host large numbers of breeding gannets. Especially Ichaboe Island, about 90 km north of Possession Island hosts the largest Cape gannet breeding colony in Namibia with over 8600 pairs (Crawford et al., 2007). In South African waters, Cape gannets from neighbouring breeding colonies use different foraging areas, thus avoiding intra-specific competition (Grémillet et al., 2004a). Competition may also arise among birds from one colony, usually increasing with increasing colony size leading to longer foraging trips and larger foraging ranges for birds from larger colonies (Lewis et al., 2001; Grémillet et al., 2004a). For birds at Possession Island, this relationship of colony size and foraging range would lead to distinctly shorter foraging distances than for birds from Mercury Island. This concept is, however, not supported by the track of the bird equipped at Possession Island. Numbers of breeding birds at Possession Island are so small that intra-specific competition should not be an important factor shaping foraging behaviour. Lewis et al. (2006) state that foraging is less successful in colonies such as Possession Island where gannet numbers are decreasing.

5 Cape Gannets (*Morus capensis*): Facing food shortage?

Cape fur seals (*Arctocephalus pusillus pusillus*), which breed at two large colonies (Atlas and Wolf Bay) about 20 – 25 km north of Possession Island and which forage within the foraging range of the Cape gannets may constitute competitors for food in waters around Possession Island. Cape fur seals feed predominantly on Cape hake but also on horse mackerel and other fish species of the same size class as the prey of Cape gannets (Thomas and Schülein, 1988; Mecenero et al., 2006b). On the other hand, gannets might also take advantage of seals foraging within the same area since several fish species might be driven to the surface by feeding marine mammals and thus become available to shallow diving birds (Duffy, 1989a; Camphuysen et al., 1995; Camphuysen, 2002).

Compared to African penguins breeding at the same islands as Cape gannets along the Namibian coast, gannets have the advantage of being able to exploit larger areas and especially different oceanographic habitats with greater chances to obtain food, even during unfavourable conditions such as sulphide eruptions. Birds in this study showed a high flexibility in foraging behaviour and a diverse prey composition. However, even the use of large areas, including waters outside the coastal upwelling zone, and the prey obtained does not seem to be sufficient to sustain the breeding population of Cape gannets in Namibia. The species is listed as *Vulnerable* (IUCN, 2006) and is considered *Endangered* in Namibia (Kemper, in press b). While numbers of breeding birds are increasing at several colonies in South Africa, numbers of birds in Namibia continue to decrease. Alterations of the trophic structure in the northern Benguela upwelling system due to changes in upwelling intensities in combination with overfishing result in limited food availability to seabirds. This seems to be one of the main reasons for the observed population decline (Roux, 2003; Lewis et al., 2006; Crawford et al., 2007).

Table 5.1: Logger deployment, departure and arrival times and trip duration for seven Cape gannets from Mercury Island, Namibia, equipped with GPS TDlog data loggers in 2005. Two birds equipped on the 17th and 18th of February returned with the devices missing and are not included in this table.

Bird	Trip	Deployment		Departure		Arrival		Trip duration hours
		Date	Time	Date	Time	Date	Time	
29-170205	1	14.2.05	13:20	14.2.05	13:29	17.2.05	13:43	72:21
27-150205	1	14.2.05	13:40	14.2.05	14:02	15.2.05	15:30	25:28
34-160205	1	15.2.05	17:00	15.2.05	17:12	16.2.05	15:31	22:19
56-170205	1	15.2.05	17:00	16.2.05	6:16	16.2.05	19:09	12:53
27-180205	1	17.2.05	10:30	17.2.05	11:20	17.2.05	15:30	04:10
	2			18.2.05	6:43	18.2.05	15:51	09:08
56-200205	1	18.2.05	17:30	19.2.05	7:06	20.2.05	13:27	30:21
27-250205	1	23.2.05	14:00	23.2.05	16:53	24.2.05	20:00	27:07

Table 5.2: Logger deployment, departure and arrival times and trip duration for seven Cape gannets from Mercury Island, Namibia, equipped with GPS TDlog data loggers in 2006. One bird equipped on the 17th of February did not return and one device, deployed on a bird on the 27th of February did not function properly. Both birds are not included in this table.

Bird ID	Trip	Deployment		Departure		Arrival		Trip duration hours
		Date	Time	Date	Time	date	time	
57-200206	1	17.2.06	15:58	18.2.06	7:01	20.2.06	17:18	58:17
83-200206	1	19.2.06	15:45	19.2.06	15:45	20.2.06	16:22	24:37
57-230206	1	21.2.06	11:20	21.2.06	11:20	21.2.06	14:00	2:40
	2			22.2.06	13:34	23.2.06	15:02	25:28
83-230206	1	21.2.06	11:28	21.2.06	11:30	21.2.06	14:48	3:18
	2			21.2.06	15:25	21.1.06	19:28	4:03
	3			22.2.06	13:12	22.2.06	18:27	5:15
	4			23.2.06	12:10	23.02.06	16:05	3:55
86-240206	1	21.2.06	12:09	21.2.06	13:30	22.2.06	14:38	25:08
	2			23.2.06	12:23	24.2.06	13:39	25:16
83-040306	1	27.2.06	13:27	28.2.06	10:41	28.2.06	19:42	9:01
	2			1.3.06	8:24	2.3.06	13:44	29:20
	3			3.3.06	6:21	4.3.06	18:20	35:59
86-010306	1	27.2.06	18:10	27.2.06	18:24	1.3.06	11:47	41:23

Table 5.4: Diet composition of Cape gannets at Mercury and Possession Islands, Namibia. Given are the percentages of each species of the entire mass of all stomach samples combined and the frequency of occurrence [%], n states the number of stomach samples.

Common name	Scientific name	Mercury 05 n = 17		Mercury 06 n = 17		Possession 06 n = 5	
		% mass	% occurrence	% mass	% occurrence	% mass	% occurrence
Anchovy	<i>Engraulis capensis</i>	1.0	11.8	7.6	23.5	0.0	0.0
Sardine	<i>Sardinops sagax</i>	60.9	47.1	22.1	23.5	16.8	20.0
Horse mackerel	<i>Trachurus capensis</i>	16.4	23.5	20.9	35.9	24.6	20.0
Saury	<i>Scorpaenopsis saurus s.</i>	1.2	11.8	13.3	11.8	44.7	60.0
Redeye	<i>Etrumeus whiteheadi</i>	17.4	23.5	5.0	11.8	14.0	20.0
Mullet	<i>Liza dumerili</i>	0.0	0.0	9.2	11.8	0.0	0.0
Snoek	<i>Thysites atun</i>	3.1	5.9	17.6	11.8	0.0	0.0
Chub mackerel	<i>Scomber japonicus</i>	0.0	0.0	4.4	5.9	0.0	0.0

Table 5.5: Length of fish and other prey organisms found in the diet of Cape gannets at Mercury and Possession Islands, Namibia. Only complete specimens were measured, n gives the number of complete fish measured in each year and at each colony.

Common name	Mercury Island 2005			Mercury Island 2006			Possession Island 2005		
	n	median length [cm]	range	n	median length [cm]	range	n	median length [cm]	range
Anchovy	2	11.5	11.0 - 12.0	8	11.9	7.5 - 13.5	0	-	-
Sardine	37	6.8	5.0 - 20.7	7	19.5	18.3 - 22.3	1	10.5	-
Horse mackerel	15	8.4	6.4 - 10.9	14	17.2	11.0 - 19.9	1	22.0	-
Saury	4	9.9	7.9 - 11.4	5	22.7	16.2 - 24.4	6	24.0	22.0 - 25.0
Redeye	120	5.9	4.3 - 13.5	12	9.25	7.0 - 11.8	1	17.0	-
Mullet	0	-	-	3	22.1	21.5 - 22.2	0	-	-

6 Distribution and foraging behaviour of the Peruvian booby (*Sula variegata*), a top-predator endemic to the Humboldt upwelling system

6.1 Introduction

Seabirds in the Humboldt upwelling system are frequently exposed to climatic and oceanographic changes due to the El Niño Southern Oscillation (ENSO), which causes - during El Niño events - a reduced productivity in this usually highly productive system (Barber and Chavez, 1983; Arntz and Fahrbach, 1991; Ribic et al., 1997). During such events birds often have to face dramatic changes in food availability which cause changes of their diet (Jahncke and Goya, 2000). If the species and/or individuals are not able to cope with those changes, they show a reduced breeding success (Kalmbach et al., 2001; Simeone et al., 2002; Hennicke and Culik, 2005) or a complete breeding failure (Jahncke and Goya, 2000). Many bird species leave the area completely, trying to outmanoeuvre the bad feeding situation (Ribic et al., 1992; Culik et al., 2000). Since breeding failure and migration of the birds seem to be directly caused by prey availability, the birds behaviour at sea plays an important role in understanding the effects of climatic changes. Unfortunately little is known about the behaviour at sea of endemic seabird species in the Humboldt upwelling system compared to a broader knowledge of their breeding behaviour. Data logger technology has enabled a better understanding of diving behaviour, distribution of birds at sea and their behaviour during foraging. These parameters have been studied for example in the Humboldt penguin (*Spheniscus humboldti*), a seabird directly affected by the El Niño phenomenon (Culik and Luna Jorquera, 1997b; Culik et al., 1998; Luna Jorquera and Culik, 1999; Culik et al., 2000). However, little is known about the endemic Peruvian booby (*Sula variegata*), one of the most abundant guano bird species of the Humboldt Current. Besides a few studies in Peru (Jahncke et al., 1998b; Tovar and Guillén, 1988; Jahncke and Goya, 2000), little is known about its feeding ecology or about its behaviour at sea. In this study, I used a combination of methods to investigate diet, diving behaviour, colony attendance patterns and at-sea activity of Peruvian boobies at Isla Pájaros, the largest colony of this species in Chile (Simeone et al., 2003). Combining the results obtained by these methods, it is assessed how this endemic seabird species may cope with changing environmental conditions. Such information will be very useful when evaluating the impact of future climate changes and upcoming El Niño events.

6.2 Methods and study site

This study was conducted over the breeding seasons of the Peruvian booby in 1998 – 99 to 2003 – 04. Fieldwork consisted of telemetry of individual birds, of observations in the colony and of ship-based counts at sea. These different methods enable the determination of important foraging areas and the at-sea behaviour of this species in Chile.

Study site Isla Pájaros (29°35'S, 71°33'W; Fig. 6.1) hosts the largest colony of Peruvian boobies in Chile (Simeone et al., 2003) as well as large numbers of breeding kelp gulls (*Larus dominicanus*) and Humboldt penguins. The island is located about 40 km north of La Serena, northern central Chile, and lies 25 km offshore. The continental coastline forms a large bay; the island itself is located on the shelf edge. Water depths within the bay are up to 200 m; west of the island, depths increase rapidly to more than 1000 m (Moraga, 1996). The predominant wind direction in the area is south-west (Marín et al., 2003). The oceanographic conditions around the island are characterised by localised upwelling at protruding points along the coast and at the island itself (Moraga and Olivares, 1993; Marín et al., 2003).

Application of data-logging units Chick-rearing Peruvian boobies were caught with a noose-pole in order to equip them with data loggers. The general procedure followed Garthe et al. (1999) and Garthe et al. (2000) for northern gannets (*Morus bassanus*). Due to hardly accessible nest sites on exposed rocks, capture and - in particular - recapture of the birds were difficult. Therefore data sets of only four birds were obtained with different types of devices in three different years (2000 and 2001 one LTD 100 tag each, 2004 one PreciTD and one CT logger). In a total of nine cases no data were obtained because the birds could not be recaptured or data loggers did not work properly (see Table 6.1). LTD 100 tags (Light-Temperature-Depth recorders; Lotek Marine Technologies, St. John's, Newfoundland, Canada) and PreciTD (Temperature-Depth recorders; earth&OCEAN technologies, Kiel, Germany) were used to derive dive depth (from a pressure sensor) and activity (in water, in air, on land - from a temperature sensor). The LTD 100 were 57 mm long with a diameter of 18 mm and a mass of 16 g; memory size was 1.5 MB. Devices were attached with Tesa[®] tape to a plastic ring placed on one leg of each bird. Pressure was recorded every 2 s over a depth range of 0 – 100 m with a resolution of 0.04 m. External temperature was recorded every 30 s. PreciTD tags were 80 mm long with a diameter of 19 mm and a mass of 23 g; memory size was 2 MB. Pressure and temperature were measured every second. The devices were located underneath the tail in order to enable the measurement of the water temperature and were attached using Tesa[®] tape to the three central tail feathers. CT loggers (compass and temperature recorders; earth&OCEAN technologies, Kiel, Germany) were used to derive flight paths (using dead reckoning technique; see Wilson et al., 1991) and birds' activity at sea. The devices were 65 mm long with a diameter of 16 mm and a mass of 14.5 g. The directional resolution was < 0.1° and the temperature resolution 5 mK. Memory size was 2 MB. Similar to the PreciTD, the compass logger was attached to the main tail feathers using Tesa[®] tape with the temperature sensor cable reaching out

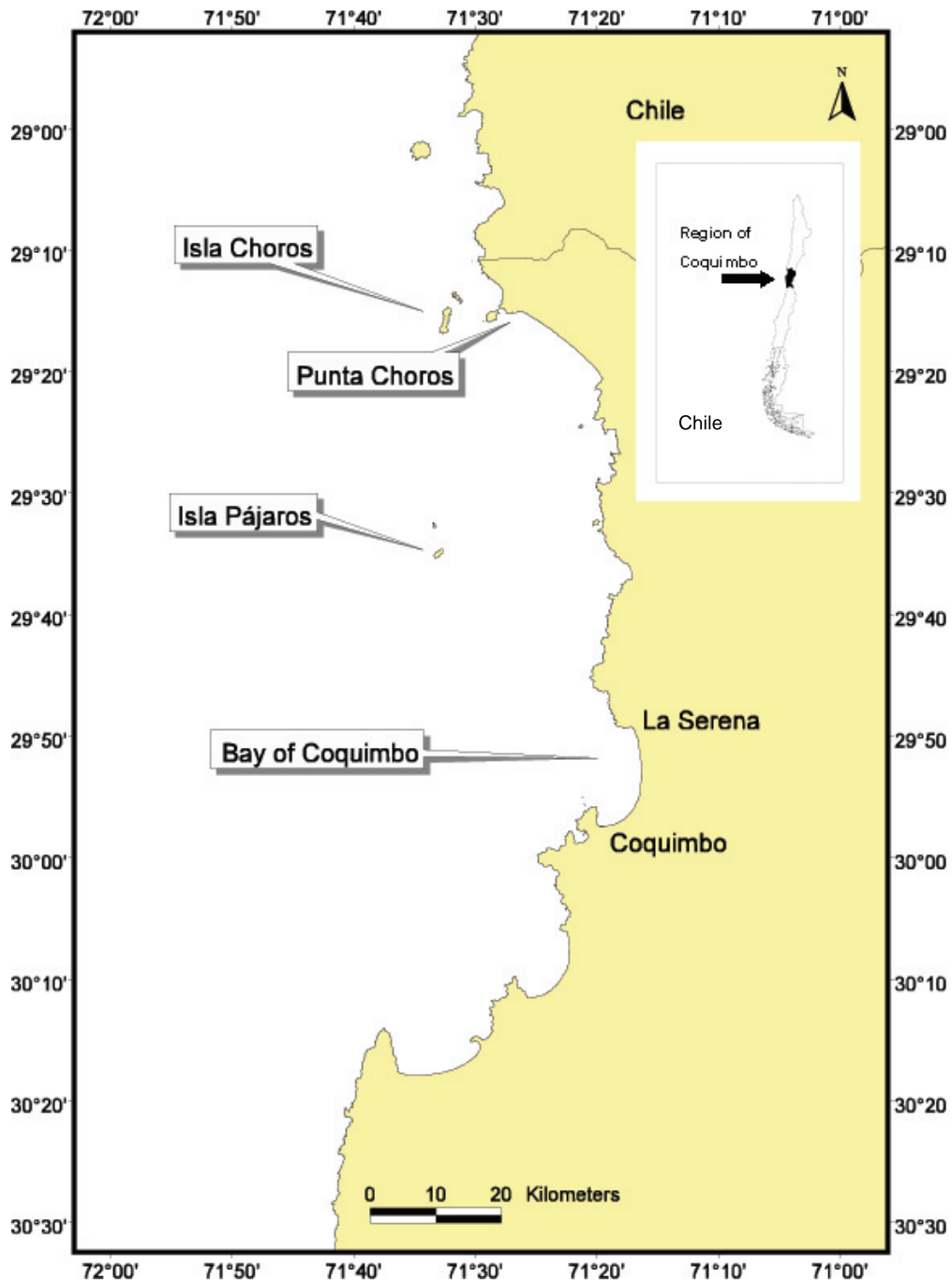


Figure 6.1: Study area corresponding to the region of Coquimbo in northern central Chile. Studies on Peruvian boobies including logger deployment, diet sampling and colony observations were conducted at Isla Pájaros. Seabird-at-sea observations were carried out in the area shown in the map.

underneath the tail. The activity of the bird was deduced from records of thermal fluctuations following Wilson et al. (1995) and Garthe et al. (1999). When the temperature remained constant, the bird was considered to be swimming or resting on the water surface with the logger submerged and measurements indicated sea surface temperature (SST). When the temperature record varied slightly within the range recorded for air temperature (a few degrees higher than sea temperature), the bird was considered flying. When the temperature varied in higher temperature ranges (as the logger was warmed by the bird's or chick's body heat and/or solar and terrestrial radiation), the bird was considered to be in the colony (i.e. at the nest most of the time). The last deduction was validated by observations with a spotting scope from outside the colony to check when marked birds carrying loggers were present. From all pressure values obtained (TDL 100 and PreciTD), measurements of less than 0.5 m were ignored because such shallow dives presumably occurred during bathing or other movements of the bird near the surface. The dive analysis was carried out using Matlab 7.0.1[®] (script written by L.-G. Ellenberg and T. Mattern). For compass logger analysis, the dead reckoning software MT Comp (Jensen Software Systems, Kiel, Germany) was used. Different activities of the bird were identified using the temperature channel as well as the compass signals similar to the method described above. During flight periods an average flight speed of 14.9 m/s was assumed (Pennycuik, 1997, for northern gannet); during diving and swimming periods flight speed was considered to be 0 m/s. Whereas diving behaviour could only be studied using the LTD 100 and PreciTD devices, foraging trip length and activities at sea (flying, diving and swimming) were calculated using CT, PreciTD and LTD data (only 2000; data from 2001 consisted of only pressure measurements).

Diving parameters were tested using linear mixed-effects models fit by REML (LMER), carried out with the statistical program R 2.4.1[®]. The median and the range of all dives are given.

Seabird-at-sea observations Seabird-at-sea observations were conducted during approximately one-week trips from the 17th to the 24th of January 2002, the 25th of January to the 1st of February 2003 and the 17th to the 23rd of January 2004, covering a counting area of in total 357, 421 and 434 km², respectively. Observations were conducted using an international standardised method following Tasker et al. (1984) and Camphuysen and Garthe (2004). Birds were counted in a 300 m strip transect parallel to the boat, recording not only numbers of birds but also their behaviour and flight directions. Densities of birds at sea were calculated and special attention was paid to birds' behaviour at sea, in the case of the boobies especially to feeding activities, i.e. plunge diving. Feeding flocks were also recorded when present as well as associations of birds with fishing vessels.

Colony attendance and foraging trip duration From the 25th of February to the 6th of March 2001, all adult Peruvian boobies were counted at different times of the day in a randomly selected part of the colony outside the area where diet was collected and where birds were captured. In total, 72 counts were performed, covering all hours. No more than

two counts per hour, interspersed by at least 30 min, were allowed on one day in order to avoid pseudoreplication of data. Data were analysed using circular statistics (Batschelet, 1981). During the breeding season 2003–04, observations of foraging trip duration and nest attendance were carried out on five days. The total time of observations summed up to 34 hrs and 37 min and a total of 20 nests were monitored constantly during this time. Trips with known departure and arrival times and a minimum duration of ten minutes were considered in the analysis. Periods when both birds were present at the nest site were analysed when lasting longer than ten minutes. Observations could only be conducted during daylight hours and all trips and/or presence at nest overnight were excluded from the analysis because late arrivals and early departures could not be precluded. Differences between chick-rearing birds and nests without chicks or eggs were tested using the program R 2.4.1[®], applying a general linear model (GLM) with a quasipoisson distribution.

Flight direction Flight directions were observed from the breeding colony at Isla Pájaros to determine the locations of the foraging areas used by the birds during the breeding season 2003–04. Birds returning to the colony were counted from five vantage points along the coast of the island between 19:00 and 20:00 h on eight days. It is known that birds leaving the colony to feed at sea do not necessarily fly directly towards the feeding spots. Birds returning to their colony after feeding are supposed to take a more direct route (Grémillet et al., 2004a), therefore only returning birds were counted. Every count lasted ten minutes at which two to four 45° areas were scanned, counting all returning birds in the entire area observed.

Diet sampling Diet samples of adults and chicks were collected at Isla Pájaros when birds voluntarily regurgitated food after approaching them. Adult samples originated from roosting adult birds in 2001 (n = 582) and from roosting and breeding birds in 2004 (n = 12), when some birds regurgitated during handling for logger attachment. In 2000, chicks samples were obtained during physiological measurements (n = 96; Sepúlveda, 2006). Ropert-Coudert et al. (2004a) found no evidence for difference in prey of adult and chick Cape gannets (*Morus capensis*). Therefore all samples were analysed without differentiating between adults and chicks. All fish were identified to species level and common and scientific fish names follow FishBase¹. Undigested fish collected from adult diet samples were weighed to the nearest gram.

¹<http://www.fishbase.org>

6.3 Results

6.3.1 Distribution at sea

Seabird-at-sea observations

Seabird-at-sea surveys in three consecutive years showed a coastal distribution of Peruvian boobies (Fig. 6.2) except for the year 2002 (Fig. 6.2a) when birds failed to breed at Isla Pájaros and fewer birds were observed at sea in the entire study area. Overall, especially foraging birds were observed close to the coast. Birds were feeding in median distances of 4.8, 3.1 and 4.1 km (means 8.7, 13.4 and 4.5 km) off the coast in 2002, 2003 and 2004, respectively. Feeding took place mainly in areas around protruding land masses such as Punta Choros in the north and the Coquimbo Peninsula in the south (see Fig. 6.3 for 2004).

Foraging tracks

One compass logger was successfully deployed for three days on one chick-rearing Peruvian booby in the breeding season 2003–04. The device was recovered containing data of four consecutive foraging trips. In all four cases the bird flew towards the coast in a easterly direction (Fig. 6.4). The first trip led the bird to a foraging spot very close to shore (2 – 3 km off the coast), which was visited again the next morning. Later the same day the bird foraged in an area further north. In all three foraging trips the bird travelled more or less directly towards the feeding ground, foraged (i.e. plunge-dived) in a restricted area (Fig. 6.4) and returned to the colony. During the fourth trip, the bird dived again near the island after returning from the foraging area close to the coast. Diving activity close to the colony was also observed from the island in all years. Feeding flocks consisting of larger numbers of birds (including other species such as penguins and cormorants) form regularly close to the island. Whether these birds leave towards the coast later or return before joining the feeding flock could not be confirmed.

Flight directions

Birds observed at sea commuted between the colony and foraging areas close to the mainland (Fig. 6.3). This pattern was asserted by counts of returning birds during the evening hours from the vantage points at Isla Pájaros. The largest number of birds returned from a south-easterly direction, presumably from the bay of La Serena and the Coquimbo Peninsula, where feeding birds were also observed during seabird-at-sea counts (see above; Fig. 6.3). Another high percentage of birds returned to the colony from a north-easterly direction where another major feeding area seems to be located around Punta Choros (see foraging tracks of equipped bird, Fig. 6.4).

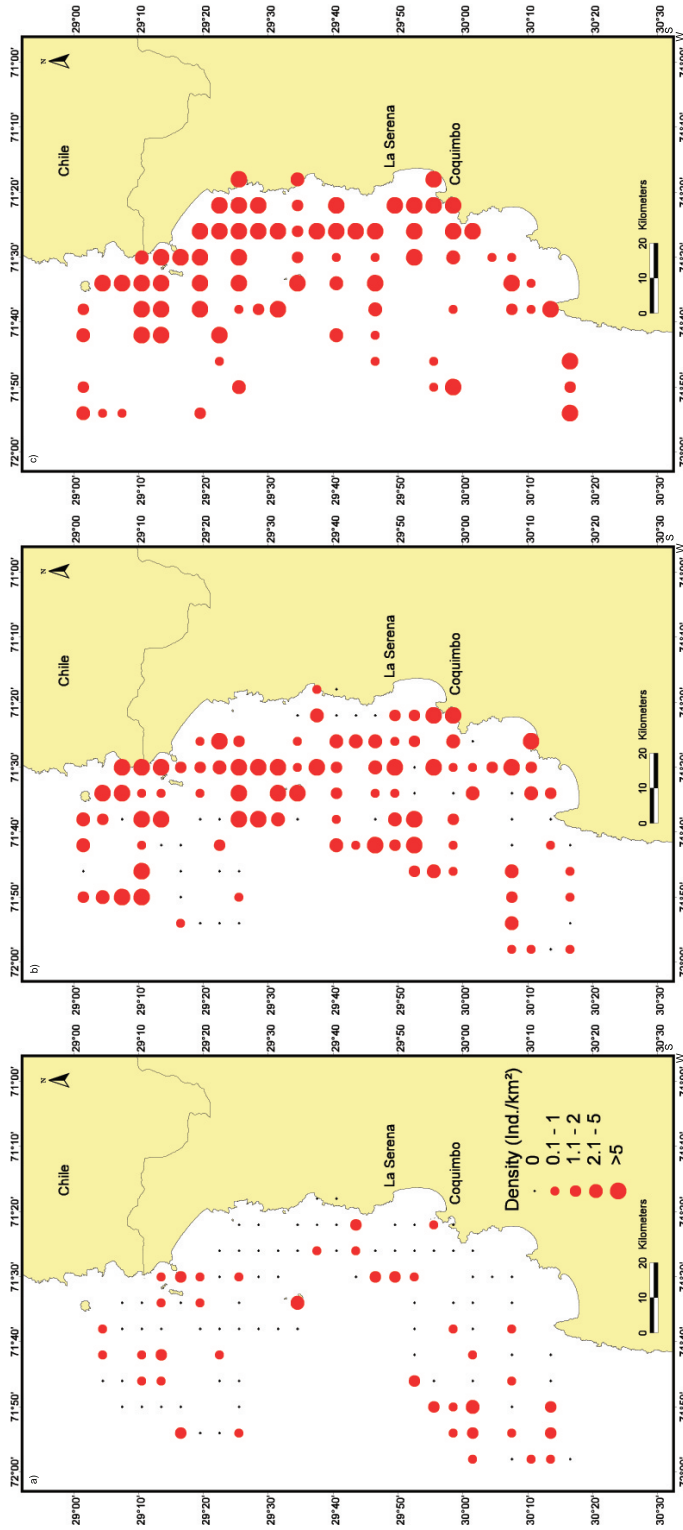


Figure 6.2: Distribution of Peruvian boobies during ship-based surveys in January a) 2002, b) 2003 and c) 2004. Data are presented as density of birds (numbers divided by area mapped).

6.3.2 Behaviour at sea

Diving behaviour

Using different temperature-depth devices (Lotek & PreciTD) in three different years, the diving activity of the Peruvian boobies at Isla Pájaros was determined. No statistical differences were found between the three different years concerning dive depth and dive duration (n.s.; $p = 0.660$ and $p = 0.825$, respectively; LMER), the data was therefore pooled from 2000, 2001 and 2004 (one bird each year). In total, 121 dives were recorded from three birds with a median dive duration of 2 s ($n = 121$; range 1 – 15) and a median diving depth of 2.4 m (range 0.5 – 8.2; Table 6.2). Maximum diving depth was 8.2 m and maximum dive duration was 15 s (Table 6.2 and Fig. 6.5).

At-sea activities

During the ship-based surveys in three different years only 12.6 % of all boobies observed in the transect were swimming whereas 58.8 % of the birds were flying; 28.6 % of all birds observed were involved in foraging behaviour, either plunge-diving or actively searching for food (Table 6.3). Differences between years were significant ($\chi^2 = 771.32$, $df = 4$, $p < 0.001$; χ^2 test of independence), with swimming being the least frequent behaviour in 2002 and 2004 whereas birds spent more time swimming than foraging in 2003. Analysis of different behaviour at sea using logger data showed that birds spend 90.2 % of their time flying, 8.8 % involved in diving activities and only 1.0 % swimming (Table 6.3).

6.3.3 Colony attendance and foraging trip duration

The average foraging trip duration of birds carrying data loggers was 74 min ($n = 13$; range 12 – 184). None of the birds left before 11:30 h and came back later than 20:15 h (Fig. 6.6a). This coincides well with observations conducted in 2001 where the number of birds in the colony decreased starting at around 11:00 h and increasing again at about 19:00 h (Fig. 6.6b). Additionally, 20 nests in the colony were observed and all leaving and returning birds were noted. In total, 45 complete foraging trips were observed of which the median length was 176 min (range 11 – 424). Maximum trip length was seven hours although the arrival of several birds possibly returning during darkness was not confirmed. Birds without eggs or chicks spent less time at sea than birds raising chicks (34 and 194 min, $n = 11$ and 34 birds, respectively; $p < 0.05$; GLM). Possibly due to the small sample size, no differences in the time spent away from the nest were found for parents raising chicks of different age classes. Not all birds left immediately after the return of the partner to forage. At 37 occasions, both birds spent on average of 37 min (range 10 – 230) at the nest site together during daytime.

6.3.4 Diet

The diet of Peruvian boobies in 2000 was much more diverse in comparison to the diet of birds in the other two years sampled. In 2000, anchovy (*Engraulis ringens*) was the main prey item with 30.2 % of all samples containing this species (Table 6.4). In 2004,

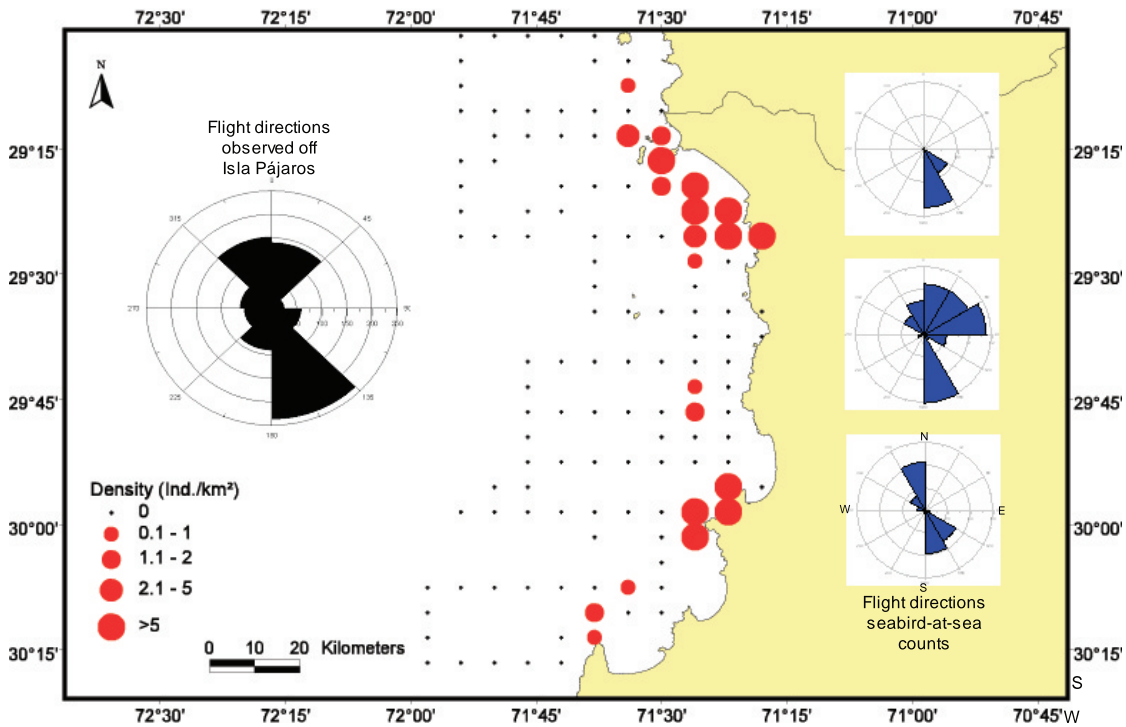


Figure 6.3: Distribution of feeding Peruvian boobies (shown as density per km², red dots) and flight directions observed during the seabird-at-sea survey in 2004 (right wind roses). Flight directions of Peruvian boobies observed from the colony in 2004 are shown in the wind rose left.

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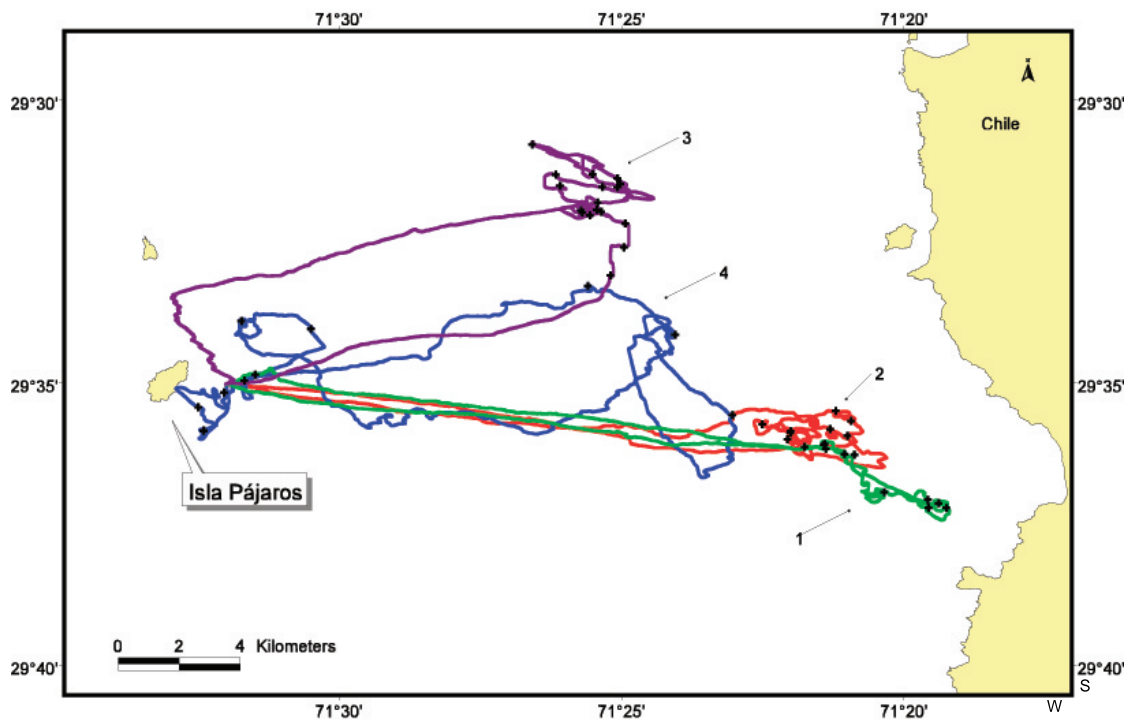


Figure 6.4: Foraging tracks of one Peruvian booby equipped with a compass logger at Isla Pájaros, Chile, in 2004. Black crosses indicate dive locations of the bird during each trip (1: 6th of February; 2 & 3: 7th of February; 4: 8th of February 2004).

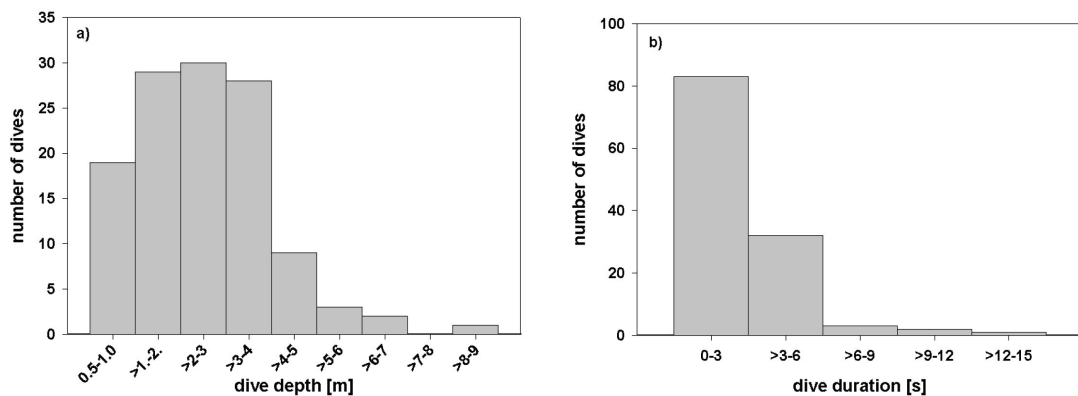


Figure 6.5: Dive depth [m] (a) and dive duration [s] (b) of Peruvian boobies from Isla Pájaros, Chile (n = 121 dives, one bird in 2001, 2002 and 2004).

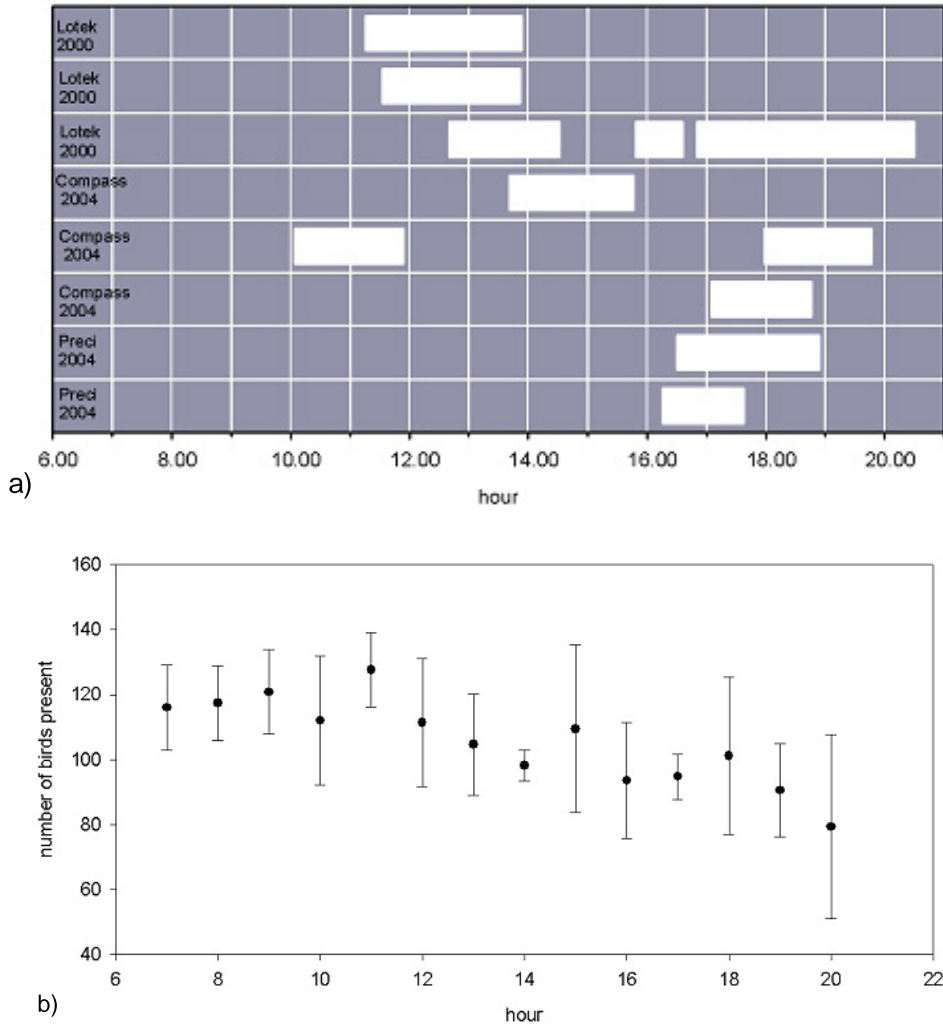


Figure 6.6: Colony attendance and timing of foraging of Peruvian boobies at Isla Pájaros, Chile; a) timing of foraging trips of birds equipped with data loggers (Lotek for 2000; Compass and Preci for 2004; each device represents several trips of one bird; white bars indicate absence from nest) and b) diurnal rhythm in colony attendance (2001; mean numbers of birds present, lines indicate standard deviation).

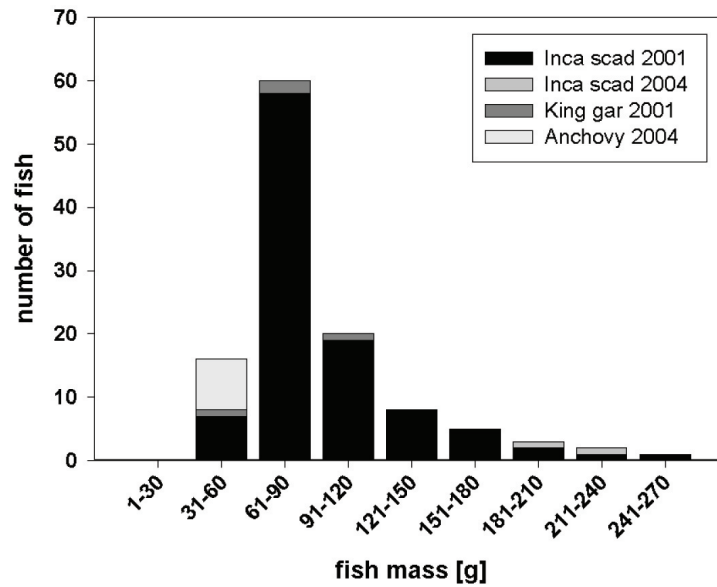


Figure 6.7: Fish mass [g] and number of fish found in diet samples of Peruvian boobies at Isla Pájaros, Chile, in 2001 and 2004.

anchovy was found in almost half of all samples, the other fish species found were Inca scad (*Trachurus murphyi*, also called Chilean jack mackerel) and to a minimal proportion cabinza grunt (*Isacia conceptionis*) (Table 6.4). Anchovy was not found in the diet in the year 2001; Inca scad made up the major part of the diet with a presence of 82.3 % of all samples that year. Araucanian herring (*Strangomera bentincki*) and silverside (*Odontesthes regia*) were found only in 2000. Unidentified squid was present in 2000 and 2004, in the latter making up 15.4 % of the samples mass (Table 6.4). In 2001, it was possible to sample large numbers of intact fishes so that fish masses could be taken. Inca scad had a mean mass of 94.4 ± 36.2 g ($n = 101$; range 33.7 – 255; Fig. 6.7). The other fish species found in 2001, king gar (*Scomberesox saurus*, also called saury) had a mean mass of 70.0 ± 18.8 g ($n = 4$; range 47 – 92). In the samples in 2004, two Inca scad were recovered entirely, which had masses of 221.2 and 208.2 g, being 27.0 and 25.2 cm in size, respectively. Anchovy found in 2004 ranged between 32 and 60 g (Fig. 6.7).

6.4 Discussion

Distribution and behaviour at sea

The Peruvian booby is one of the most abundant seabird species in the Humboldt upwelling system along the Peruvian and Chilean coasts (Jahncke et al., 1998a,b; Weichler et al., 2004) but little is known about its distribution at sea. The results of this study indicate that the birds show preferences for coastal waters and use those almost exclusively

in order to forage. The at-sea distribution coincides well with Weichler et al. (2004), who found decreasing numbers of boobies with increasing distance to the coast. Similarly, Jehl (1973) observed birds within one mile of the beach. Birds in our study were observed feeding at an average distance of 6.5 km from the mainland in 2002 to 2004. Ship-based observations as well as telemetry data indicate special foraging areas around protruding coastal points such as the Coquimbo Peninsula and Punta Choros. Such coastline geometry together with bottom topography and local wind forcing lead to stronger upwelling (Moraga, 1996; Marín et al., 2003; Mesías et al., 2003) and to retention of planktonic organisms in bays between such points (Marín and Moreno, 2002). The use of foraging areas where bathymetric features enhance primary production is also known for birds feeding further offshore, such as northern gannets in the North Sea (Hamer et al., 2000) and off Mauritania (Camphuysen and van der Meer, 2005). Feeding very close to the coast has also been found in northern gannets in the north-west Atlantic, where birds breed on a small offshore island and commute to the coast to feed on spawning capelin (*Mallotus villosus*), a small forage fish (Montevecchi et al., 2006; Garthe et al., 2007a). Peruvian boobies in our study fed on a variety of pelagic fish species which all occur relatively close to the coast (Acuña et al., 1989). The diet consisted of several fish species as well as squid and varied strongly between years but also between individuals. Anchovy never made up more than 50 % of the diet and were even absent at times, when substituted by other species such as Inca scad. In contrast, anchovy makes up between 70 and 100 % of the prey items found in the boobies diet in Peruvian waters (Nelson, 1978; Jahncke et al., 1997; Jahncke and Goya, 1997, 2000). Even more obvious, the at-sea distribution of Peruvian boobies has been found to correlate strongly to anchovy distribution in Peru (Jahncke et al., 1998a). In this study, despite a relatively small sample size, it could be shown that birds exhibit a fidelity to certain foraging areas, where they feed on a variety of pelagic coastal prey species. The other fish species consumed by the boobies, especially pelagic species (*T. murphyi*, *S. saurus*), are closely related to upwelling coastal zones around Isla Pájaros and Isla Choros, as well as to the protruding points along the coast of Coquimbo (Acuña et al., 1989).

Peruvian boobies from Isla Pájaros conducted relatively short foraging trips and left the colony several times a day. Birds left the colony up to three times a day in order to forage and the longest observed foraging trips lasted seven hours. In Peru, Duffy (1987) observed foraging trips of boobies with a mean duration of about two hours. Cape gannets in the Benguela Current show much longer foraging trips, occasionally staying out overnight (Ropert-Coudert et al., 2004a). Those birds show a bimodal foraging strategy, feeding for themselves during the first part of the trip and obtaining food for their offspring during the second part. In addition, overnight trips were interpreted to indicate poor feeding conditions (Ropert-Coudert et al., 2004a). The same phenomenon has been observed in northern gannets (Garthe et al., 2003), although foraging trips in that species were found to last up to two days (Lewis et al., 2004a). In this study, birds seemed to be feeding either for themselves or for their chicks and feeding grounds located near the colony enabled them to perform several trips a day, implying that they do not necessarily have to feed their chicks after every trip. This behaviour seems to rely on the predictability of prey at certain foraging areas as mentioned above. Another

6 *Distribution and foraging behaviour of the Peruvian booby*

indication for predictable and sufficient prey availability is the fact that both partners spent considerable time phases together at the nest. Other species even leave chicks unattended when their nutritional requirements increase (Lewis et al., 2004b) or when unfavourable feeding conditions are encountered (Lewis et al., 2006). A foraging strategy of only short trips also implies a different behaviour at sea. The Peruvian boobies do not spend much time swimming at the surface. Calculations of the percentage of time swimming varied between less than 1 % from the data logger sets and 12.6 % from the seabirds at sea cruises. The time spent diving might include short periods on the water, but swimming activity refers to resting on the surface independent of foraging. Cape gannets and northern gannets spend more than half of their time at sea swimming at the surface (Garthe et al., 1999; Hamer et al., 2000; Grémillet et al., 2004a; Ropert-Coudert et al., 2004a). This is partly due to overnight foraging trips since birds do not show foraging behaviour at night (Garthe et al., 1999; Hamer et al., 2000) and often just drift but also during day trips, other gannet species spend long time swimming at the surface (Ropert-Coudert et al., 2004a).

Variation of the marine environment

Since most methods for studying seabird ecology depend on the accessibility of the birds in the colony, only little may be said about the birds foraging behaviour in years of breeding failure such as the El Niño year 2002. Only seabird-at-sea observations were conducted during that year and birds were observed at much lower densities than in other years. Birds were also found further away from the coast. The birds had started breeding at Isla Pájaros, however, by February all birds had abandoned their nests. Strong El Niño events such as the one in 2002 (see MEI values, Climate Diagnostic Center NOAA, K. Wolter) do not necessarily lead to adult mortality (Anderson, 1989) but birds may migrate to more productive areas. In Peru, population decreases of more than 85 % have been found (Jahncke et al., 1998b), while birds were absent from major breeding colonies during the El Niño 1997-98 (Jahncke and Goya, 2000). Birds do return to their normal breeding range usually by the next season (Nelson, 1978; Jahncke et al., 1998b), although numbers of breeding birds might still be smaller than normal (Jahncke et al., 1998a). In the study area, birds had returned to the area by 2003 and were abundant at sea, although the number of breeding pairs was still low (Table 6.5). At-sea densities of birds in 2004 were similar to the values in 2003 and the number of breeding pairs reached a maximum of 5000 pairs, the largest number counted in the previous five years. Unchanged population numbers after El Niño events might also be due to increased recruitment of non-breeders (Duffy, 1989b).

The factors that trigger such a breeding failure and migration are still unknown. It still needs to be investigated whether the birds respond to reduced food availability or directly to hydrographic and climatic factors such as a rise in sea surface temperature or changes in the wind field. Furthermore, it needs to be investigated whether long-term changes in the environment lead to changes in the foraging behaviour, including foraging trip length and diving behaviour. Birds in the Humboldt upwelling system are well adapted to their environment over the ENSO cycle. In El Niño years, birds encounter severe

problems ranging from reduced breeding performance to adult mortality (Duffy, 1989b) but fast population recoveries after strong El Niño events are made possible through large clutch sizes and rapid breeding as may also been detected in other guano birds in the region (Nelson, 1978; Kalmbach et al., 2001; Luna Jorquera et al., 2003). The knowledge of distribution and basic foraging parameters of this species will enable to evaluate the birds' response to further changes in the climate and hydrography in the Humboldt upwelling system.

6 Distribution and foraging behaviour of the Peruvian booby

Table 6.1: Logger types and number of Peruvian boobies equipped (n) at Isla Pájaros, Chile. Data sets correspond to data included in this study.

Year	Logger type	n	Data sets	Malfunctioning	Not recovered
2000	LTD 100	2	1	0	1
2001	LTD 100	5	1	2	2
2004	PreciTD	3	1	0	2
2004	CT	3	1	2	0

Table 6.2: Diving depth [m] and dive duration [s] of three Peruvian boobies (n = number of dives recorded by each device) at Isla Pájaros, Chile.

device	diving depth [m]		dive duration [s]	
	median	range	median	range
Lotek 2000 (n = 15)	3.6	(0.6 – 6.3)	4	(2 – 10)
Lotek 2001 (n = 41)	2.7	(0.5 – 5.8)	4	(2 – 8)
Preci 2004 (n = 65)	2.3	(0.5 – 8.2)	2	(1 – 15)
total (n = 121)	2.4	(0.5 – 8.2)	2	(1 – 15)

Table 6.3: Different behaviour (swimming, flying and foraging, i.e. plunge diving and actively searching for food) of Peruvian boobies observed during seabird-at-sea counts and logger deployment (n = number of birds observed inside the 300 m transect; min = minutes of logger recording for the respective behaviour; * birds equipped with loggers: 2002 n = 1, 2004 n = 2).

	2002		2003		2004		2002-2004		Logger 02/04 *	
	n	%	n	%	n	%	n	%	min	%
swimming	8	6.7	504	23.9	69	2.9	581	12.6	9	1.0
flying	92	77.3	1325	63.0	1295	54.3	2712	58.8	839	90.2
foraging	19	16.0	276	13.1	1023	42.9	1318	28.6	82	8.8

Table 6.4: Percentage of prey items in freely regurgitated diet samples of Peruvian boobies at Isla Pájaros, Chile (n = number of samples).

Year	n	Inca scad <i>T. murphyi</i>	King gar <i>S. saurus</i>	Anchovy <i>E. ringens</i>	Araucan. herring <i>S. bentincki</i>	Silverside <i>O. regia</i>	Cabinza grunt <i>I. conceptionis</i>	Squid
2000	96	20.8	18.8	30.2	10.4	15.6	0.0	4.2
2001	582	82.3	17.5	0.0	0.0	0.0	0.2	0.0
2004	12	38.5	0.0	46.2	0.0	0.0	0.0	15.4

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Table 6.5: Number of breeding pairs of Peruvian boobies at Isla Pájaros, Chile. Censuses were conducted in January and February of each year (data from Simeone et al., 2003, G. Luna Jorquera, E. Hanshing, R. Villablanca, pers. counts).

Year	2000	2001	2002	2003	2004
Breeding pairs	1300	3000	0	410	5000

7 Conclusions

This thesis has identified and characterised important foraging areas of seabirds in two coastal upwelling systems. Three species, African penguins (*Spheniscus demersus*) and Cape gannets (*Morus capensis*) living in the Benguela system and Peruvian boobies (*Sula variegata*) in the Humboldt system were chosen in order to investigate the implications of biological and hydrographic conditions for their foraging at sea. The Benguela Current runs along the coast of southern Africa and the Humboldt Current is found along the coasts of Chile and Peru off South America. Both systems are wind-driven coastal upwelling areas along the western coasts of the continents. They resemble each other in main oceanographic conditions as well as in productivity (Shannon, 1985; Mann and Lazier, 2006). Fisheries, especially for small pelagics such as anchovies and sardines, are the most important ones in the world (or were before the collapse of fish stocks; Schwartzlose et al., 1999). The most abundant seabird species in both systems belong to the same families, *Spheniscidae* (penguins), *Sulidae* (gannets and boobies) and *Phalacrocoracidae* (cormorants) with individual species of each family being endemic to each upwelling area (Gaston, 2004).

The study species were chosen because they constitute the most abundant seabird species in both systems, occupying similar ecological niches (Duffy, 1989a; Crawford et al., 2006b). Fortunately, their body size allows the use of modern remote-sensing technology and their ability to dive allows the analysis of water column characteristics.

Characteristics of foraging behaviour of seabirds in upwelling systems

Penguins, being unable to fly, mostly cover smaller areas in terms of horizontal displacement during foraging compared to flying seabirds such as gannets and boobies. They rely on food patches close to their colonies, however, though they are able to explore food resources inaccessible to non-diving birds by diving to greater depths (Wilson et al., 1989b; Davis and Renner, 2003). African penguins are inshore feeders and do not migrate during the non-breeding period. This also applies to two of the other three *Spheniscus* species, the Humboldt and the Galápagos penguins. Only the Magellanic penguin is an offshore forager and migrates during its non-breeding season (Stoakes et al., 1998; Davis and Renner, 2003; Boersma et al., 2007). The Humboldt penguin might travel larger distances away from its colony especially during times of severe oceanographic anomalies such as an El Niño (Culik and Luna Jorquera, 1997a; Wallace et al., 1999; Culik et al., 2000). Their ability to dive to great depths enables penguins to extend their foraging range vertically compared to the comparatively greater horizontal distances covered by flying birds. The foraging range of chick-rearing African penguins at Mercury Island, Namibia's largest breeding colony, was on average about 20 km. The birds travelled

7 Conclusions

about 60 km during single trips and covered a median vertical distance of little more than 10 km (see Chapter 2). The entire area covered by foraging penguins in 2005 and 2006 around Mercury Island was about 500 km². Considering a maximum diving depth of 75 m, birds were able to exploit 37.5 km³ of water within their foraging range. In comparison, Humboldt penguins foraged between 20 and 35 km away from their colonies (Culik and Luna Jorquera, 1997b; Culik et al., 1998; Boersma et al., 2007) and dived to maximum depths of 40 – 50 m (Luna Jorquera and Culik, 1999; Hennicke and Culik, 2005). They were not found to prefer particular areas around their breeding site at Pan de Azúcar, Chile, and stayed inshore to forage (Culik and Luna Jorquera, 1997b; Luna Jorquera et al., 2000; Weichler et al., 2004). Penguins at Mercury Island, Namibia, did show preferences for an area north-west of the island in both years studied. African and Humboldt penguins both forage in areas with coastal upwelling close to their breeding sites where prey availability is elevated. In the case of African penguins at Mercury Island, the use of one particular area, even during sulphide eruptions, might indicate the lack of other profitable feeding sites in the vicinity of the colony.

Cape gannets breeding at Mercury Island, Namibia, used a greater area to forage due to their ability to fly. Within their median foraging range of 100 km, they were able to explore different water masses. Birds were able to explore cold coastal waters as well as warmer offshore waters, presumably feeding on different prey in the two habitats. In 2005, they covered an area of about 15300 km² and in 2006 foraging took place in an area of about 7400 km². Taking into account their maximum dive depth of 8 m measured in this study, they were able to explore a water volume of about 120 and 60 km³ in 2005 and 2006, respectively. The ability to explore larger areas seems to be advantageous when facing food shortage. Cape gannets in 2005 were able to forage outside of the area affected by sulphide eruptions feeding on pelagic prey species, although penguins were able to switch to benthic prey, such as pelagic goby (*Sufflogobius bibarbatu*s), by diving to greater depths.

Peruvian boobies in the Humboldt upwelling system differed in their foraging behaviour in terms of foraging range and time spent at sea compared to Cape gannets in the Benguela system. Boobies breeding at Isla Pájaros, Chile, foraged close to the coast within a foraging range of about 25 km. Birds spent several hours at sea, some leaving for more than one trip per day. Cape gannets had longer foraging trips; several birds spent more than one day at sea. Whether Peruvian boobies also foraged offshore could not be determined due to the small sample size of logger equipped birds but observations at sea confirmed the coastal distribution of foraging boobies.

All species investigated in this study rely on predictable food availability within the coastal upwelling systems. They all show similar flight and swimming patterns when leaving for their foraging areas. African penguins as well as Cape gannets and Peruvian boobies commuted relatively directly between colonies and feeding areas, swimming and flying in straight lines until reaching areas with presumably higher food abundance. When reaching the main foraging area, flight or swimming speed was reduced and searching actively for food increased. Upwelling areas constitute meso-scale events in terms of predictability of prey (Hunt and Schneider, 1987). Within those highly productive areas, seabirds depend on prey patches on a smaller scale, which in upwelling systems seem to

be predictable over long periods (Weimerskirch, 2007). Birds in the present study showed foraging site fidelity to different extents. African penguins foraged in a limited area in two consecutive years and Peruvian boobies were observed foraging along the coast for several successive years. Cape gannets showed site fidelity on a broader scale. Although they did commute to an area north-west of the island, birds showed more looping flight patterns (Weimerskirch, 2007), searching for food over larger areas. Birds did not necessarily return to the colony from the same direction as on the outward flight because they often foraged in- and offshore before returning to the colony. Site fidelity of individual birds could be observed in Cape gannets as well as in Peruvian boobies. In African penguins, only one bird made two trips before the device was taken off; this bird foraged in the same area on both occasions. Foraging behaviour was similar in all three species studied here; it was evident that morphological and physiological constraints caused differences in foraging ranges and diving depths but all birds relied on predictable food patches within the respective upwelling systems.

Biological and hydrographic parameters influencing foraging

Many studies have related seabird distribution at sea to prey abundance and oceanographic conditions (e.g. Abrams, 1985; Hunt et al., 1990; Shealer, 2001; Weichler et al., 2004; Ballance et al., 2006). Upwelling systems constitute particular conditions with cold, nutrient-rich waters along the coasts and a high prey abundance, especially of small pelagic fish species, exploited by numerous seabirds living in these systems (Furness, 1981; Furness and Cooper, 1982; Duffy and Siegfried, 1987; Crawford et al., 1991). In this study, biological and hydrographic parameters influencing the foraging behaviour of the seabird species studied were investigated. Prey is one of the main factors shaping foraging behaviour in seabirds (Furness and Monaghan, 1987; Shealer, 2001; Garthe et al., 2007b). Differences in prey availability led to distinct foraging behaviour in African penguins breeding along the Namibian coast. Birds breeding at Mercury Island foraged in an area about 20 km north-west of the island. Penguins covered relatively large distances in order to reach their foraging grounds, however though prey availability seemed to be predictable. The energetic gain by feeding in these areas should hold up for the costs of travelling relatively long distances (Ellis and Gabrielsen, 2001). Nonetheless, food limitation seems to be a key factor for the population decline of African penguins at Mercury Island (Kemper, 2006).

Possession Island used to host the largest population of African penguins in Namibia with an estimated 46000 adults (Rand, 1963); nowadays only 500 nests are occupied during the main breeding period (Kemper et al., 2001). Reasons for this strong population decline may be found in the prey availability around the island. Birds breeding at Possession Island spent almost as much time at sea as birds breeding at Mercury Island but had a much smaller foraging range. Unfavourable prey availability presumably inhibited larger foraging ranges. Fish larvae, the main prey of African penguins at Possession Island, have lower energy contents than other fish species found in the diet of penguins at other islands. Additionally, mining activities within Elizabeth Bay seem to have a negative impact on food abundance around Possession Island (Simmons, 2005).

7 Conclusions

Differences in food abundance and the resultant breeding success of penguins along the Namibian coast may be caused by local oceanography. Mercury Island is located downstream of the main upwelling cell off Lüderitz and appears to profit from enhanced productivity. The strength of the upwelling cell inhibits large phytoplankton growth because of strong wind-induced mixing and a deeper surface layer around the Lüderitz area (Demarcq et al., 2003). Fish stocks are mainly concentrated between Lüderitz and the Angola-Benguela Front in the north (Roux, 2003). Pelagic goby, the main prey of birds at Mercury Island, is not present around Possession Island. Goby distribution shows a gap between south of Lüderitz and the Orange River (Cruickshank et al., 1980) and birds at Possession Island are not able to compensate for the lack of sardine by feeding on pelagic goby as birds at Mercury Island do (Crawford et al., 1985; Cordes et al., 1999).

Water temperature may directly influence prey abundance (Castillo et al., 1996; Cole and McGlade, 1998) and may therefore be directly correlated with the distribution of birds at sea. Additionally, cold water reduces swim speed in most fish species (Oezbilgin, 2002) and thus enables seabirds to capture fast swimming prey (Garthe et al., 2000). This phenomenon might explain why no seabird species uses pursuit diving in tropical waters, pursuit divers (e.g. penguins and auks) being mainly distributed in higher latitudes (Gaston, 2004). African penguins at Mercury Island, Namibia, foraged exclusively in cold coastal waters (Demarcq et al., 2003); Cape gannets also showed most diving activities along the coast where cold water temperatures dominate.

Analyses of the water temperature measured through devices attached to penguins showed that birds were foraging in water masses with little temperature variations. These temperatures correspond to water masses in upwelling cells; those playing an important role in prey accumulation (Haney, 1986a; Hunt and Schneider, 1987). Additionally, cold water conditions favour for example anchovy recruitment (Cole and McGlade, 1998). Small pelagics are difficult to sample (Hunt et al., 1991) and little is known about their small scale distribution (Boyer and Hampton, 2001). The combination of known seabird distribution and water temperature might therefore allow conclusions to be drawn about the distribution of fish species (Montevecchi and Myers, 1995). Wide ranging seabirds are able to explore different oceanographic environments and therefore different prey types during foraging (Stahl et al., 1985; Cherel and Weimerskirch, 1995; Sokolov et al., 2006; Garthe et al., 2007a,b). Prey species found in the diet of seabirds may thus be correlated to certain environments and water temperatures. Cape gannets in Namibia foraged in cold coastal waters as well as in warmer waters offshore. Saury (*Scomberesox saurus scombroides*) and horse mackerel (*Trachurus capensis*) were presumably caught in warmer offshore waters (Klages et al., 1992; Boyer and Hampton, 2001) whereas other prey species, e.g. sardine (*Sardinops sagax*) and redeye (*Etrumeus whiteheadi*), were caught inshore. Prey availability seems to be the most important parameter influencing foraging in the seabird species studied in upwelling systems, however, distribution of prey is closely linked to hydrographic parameters. Therefore, hydrographic parameters have to be taken into account when evaluating foraging areas of seabirds.

Implications of changes in the system

The Humboldt and Benguela upwelling systems are both affected by alterations in the marine environment. Large-scale phenomena, such as El Niño, are well known for their global impact on seabird populations (Barber and Chavez, 1983; Arntz and Fahrbach, 1991; Ribic et al., 1992; Boersma, 1998; Schreiber, 2001). Events at smaller scale may affect localised populations and may influence the foraging behaviour of single bird species, often causing reduced breeding success (Velando et al., 1999; Schreiber, 2001; Simeone et al., 2002).

The effects of an El Niño occurring in the Humboldt Current in 2002 were noted in the breeding performance and distribution of Peruvian boobies in this study. Boobies, usually widely distributed over the study area off the coast of north-central Chile, were observed in smaller numbers and further offshore in 2002 (see Chapter 6). Birds which had already started to breed abandoned their nests including eggs and chicks which led to a complete breeding failure at Isla Pájaros, Chile. Due to the exodus of birds, no diet studies or logger deployment could be carried out and the knowledge about the birds' behaviour at sea during El Niño events remains limited. It also remains unclear what factors lead to breeding failures; whether birds react directly to changes in the water temperature, increasing with a beginning El Niño or whether the birds stop breeding due to food scarcity caused by such events. For Humboldt penguins breeding in the same region of the south-east Pacific, it is known that birds leave their usual foraging and breeding areas during periods of increased water temperatures (Simeone et al., 2002). El Niño phenomena also affect birds breeding at the Galápagos Archipelago, equatorial Pacific, causing reduced breeding success and population declines in several seabird species (Anderson, 1989; Boersma, 1998).

A small scale phenomenon is the occurrence of sulphide eruptions as observed in Namibian waters in 2005 (see Chapter 3). Sulphide eruptions cause hypoxic conditions in the water column and lead to prey depletion (Hamukuaya et al., 1998; Weeks et al., 2004). Birds in 2005 were almost exclusively feeding on pelagic goby, a demersal fish species able to tolerate low-oxygen conditions. In 2006, birds were feeding on anchovy and sardine in addition to pelagic goby. The distinct prey composition was also reflected in the diving behaviour; birds in 2005 presenting deeper and in some cases presumably benthic dives whereas birds in 2006 presented more pelagic diving behaviour. Pelagic goby has lower energetic contents than other pelagic fish species (Cruickshank et al., 1980; Crawford et al., 1985) and may constitute an alternative prey for lack of higher energetic fish. Cape gannets were able to reach water masses that were unaffected by the sulphide eruptions but dived less frequently in a larger area and prey items obtained were smaller in 2005 than in 2006. All three species studied presented changes in their foraging behaviour during times of alterations in the ecosystems, indicating that their main implication for seabirds was food limitations to which the birds had to react.

Seabirds as oceanographers

The use of remote-sensing technology provided sufficient data to test the use of penguins as monitors of the marine environment. Penguin-derived temperature data have been used to analyse circulation patterns of the Polar Front and to identify subsurface currents in the Southern Ocean (Charrassin et al., 2004; Sokolov et al., 2006). Data on temperature patterns in the northern Benguela system are scarce and mostly based on satellite measurements leading to a relatively broad scale and limited to the sea surface (Cole and McGlade, 1998; Demarcq et al., 2003). Dive data of African penguins in this study were used to produce a fine-scale three-dimensional temperature distribution map by applying an oceanographic model. Features of the upwelling area north-west of Mercury Island, Namibia, were mapped for the entire water column down to depths of 70 m. Cold water cells were found mainly along the coast flanked by warmer water further offshore. In greater depths, water temperature distribution was more homogeneous. Temperature differences between both years included in the model were significant. Water temperatures in 2006 were higher than in 2005, which partly explains the different prey composition in penguin diet samples. Short term analyses revealed the impact of wind conditions on temperature distribution over short time periods. Changes in wind direction cause temperature changes in the water column due to up- or downwelling, which also leads to changes in the oxygen concentration and may cause phytoplankton blooms (Peard et al., 2005). The productivity of the northern Benguela upwelling systems relies on such frequent changes in wind directions. Optimal biological productivity occurs when strong upwelling is followed by several days of weaker wind stress allowing the phytoplankton biomass to increase using the upwelled nutrients in the euphotic zone (Cole and McGlade, 1998; Demarcq et al., 2003; Mann and Lazier, 2006). The study of penguins foraging along the Namibian coast provides important insight into small scale patterns of upwelling and temperature distribution in the northern Benguela system. This information is essential for understanding oceanographic parameters that effect all trophic levels of the ecosystem.

Synopsis

Seabirds present a number of different methods when obtaining their food. Surface feeders only explore the uppermost part of the water column whereas pursuit divers, such as penguins and auks, may forage in considerable depths (Ashmole, 1971; Furness and Monaghan, 1987). Plunge-divers, such as gannets, may only dive to several metres of depth although underwater pursuit diving has been observed in brown boobies (*Sula leucogaster*) (Nelson, 1978), northern gannets (*Morus bassanus*) (Garthe et al., 2000) and Cape gannets (Ropert-Coudert et al., 2004b). While many seabird species have been used to monitor prey availability (Montevecchi, 1993; Cherel and Weimerskirch, 1995; Montevecchi and Myers, 1995; Grémillet et al., 2004b), the monitoring of hydrographic parameters is limited to the sea surface when studying surface feeding seabirds (Weimerskirch et al., 1995). Only diving birds are able to sample the water column in a greater vertical extension (Wilson et al., 1994; Watanuki et al., 2001; Charrassin et al.,

2004; Sokolov et al., 2006). In this study, the use of data loggers on diving seabirds has provided informations about biological and hydrographic parameters affecting the foraging behaviour of three seabird species in upwelling systems. It has been shown that prey availability is reflected in the areas used by the birds when foraging as well as by the diving behaviour exhibited. Birds react to changes in their environment and might be capable of buffering against reduced food availability (Croxall et al., 1988; Hennicke and Culik, 2005; Clarke et al., 2006; Quillfeldt et al., 2007). A certain degree of plasticity in foraging behaviour and prey taken by the birds in this study could be observed. The use of similar foraging areas on consecutive trips and even over several seasons indicated a predictable prey availability for birds in both upwelling systems. Nonetheless, penguins and gannets in Namibia undergo strong population declines, mostly due to limited food abundance (Kemper et al., 2001; Kemper, in press b). Peruvian boobies in Chile reacted strongly to changes in the environment, i.e. El Niño events, however populations of seabirds in the Humboldt system are not listed as threatened (Schlatter, 1984; IUCN, 2006), except for the Humboldt penguin which is listed as *Endangered* (IUCN, 2006) due to uncertainties in population size (Luna Jorquera et al., 2000; Mattern et al., 2004). An on-going degradation of the Benguela ecosystem with further reduction of pelagic fish stocks and increasing abundance of low-energetic prey such as goby and jellyfish (Bakun and Weeks, 2004; Moloney et al., 2005) will deteriorate food availability for seabirds. Different scenarios about possible consequences of global change are considered by Roux (2003), mostly with negative consequences for African penguins and Cape gannets. Seabirds in the Humboldt upwelling system seem to be better adapted to changes in the environment. Life-history parameters, such as clutch size, age of first breeding and numbers of successful broods per year, indicate the ability of fast recoveries after population declines due to El Niño events (see Luna Jorquera et al., 2003; Crawford et al., 2006b, and citations therein). Nevertheless, it may be doubted whether birds would be able to buffer against increasing frequency of warm water events, such as El Niño and other changes due to global warming. Bird populations might not be capable of recovering from breeding failures if those would occur in shorter intervals.

This study shows the importance of monitoring the foraging behaviour of seabirds in order to understand population changes. Foraging is a main factor for breeding success and food limitations strongly affect seabird populations. Upwelling systems with their high productivity and predictability of prey host large numbers of seabirds but environmental changes as well as human impacts may lead to declining populations. Monitoring of seabird behaviour at sea in combination with monitoring of biological and hydrographic parameters becomes more and more feasible due to advances in logger technologies. These methods state an important tool for understanding complex processes in upwelling systems as shown in this study.

7 Conclusions

A Logger deployment

The following appendix is my contribution to a manual for seabird monitoring techniques which was compiled for a Benguela Large Marine Ecosystem (BCLME) project on top predators as indicators of ecosystem health. The title of the document is MONITORING SEABIRDS IN THE BCLME - DATA COLLECTION MANUAL (J. Kemper, with contributions from: J. Braby, B. Dyer, J. James, R. Jones, K. Ludynia, R. Mullers, J.-P. Roux, L. Underhill and A. Wolfaardt)¹. The BCLME Programme is a joint initiative of the governments of Angola, Namibia and South Africa concerning the sustainable use of the resources within the Benguela upwelling system. The manual is directed towards technical staff working in the field taking part in scientific studies, such as population counts, diet sampling and remote sensing, i.e. logger deployment. The methods described in this manual are based on Wilson and Wilson (1989); Wilson and Culik (1992); Wilson et al. (1997) and on personal experiences during field work.

A.1 Theoretical background

Preparation for logger deployment

In order to study the at-sea behaviour, especially the diving behaviour, and to determine the areas at sea used by African penguins for feeding, new technologies, such as remote sensing devices may be applied. In our study, we used GPS TDlog data loggers (following referred to as GPS loggers), designed and manufactured by earth&OCEAN technologies, Kiel, Germany.

Since an extensive manual is supplied by the manufacturer, explaining the functions and programming of the devices, this manual will focus on the proper attachment of the GPS logger onto the bird at the colony.

How to start the logger

Logger preparations and programming are extensively explained in the manufacturer's manual and instructions should be read carefully before using the device. A test run using the logger *on land* before handling birds should be done to get accustomed to preparing, programming and data downloading. Different settings for the GPS receiver, the temperature and the pressure sensors may be used according to the questions asked and to the animal's behaviour and the time spent at sea. In our study with African

¹Contribution to the project LMR/EAF/03/02 of the Benguela Current Large Marine Ecosystem (BCLME) Programme

A Logger deployment

penguins at Mercury Island, Namibia, following logger settings have shown to give successful results. We have set the GPS interval to 5 minutes and the temperature/pressure sensor to 1 second. Enabling the pressure control, we have chosen the pressure mode to start the GPS after each resurfacing (not cycle-dependent). This way, as the bird starts diving, the GPS receiver tries to get a position after every dive. At the colony and during prolonged periods at the surface during night time, the logger obtains a position every 5 minutes. Due to the 1 second interval of recording temperature and pressure, very exact information about water temperature and diving behaviour is obtained.

Deployment of the logger

Things needed for deployment - have everything ready and at reach before catching the bird in order to reduce time of handling:

- GPS Logger – started and closed properly
- Tesa[®] Tape – black for penguins
- Pattern/ shape
- Scissors
- Scalpel or knife
- Scale and strep
- Rubber glue (Pattex[®])
- Pencil and paper

What birds to deploy?

Choose nests with small to medium downies, since at that chick age one parent usually leaves to sea while the other one stays at the nest site during the day. Chances that the bird leaving to sea returns in the evening in order to feed and swap nest duties with the other parent are high and makes recovery of the logger easy.

Check beforehand the nest attendance of birds in the study colony. If birds leave early in the morning or during night hours, as in our case on Mercury Island, the attachment of the logger may take place in the late evening hours when the partner has returned from sea and both parents are present at the nest site. Make sure to deploy the partner that has spent the day at the nest and who will leave the same night or next morning to sea. The bird having been at the nest is usually dry and quite dirty while the one that has just returned from sea might still be wet and feeding the chicks. Deploying the bird after the partner has returned has the advantage that, while one takes out the bird in order to attach the logger, the other partner may protect the chicks from any danger (e.g. picking of neighbouring birds) and may continue feeding. This way little disturbance to the chicks is caused while working with the bird.

How to catch the bird?

Always try to cause as little disturbance as possible while working in the colony. It's best to work with two people, one catching and holding the bird while the other one prepares the deployment and attaches the logger to the bird. Slowly approach the nest, trying not to chase off any birds, and cautiously grab the bird you want to equip (the dry one that has been on the nest). Take it out of the main nesting area. When working with the bird, try to cover its eyes slightly with your hand, as this reduces the bird's stress.

Logger attachment

How to attach the logger?

Before attaching the logger, weigh the bird by using a spring scale and a strap around the penguin's body underneath the flippers. Note down the weight.

After weighing, one person has to hold the bird calmly on his lap, slightly covering the bird's eyes, holding the bird's back straight towards the other person.

Stick your logger outline pattern with some pieces of tape to the bird's lower back.

Rip a piece of tape about 10 – 15 cm long and hold it in-between your fingers with the sticky side up. Use the scalpel or the knife to lift some feathers in the upper part of the outline and place the tape with its sticky side facing upwards underneath the feathers. That way, the feathers will stick onto the tape, leaving the remaining ends of the tape on the left and right side hanging down. Repeat the procedure with the next layer of feathers downwards from the strip of tape just applied. When reaching the lower end of the outline, i.e. the lower end of the logger, you should have placed 4 to 5 stripes of tape. Now place the logger onto the feathers which are sticking to the tape and fasten the tape around the logger. Always start with the right end of the tape sticking it tight onto the logger without leaving crevices or folds in the tape, then take the left end of the same stripe. For the top stripe which is at the narrow end of the logger you might need to cut into the tape in order to prevent folds. Repeat this for all stripes of tape. If you always start with the right end and stick the left end afterwards, it will help you to undo the tape when taking off the device, especially when working at night time and/or with very nervous birds.

When all layers of tape are applied, the logger should be attached firmly to the penguin's back. Now you may take off the plastic outline. Do so by pulling it gently downwards over the logger. To secure the endings of the tape, lay another stripe of tape around the entire logger (not the bottom part because you might cover the pressure sensor), cut into the tape at the narrow end of the logger to prevent folds again. After having all the tape attached firmly you may apply a little bit of rubber glue to the logger (it should not get into contact with the feathers) to prevent the tape from loosening in the water. When applying only a thin layer of glue, it dries quickly and the bird may be released immediately. Take the bird back to its nest site as close as possible without distracting all other birds.

Recovering the device

How to retrieve the logger?

Check the next evening for the returning bird regularly at its nest site. When the bird has returned, remove the logger as soon as possible since other birds might pick at it when the bird is in the colony. The same caution has to be applied for catching the bird when taking off the logger as has for deployment. One person should again hold the bird calmly while the other takes off the tape layer by layer. Peel the tape off the device until the logger is freely detachable. When the logger is taken off, the tape is still sticking underneath the feathers. It may now be easily removed by pulling gently downwards while holding the feathers base down with the finger preventing the feathers from pulling out. Once the logger and the tape are completely removed from the bird's back, the penguin may be released.

How to analyse the data?

Once downloaded from the GPS logger, the positional data may be visualised using for example ArcView[®] or any other GIS program. For the dive analysis a program called MT Dive may be obtained through earth&OCEAN technology but self-written programs, such as Matlab[®], may also be used to analyse the data.

A.2 Steps for logger attachment

Step 1 After catching and weighing the bird, attach the logger outline cut out of strong plastic onto the birds back with some stripes of tape. Make sure it is positioned straight and centered on the lower back.

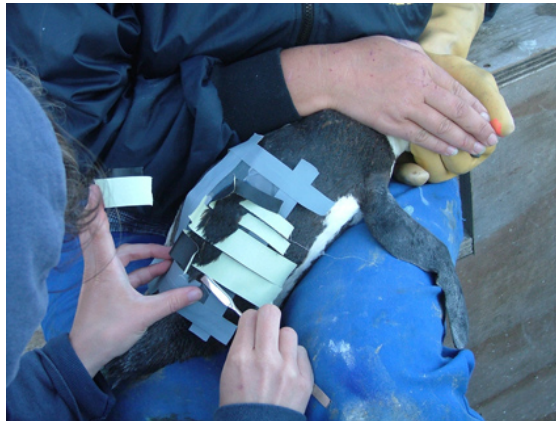


Step 2 Lift the first row of feathers inside the outline using the scalpel or knife and apply the first stripe of tape with the sticky side up so that the feathers stick on top of the tape and the ends hang down on each side.



A Logger deployment

Step 3 Continue applying tape underneath the feathers row after row until reaching the bottom end of the outline. You should need 4-5 rows depending on the tape's width.



Step 4 After positioning the logger onto the feathers and tape inside the outline start wrapping the tape tightly around the logger. Always start with the right side of the tape's end, then wrap the left side. This makes it easier to find the tape's end when taking off the logger.



A.2 Steps for logger attachment

Step 5 When all loose ends are wrapped around the logger, it should stick firmly to the birds back. Take off the outline by pulling it carefully downwards (to prevent pulling on the feathers) over the logger.



Step 6 To minimize the gaps between logger, tape and feathers where the bird could pick, wrap one long stripe of tape around the border of the device. Leave out the bottom part where the pressure sensor is located. In order to stick the tape without folds, you might need to make some small cuts in the tape at the upper area of the logger.



A Logger deployment

Step 7 When finished wrapping the tape around the logger, apply a little bit of rubber glue in order to prevent the ends from loosening. Make sure the rubber glue does not get into the feathers.



That's what it should look like when the logger is attached properly. Release the bird as close to its nest as possible.



All photos taken by Rian Jones and Joan James, Mercury Island, Namibia

B Establishing a Marine Protected Area (MPA) in Namibian waters based on penguin foraging data

Marine Protected Areas (MPAs) have become an important tool for the conservation of ecosystems, habitats and/or species assemblages in the marine environment (Hyrenbach et al., 2000; Garthe and Skov, 2006; Mann et al., 2006). The benefits of closed area management are increasingly becoming apparent and being recognised, both from a conservation as well as a resource management perspective (Currie, 2006b). Several countries have recently established MPAs that include the protection of important seabird breeding sites (Lombard et al., 2005; Garthe and Skov, 2006).

The Namibian government has declared its disposition to install a MPA in Namibian waters. Scientists of the Ministry of Fisheries and Marine Resources in Namibia together with the WWF South Africa have started to work on a proposal for a Marine Protected Area along the southern Namibian coast, including the main breeding islands of seabirds within the northern Benguela upwelling system.

Species, that are considered to be protected through the MPA in Namibia are mainly species listed as *Endangered* or *Vulnerable*, e.g. African penguins (*Spheniscus demersus*), Cape gannets (*Sula capensis*), bank cormorants (*Phalacrocorax neglectus*), crowned cormorants (*P. coronatus*) (IUCN, 2006) but also species that are commercially used, such as rock lobsters (*Jasus lalandii*). Whale calving sites of southern right whales (*Eubalaena australis*) are also to be included in the MPA.

In the following appendix, the results of several meetings at the Ministry of Fisheries and Marine Resources during the process of developing an adequate outline for the planned Marine Protected Area in Namibia are presented. The process of declaration of the MPA has not been finalised yet but will hopefully be continued and lead to a Marine Protected Area along the southern Namibian coast. Meetings with scientists of the MFMR as well as with stakeholders, such as fishing and mining companies have so far led to an outline presented to the Namibian government.

The following section gives an overview about planned general protection measurements as well as island-specific zoning and management activities for specific islands. The information given here is taken from several reports written by Heidi Currie, legal adviser in the process of the proclamation of Namibia's offshore islands and surrounding waters as Marine Protected Area (Currie, 2006b,a). One of several MPA workshops took place at the Ministry of Fisheries and Marine Resources in Lüderitz on the 29th and 30th of March, 2006, where I was invited to give a presentation of the preliminary results of my study using logger technology on African penguins and Cape gannets at several

Namibian islands. Especially the outer limits of a potential Marine Protected Area were defined based on the results of my study as shown in Section *Method of defining the broader buffer zone VI*, page 146.

B.1 Scientific baseline

Following areas and species are considered to possibly be included in the potential MPA:

- Orange River Wetland (already declared as RAMSAR site)
- All islands and islets between Hollamsbird in the north and Sinclair Island in the south including surrounding waters.
- Main breeding and foraging sites for endangered seabird species, such as African penguin and bank cormorant, as well as other seabird species, such as crowned cormorant, Cape gannet and others.
- Rock lobster sanctuaries already established at Ichaboe Island and Lüderitz as well as potential additional lobster sanctuaries.
- Calving sites of the southern right whale.
- Airspace within 3000 feet above all islands and main seal colonies.

A zonation system has been applied, consisting of a broader buffer zone, equivalent to the IUCN category VI and several zones around each individual island, taking into account special protection measurements considering the islands characteristics, the species inhabiting the islands as well as commercial use and man-made activities planned.

Not all islands will be considered in the following section but only islands dealt with in the scientific work of this thesis (Mercury, Halifax and Possession Islands) will be presented as examples.

Broader buffer zone VI

Recommendations made for the outline of the broader buffer zone as well as the management of thus are suggested to be incorporated as a flexible management plan, which should be reviewed on a periodic basis, as new scientific information becomes available and monitoring technologies improve. It is also important to stress, that the suggestions made below have to be considered in the context of minimal interference with existing activities in the area, such as fishery and mining activities and that the co-operation of all stakeholders has been essential to the planning process. Stricter conditions apply closer to the islands, as further described below.

- Fishery: Lobster, mullet (*Liza dumerili*) and line-fishing is allowed. Long-lining, fishing with drift nets, trawling and purse seining is prohibited. The impact on commercial fisheries is kept to a minimum since trawling only takes place outside

the 200 m depth contour (the entire MPA lies within the 200 m bathyline) and purse seining almost ceased due to strongly reduced capture rates within the area. Any possible new fishing methods have to be evaluated.

- Kelp harvest: No kelp (*Laminaria pallida*) cutting is allowed.
- Underwater exploration: No underwater explosions or blasting is allowed.

Zone 1 Zone 1 applies to all islands and islets within the broader buffer zone constituting the Marine Protected Area.

- No mining.
- No anchoring.
- Ecotourism limited to boat-based activities with restrictions on numbers and distance to the islands.
- Overflight regulations of 3000 feet over all islands and main seal colonies. Exceptions for scientific and medical purposes.
- No commercial sealing on the islands.

Zone 2 Zone 2 includes the proposed lobster sanctuary including Albatross, Pomona, Plumpudding and Sinclair Islands and deals with the effects of mining activities in the area. No mining discharge is allowed in the area and destruction of kelp beds and the build-up of land bridges have to be prevented.

Island specific zonation

Zone 3 covers an area of 120 m around each island (measured from the low water mark, l.w.m.) and Zone 4 refers to the island itself.

Mercury Island

Objectives for protection:

- Largest African penguin breeding site in Namibia. Numbers are decreasing by 3.7 % per year and species is classified as *Endangered* in Namibia.
- Second largest breeding site for Cape gannets in Namibia. Species is classified as *Endangered*.
- Worlds largest breeding site for bank cormorants. Species is classified as *Endangered* and ≈ 75 % of the global population breeds at Mercury Island.
- Important breeding site for other seabird species, such as crowned and Cape cormorants (*Phalacrocorax capensis*).

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- Passage and/or breeding path for southern right whales and Heaviside's dolphins (*Cephalorhynchus heavisidii*).

Controlled activities:

Zone 4:

- No guano scraping allowed.

Zone 3:

- Mining only allowed under strict regulations protecting the benthos, lobster habitat and biodiversity.
- No anchorage.
- Lobster fishing allowed but limited to 50 m from the l.w.m. and outside the area stretching between the jetty and North Island. Traps must be marked and removed after fishing. Missing traps have to be reported.
- Mariculture only allowed outside Zone 3 and outside the passage ways of southern right whales, Heaviside's dolphins and African penguins.
- Boat-based ecotourism only allowed outside Zone 3.

Halifax Island

Objectives for protection:

- Third largest breeding site for African penguins in Namibia and only colony with increasing numbers in Namibia ($\approx 8\%$ per year).
- Damara tern (*Sterna balaenarum*) feeding off the island. The species is the most endangered tern in southern Africa and states as a flagship conservation species.
- Densest population of Heaviside's dolphins in Guano Bay.
- Breeding site for other seabird species, such as crowned cormorant, kelp gull (*Larus dominicanus vetula*) and African black oystercatcher (*Haematopus moquini*).

Current activities:

- Two boat-based tour operators approaching Halifax Island.
- Mining vessels offshore, threat of pollution.
- Persons landing illegally on the island and recreational fishing close by.

Controlled activities:

Zone 4:

- No tourism on the island and no access of private persons allowed.
- No guano scraping allowed.

Zone 3:

- No mariculture allowed.
- No activities or operations allowed that could obstruct the passage ways of Heaviside's dolphins and African penguins.
- No anchorage within 50 m from the island (l.w.m.).
- Boat-based tourism only in limited numbers and not within 20 m off the island (l.w.m.).
- Recreational lobster fishing allowed but not within 50 m off the island.
- Commercial lobster fishery allowed except for the area between Diaz Point and Grossebucht.

Possession Island

Objectives for protection:

- Largest kelp bed in the area, important for lobster recruitment and marine biota.
- African penguin colony, once the largest in Namibia, nowadays the 4th largest decreasing at a rate of 8 % per year. In the last 50 years, numbers have decreased from 46000 to 1400 individuals.
- Smallest of the three Namibian Cape gannet colonies.
- Largest concentration of African black oystercatcher.
- Damara terns breed and feed around the island (breeding site at the nearby mainland).
- Bird species are particularly nervous because of small colony sizes and are therefore more vulnerable to disturbance.
- Food limitation is most pronounced around the island compared to other islands.
- Southern right whale calving site in Elizabeth Bay. Several calves have been born there recently.

Current activities:

- Mining is not currently taking place in close distance to the island but could be implemented by boat-based mining.
- Several aquaculture activities are planned within Elizabeth Bay but no permissions are given yet.

Controlled activities:

Zone 4:

- No guano scraping allowed.
- If ecotourism will be allowed, strict conditions would have to be followed, such as seasonal limitations, limited numbers of persons, guided tours only along a walking trail not passing close to the gannetry.

Zone 3:

- Only limited mining activities and no anchorage in front of settlement.
- No boat-based tourisms within 120 m of the coast.
- No lobster fishery within Zone 3 (no such activity currently).
- Aquaculture activities allowed only without obstructing the passage ways of southern right whales. No line culture including moorings.

B.2 Method of defining the broader buffer zone VI

When defining the extension of the broader buffer zone VI, all areas listed above were considered except for the Orange River Wetland area, which is already proclaimed as RAMSAR site. Based on the results of my study using logger technology on African penguins and Cape gannets at Mercury, Halifax and Possession Islands, the maximum foraging distance of African penguins was taken as a baseline for the minimum extension of a potential MPA. Although the protection of foraging areas of Cape gannets would be desirable from an ecological point of view, the large foraging distances of Cape gannets could not be included in the MPA outline. Gannets reach areas which constitute important fishing grounds; therefore, a MPA of such large dimension would have an socio-economic impact not desirable in this context. African penguins breeding at Mercury Island covered the largest area when foraging, travelling up to 30 km to the north and about 20 km to the west of the island. Birds at Possession Island only covered about 10 km to the north and south, staying within Elizabeth Bay and birds breeding at Halifax Island travelled a maximum of 12 km away from the coast when foraging (see Chapter 2). The two birds covering exceptional large distances were not considered in this context.

B.2 Method of defining the broader buffer zone VI

Based on these results of my study, an offshore extension of 20 km for a potential MPA was defined. Taking into account that birds could forage in a northerly as well as in a southerly direction of the islands, the 30 km maximum distance was plotted around each island towards the north and the south (Fig. B.1). Unprotected areas between buffer zones of each island would have no ecological advantages, therefore a large, continuous area covering all islands and surrounding waters between Hollamsbird Island in the north and Sinclair Island in the south was considered. Such an approach would be better feasible for management, implementation and enforcement. Several possible outlines of the Marine Protected Area have been designed, either along degrees of latitude and longitude or along a line running approximately 20 km off the Namibian coast. Included in this MPA design are the existing (and planned) lobster sanctuary, whale calving sites and line-fishing sanctuary (Fig. B.3). The maps also indicate Namibia's Exclusive Economic Zone (EEZ), showing that the MPA would cover about one third of the Namibian coastline but only small part of its national and economically used waters (Fig. B.4).

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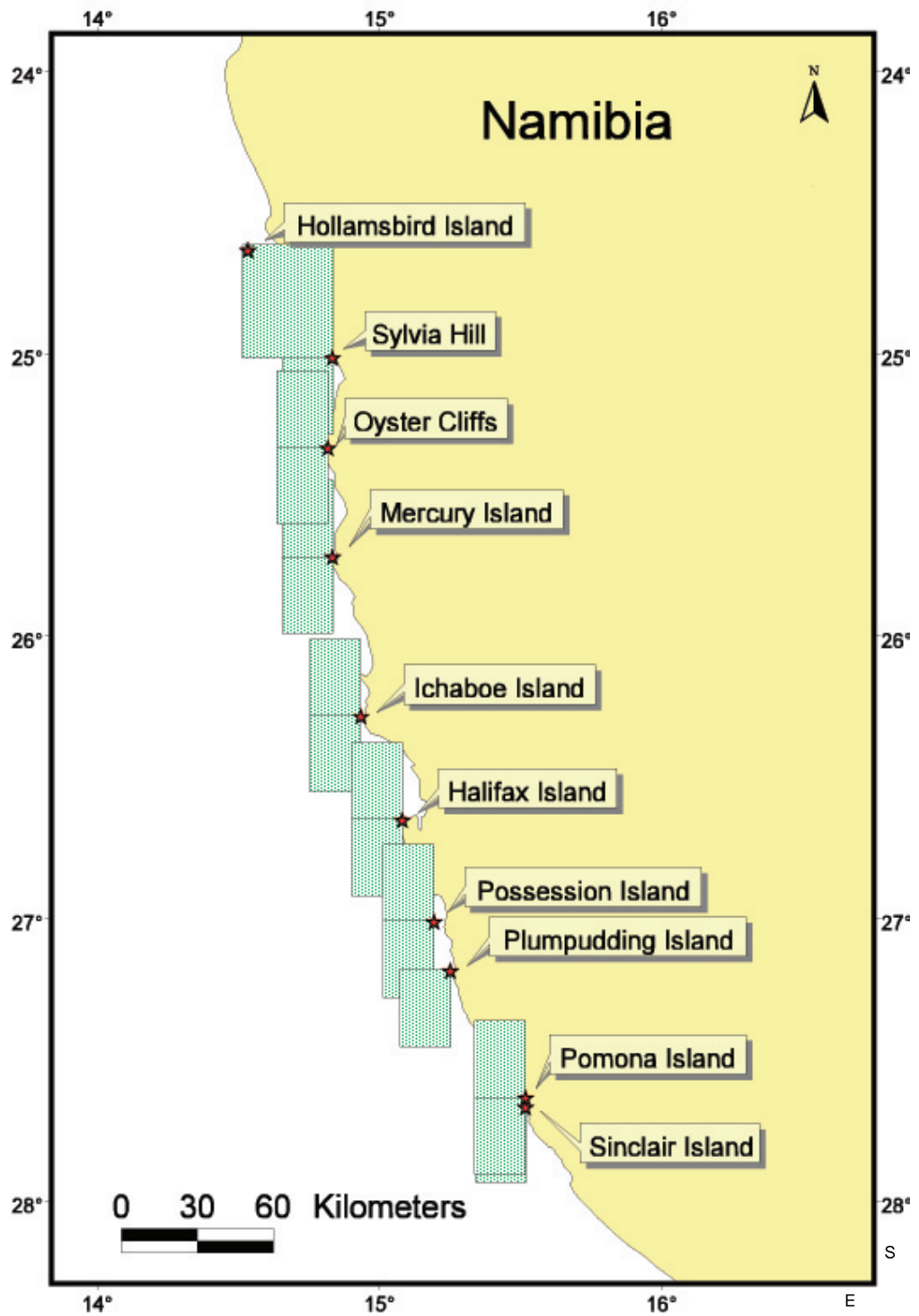


Figure B.1: First design for possible outlines of protected areas based on a maximum foraging distance off the coast of 20 km and a maximum north and south extension of 30 km of foraging areas of African penguins around Namibian breeding sites.

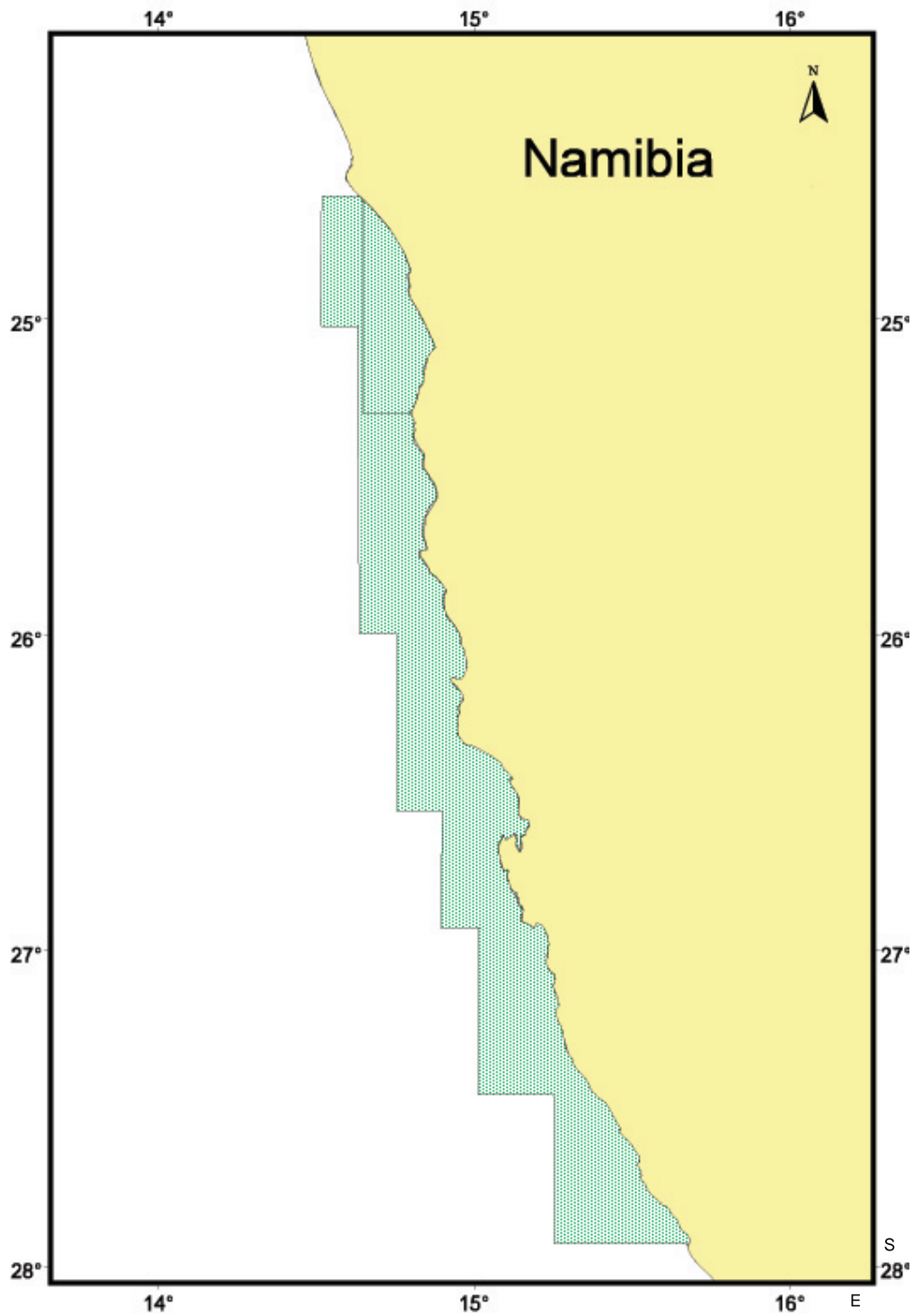


Figure B.2: Possible design of the proposed MPA in Namibian waters with its border running along degrees of latitude and longitude.

B Establishing a Marine Protected Area (MPA) in Namibian waters

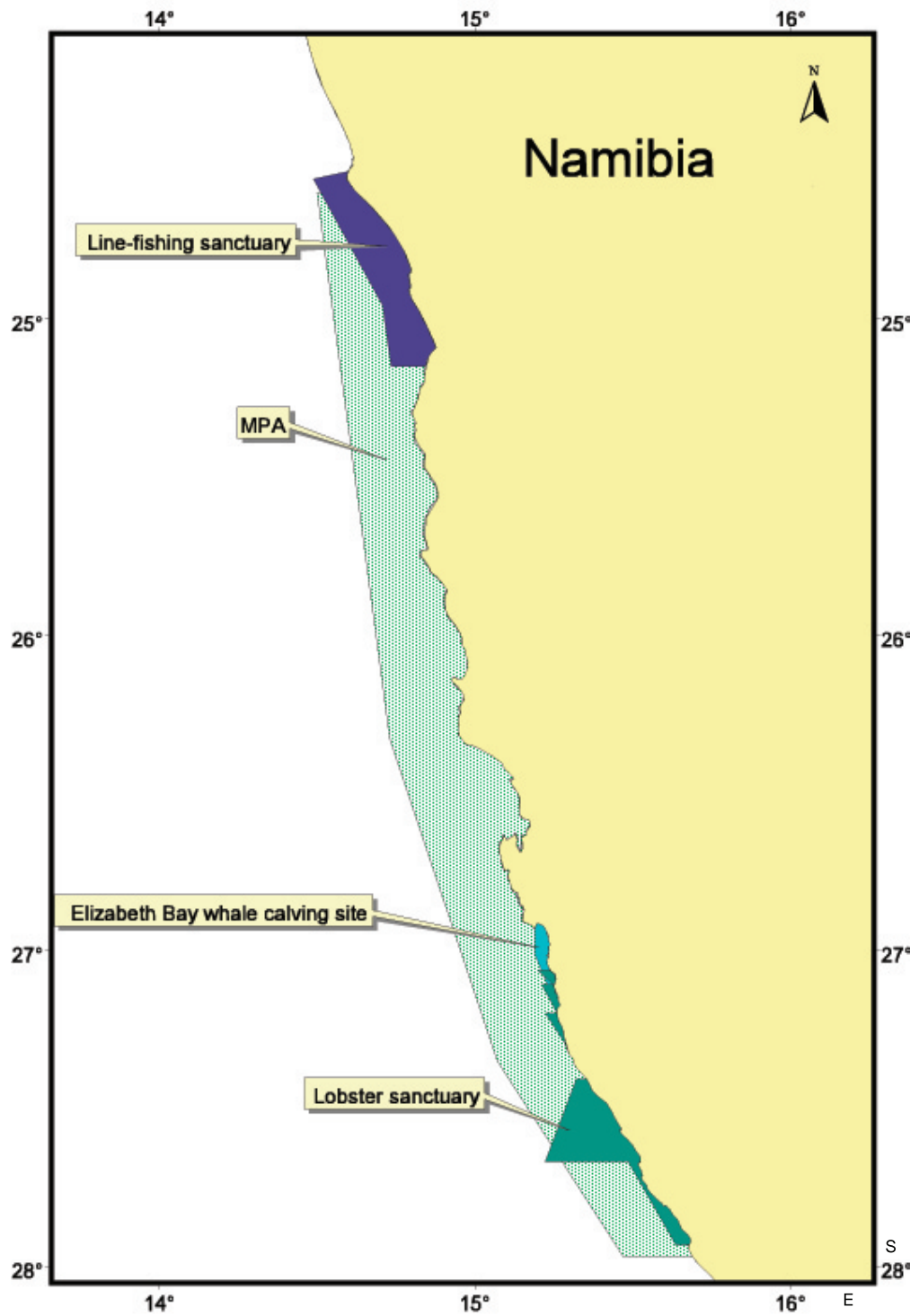


Figure B.3: Possible design of the proposed MPA in Namibian waters with its borders running about 20 km offshore.

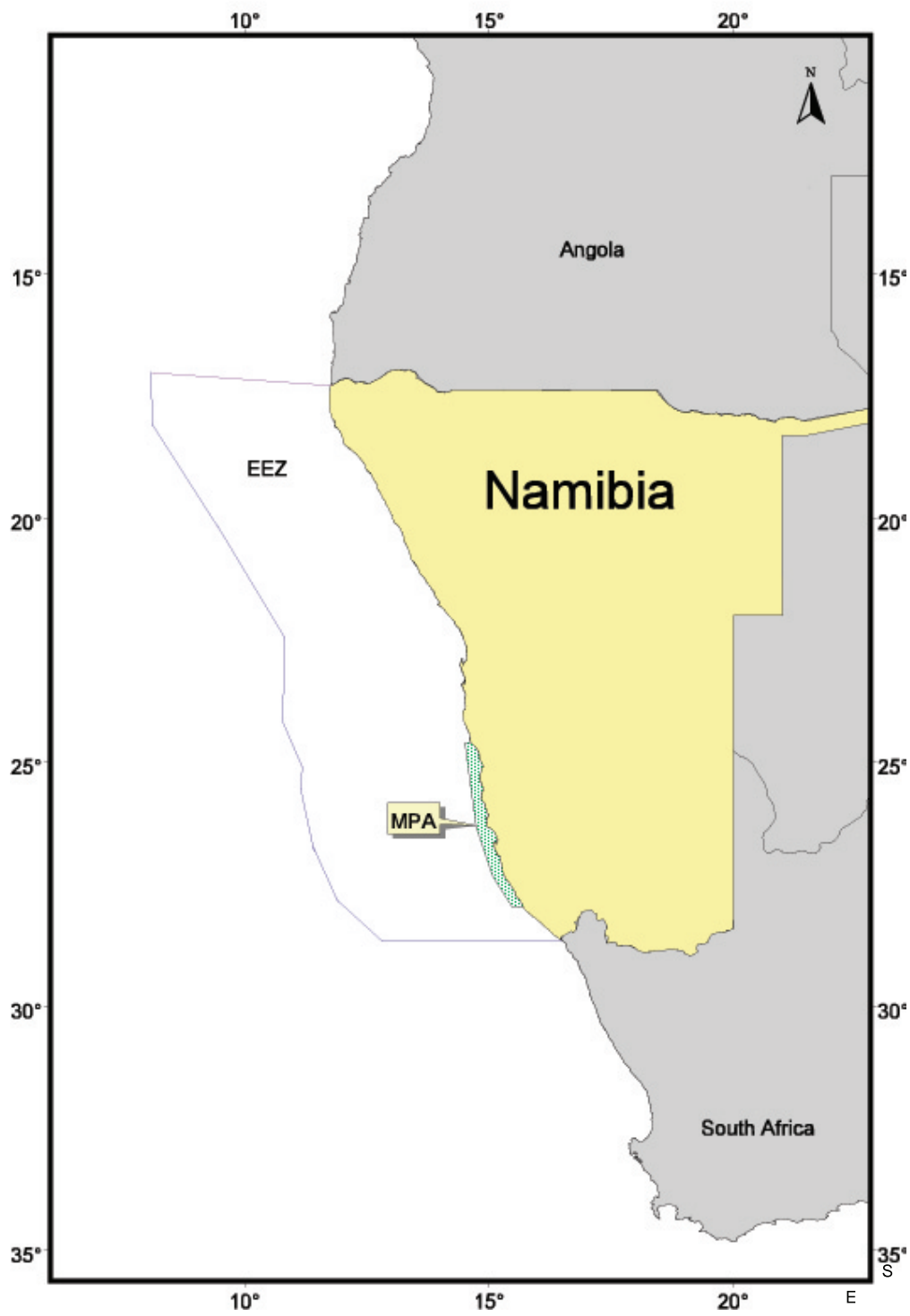


Figure B.4: The proposed Marine Protected Area (MPA) and the Exclusive Economic Zone (EEZ) of Namibia.

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Bibliography

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Erklärung

Hiermit erkläre ich, dass die vorliegende Dissertation - abgesehen von der Beratung durch meine akademischen Betreuer - nach Inhalt und Form meine eigene Arbeit ist. Sie wurde keiner anderen Stelle im Rahmen eines Prüfungsverfahrens vorgelegt. Die Arbeit wurde unter Einhaltung der Regeln guter wissenschaftlicher Praxis erstellt. Dies ist mein erster Promotionsversuch. Der Zulassung von Zuhörerinnen und Zuhörern bei der mündlichen Prüfung wird nicht widersprochen.

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